SYMPOSIUM ON
MOLLUSCA

PART I

MARINE BIOLOGICAL ASSOCIATION OF INDIA
MARINE FISHERIES P.O., MANDAPAM CAMP
INDIA

SYMPOSIUM ON MOLLUSCA

PART I

MARINE BIOLOGICAL ASSOCIATION OF INDIA
MARINE FISHERIES P.O., MANDAPAM CAMP
INDIA

PROCEEDINGS

OF THE

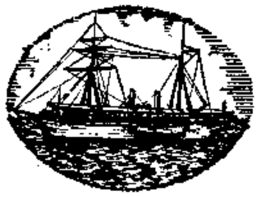
SYMPOSIUM ON MOLLUSCA

HELD AT

COCHIN

FROM JANUARY 12 TO 16, 1968

PART I



SYMPOSIUM SERIES 3

MARINE BIOLOGICAL ASSOCIATION OF INDIA
MARINE FISHERIES P.O., MANDAPAM CAMP
INDIA

PRINTED IN INDIA
AT THE BANGALORE PRESS, BANGALORE
1968

CONTENTS

PART I

LIST OF PAPERS—

PREFACE

THE SYMPOSIUM ON MOLLUSCA was organised under the auspices of the Marine Biological Association of India at Cochin from 12th to 16th January 1968 and the present volume contains the first part of its proceedings.

Molluscs have held a prominent place in the animal kingdom. In numerical abundance they are second only to arthropods. Having originated from a flatworm-like ancestral form in the distant past in the geological history of the earth, the group has radiated and come to occupy almost every type of ecological niche. Varied are their forms to adapt themselves to diverse habitats. They have played a large role in human welfare. Clams, mussels, oysters and squids, to mention a few among the shellfish, serve as food for man. Pearls from pearl oysters are among the costliest of the gems. Most molluscan shells are used as ornaments or shaped into a variety of household articles. The pearl and the chank have so much inspired the common man from the very ancient times that they have entered the folklore and the legendary tales. A detailed account of this may be found in "Molluscs in Indian Tradition and Economy" given elsewhere in this volume.

Taxonomic accounts of the molluscan species are numerous coming from the systematists and conchologists all the world over, the notable among the earlier works being Reeve's (also Sowerby and Reeve) *Conchologia Iconica* (1843–1878), Forbes and Hanley's *History of British Mollusca and Their Shells* (1848–1853), Jeffre's *British Conchology* (1863–1869) and Alder and Hancock's *British Nudibranchiate Mollusca* (1845–1855). Most outstanding are the Ray Society's recent publication on the *British Prosobranch Molluscs, Their Functional Anatomy and Ecology* by Fretter and Graham (1962) and *The Invertebrates*, Vol. VI, *Mollusca I* by L. H. Hyman (1967). On varied aspects of molluscan studies quite a good number of scientific papers and treatises have appeared in the periodicals of the learned societies of the world. As most molluscan shellfish lend themselves to culture, these aspects of study have also been dealt with in detail by numerous workers, especially those on oyster farming. Scientific aspects of pearl culture also have shown much progress in the past fifty years. The production of the perfectly round culture pearl heralded the day when the impossible was achieved giving rise to a flourishing industry.

In India the molluscan species occur in a wide range of habitats characteristic of the tropical zones. The species abundance and the economic resources pertaining to this group are vast. Though some taxonomic studies have been made in the past, there is still a large field to cover especially in regard to the deeper waters. The pearl and chank resources and their fishery management have received much attention of the ruling governments at all times for the large revenues they have been yielding. In recent years a good deal of information has been published on the biology of edible molluscs as mussels, clams, oysters, squids and cuttlefishes. Still, the utilization of these items is poor as the molluscan shellfish are looked down by the common man and culture of shellfish is little practised. Parasitology related to molluscan species transmitting dreadful diseases to man and farm animals has received considerable attention. Studies on boring and fouling molluscs in marine habitats, which cause heavy economic losses, have in the past two decades made rapid strides. Studies on problems of water pollution and radiation biology in relation to coastal and brackish water shell fisheries are in their infancy although a good beginning has been made.

The aims of this Symposium have been to consolidate information on work done so far, to highlight the recent advances and to enable formulation of future programmes, both in the academic and applied fields of research, at national and international levels. The response from the eminent scientists all over the world has been immensely great. The number of contributions received from them was large covering such varied aspects of molluscan studies as taxonomy, phylogeny and evolution, distribution, morphology and anatomy, general biology, radiation biology, reproduction and larval development, ecology and behaviour, physiology, boring and fouling molluscs, parasitism and commensalism and culture, economics and fisheries. The 'Abstracts of Papers' would provide an idea of the particular subjects dealt with. Nearly 100 papers were presented and the discussions were lively and enlightening. It gives us pleasure to note that the objectives of the Symposium have been more than fulfilled.

The Symposium is the outcome of the very ardent enthusiasm evinced, able planning and successful execution in every detail of the entire proceeding by Dr. S. Jones, President of the Marine Biological Association of India who has been the driving force behind all the achievements of this august body devoted to the cause of marine biological sciences, since its inception in 1958. An account of the Marine Biological Association of India is included later in this volume. The *Symposium on Mollusca* is the third in the series after the *Symposium on Scombroid Fishes* held in 1962 and the *Symposium on Crustacea* in 1965, the proceedings of which have made a headway as authentic and exhaustive contributions in the respective fields for the advancement of biological and fisheries sciences.

The 'Summary of the Proceedings' and the other sections that follow give an account of the Symposium during the five days, 12-16 January, 1968 and the acknowledgements to various scientists and other individuals and institutions who have extended their co-operation in organising the Symposium and other functions, and have participated in the various programmes.

Professor (Dr.) Ralph W. Dexter of the Kent State University, Ohio, U.S.A., has kindly done the onerous job of editing the scientific papers presented at this Symposium.

As Convener, I have great pleasure to express my deep appreciation and gratitude to one and all concerned whose enthusiasm and efforts made the Symposium a success.

K. VIRABHADRA RAO,
Convener.

SUMMARY OF THE PROCEEDINGS

The Governor of Kerala, His Excellency Mr. V. Viswanathan, inaugurated the *Symposium on Mollusca* organised by the Marine Biological Association of India, at the Central Institute of Fisheries Operatives, Cochin, on Saturday, the 13th January 1968, at 11 A.M., and released the first Memoir of the Association on *The Ribbon-fishes of the Family Trichiuridae of India.* Dr. S. Jones, President, Marine Biological Association of India and Director, Central Marine Fisheries Research Institute, presided over the function. Mr. R. Madhavan Nayar, Chairman, Committee of Hosts, welcomed the gathering. Mr. K. Virabhadra Rao, Convener of the Symposium, introduced the foreign participants. Professor (Dr.) R. W. Dexter of the Kent State University, Ohio, U.S.A., Mr. K. P. A. Menon, Secretary, Indian Council of Agricultural Research and Mr. G. N. Mitra, Joint-Commissioner (Fisheries), Ministry of Food, Agriculture, Community Development and Co-operation (Government of India) spoke offering messages to the Symposium on behalf of the foreign delegates, the Indian Council of Agricultural Research and the Ministry respectively. Dr. S. Jones in his speech stressed the need for the development of molluscan fisheries in India. Mr. M. C. Perumal, Chairman, Reception Committee, proposed a vote of thanks.

Mr. K. P. A. Menon inaugurated the Special Lectures held prior to the formal inauguration of the Symposium, at 10 A.M. on 12th January 1968, and released a *Souvenir*, depicting in special the cultural heritage of Kerala, brought out on the occasion by the Association. Mr. G. N. Mitra presided over the function. As the inauguration of the Symposium had to be postponed by one day for the convenience of His Excellency the Governor of Kerala, the special lectures scheduled for the 13th were shifted to the previous day. Details of the special lectures are given in the 'Programme'.

The scientific sessions began in the afternoon of 13th January 1968 and were spread over a period of four days, concluding on the afternoon of 16th January 1968. Dr. S. Jones served as the general president. The sections dealt with during the scientific sessions and the respective sectional chairmen and rapporteurs are indicated elsewhere in this volume. At the close of the concluding session resolutions were passed. Dr. S. Jones proposed the vote of thanks. Professor (Dr.) Ralph W. Dexter spoke on behalf of the participants.

Besides scientific sessions there were light entertainment programmes in the evenings details of which are included in the 'Programme'.

PRESIDENTIAL SPEECH BY DR. S. JONES

Your Excellency, Ladies and Gentlemen,

Though the formal welcome is over and the vote of thanks is to follow the inauguration I will be failing in my duty if I do not say a word of welcome on behalf of the Association and express our grateful thanks to you all for gracing the function. We are deeply grateful to Your Excellency, Sir, for honouring us by accepting our invitation to inaugurate the Symposium and release the first Memoir. Similarly, we are most happy that Mr. K. P. A. Menon, Secretary, Indian Council of Agricultural Research, representing the Council and Mr. G. N. Mitra, Joint-Commissioner for Fisheries, representing the Ministry of Food, Agriculture, Community Development and Co-operation, Government of India, could be present here and give us messages. We are most gratified and overwhelmed by the presence of such a large gathering of eminent scientists and citizens. Our welcome and thanks to everyone. Leaving out the members of the Association and my own colleagues I should express my special thanks to Mr. R. Madhavan Nayar, Chairman of the Committee of Hosts and Mr. M. C. Perumal, Chairman of the Reception Committee. It is necessary that I should make special mention of Mr. Perumal since he is to give the vote of thanks and naturally will not thank himself. On my own behalf and on behalf of the Association, I wish to express my sincere thanks to him for permitting us to hold the Symposium here and agreeing to serve as Chairman of the Reception Committee. He and the devoted members of his staff have spared no pains to make the function a success. A great deal of what you see here would bear testimony to his organising capacity and spirit of co-operation.

We have received quite a large number of messages for the success of the Symposium from institutions and individuals from different parts of the world including the FAO, UNESCO and Director-General, Council of Scientific and Industrial Research, New Delhi. For want of time they are not being read here.

Now coming to the Symposium it may be said that the subject was selected with due consideration to its potential importance. Among the living resources of the sea, molluscs come next in importance to fishes and crustaceans. The world contribution of edible molluscs is estimated at over 3 million tonnes of which India's share at present is very little. In spite of its high protein value as food it is the least developed compared to the other marine resources in this country. Molluscs have played an important role in the religion, customs, and traditions of our country and also in our economics. The successive struggles for power by the Moors, Portuguese and Dutch in the Gulf of Mannar and Palk Bay till the British took over have been mainly for the control of the pearl and chank beds there.

In all, we have received for the symposium nearly 100 contributions from 17 countries including several from India. The 'Abstracts of Papers' have been supplied to all participants and others. About 150 scientists are participating in the meetings including several from foreign countries. *The Proceedings of the Symposium* when published would come to over 1000 pages and serve as an important work of reference on the subject. The special lectures held in advance of the Symposium on the 12th January have been well attended. These would show the importance of the subject and the wide interest the Symposium has created.

My thoughts now go back to January 1962 when we held the first Symposium at Mandapam Camp on Scombroid Fishes. We were then in a state of uncertainty as we were confronted with the formidable task of publishing the proceedings with hardly any financial resources at our command. We faced the issue with courage and determination. We learnt the lessons of survival in the hard way and the whole picture has changed now.

It is hardly necessary to say anything in special about the Association and its activities. It is just 9 years old and a brief history of the same has been given in the *Souvenir* issued in connection with this Symposium. The Association by its various activities, especially by the publication of its Journal and holding Symposia, has strived its utmost to promote the cause of marine sciences in this part of the world and in this it has met with considerable success on account of the co-operation extended by all.

The release of the first Memoir of the Association on *The Ribbon-fishes of the Family Trichiuridae of India* is another landmark in the history of the Association. It can be said to be the most detailed account ever attempted on any economically important group of fishes in the Indian region. This and the others to follow would go a long way to broaden our knowledge of marine life, and it is hoped that they will be well received.

As one with about three-and-a-half decades of research background with close contacts with the rising generation of scientific workers in the country I can say without hesitation that given proper guidance and encouragement our young workers would compare favourably with the best anywhere in the world. While understanding their hopes and aspirations I would repeat to them the advice given thousands of years ago in that great battlefield of Kurukshetra:

> Set thy heart upon thy work and not on its reward
>
> Work not for a reward but never cease to do thy work

I request Your Excellency to kindly inaugurate the Symposium and release the first Memoir of the Association.

Thank you all.

INAUGURAL ADDRESS BY HIS EXCELLENCY THE GOVERNOR OF KERALA, MR. V. VISWANATHAN

Dr. Jones, Ladies and Gentlemen,

I thank you for your very kind invitation to me to be present here on this important occasion of the inauguration of your Symposium on Mollusca. I am happy to note that the Marine Biological Association of India has, within the span of a decade, done much to further the study of marine sciences in India and that this is the third International Symposium it is organising. This is quite a substantial record for the Association. I was particularly anxious to participate in this Conference, because, of all the States bordering on the sea, the importance of the sea and sea-food is greater at the moment to Kerala than to other States.

You are all gathered here a body of very distinguished scientists but I should speak to you today only as a layman and as an administrator. A body of distinguished scientists like this makes you ask the first question: what is the object of these Seminars and Conferences and of the research work. The purposes of science have always been recognised to be twofold. The chief aim of scientific pursuits is the search for truth, truth for its own sake. All philosophy and all science primarily get directed towards a proper apprehension, a perception of the truth in nature and if possible beyond. Truth is an end in itself and has to be sought for its own sake. When Newton made the discovery of the law of gravitation he experienced a state of happiness and bliss, not because the discovery of the law of gravitation was of any practical use to anyone, but because he had now come into an apprehension of the further region of truth in nature. The whole idea of looking for truth for itself is expressed in the toast of the pure Mathematical Society of one of the Universities. The toast is "Here is to pure mathematics though it be of no damned use to anyone". That is one of the most profound and fundamental objects of science and not only of science but of all philosophical exploration. But to-day as an administrator I must speak to you of the other great object of science, of the utilitarian aspect of scientific research, of science serving the day-to-day needs, the material needs, of man. That is an aim which many may consider of secondary importance, but you can no longer ignore it or consider it as of less importance.

Now therefore coming to the subject of marine biology, what has been man's approach to the sea and how has he faced this problem? Man, in the course of evolution of a quarter of a million years, sought for sustenance from his environment and he became a food-gathering animal like all other animals in nature. On land he started gathering food but equally so, from the very early times, from the sea also. But in the course of some millennia man, who is essentially a land animal, developed in a new direction in the matter of getting food from the land. He gave up the habit of being a food gatherer and became a food producer or food creator. He domesticated animals and cultivated land. He was not creating anything new, but was helping nature and directing the course of nature to subserve his ends in a way in which he became essentially a producer of food. Yet after these millennia in which he has been a food producer on land he largely remained a food gatherer on sea. Even today he is very largely a food gatherer on sea. I have no doubt that in the course of some decades man will develop the capacity to become a food producer even in the sea. In Japan and other eastern Pacific countries the cultivation of the pearl oyster has become a producing activity instead of merely a gathering activity. But along our sea coasts we are still in food gathering stage. Even this food gathering stage is not to be despised. The problem before us in India is that as food gatherers we are not so efficient as we should be. We had better apply the principles of food gathering on land to the sea also. We know that the forest has to be exploited to the maximum, but conserved also to the maximum. The gathering of wealth from the sea, as from the land, is the problem of optimum exploitation, regeneration and conservation. But are we doing it efficiently in the sea? So far as we Indians are concerned our food gathering methods from the sea are still rather primitive. We are not gathering from the sea that amount of food which we can gather from our own continental shelf and from beyond. But such an increase of food gathered from the sea will immediately place on you the responsibility of conserving the sources of food. That is to say, conservation must accompany better exploitation. We have therefore this problem before us which I invite you scientists to give your attention to and help us administrators, by applying yourselves to the problem, of how we can gather more sea-food without destroying resources—without eating up the goose that lays the golden egg. This way we can organise the supply of food from the sea and later on, perhaps, when science develops, I have no doubt, we would reach the stage when we should begin proper process of producing food from the sea itself. That is the problem which I invite you to address yourselves. I know that you are concerned with a variety of details of biological importance, but these are the problems which confront us in the country and I seek your assistance in evolving final solution to this problem. I am very happy as I said particularly in my capacity as the Administrator of Kerala to be here where you discuss a problem which concerns this State and other parts of India so intimately and vitally.

I thank you once again for the cordiality with which you have welcomed me here. I have great pleasure in inaugurating this *Symposium on Mollusca* and in releasing the Memoir on *The Ribbonfishes of the Family Trichiuridae of India.*

VOTE OF THANKS BY DR. S. JONES *

Friends,

I am taking the privilege of proposing the vote of thanks since as most of you are aware I have been, from the very beginning, associating myself closely with the organisation and conduct of this Symposium. Perhaps more than anyone else here, I am aware of the interest taken by various persons and the efforts put in by them in making the Symposium a success and it gives me great pleasure to thank them all on behalf of the Association.

From the time of conceiving the idea of holding this Symposium until Mr. K. Virabhadra Rao, the Convener, took charge a few weeks back the onerous duties of the Convener were looked after by a number of my colleagues. To begin with I would like to mention the name of Mr. K. Alagarswami who made a good beginning by issuing the various circulars and contacting prospective contributors and participants. He had to leave the country for a while and the work was carried on by Dr. V. S. Durve for some time followed by Dr. P. S. B. R. James assisted by Mr. K. S. Sundaram who brought the same to the final stages until formally taken over by Mr. K. Virabhadra Rao. My sincere thanks to all of them and the Convener.

We are grateful to His Excellency, the Governor of Kerala Mr. V. Viswanathan for kindly inaugurating the Symposium and releasing the first Memoir of the Association. Our thanks are due to the Indian Council of Agricultural Research and the Ministry of Food, Agriculture, Community Development and Co-operation, Government of India, for the messages of greetings and good wishes sent for this occasion through Mr. K. P. A. Menon, Secretary and Mr. G. N. Mitra, Joint Commissioner (Fisheries), respectively. We thank Mr. Menon for inaugurating the special lectures connected with the Symposium and releasing the *Souvenir* and Mr. Mitra for presiding over the above function. Our thanks to Dr. R. W. Dexter, Professor of Biological Sciences, Kent State University, Ohio, for the message given on behalf of the foreign participants.

We are grateful to Dr. B. P. Pal, Director-General, Indian Council of Agricultural Research, for kindly making it convenient to attend the evening function yesterday in spite of various pressing engagements.

We are indebted to Mr. M. C. Perumal, Director, Central Institute of Fisheries Operatives, for permitting us to hold the Symposium within the premises of the Institute and wish to place on record our grateful thanks to him and his staff for all the co-operation extended and assistance rendered in this connection.

Mr. R. Madhavan Nayar as Chairman of the Committee of Hosts, Mr. M. C. Perumal as the Chairman of the Reception Committee did their best to make the Symposium a success. Our sincere thanks and appreciation to them and members of the above Committees.

Our grateful thanks to the Conveners and Members of the Souvenir Committee, the Programme Committee, the Hospitality Committee and the Information Committee. For the active interest evinced in the various matters connected with the Symposium we are thankful to Mr. Balasubrahmanyan, Dr. R. Subrahmanyan and Mr. K. K. P. Menon.

During these four days we have enjoyed the hospitality and courtesies from various organisations: The Seafood Canners' and Freezers' Association of India, Cochin and its President Mr. R. Madhavan Nayar; the Indian Seafood Exporters' Association, Cochin and its President Mr. Kuruvath Damodaran; the Kathakali Club, Ernakulam; The Amateur Artists' Association; Ernakulam; and the Ernakulam Fine Arts Club and specially Mr. V. R. Krishna Ayyar and

---

* At the concluding session on January 16, 1968.

Mr. K. Baskaran Nair for arranging the Veena performance by Mr. S. Balachandar and Bharatanatyam by Miss Sashikala Chandramouli. To them all we offer our sincere thanks.

The success of the Symposium has been greatly due to the large number of contributions received and very good attendance by scientists from within this country and outside. Our sincere thanks to all of them. Our thanks are due to the distinguished scientists who served as Members of the Advisory Committee, Chairmen of the various sections and also the Rapporteurs. To those participants who have come from abroad and gave an international touch to the Symposium we owe our sincere thanks. They have actively participated in all the Sessions and connected functions and have cheerfully put up with the discomforts, if any, experienced here. It is hoped that they would carry with them pleasant memories of their brief sojourn in this country.

We are thankful to Mr. P. V. Ramachandran Nair and Dr. E. G. Silas who had been associated with this Symposium arrangements since a very early stage and did their best to bring out the *Souvenir* and the *Abstracts*.

Our thanks to Mr. P. Vedavyasa Rao through whom we were able to put up the nice tea stall adjacent to our conference hall. Our appreciation and thanks to Mr. K. K. R. Kumar for personally attending to our various needs here and to Mr. M. P. Cherian for attending to the slide projector and amplifier arrangements.

We thank Messrs. City Printers, Ernakulam, for their active co-operation in bringing out the *Souvenir* and the *Abstracts* in time. We also thank Messrs. Kerala Travels, the postal authorities at Ernakulam and the Bharat Cafe for kindly offering their services to the participants.

For the success of this Symposium so many individuals, too numerous to mention their names here, have extended their willing co-operation and help. To them we offer our appreciation and sincere thanks. My personal thanks to all for the courtesy and co-operation.

Thank you all.

CONCLUDING STATEMENT BY DR. RALPH W. DEXTER, ON BEHALF OF THE PARTICIPANTS

Dr. Jones, Ladies and Gentlemen,

On behalf of the participants, I should like to express our profound gratitude to you, Dr. Jones, and to the Marine Biological Association of India, for organising this eminently successful *Symposium on Mollusca* and for leaving no shell unturned to make the occasion an enjoyable and profitable one. Ladies and Gentlemen, I give you, Dr. Jones! (standing ovation).

RESOLUTIONS

1. *Resolved* that the Marine Biological Association of India on the occasion of the Symposium on Mollusca at Cochin in January 1968 shall send its greetings and good wishes to the Third International Malacological Congress (European Unit) to be held in September 1968, at University of Vienna, Vienna and request Dr. Ferdinand Starmühlner of the University of Vienna now attending the Symposium to convey the same on the occasion personally on behalf of the Association.

2. It is noted with concern that the systematics of no major group of molluscs in the Indian region has been studied in a comprehensive manner in the past few decades and it is therefore recommended that steps be taken by concerned organisations to make vigorous efforts to undertake taxonomic studies of at least the economically important groups.

3. It is *resolved* to recommend that in view of the importance of molluscs as food resource and to enable their optimum utilization a survey of the edible molluscan fishery resources especially of the developing countries be taken without delay.

4. *Resolved* to recommend that investigations be undertaken to ascertain the feasibility of transplanting economic varieties of molluscan species from well-established areas to other similar and suitable habitats where they are not found at present.

5. *Resolved* to recommend that studies on the biology and fishery of economically important molluscs be intensified to include various aspects, especially these relating to mussel, oyster and clam farming and pearl culture.

6. In view of the great importance of some molluscs as borers and foulers, it is *resolved* to recommend that a suitable illustrated review of these groups be undertaken on a global basis.

7. *Resolved* to recommend that suitable methods of preservation and processing of mussel, oyster, clam and squid meat be tried in India for export to create an interest for better utilization of the available resources.

8. Molluscan shellfish at present being utilised only by the poorer classes of people in India, it is *resolved* to recommend that steps be taken to popularise their being utilised to a larger extent than is obtained at present.

9. The participants both Indian and foreign, at the Symposium on Mollusca express their sincere thanks and appreciation to the Chairman and Members of the Committee of Hosts and Reception Committee and to the Convener and Members of the Hospitality Committee and to the Seafood Canners' and Freezers' Association of India, the Kathakali Club, Kerala Fine Arts Association, Amateur Artists' Association, Ernakulam and the Indian Seafood Exporters Association and the citizens of Cochin in general for the hospitality and courtesy shown to them in the course of their stay and request the President to convey the same to the respective individuals and organisations.

THE SECTIONS DEALT WITH DURING THE SCIENTIFIC SESSIONS AND THE RESPECTIVE SECTIONAL CHAIRMEN AND RAPPORTEURS

I. PHYLOGENY

Chairman: Prof. (Dr.) Ralph W. Dexter
Rapporteurs: Dr. M. C. Mercer and Dr. E. G. Silas

II. GENERAL DISTRIBUTION

Chairman: Prof. (Dr.) F. Starmühlner
Rapporteurs: Dr. A. H. Atapattu and Mr. S. Mahadevan

III. MORPHOLOGY AND ANATOMY

Chairman: Dr. A. D. Ansell
Rapporteurs: Mr. K. Nagappan Nayar and Dr. V. V. Srinivasan

IV. RADIATION BIOLOGY

Chairman: Dr. A. D. Ansell
Rapporteurs: Mr. J. R. Naidu and Mr. P. V. Ramachandran Nair

V. REPRODUCTION AND LARVAL DEVELOPMENT

Chairman: Mr. K. Virabhadra Rao
Rapporteurs: Mr. S. Mahadevan and Mr. R. Sarvesan

VI. ECOLOGY AND BEHAVIOUR

Chairman: Dr. A. J. Kohn
Rapporteurs: Mr. S. Mahadevan and Dr. M. Saraswathy

VII. PHYSIOLOGY

Chairman: Dr. G. M. Davis
Rapporteurs: Dr. M. Narayanan Kutty and Dr. P. S. B. R. James

VIII. CYTOLOGY

Chairman: Dr. J. B. Burch
Rapporteurs: Dr. C. M. Patterson and Mr. S. Mahadevan

IX. BORING AND FOULING MOLLUSCS

Chairman: Dr. N. Balakrishnan Nair
Rapporteurs: Mr. R. Balasubramanyan and Dr. A. A. Karande

X. PARASITOLOGY AND COMMENSALISM

Chairman: Dr. M. Anantaraman
Rapporteurs: Dr. P. S. B. R. James and Mr. D. B. James

XI. CULTURE, ECONOMICS AND FISHERY

Chairman: Mr. G. N. Mitra
Rapporteurs: Mr. S. Mahadevan and Mr. E. J. Rasalam

COMMITTEES CONSTITUTED AT THE TIME OF THE SYMPOSIUM

COMMITTEE OF HOSTS

Mr. R. Madhavan Nayar, *Chairman*
Mr. M. S. Bhaskaran Nayar
Mr. N. J. Chacko
Mr. K. Gopinatha Pillai
Mr. John P. George
Mr. V. R. Krishna Iyer
Mr. Kuruvath Damodaran
Mr. P. Lakshmanan
Mr. V. M. Srikumaran Nayar
Mr. Salay Mohamed Ebrahim

RECEPTION COMMITTEE

Mr. M. C. Perumal, *Chairman*
Mr. V. Ananthanarayanan
Mr. M. Devidas Menon
Rev. Sr. Digna
Mr. P. K. Eapen
Dr. C. V. Kurian
Mr. G. K. Kuriyan
Mr. Lahn Johannessen
Mr. K. M. Mathew
Dr. S. Z. Qasim
Dr. E. G. Silas
Rev. Fr. Theobald
Mr. P. M. G. Menon

SOUVENIR COMMITTEE

Mr. P. V. Ramachandran Nair, *Convener*
Mr. K. K. P. Menon
Mr. K. K. R. Kumar

PROGRAMME COMMITTEE

Mr. K. K. P. Menon, *Convener*
Mr. K. C. George
Mr. K. P. V. Unni

HOSPITALITY COMMITTEE

Mr. R. Balasubrahmaniam, *Convener*
Mr. T. R. Menon
Mr. R. Satyarajan
Mr. K. B. C. Menon
Mr. P. Vedavyasa Rao
Mr. N. M. Shah

INFORMATION

Dr. R. Subrahmanyan
Mr. K. K. P. Menon

PROGRAMME

January 11, 1968

10–00 a.m. to 12–30 p.m. and 2–00 p.m. to 5–00 p.m.	Registration of Participants.
3–00 p.m.	Meeting of the Advisory Committee and Sectional Chairmen.

January 12, 1968

9–00 a.m. to 10–00 a.m.	Registration of Participants
10–00 a.m.	Inauguration of Special Lectures.
10–15 a.m. to 11–15 a.m.	Lecture: *Defensive Adaptations in the Mollusca* by Dr. Alan D. Ansell, Marine Station, Millport, U.K.
11–30 a.m. to 12–30 p.m.	Lecture: *Some Problems of Cephalopod Locomotion* by Dr. Anna M. Bidder, University of Cambridge, U.K.
2–30 p.m. to 3–30 p.m.	Lecture: *The Problem of Timber Destroying Molluscs of Indian Coast* by Dr. N. Balakrishnan Nair, University of Kerala, India.
3–30 p.m. to 5–00 p.m.	Lecture: *The Resistance of Intertidal Snails to High Temperature* by Dr. G. Fraenkel, University of Illinois, U.S.A.
7–00 p.m.	Film Shows—*Fishing at Sea* and *Feeding Habits of* Conus.

January 13, 1968

9–00 a.m. to 10–30 a.m.	Registration of Participants.
11–00 a.m.	Inaugural Meeting.
2–00 p.m. to 5–00 p.m.	Scientific Session.
5–30 p.m.	Tea by the Seafood Canners' and Freezers' Association of India, at T.D.M. Hall.
6–30 p.m.	Kathakali (*Rugmangatha Charitham*) at T.D.M. Hall.

January 14, 1968

9–30 a.m. to 12–30 p.m.	Scientific Session.
2–00 p.m.	Sight-seeing Trips.
5–00 p.m.	Tea by the Marine Biological Association of India, at the Central Institute of Fisheries Operatives.
5–45 p.m. to 6–30 p.m.	Bharatanatyam by Kumari Sashikala Chandramouli at Fine Arts Theatre.
6–30 p.m.	Music (Veena performance) by Mr. S. Balachander at Fine Arts Theatre.

January 15, 1968

9-30 a.m. to 12-30 p.m. ..	Scientific Session.
2-00 p.m. to 5-00 p.m. ..	Visit to Fisheries and Oceanographic Institutes.
5-30 p.m. ..	Tea by the Indian Seafood Exporters Association, at the International Hotel.
6-30 p.m. ..	Music performance organised by the Amateur Artists' Association, Ernakulam, at the International Hotel.

January 16, 1968

9-30 a.m. to 1-30 p.m. ..	Concluding Session.

PARTICIPANTS

Achari, G. P. Kumaraswamy,
* C.M.F.R. Institute,
Mandapam Camp,
India.

Adolph Clement,
Department of Zoology,
Malabar Christian College,
Calicut,
India.

Alexander, K. M.,
Department of Zoology,
University of Kerala,
Calicut,
India.

Ansell, A. D.,
The Marine Station,
Millport,
Scotland.

Anantaraman, M.,
Veterinary College,
Madras-7,
India.

Appukuttan, K. K.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Aravindakshan,
Indian Ocean Biological Centre,
Ernakulam,
India.

Atapattu, D. H.,
Department of Zoology,
University of Ceylon,
Colombo-3,
Ceylon.

Babu, S. K.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Balakrishnan, G.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Balan, V.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Balasubramanyan, R.,
Central Institute of Fisheries Technology,
Cochin,
India.

Banerji, S. K.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Bennet, P. S.,
C.M.F.R. Sub-Station,
Calicut,
India.

Bidder, A. M.,
Department of Zoology,
University of Cambridge,
Cambridge,
England.

Burch, J. B.,
Museum and Department of Zoology,
University of Michigan,
Ann Arbor,
Michigan,
U.S.A.

Chacko, P. I.,
Department of Fisheries,
Madras,
India.

Chakraborty, D.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

---

* C.M.F.R. = Central Marine Fisheries Research

Cherian, C. J.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Cherian, T.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Cheriyan, P. V.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Damodaran, R.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Davis, G. M.,
406th Medical Laboratory,
USAMCJ,
APO San Francisco,
U.S.A.

Desai, B. N.,
National Institute of Oceanography,
Ernakulam,
India.

Dexter, R. W.,
Kent State University,
Kent,
Ohio,
U.S.A.

Dhandapani, P.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Dharma Raja, S. K.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Dora, Y. L.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Fraenkel, G. S.,
Department of Entomology,
University of Illinois,
Illinois,
U.S.A.

George, A. I.,
Department of Fisheries,
Trivandrum,
India.

George, K. C.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

George, K. V.,
C.M.F.R. Sub-Station,
Calicut,
India.

George, M. J.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Girijavallabhan, K. G.,
C.M.F.R. Sub-Station,
Calicut,
India.

Gopalan, U. K.,
National Institute of Oceanography,
Ernakulam,
India.

Hameed, D. M. A.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

James, D. B.,
C.M.F.R. Institute,
Mandapam Camp,
India.

James, P. S. B. R.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Jones, S.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Jose, P. J.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Joseph, M.,
Oceanographic Laboratory,
Ernakulam,
India.

Joshi, P. V.,
N. Wadia College,
Poona-2,
India.

Karande, A. A.,
Naval Chemical and Metallurgical Laboratory,
Naval Dockyard,
Bombay,
India.

Kewalramani, H. G.,
Taraporewala Aquarium,
Bombay,
India.

Kohn, A. J.,
University of Washington,
Seattle,
Washington,
U.S.A.

Kuriakose, P. S.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Kurian, C. V.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Kutty, M. Krishnan,
National Institute of Oceanography,
Ernakulam,
India.

Kutty, M. Narayanan,
C.M.F.R. Institute,
Mandapam Camp,
India.

Lahn-Johannessen, J. H.,
Indo-Norwegian Project,
Ernakulam,
India.

Luther, G.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Mahadevan, S.,
C.M.F.R. Unit,
Tuticorin,
India.

Mathai, P. G.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Mathew, K. J.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Meeran, N. K.,
Fisheries Research Station,
Edathua,
Kerala,
India.

Meiyappan, M. M.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Menon, K. K. P.,
Off-shore Fishing Station,
Cochin,
India.

Menon, K. P. A.,
Indian Council of Agricultural Research,
Krishi Bhavan,
New Delhi,
India.

Menon, K. R.,
National Institute of Oceanography,
Ernakulam,
India.

Menon, N. Gopinatha,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Menon, T. P. Rema,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Mercer, M. C.,
Fisheries Research Board of Canada,
Biological Station,
St. John's,
Newfoundland,
Canada.

Mitra, G. N.,
Ministry of Food, Agriculture, Community Development and Co-operation,
Government of India,
New Delhi,
India.

Mohammed, K. H.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Mukundan, C.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Murty, A. V. S.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Naidu, Janik Ram,
Health Physics Division,
Bhabha Atomic Research Centre,
Bombay,
India.

Nair, P. Karunakaran,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Nair, N. Balakrishnan,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Nair, N. Unnikrishnan,
Central Institute of Fisheries Technology,
Cochin,
India.

Nair, K. Prabhakaran,
C.M.F.R. Centre,
Neendakara,
India.

Nair, P. N. Radhakrishnan,
Oceanographic Laboratory,
Ernakulam,
India.

Nair, P. V. Ramachandran,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Nair, R. Vijayalakshmi,
Indian Ocean Biological Centre,
Ernakulam,
India.

Neelakantan, B.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Natarajan, R.,
Marine Biological Station,
Porto Novo,
India.

Nayar, K. Nagappan,
C.M.F.R. Unit,
Tuticorin,
India.

Nayar, R. Madhavan,
Cochin Company (P.) Ltd.,
Cochin,
India.

Noble, A.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Oommen, P. V.,
Oceanographic Laboratory,
Ernakulam,
India.

Panikkar, N. K.,
National Institute of Oceanography.
New Delhi,
India.

Parvathy, V. S.,
Oceanographic Laboratory,
Ernakulam,
India.

Patterson, C. M.,
Museum of Zoology,
University of Michigan,
Ann Arbor,
Michigan,
U.S.A.

Perumal, M. C.,
Central Institute of Fisheries Operatives,
Ernakulam,
India.

Peter, K. J.,
Indian Ocean Biological Centre,
Ernakulam,
India.

Pillai, C. S. Gopinatha,
C.M.F.R. Institute,
Mandapam Camp,
India.

Pillai, N. Neelakanta,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Pillai, P. Parameswaran,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Prasad, N. K.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Prasad R. Raghu,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Qasim, S. Z.,
National Institute of Oceanography,
Ernakulam,
India.

Radhakrishnan, N.,
C.M.F.R. Unit,
Vizhingam,
India.

Rajagopal, M. S.,
C.M.F.R. Unit,
Vizhingam,
India.

Rajan, S.,
National Institute of Oceanography,
Ernakulam,
India.

Rajan, S. J.,
C.M.F.R. Sub-Station,
Calicut,
India.

Ralph, Ann,
Marine Laboratory,
Aberdeen,
Scotland.

Ramamritham, C. P.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Rao, J. Advi,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Rao, K. Virabhadra,
C.M.F.R. Sub-Station,
Bombay,
India.

Rao, P. Vedavyasa,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Rasalam, E. J.,
L.S.A. Station,
Kumarakom,
Kerala,
India.

Rass, T. S.,
Institute of Oceanography,
Academy of Sciences,
USSR,

Ronkin, R. R.,
U.S. National Science Foundation,
9, Ring Road,
New Delhi,
India.

Sait, M. S. M.,
XX/238 Chittoor Road,
Ernakulam,
India.

Sakthivel, M.,
Indian Ocean Biological Centre,
Ernakulam,
India.

Sankarankutty, C.,
Indian Ocean Biological Centre,
Ernakulam,
India.

Santhakumari, V.,
Oceanographic Laboratory,
Ernakulam,
India.

Saraswathy, M.,
Indian Ocean Biological Centre,
Ernakulam,
India.

Sarvesan, R.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Sathananthan, A. H.,
Department of Zoology,
University of Ceylon,
Colombo-3,
Ceylon.

Sebastian, M. J.,
State Fisheries Department,
Kerala,
India.

Seshappa, G.,
C.M.F.R. Sub-Station,
Calicut,
India.

Shah, N. M.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India,

Shanbhogue, S. L.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Sharma, G. S.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Shenoy, J. S.,
Oceanographic Laboratory,
University of Kerala,
Ernakulam,
India.

Shukhanov, B. N.,
Consulate of USSR,
2, Kasturi Ranga Iyengar Road,
Madras,
India.

Silas, E. G.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Srinivasan, M.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Srinivasan, V. V.,
Marine Organisms Scheme,
Forest Research Institute,
Madras,
India.

Sriramachandramurthy, V.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Starmühlner, F.,
1st Zoological Institute,
University of Vienna,
Austria.

Subramanyan, R.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Sugunan, V. V.,
Oceanographic Laboratory,
Ernakulam,
India,

Sundaram, K. S.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Sunny, K. G.,
Oceanographic Laboratory,
Ernakulam,
India.

Suryanarayanan, H.,
Department of Zoology,
Kerala University,
Calicut,
India.

Suseelan, C.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Thomas, M. M.,
C.M.F.R. Institute,
Mandapam Camp,
India.

Thomas, P. A.,
C.M.F.R. Sub-Station,
Ernakulam,
India.

Tranter, D. J.,
Indian Ocean Biological Centre,
Ernakulam,
India.

Venkataraman, G.,
C.M.F.R. Sub-Station,
Calicut,
India.

Vincent, T. J.,
Marine Biological Station,
West Hill,
Calicut,
India.

Warrier, V. T. G.,
C.M.F.R. Sub-Station,
Calicut,
India.

THE MARINE BIOLOGICAL ASSOCIATION OF INDIA[1]

S. JONES

President, Marine Biological Association of India and Director, Central Marine Fisheries Research Institute, Mandapam Camp

THE Marine Biological Association of India was organised on the 30th December 1958 with its headquarters at Mandapam Camp and was formally inaugurated on 3rd January 1959 by the Minister for Fisheries, Madras State. Its aim is to promote the cause of marine sciences in the Indian Region: "(*a*) by organising lectures, symposia and seminars on specific subjects, (*b*) by offering requisite information to research workers and students undergoing training in Marine Biological Sciences, (*c*) by publishing a journal which shall be called the *Journal of the Marine Biological Association of India*, (*d*) by issuing occasional Memoirs and Monographs, (*e*) by instituting fellowships and studentships for research workers at the various recognised institutions, (*f*) by sponsoring and aiding expeditions and (*g*) by instituting prizes to be awarded in recognition of outstanding contributions towards the advancement of the Marine Biological Sciences from the research workers of India, as funds permit". The Association has as its Patron-in-Chief His Excellency the Governor of Madras State and as patrons the Hon'ble Minister of Fisheries, Madras State, and the Vice-Chancellors of the Aligarh Muslim University, the Annamalai University and the Kerala University.

The initiative for organising the Association was taken by the scientific staff of the Central Marine Fisheries Research Institute at Mandapam Camp, who continue to be mainly responsible for conducting its affairs in an honorary capacity. The Association has grown from an initial individual and institutional membership of 563 in 1959 to 837 by 1967. Of these 480 are from within India and 357 from countries outside. Foreign component in the membership of the Association is from nearly 50 countries, *viz*., Argentina, Australia, Austria, Belgium, Bermuda, Brazil, Canada, Ceylon, Chile, Denmark, France, Germany, Ghana, Guyana, Hongkong, Hungary, Iceland, Italy, Indonesia, Israel, Japan, Kenya, Korea, Liberia, Malagasi, Malaysia, Mauritius, Mexico, Netherlands, New Caledonia (Oceania), New Zealand, Nigeria, Norway, Pakistan, Papua, Peru, Republic of Congo, Rumania, Singapore, Spain, Tanzania, Thailand, United Arab Republic, United Kingdom, United States of America, Union of Soviet Socialist Republics, Venezuela and West Indies. In addition to the above it is possible that the publications of the Association reach several other countries also through book sellers. There is hardly any country in the world where researches on marine sciences are in progress which does not subscribe for or procure the *Journal* and other publications of the Association directly or indirectly.

The above statistics will speak for themselves to indicate the wide recognition that the Association enjoys and this is in no small measure due to its *Journal* being issued since 1959. The periodical had from its very inception achieved its present international status owing largely to the standard of the scientific papers published in the same.

A significant step that the Association took in the furtherance of its objectives was by organising symposia periodically. The first symposium was held in Mandapam Camp in January 12–16, 1962, on "Scombroid Fishes" constituted by mackerel, tunas, seerfishes and billfishes, with 72 contributions from 14 countries and with participation by Indian as well as foreign contributors. The proceedings of the symposium coming to over 1,400 pages issued in four volumes have already

---

[1] Reprinted from: *Souvenir, Symposium on Mollusca*, Cochin, Jan. 12–16, 1968: 1–3

been recognised as the most outstanding contribution to fishery science from this part of the world. The second symposium held at Ernakulam from January 12 to 15, 1965 was on 'Crustacea' the group that includes prawns, lobsters and crabs and a variety of smaller forms which are in one way or other directly or indirectly of importance to man. The symposium received 124 contributions from 20 countries and was attended by quite a large number of contributors and other scientists from within and outside India. The proceedings consisting of about 2,000 pages are to be brought out in six volumes and of these four volumes coming to over 1,500 pages have already been issued. This has become an indispensable work of reference on this interesting and important group of animals. The third symposium in connection with which the present *Souvenir* is being issued is on "Mollusca", the important group of animals consisting of squids, oysters, mussels, clams, gastropods (chanks), etc. It has received nearly a hundred contributions from over 15 countries and the proceedings are expected to come to over 1,000 pages to be issued in four volumes. The fourth symposium will be on "Corals and Coral Reefs" and is proposed to be held at Mandapam Camp from January 12 to 16, 1969. The popularity and recognition enjoyed by the Association both within the country and outside are already evident not only from the wide range of membership but also from the response we have been receiving for the symposia which are held regularly.

The *Journal of the Marine Biological Association of India* and the proceedings of the symposia have helped to highlight the work done in fisheries and cognate sciences in this country and thereby place India on the map of marine sciences in general and fishery sciences in particular. In addition to the above, the Association has just started a new series of publications, *viz.*, Memoirs, which consist of monographs and other comprehensive accounts on marine organisms. Over six of them are under various stages of publication and of these the first two on the Ribbon-fishes of India and *Ceratium* are under issue.

It should perhaps surprise many to know that the Association has been able to do all this without any grant or subsidy from any organisation from within this country. The annual subscription for individual members in India is purposely kept as low as Rs. 10 to enable the maximum number of scientific workers to take advantage of the services of the Association. Every member is entitled to receive free a copy of the Journal of the Association, the publication cost of which comes to very much more than this amount!

The Association has never looked back since its inception. That it is in a position to thrive in a self supporting manner by membership subscription and sale of publication is a matter of gratification to all, especially when few other scientific associations of this kind could make such a claim. As against about Rs. 350 on postage and about Rs. 2,600 on printing spent in 1959 our expenses in 1967 came to about Rs. 4,000 on postage and about Rs. 60,000 on printing! Our printing programme for 1968 is expected to be much larger than for the previous year but we hope to meet all these commitments from our own resources apart from the expenses that are being incurred for conducting the present Symposium. Incidentally it may be mentioned that in addition to the scientific service, the Association has been able to contribute its mite to the nation's economy by bringing in foreign exchange to the tune of Rs. 10,000 to Rs. 15,000 a year into the country.

The above might probably give a rather rosy picture about the Association but the teething troubles and the ordeals it had to undergo in the early years have remained an untold story. Ours was perhaps not unlike the case of the shepherd in the Virgil who at last got acquainted with Love and found him a native of the rocks. The efforts to get grants met with no response when we really wanted them and it was ultimately decided to depend on self-reliance, and in this we have fortunately succeeded, due entirely to the untiring and unostentatious work and unstinted co-operation shown by my colleagues at the Central Marine Fisheries Research Institute. We have now decided not to seek, as far as possible, for any aid and if necessary to go a step further by offering aid to the maximum possible extent in deserving cases. The Association has been in a way able to demonstrate that it is man that makes money but not quite the other way about.

The success of the Association is a challenge to others and it is hoped that it will give food for thought to the authorities giving subsidies and grants for such organisations. This also brings in a poser for others as to whether subsidies and grants are indispensable. It is understood that no Association could expect to get a grant unless there is a deficit and this unfortunately gives incentive to develop a tendency to create deficit, which is a most negative approach! It is, therefore, time for a reappraisal of the whole procedure so as to encourage incentives of a positive and constructive nature and *not* of a negative nature as at present.

The Association has a programme of expansion of its activities which includes a proposal to establish a laboratory also in the pattern of the Naples Zoological Station or the Marine Biological Laboratory at Plymouth. It would not be possible to do this with its own resources. The materialisation of this will depend on the co-operation and support received from the scientists and the public.

What little the Marine Biological Association of India has been able to do within the short period of its existence from its humble beginning hardly a decade ago is in a way unique. We could say with pardonable pride that it has blazed a trail which has no parallel in this country. It is doubtful if there is any scientific association or society in India, probably for that matter anywhere else, which could claim to have served the cause of science to such an extent and against such odds on its own resources. The achievements of the Association will go down in the history of science in India as a classical example of what could be accomplished by the united and dedicated efforts of a devoted few.

MOLLUSCS IN INDIAN TRADITION AND ECONOMY[1]

C. MUKUNDAN

Central Marine Fisheries Research Institute, Mandapam Camp

THE molluscs constitute a natural resource of sizeable magnitude in many parts of the world. They are an age-old group represented among the early fossils, a group of great diversity in size, distribution, habitat and utility. The range of their distribution is as extensive in space as in time for it covers terrestrial, marine and freshwater habitats. They include members from the tiny estuarine gastropod *Bithynia* and small garden snails to the Giant Clam *Tridacna* or the Giant Squid *Architeuthis*. Their use as ornaments, utility articles and medicine has been widespread from ancient days. Not all molluscs, of course, are so helpful or even harmless. Even as in the humans that exploit them, there is in their midst an effective section that hides behind the goodness of others to indulge in a spot of mischief of their own. The sacredness of the Chank is countered by the sin of the snail-carriers of *Schistosoma* or by the destructive talents of the ship worms and fouling molluscs. This, in a way, but adds to the importance of their study; it does not diminish the positive qualities of the group. Though the recognition of their full potential, including their role as nutritious, even delectable, food is of relatively recent date, it is clear that man has exploited the shell resources to varying extents ever since he started utilizing nature's gifts for his own personal or social needs.

In India the molluscs have occupied a marked place in the affairs of man from time immemorial, in his affairs of state and economy, of mind and aesthetic values, of religion and rites of worship. From their pride of place in mythology and legend they have inspired countless tales in folklore, caused long-standing customs and traditions, and in more recent times come to occupy prominent positions in heraldry and royal insignia, besides featuring conspicuously in the economy of vast sections of the people.

The most renowned of these molluscs, in lore and in literature, is perhaps the pearl oyster, as the very mention of the fabulous pearls strikes a responsive chord rich in associations. History and legend here bring forth such an admixture of fact and fiction, wherein for some historical pearl or other, kingdoms have fallen, fortunes changed hands or widespread destruction has followed. The pearls have also inspired countless ancient poets to moralise and gush forth lyrical, even if unscientific, accounts of their origin and occurrence.

MOLLUSCS IN ANCIENT INDIA

Evidence of long-standing association between man and molluscs in India is afforded by the shell remains discovered in human habitations of pre-Vedic Mohanjedaro, Harappa, Amri, Nal, Nundara and Rupar. These included not only the cowries (*Cypraea*) and the Chank (*Xancus*) but also their products—bangles and cores of shells from which the bangles have been sawn out. In Vedic times, despite the relative rarity of references to marine life in the Vedas, possibly because of the predominantly agricultural or pastoral nature of Vedic civilization which had very little contact with the sea, the few references that occur relate mainly to the molluscs—the *sankha* (Chank), *sukti* (pearl oyster), *sambuka*, *valluka* and *vodika* (generally held to be spiral-shelled gastropods).

---

[1] Reprinted from: *Souvenir, Symposium on Mollusca*, Cochin, Jan. 12-16, 1968: 45-52.

But to know the hold of the molluscs over ancient Indian mind, one has to start from the dim ages of mythology and legend.

(*a*) *In mythology*

The sacred chank, for instance, is so much a symbol of Hindu worship and mythology that it is integrated with almost every aspect of early Indian thought and culture. Vishnu, in his original aspect, has it as one of his four emblems; some of his avatars too are depicted as holding it. Possibly from this close affinity the chank is used in all Hindu temples, irrespective of sects, as an indispensible instrument of worship, as a container for holy water, as an instrument of invocation and call to the devout for worship. The mystic wail of the sacred chank resonant in the fading twilight of day-break or dusk is part of the spiritual aura that surrounds most Hindu temples. Particularly the sinistral chank, by its very rarity, is held in such esteem that all major temples in India have one or more of these.

Such adoration does not appear to be confined to the chank alone, nor to Hinduism alone. The fossil cephalopod *Ammonites* of the sub-Himalayan region, known to the Vaishnavite devout as *salagram*, is held in high veneration as the very abode of Vishnu. And the Buddhist monasteries in Tibet have been known to keep sinistral chanks; the one at the Sakya Monastery, for instance, is believed to have been gifted by the great Kublai Khan himself in late 13th century. In some of the neighbouring countries of India too these shells are preserved as priceless treasures, at some time their value having been assessed at their weight in gold!

(*b*) *In folklore and superstition*

From its intimate association with the religious and emotional life of the people, the chank gradually slid into man's diverse walks of life. The folklore of different parts of India is replete with tales that have found concrete expression in many social customs as well. The lore relating to the place of chank and chank products in the marriage rites is vast, particularly in Bengal where the wearing of a lacquered chank bangle is part of the traditional ceremony. There is evidence to show that similar customs were prevalent elsewhere too, though non-existent now. Anthropologists refer to agricultural and pastoral communities like the Vellalans and Idaiyans, where the married women wear chank bangles customarily. The lore sometimes links the shell to Shiva who, as the story goes, laughingly chided Parvati at the time of her wedding, as not as charming as she might be, and proceeded to create out of his braided hair a Being who brought chank bangles for the adornment of the bride. Or, as in the story from South India, it is linked with Sri Krishna who, after abducting Rukmini from her marriage with Sishupala, married her himself by placing a chank bangle on her wrist.

The influence that the shells exerted on the imagination of the ancient world is also borne out by the wealth of proverbs about the shells in different Indian languages.

From religion and folklore it is but a short step to superstition and the shell pervades the superstitious world just as extensively. From innocent, amusing beliefs, such as that sinistral shells blow of their own accord during the nights (a superstition once so entrenched in Tamil areas that even Christian divers felt concerned at this!) to stories of their power to ward off evil, all sorts of superstitions have been reported. Tattooing or branding with heated metal the form of a chank, or burying a chank beneath the first stone laid for the construction of a temple or a house, all were once considered purificatory acts to ward off evil omens.

(*c*) *In social customs and traditions*

Apart from the uses already mentioned as inspired by folktales and superstitions, shells as traditional personal adornment were in use among many communities. It is quite possible that these were originally worn as amulets or mascots tied round the neck, but their form and use acquired a range in later years from finger rings and necklaces to disc ornaments for hair or head dresses. Rings cut out from *Stombus* shells were used either as finger rings or strung on a cord and interspersed with coral beads as necklaces. Necklaces were also made with discs cut out of shells or from bisected shells merely strung together. The wearing of these necklaces once a girl had attained a particular age was an obligatory custom in many tribes in the past. The shell discs as ornaments for the ear or as decoration for head-dresses appear to have been popular till recent times among peoples of the northern border—the Bhutanese, the Assamese and the Nagas.

Other shells used as ornaments included the ring-cowry *Ornamentaria*. This cowry and also the money-cowry *Monetaria* were considered a symbol of wealth and prosperity and found a place in many social functions like marriages, rice-giving ceremonies, *sradaha* (death anniversaries), etc. Sometimes cowries or chanks were placed with the dead body as part of funereal rites.

The cowries were also widely used in gambling and many other indoor games.

(*d*) *In trade and handicrafts*

Ancient Indians rarely left any records of their commerce or trade, when foreign sources have often filled in much information. As one leaves the dim past of myths and legends and comes into years of early history, indications of the commercial importance of molluscs are forthcoming. The accounts of foreign travellers mention the brisk trade that went on in shells from the fishing grounds of the Gulf of Mannar and Kathiawar coasts. The chank bangle trade is referred to in ancient Tamil writings and its prevalence proved by archaeological evidence. The travelling monk Cosmas Indico-Pleustes in the 6th century referred to the export of conch shells from India. The disputes and rivalries that went on between the foreign powers on this score, particularly at the time of the Portugese and the Dutch, are part of more recent history. Rings, bangles plainly or elaborately carved, and disc ornaments appear to have been the main handicraft products of the past.

The "ink" extracted from the cuttle fish *Sepia* was used as a drawing ink till recently and was known to keep the clarity and intensity of colour for long. Similarly the "purple" extracts from some gastropods were also used as dyes and pigments.

(*e*) *As currency*

The shells, particularly the cowries, constituted the currency among many civilized and uncivilized peoples of the world. The most commonly used were the money-cowries *Monetaria*. Some ancient Hindu treatises about the 5th century mention the use of cowries as currency. Because of similar use of cowries in many parts of Africa, the trade in cowries flourished. There are records of annual despatch of cargoes of cowries fished from Laccadive-Maldive waters to Wydah and Lagos, where they were exchanged for Spanish doubloons brought by the slave traders. Many European nations also imported cowries from India and other places for payment to West Africans in exchange for their products. Marco Polo, in the account of his voyage to China, recorded the finding of cowries circulating as currency in Yunnan in the 13th century.

Many Indian hill tribes, including the Nagas, employed it almost until the appearance of the Rupee. Till about a century ago the shells appear to have had a fixed and well-worked-out exchange value among the Nagas. Slaves and cattle were traded in shells. The villages captured during raids paid their ransom in shells as well as in other kind.

(*f*) *As medicine*

Many molluscs, predominantly the chank, appear to have been extensively used medicinally in ancient India. Chank shells, powdered and mixed with water, was considered an effective salve for ailments ranging from skin diseases to rickets and asthma. Chank ointment was similarly held as cure for eye inflammation or granulation on inner side of eyelids, for piles or even for leprosy. Sometimes chank powder was prescribed, mixed with ghee and taken internally, for skin troubles, consumption and such. Another remedy compounded of partially burnt camphor, chank powder and human milk or white of egg was considered a speedy cure for soreness of eyes. The chank powder was, in short, a panacea for diverse illnesses like jaundice, cough, phthisis and general debility. The dried egg capsule of chank, powdered with pepper and coriander in til oil, was considered effective to relieve headache, while the dried visceral mass was thought efficacious for enlarged spleen.

Some of the remedies appear scientifically possible of explanation. The use of chank powder as remedy for dyspepsia seems based on the carbonate of lime counteracting the hyperacidity of gastric fluids. Similar may be the case of rickets—an illness characterized by insufficient deposition of lime in bones. In many cases, however, it may be the religious association of the chank and the consequent faith in it that proved responsible for many cures.

Other molluscs that were put to medicinal uses included the cowries (*Cypraea*), the apple snails (*Pila*) and the widowpane oysters (*Placenta*).

Molluscs in Modern India

The molluscs in India are playing a living role yet, shedding many of their past associations and reported miraculous properties (the impact, no doubt, of the so-called ungodly present-day generations!) but assuming newer and vastly more utilitarian roles.

(*a*) *Surviving customs and traditions*

However, traditions and habits die hard and superstitions assume modern garb and survive, if only in name. Chanks or other shells tied to the forehead of draft bullocks or around the neck of cows and cow-buffaloes to keep them in milk are still sights not very uncommon. True, they are often put on as mere ornamentation now, their owners having no idea of the origin of this practice. Such is also the case of the shell necklaces that continue to be worn by many tribes even today. The mark of sophistication is not altogether absent, either—the shells that were once used to cut out discs for the ears and the hair, now turn out dress buttons.

Even the role of the conch as a clarion call to duty and action, exemplified in ancient days in times of war (when every great warrior had his own individual and renowned conch which he blew lustily while going into action)—even this role appears to have survived in the custom in Bengal of blowing the conches in times of emergencies such as eclipses or earthquakes. The resounding booms proceeding from almost all houses in a locality is kept up until the calamity is over (or, may be, until the deafened neighbourhood is past caring!).

(*b*) *In heraldry and design*

The nobler, more elevated roles of the shells also have survived in part. Apart from the continued use of the chanks in Hindu temples, the heraldic designs of the royal houses as well as the State emblems of both Travancore and Cochin had the sinistral chank as a prominent motif. Perhaps reminiscent of the early use of shells as currency, the chank shell was a symbol on coins issued by many ancient rulers, especially of the Pandyan and Chalukyan dynasties. In more recent times Travancore and Cochin again used them on coins and early stamps. What is perhaps significant here is that in these cases the chank symbol was often used in place of and to the exclusion of the sovereign's head. What higher status can one ascribe to these shells?

(*c*) *In trade and handicraft*

The trade in shells as raw material for the traditional handicraft products appears to have fallen, with glass and plastics displacing the chank in the bangle and bead-necklace manufacture, to a large extent. The chank bangle industry, however, still survives in Bengal. New forms of handicrafts have evolved in place of old. The old-world infant's drinking-spout fashioned out of chank lingers among some of the poorer classes, while the richer strata are supplied with carved shell ash-trays or *Nautilus* reading lamps or window-pane oyster lamp shades. A glue made out of the powdered horny operculum of the chank is still in use in some places as an adhesive base in the manufacture of incense sticks.

(*d*) *Fisheries*

Apart from the well-established fisheries for the pearl oyster and the chank along the Gulf of Mannar and Kathiawar coasts many clams, mussels, squids and other minor shell-fishes constitute smaller fisheries of local importance in many other regions as well.

(i) *Pearl oyster.*—The fishing grounds for the pearl oyster (*Pinctada fucata*) are in the Gulf of Mannar on the east coast. The inshore areas here afford a suitable habitat for the growth of oysters. The oyster beds are dispersed on patches of rocky sea-bottom (called *paars*) 8–12 miles from the shore at depths of 7–12 fathoms.

The pearl fishery, though well known since ancient days, was neglected for a considerable part of the first half of this century. But the operations were revived in 1955, after a lapse of nearly three decades, and for successive years up to 1961 yielded lucrative fisheries.

A pearl oyster fishery in the Palk Bay off Tondi was held in the early second decade of this century. In the Gulf of Kutch off Jamnagar and nearby places pearl fisheries of very small magnitude are annually harvested, the oysters exposed on rocky reefs at low tides being hand-picked by fishermen.

(ii) *Chank.*—The chank (*Xancus pyrum*) is peculiar to the waters of India (and Ceylon) and the Andamans, its nearest relatives being found only in Brazilian waters. Among the distinct traditional fisheries for the chank (Tirunelveli-Ramanathapuram, South Arcot-Tanjore, Kanyakumari-Trivandrum and Kathiawar) only the fishery in the Gulf of Mannar and Palk Bay is well organized and carried on systematically. The chank beds off Kathiawar coasts are probably next in importance. As in the case of the pearl oysters here, at Okhamandel, the chanks are not dived for, but are collected at spring tides when extensive littoral areas are uncovered.

The Tirunelveli-Ramanathapuram chanks have been noted for their solidity, weight and hardness. The chank beds lie in fine sandy areas (called *pirals*) interspersed with the rocky pearl oyster beds in the Gulf of Mannar and also extend further into the Palk Bay. The Tirunelveli-Ramnad chanks now constitute the bulk of the production that meets the demand of the Bengal chank-bangle industry.

(iii) *Mussels and clams.*—These form regular fisheries of considerable local importance along the east and west coasts. The meat is widely eaten, even considered delicious by those who develop a taste for it. The brown and green mussels (*Mytilus* spp.) form particularly good fisheries in Kerala, the former occurring in patchy but extensive beds from Kovalam to the Cape, while the latter is abundant in the northern districts. There are similar fisheries in many other States for edible bivalves like the weaving mussel (*Modiolus* sp.) wedge clams (*Donax* spp.), the backwater clams (*Meretrix* spp.) and backwater oysters (*Ostrea* spp.).

(iv) *Squids and miscellaneous shellfishes.*—Besides the above-mentioned, many widely distributed fisheries such as for the squids, edible gastropods and the like are existent. The most important of these is the fishery for the squid (*Sepioteuthis*) centred along the coast of Ramanathapuram District, where large shoals appear in April–July. They are consumed locally or, in times of poor demand, sun-dried and sold in the interior.

The cuttlefishes (*Sepia*) do not form any regular fishery in these areas, but are taken occasionally in cast nets or shore seines. Though they are eaten, it is the cuttle-bone that is more important commercially. These bones are washed ashore in large numbers and are gathered for sale. A considerable quantity of cuttle-bones is sold from Kerala too. The demand for cuttle-bone from abroad adds to the value of this trade.

Among the miscellaneous molluscs serving as food may be mentioned the edible whelks (*Pellia*) consumed by the poorer classes along the Konkan coasts, the olives (*Oliva* spp.) extensively used as food by certain sections of fishermen on the Coromandel coast and the common apple-snail (*Pila*) which is eaten and also used medicinally.

The window-pane oyster (*Placenta*), though not edible, is important commercially and a small industry for this exists in the Gulf of Kutch. The shells, transluscent and mica-like, are raw material for many handicraft products, and the animals produce an abundance of seed pearls which are not valuable as jewellery but are held to have medicinal properties.

Besides their use as food, many of these shellfishes mentioned earlier, particularly the squids and to a lesser extent mussels and clams, are in great demand as fish baits.

The fishery for *Trochus* and *Turbo* in the Andaman and Nicobar islands is of importance because of the commercial demand for "mother of pearl" in the manufacture of shell buttons, buckles and other artistic fancy goods. This fishery, like those of the pearl oyster and the chank, is under State control and the beds situated on rocky ledges at 8-10 fathoms are leased out for exploitation. As in the case of the chank, however, the industry for "mother of pearl" has also been affected by the recent introduction of plastics and synthetic materials.

(*e*) *In industry*

The shells are used in modern industry primarily for the manufacture of lime and cement. Especially in this country where in the mortar used in building construction as well as in the white-wash needed for its maintenance lime is an essential commodity, the industry though scattered and so individually on a small scale, is cumulatively a large one. Though mussel and clam shells are usually used for preparing lime, chanks are used for special needs and occasions, as the lime produced by the chank shell is found to be of superior quality. Similarly, though carbonate deposits are widely used in the manufacture of cement, the factory at Kottayam in Central Kerala makes use of the dead and subfossil shells from the Vembanad Lake as their chief raw material.

(*f*) *As enemy of man*

This account has so far dealt with some of the useful or at any rate harmless aspects of molluscs in their relationship with man. There is a reverse side to this too. The molluscs can also be agents of large-scale destruction or dreaded carriers of death to livestock or to man himself.

They cause destruction to property by fouling or by boring. Many bivalves, particularly of the oyster and mussel group, are chief components of fouling communities that encrust submerged objects like piles and boats, causing considerable loss of timber or in case of vessels, reducing their speed and spoiling their streamlined efficiency in water. The wood-borers (like *Bankia*, *Teredo*, *Martesia*, etc.) or ship-worms, even as their latter popular name suggests, eat away submerged timber and cause extensive damage to wooden hulls of sea-going vessels. These molluscs thus have a significant place in the economy of a maritime people.

The importance of molluscs as a hazard to health stems from their close association with many helminth parasites. The well-known Schistosomiasis (Bilharziasis) or snail fever is spread through the agency of amphibian or freshwater snails that are intermediate hosts to these parasites. This dreaded disease is rampant in Africa, Middle East, South-East Asia and tropical South America. But India has so far been free from it though allied helminth species have been recorded from many common freshwater snails, like *Lymnea* and *Indoplanorbis*. These snails are also active in the spread of many serious trematode infections in livestock.

PRESENT RESOURCES—NEED FOR SURVEY AND UTILIZATION

As mentioned earlier the resources of molluscs that can sustain regular and very productive fisheries are abundant in our waters. The primary need is to survey these resources and gather data on the existing level of their exploitation—which is bound to be low. Only the pearl oyster and chank fishing grounds had received some early attention in this regard, and even here a recent co-operative underwater survey conducted by the Central Marine Fisheries Research Institute and the Madras Fisheries Department with the aid of aqualung or SCUBA diving revealed many changes in patterns from that recorded by earlier surveys done decades ago, and also indicated fresh grounds that could be exploited commercially. Such systematically carried out surveys and preliminary studies should be made for other resources as well.

Great as the industrial use of molluscs is, perhaps the significance of molluscs in future would be greater as a potential source for human consumption. Only a few of the mussels, clams and oysters are now generally eaten and even these are more a poor man's food and have not attained their place on the gourmet's table that they could. The need for popularising molluscs as food is great, particularly in a country like ours where provision of nutritious food is a long-standing problem and any means to tackle it should be tried and, if successful, popularized. From the nutritional point of view the molluscs have many advantages such as easy digestibility coupled with high contents of minerals and vitamins. They have approximately 8–10% of proteins (by weight), 4–5% of carbohydrates, 2–3% of minerals with but 1–2% of fat. It has been calculated that a good serving of oysters, for example, would supply more than the needed daily allowance of iron and copper, about half the required amount of iodine, about one-tenth the daily need of protein, calcium, phosphorus, vitamin A, thiamine, riboflavin and nicotinic acid. Thus the role that the molluscs can play, along with fishes, in meeting the country's quest for balanced, nutritious diet has to be more widely recognized.

NEW SPECIES OF *NEOPILINA* OF THE CAMBRO-DEVONIAN CLASS MONOPLACOPHORA FROM THE MILNE-EDWARDS DEEP OF THE PERU-CHILE TRENCH, R/V ANTON BRUUN

ROBERT J. MENZIES*

Duke University Marine Laboratory, Beaufort, N.C. and Department of Zoology, Duke University, Durham, North Carolina, U.S.A.

ABSTRACT

Two apparently new species of *Neopilina, N. (N.) bruuni* and *N. (Vema) bacesui* are described from Milne-Edwards Trench off Peru. A larval shell or protoconch is described as a bulbar uncoiled shell. The horizontal and vertical distribution of the species is reviewed and it is suggested that *Neopilina* will be found to occur between Alaska and California and possibly in the Caribbean.

INTRODUCTION

THE genus *Neopilina* was first reported by Lemche (1957) based on *Neopilina galatheae* Lemche from off Costa Rica. A second species was reported by Clarke and Menzies (1959) who also split the genus into the two subgenera *Neopilina* (*Neopilina*) and *Neopilina* (*Vema*) with the former having 5 pairs of gills and the latter having 6 pairs of gills. A third species belonging to *Neopilina* sens. str. was reported by Menzies and Robinson (1961) and described in more detail by Menzies and Layton (1963).

The anatomy of *Neopilina* has been exhaustively treated by Lemche and Wingstrand (1959). A coiled protoconch was described by Lemche and Wingstrand, whereas a simple bulbar protoconch was photographed by Menzies and Layton (1963). The ecology of *Neopilina* (*Vema*) *ewingi* was described by Menzeis, Worzel, Ewing, and Clarke (1959). The shell chemistry has been reported on by Watabe *et al.*, 1966.

This report is based on the discovery of two apparently new species of *Neopilina* from the Milne-Edwards deep of the Peru-Chile Trench. The specimens were collected on Cruise 11 of the R/V ANTON BRUUN. This cruise was sponsored by the National Science Foundation under the guidance of Dr. Edward Chin, Texas A & M Marine Laboratory, Galveston, Texas. Preliminary results of this cruise appeared in a report on that cruise by Menzies and Chin (1966).

Aboard the vessel the writer was ably assisted by the ship's complement, as well as by a scientific support party. While all members of the invited scientific party of 14 individuals aided in the collections in one way or another, the indefatigable efforts of the "Scientific Bosun," Mr. Shiggura Yano, are especially noteworthy. Work on this project was supported by NSF Grant GB-1117 for study on *Neopilina*.

Previously so few species of *Neopilina* were known that an assay of the specific value of shell differences was not possible. The added two species reported herein which bring the number of species to 6, suggest that differences exist in the microstructure of the shell and in the shell sculpture as well as differences in the soft parts. These differences are similar to the criteria used in separating other species of molluscs.

---

*Present Address: Department of Oceanography, Florida State University, Tallahassee, Florida, U.S.A.

SYSTEMATICS

Neopilina (Neopilina) bruuni n. sp.

(Figs. 1 *c*, 4 A–E, 5)

Diagnosis.—*Neopilina,* sens. str. having 5 pairs of gills, with the postoral tentacles six in number and unbranched on each side of mouth. Foot circular and widely separated from the mouth. Prisms of shell usually longer than wide, irregularly arranged with some much wider or much longer than others. Color dull gray, or bluish-gray.

Measurements.—Length 15 mm.

Type Locality.—Milne-Edwards Deep, Peru-Chile Trench, Anton Bruun Cruise 11, Sta. 197.

Location of type.—The holotype is located in the United States National Museum, Cat. No. 678167.

Relationships.—This species is closely related to *Neopilina galatheae* Lemche from which it differs in the characteristics cited in the diagnosis. The main point of difference lies in the reduction of the postoral tentacles to near papillae and the small foot.

This species is named in honor of the late Dr. Anton Bruun. He was the friend of all who probed the deep-sea in search of the solution to interesting questions and the discovery of species new to science from the abyssal depths.

Neopilina (Vema) bacescui n. sp.

(Figs. 1 *a*, 2 A–C, 3)

Diagnosis.—*Neopilina* with six pairs of gills. Postoral tentacles exceed 20 on each side. Shell pitted in reticular pattern from margin to apex. Prisms of shell irregularly spaced, usually no wider than long, irregular in shape. Colour golden.

Relationships.—This species has close affinities with *Neopilina (Vema) ewingi* Clarke and Menzies, but the reticular pattern on the shell surface is distinctive, and the postoral tentacles are more abundant.

Measurements.—Length 28 mm.

Type Locality.—Milne-Edwards Deep, Peru-Chile Trench.

Location of type.—United States National Museum, Cat. No. 678169.

This species is named in honor of my scientific colleague Dr. Mihai Bacescu, Director Gr. Antipa Museum, Bucharest Rumanian Socialist Republic, and corresponding member of the Rumanian Academy, Bucharest, Rumania. He was a guest of the National Science Foundation on Cruise 11 of the Anton Bruun and first pointed out the differences between this species and *N. (V.) ewingi* Clarke and Menzies. His indefatigable efforts in aiding the scientific mission and friendly co-operation through diligent work toward the goals that were established, were an inspiration to senior scientists and graduated students alike.

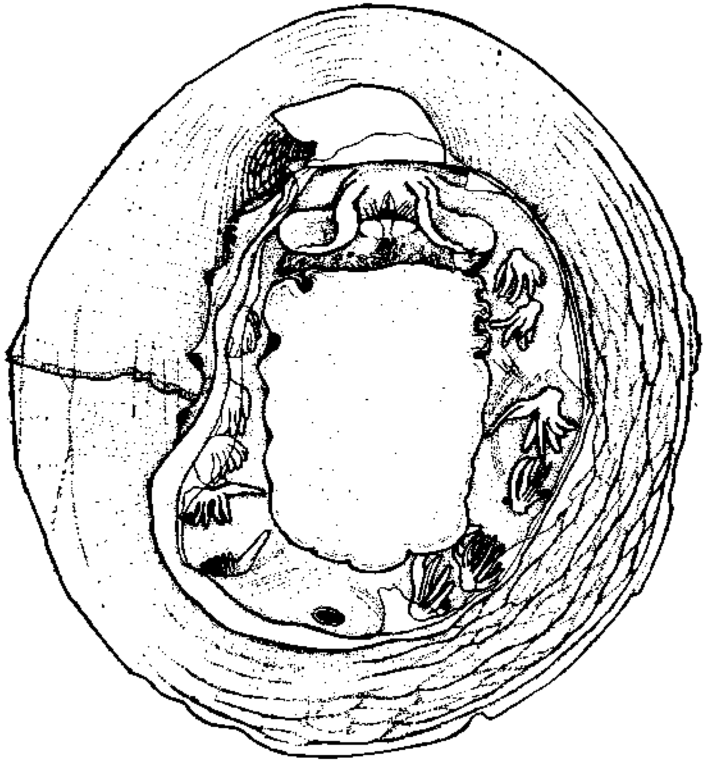


FIG. 3. *Neopilina* (*Vema*) *bacescui* n. sp., holotype, ventral view; length 28 mm., Anton Bruun Cruise 11, Sta. 113.

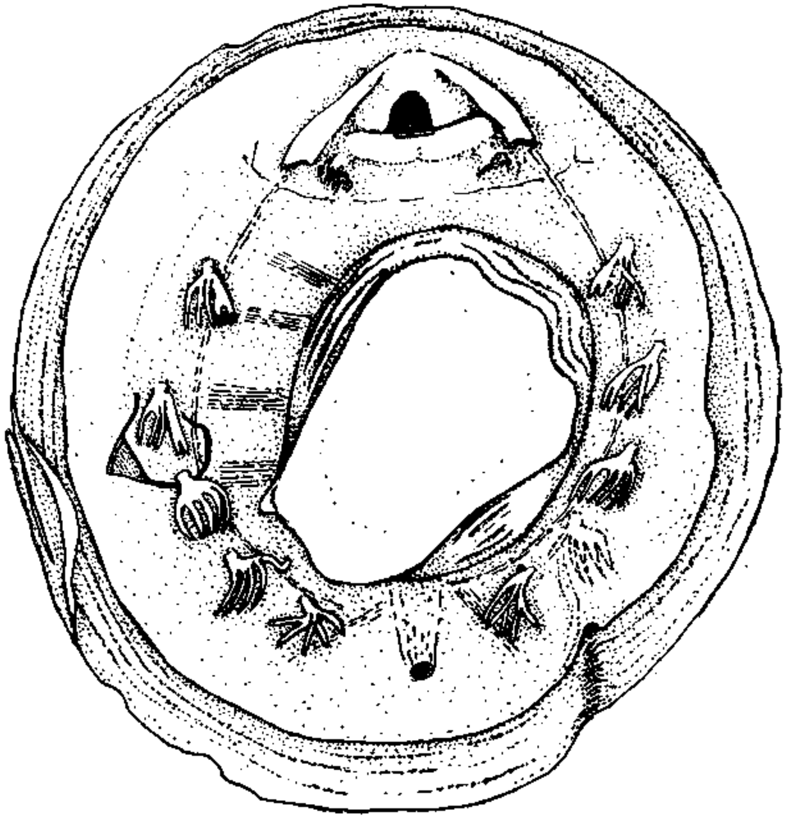


FIG. 5. *Neopilina* (*Neopilina*) *bruuni*, n. sp., holotype ventral view; length 15 mm.

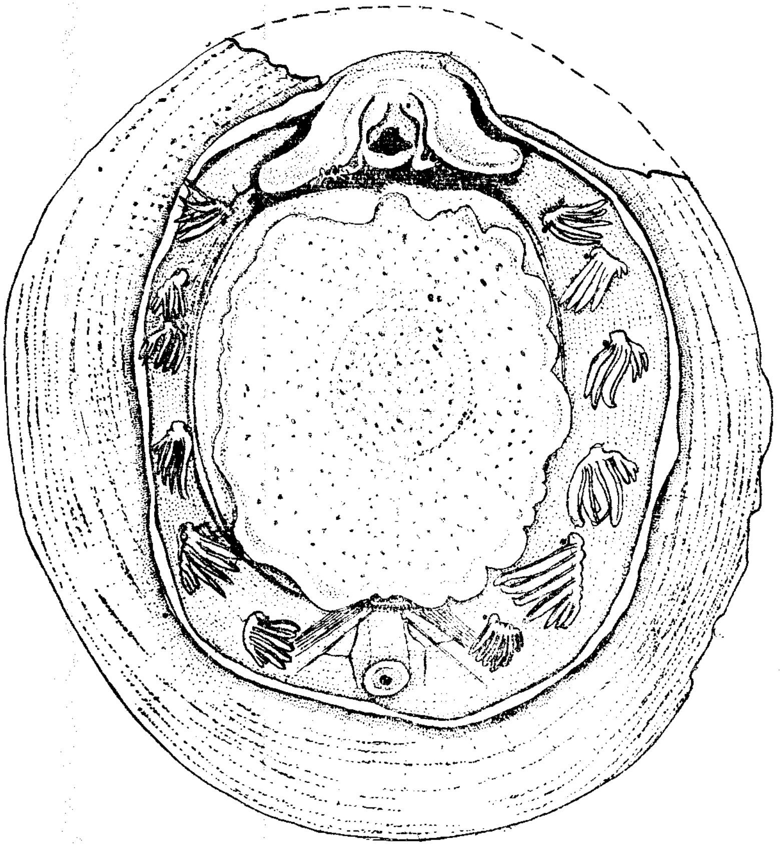


FIG. 7. *Neopilina* (*Vema*) *ewingi* Clarke and Menzies, topotype, length 25 mm., ventral view, Sta. 197, Anton Bruun Cruise 11.

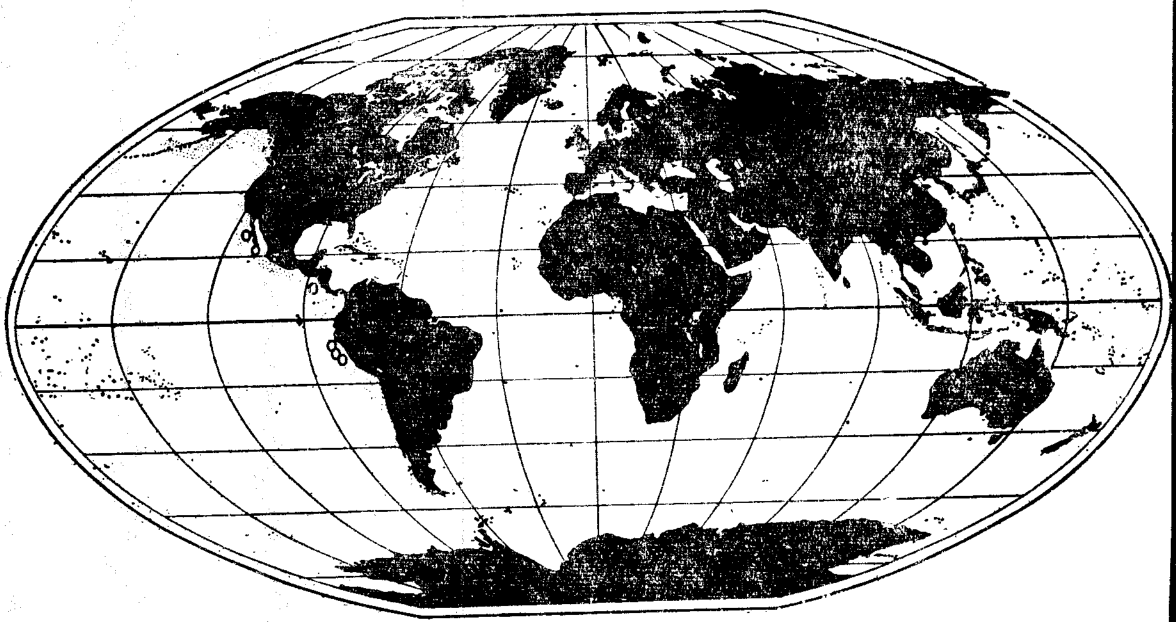


FIG. 9. Horizontal distribution of *Neopilina*. Probable distribution indicated by shaded area. Known distribution indicated by "0".

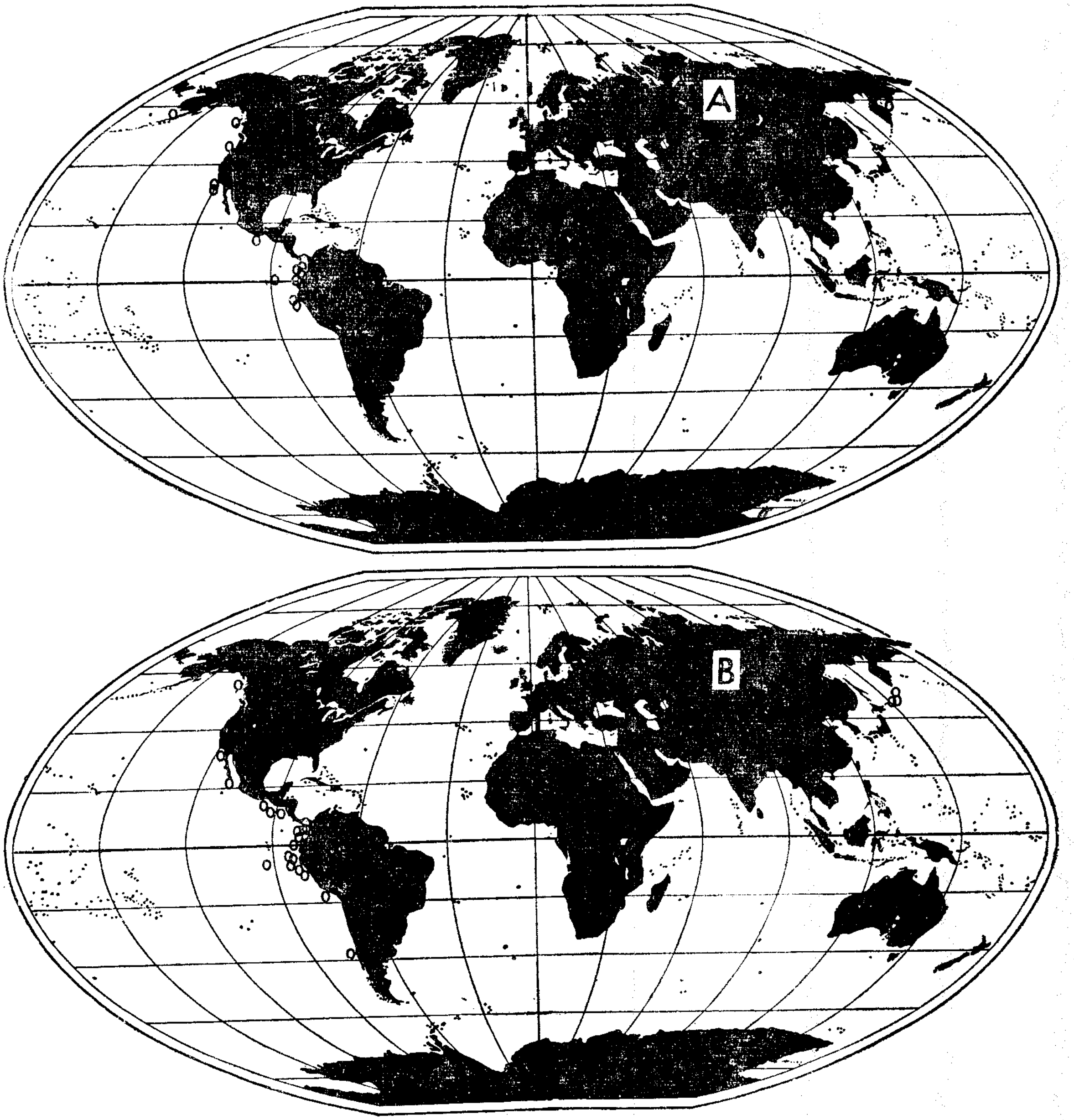


FIG. 10. Distribution of *Eremicaster*. A, *E. gracilis*; *B*, *E. pacificus*, both from Menzies, 1963 (after Madsen, 1961).

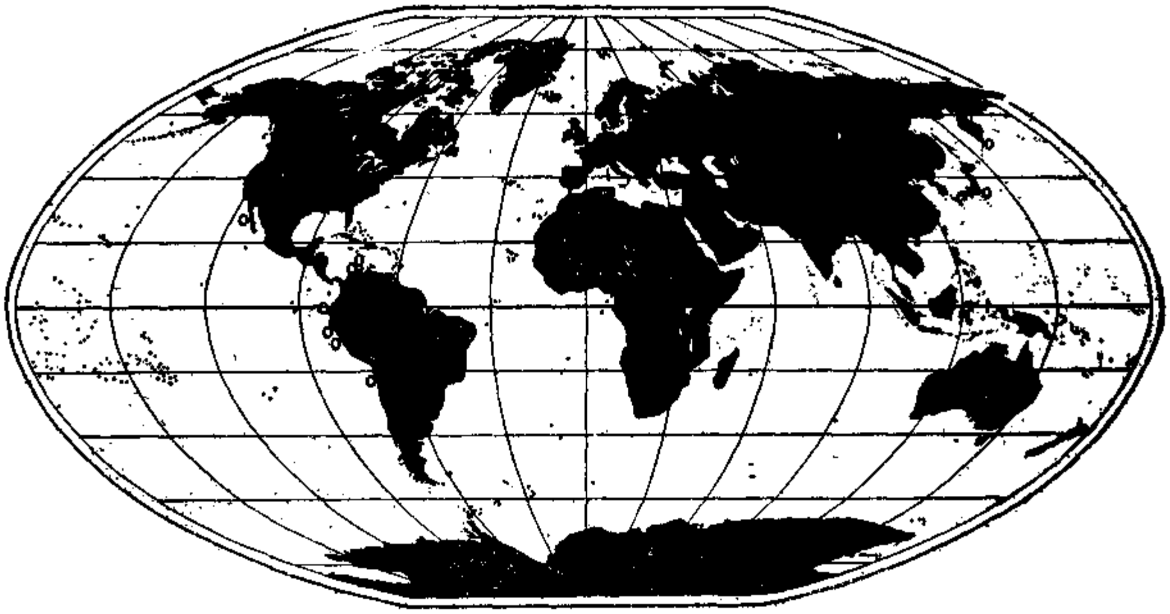


FIG. 11. Distribution of isopod genus *Mesosignum*.

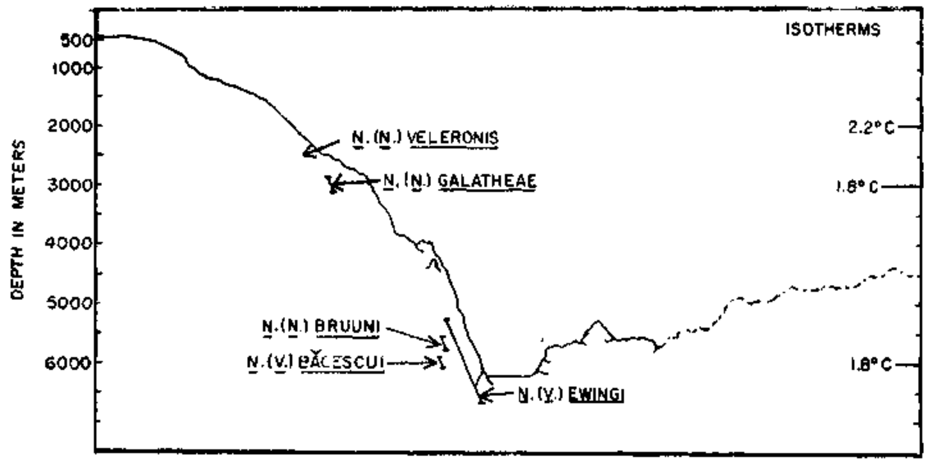


FIG. 12. Idealized profile showing vertical distribution of various species of *Neopilina*. *Neopilina adenensis* omitted from all figures.

Neopilina (Vema) ewingi Clarke and Menzies

(Figs. 1 *b*, 6 A–C, 7)

Diagnosis.—*Neopilina* with 6 pairs of gills, with numerous branched postoral tentacles. Major prisms of shell regularly spaced, higher than wide with clusters of minute prisms between regular prisms. Shell near apex without reticulations; instead, lines of growth regularly arranged, color white to yellow.

Measurements.—Length 3·5–10·7 mm. (holotype), 25 mm. (topotype).

Type locality.—Milne-Edwards Deep, Peru-Chile Trench, R/V VEMA, Cruise 12 (Clarke and Menzies, 1959).

Location of type.—United States National Museum, topotypes Cat. No. 678166 (Clarke and Menzies, 1959).

Relationships.—This species is closely related to *Neopilina* (*Vema*) *bacescui* n.sp., from which it differs most markedly in not having the reticular shell sculpture near the shell apex and in having the shell made up of large prisms which are regularly arranged and higher than wide.

Distribution.—Milne-Edwards Deep, where the species has been collected at 9 locations (Table I). In depth the species ranges between 5800 and 6400 meters.

PROTOCONCH

On the USNS *Eltanin* cruise to Valparaiso from Panama, the writer collected a minute specimen which appeared to be a *Neopilina*. This specimen was reported on by Menzies (1963) and since has been examined in considerable detail. Most regrettably the shell contained no organized tissue and a positive identification was therefore not possible. Nevertheless the shell looked so much like a *Neopilina* shell that it is highly probable that it was correctly identified. This shell showed a *bulbous uncoiled* protoconch. Loss of the protoconch shell would produce a simple circular scar-like that reported by Clarke and Menzies (1959) Fig. 8, and except for the coiled superficial sculpture is similar to that reported by Lemche and Wingstrand (1959). In molluscs quite commonly the larval shell is lost at metamorphosis and this seems to be the case for *Neopilina* also. This evidence which is about as definitive as one can expect until *Neopilina* are cultured in the laboratory strongly suggests that *Neopilina* has a larval stage; that this stage shows no indication of coiling; that the protoconch is lost from the adult shell leaving only the scar where the protoconch was firmly attached.

SIZE

Adult specimens range in maximum diameter from 2·5 mm. (*veleronis*) to 37 mm. (*galatheae*) and accordingly one can expect to collect specimens within that range. It appears that the larva is around 0·2 mm. in diameter and about 0·4 mm. in length and this might represent a minimum diameter for specimens. These data imply that small mesh nets should be used in attempts to collect specimens. This writer has used the Small Biology Trawl (auct. Menzies Trawl) (Menzies, 1963) in the collection of all species mentioned in this paper. This trawl has a mesh diameter of 0·55 mm.

DISTRIBUTION

The horizontal distribution of recent Monoplacophora is shown in Fig. 9. There it is apparent that the animals extent from 27° N to 15° S along the margin of the Eastern Tropical Pacific Ocean. This distribution is so similar to the distribution of the abyssal genera *Eremicaster* (Echinodermata) Fig. 10 and *Mesosignum* (Isopoda) Fig. 11, that it is safe to predict that *Neopilina* will also be found Northward to Alaska and Southward to Chile. The possibility that a Caribbean species will be found should not be excluded. It has since been collected from the Gulf of Aden (Table, 1967).

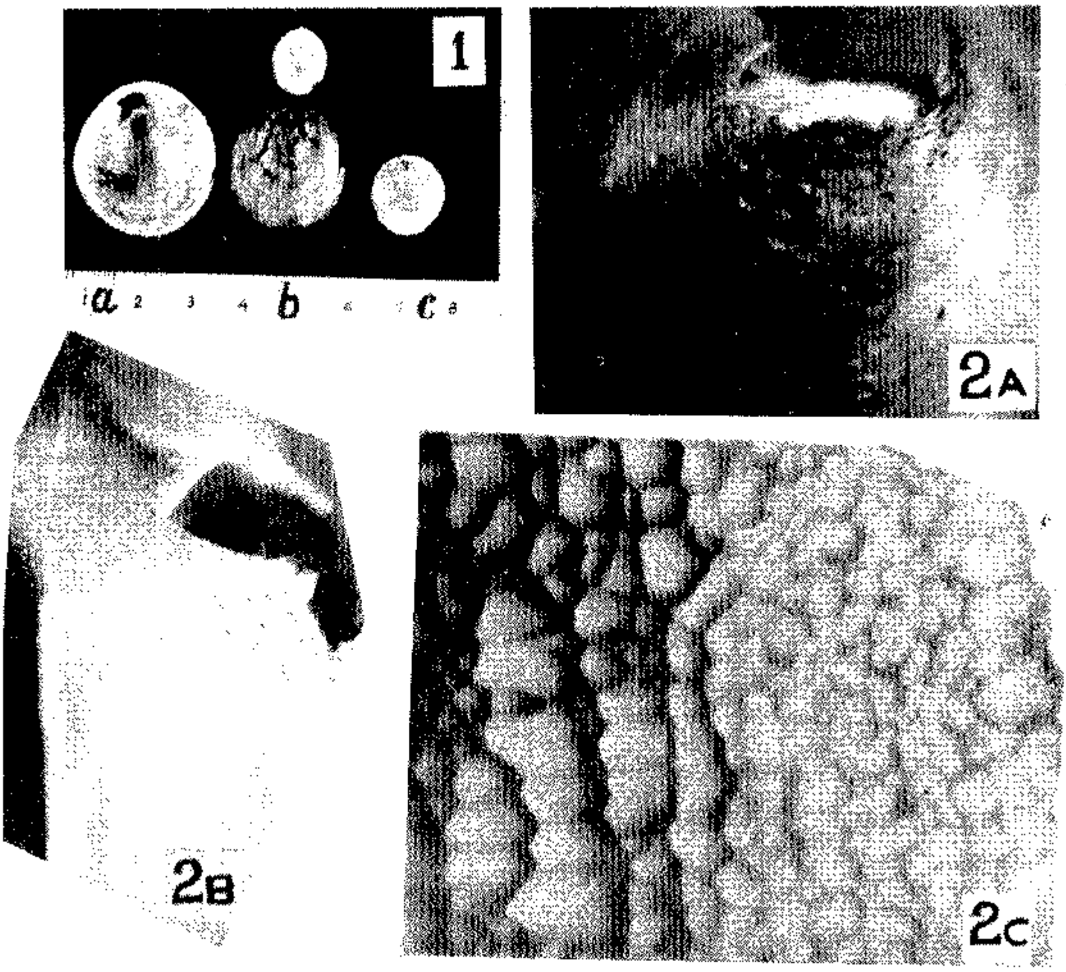
TABLE I

Positions at which Neopilina *has been collected to date* (*after Menzies, in press*)

Species	Date	Lat.	Long.	Depth (meters)	Vessel (Sta. No.)	Reference
Neopilina (*Vema*) *ewingi* Clarke and Menzies	12- 6-1958	07° 35′ S	81° 24′ W	5817–5834	*Vema* (150)	Clarke and Menzies, 1959
	12- 6-1958	07° 30′ S	81° 25′ W	5841–5854	*Vema* (151)	Clarke and Menzies, 1959
	12- 9-1958	10° 13′ S	80° 05′ W	6324–6329	*Vema* (154)	Clarke and Menzies, 1959
	12-19-1958	12° 02′ S	79° 08′ W	5607–5614	*Vema* (158)	Clarke and Menzies, 1959
	10-12-1965	08° 25′ S	81° 05′ W	6260–6052	Anton Bruun (72)	This paper
	10-12-1965	08° 20′ S	81° 04′ W	6260–6364	Anton Bruun (76)	This paper
	10-16-1965	08° 16′ S	81° 05′ W	6156–6489	Anton Bruun (100)	This paper
	11- 8-1965	11° 30′ S	79° 25′ W	6146–6354	Anton Bruun (197)	This paper
	6- 8-1962	08°10.5′S	81°8.1′ W	6002	*Eltanin* (37)	Menzies, 1963
Neopilina (*Vema*) *bacescui* n. sp.	10-19-1965	08° 44′ S	80° 45′ W	5986–6134	Anton Bruun (113)	This paper
Neopilina (*Neopilina*) *galatheae* Lemche	5- 6-1952	09° 23′ N	89° 32′ W	3591	*Galathae* (716)	Lemche, 1957
	11-11-1958	10° 07′ N	89° 50′ W	3718	*Vema* (133)	Menzies and Layton, 1962
	(?)	approx. 23° N	110° W	(?)	Horizon	Parker (unpublished)
Neopilina (*Neopilina*) *veleronis* Menzies and Robinson	12-31-1960	27° 52′ N	115°45 W	2730–2769	Velero IV (7230–60)	Menzies and Layton, 1962
Neopilina (*Neopilina*) *bruuni* n. sp.	11- 4-1965	08° 54′ S	80° 41′ W	4823–4925	Anton Bruun (179)	This paper
Neopilina sp. indet.	11- 2-1965	08° 46′ S	80° 44′ W	3909–3970	Anton Bruun (169)	This paper
	11- 8-1965	11° 30′ S	79° 25′ W	6146–6354	Anton Bruun (197)	This paper
	11- 6-1965	08° 52′ S	80° 47′ W	6313–6146	Anton Bruun (191)	This paper
Neopilina (*N.*) *adenensis* Tebble	2-22-1967	13° 50′ N	51° 47′ E	3000–3950	R.R.S. Discovery (6213)	Tebble, 1967

The vertical distribution of the species of *Neopilina* is shown on an idealized sketch of a profile of the Peru-Chile Trench, Fig. 12. This sketch combines northern and southern localities and therefore is idealized. Isotherms at various localities are indicated.

The known localities from which specimens of *Neopilina* have been taken are shown in Table I. Stations on which this report is based are included in the tabulation.



Figs. 1–2. Fig. 1 Three species of *Neopilina* from the Milne-Edwards Deep, Peru-Chile Trench; *a*, holotype, *Neopilina (Vema) bacescui* n. sp.; *b*, topotypes, *Neopilina (Vema) ewingi* Clarke and Menzies; *c*, holotype, *Neopilina (Neopilina) bruuni* n. sp., millimeter scale as indicated. Fig. 2. *Neopilina (Vema) bacescui* n. sp., holotype, L. 28 mm.; A, dorsal view near apex showing reticulations in shell; B, lateral view of shell showing reticulations; C, magnified view of shell prisms from near margin of shell. Anton Bruun Cruise 11, Sta. 113.

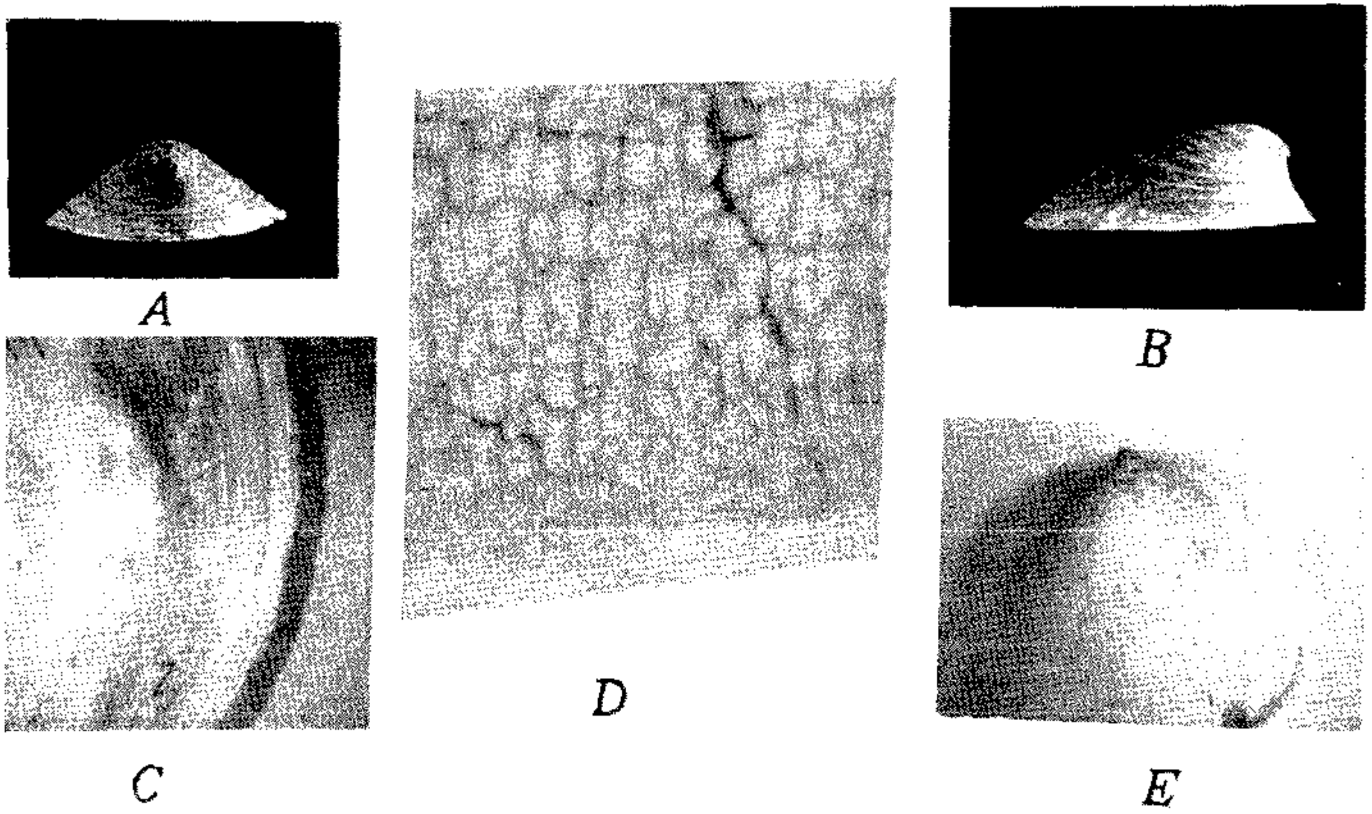


FIG. 4. *Neopilina (Neopilina) bruuni*, holotype, length 15 mm.; A, shell apical view; B, shell lateral view; C, margin of shell; D, prisms at edge of shell; E, shell apex.

Plate III

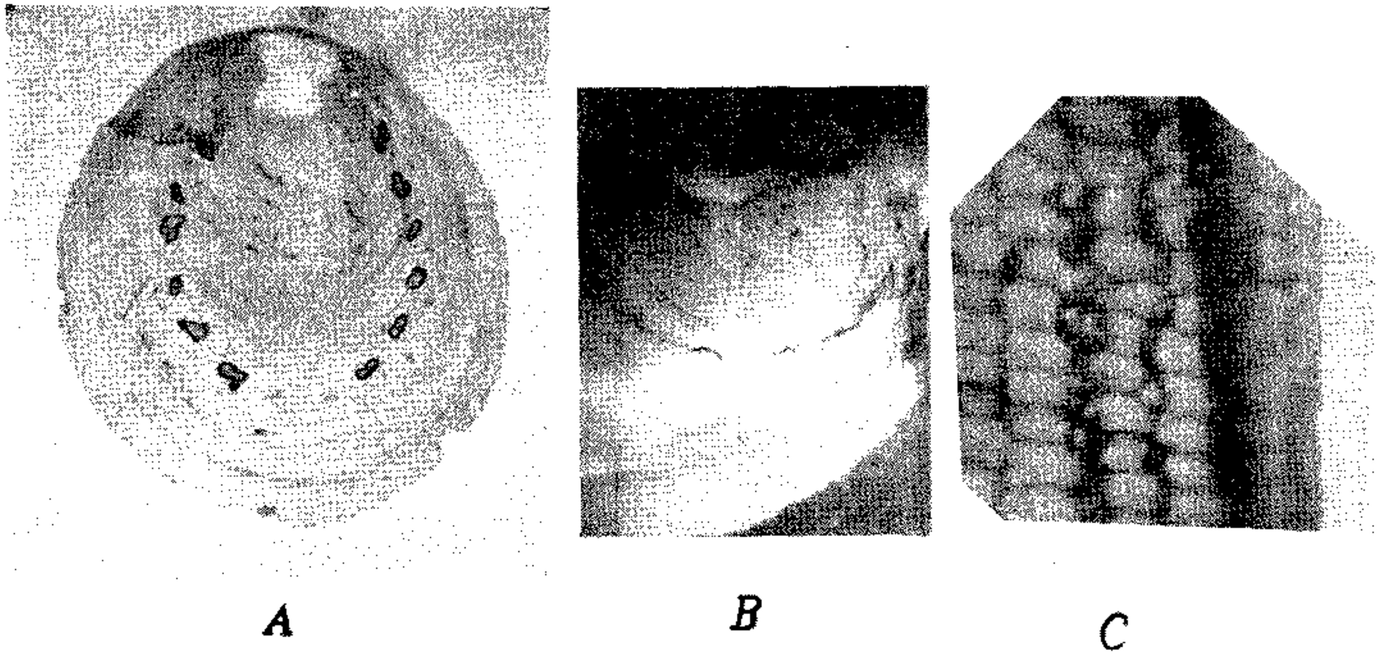


FIG. 6. *Neopilina (Vema) ewingi* Clarke and Menzies, Sta. 197, Anton Bruun, Cruise 11; A, ventral view of shell showing muscle scars (stained shell courtesy Karl Wilbur, Duke University); B, shell near apex; C, shell prisms.

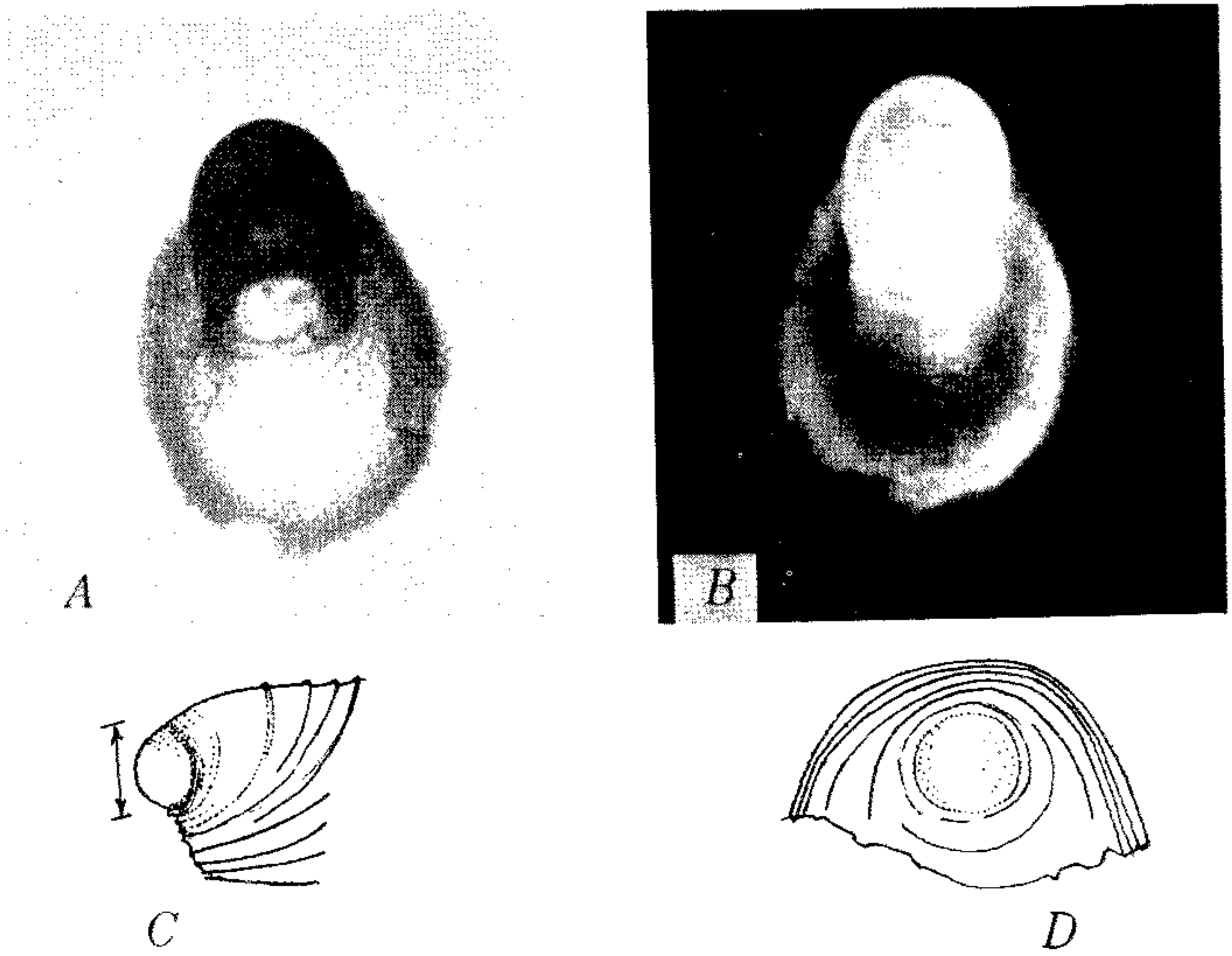


FIG. 8. Protoconch and protoconch scar of *Neopilina* sp. A, protoconch in shell, transmitted light; B, protoconch on shell, reflected light (Photos A and B courtesy Dr. William Layton, Jr., M.D.); C, protoconch scar, lateral view; D, protoconch scar, apical view. All specimens from floor of Maine-Edwards Deep. Scale indicated is 0·2 mm

LITERATURE CITED

LEMCHE, HENNING 1957. A new living deep-sea mollusk of the Cambro-Devonian Class Monoplacophora. *Nature*, **179** (4556): 413–416.

—— AND KARL G. WINGSTRAND 1959. The anatomy of *Neopilina galatheae* Lemche, 1957 (Mollusca Tryblidiacea). *Galathea Reports* 3, 71, Danish Science Press, Copenhagen.

MENZIES, ROBERT, J. 1963. Investigations on the deep-sea fauna made on the U.S.N.S. Eltanin (U.S.A.R.P.) during Cruise 3 between Panama and Valparaiso, Chile in 1962, *Int. Revue ges Hydrobiol*, **48** (2): 185–200.

——, M. EWING, J. L. WORZEL AND A. CLARKE, JR. 1959. Ecology of the recent Monoplacophora. *Oikos* **10** (2): 168–182.

—— AND A. CLARKE, JR. 1959. *Neopilina (Vema) ewingi*, a second living species of the Paleozoic Class Monoplacophora. *Science*, **129** (3355): 1026–1027.

—— AND D. ROBINSON 1961. Recovery of the living fossil mollusc, *Neopilina*, from the slope of the Cedros Trench, Mexico. *Ibid.* **134** (3475): 338–339.

—— AND W. M. LAYTON, JR. 1963. A new species of monoplacophoran mollusc, *Neopilina (Neopilina) veleronis* from the slope of the Cedros Trench, Mexico. *Ann. Mag. Nat. Hist., New Ser.* 13, 401–406, pls. VII-X.

—— AND EDWARD CHIN 1966. Cruise Report, Research Vessel ANTON BRUUN, Cruise 11. *Special Report Number 1, Texas A & M University, Galveston, Texas.*

TEBBLE, NORMAN 1967. A *Neopilina* from the Gulf of Aden. *Nature* **215**: 663–664.

WATABE, N., V. R. MEENAKSHI, P. E. HARE, R. J. MENZIES AND K. M. WILBUR 1966. Ultrastructure, histochemistry and amino-acid composition of the shell of *Neopilina* sp. *The Physiologist* **9** (3).

A SEROLOGICAL APPROACH TO MOLLUSCAN TAXONOMY[*]

J. B BURCH[‡]

Museum and Department of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A.

ABSTRACT

In many groups of molluscs classical morphological studies at their current level of perfection have not been able to establish a satisfactory systematic arrangement of taxa in the lower taxonomic categories. This is especially true of the African freshwater snail genus *Bulinus* (Basommatophora: Planorbidae), some species of which transmit human urinary schistosomiasis. The subgenus *Bulinus* s.s. is generally considered to contain two species groups, both morphologically very similar, but one is believed to contain only diploid species and the other only polyploids. Species currently are placed into these species groups according to the shapes of their radular mesocones, which do not always correspond to their chromosome numbers. Therefore, an immunological test was used in the present study to ascertain whether or not the two species groups were cytologically distinct, and to assess the reliability of the radular characters for species-group placement.

Antisera were produced against snail foot muscle proteins of three species: the Rhodesian *Bulinus natalensis* ($n=16$), the Tanzanian *B. coulboisi* ($n=36$) and an unnamed octoploid ($n=72$) Ethiopian species. We studied the reactions of these three antisera with antigens prepared from foot muscle tissue of thirty-four populations representing fifteen species and subspecies throughout the African continent and from the Middle-East and Corsica. The use of the specific absorption technique demonstrated "identity" or "non-identity" of antigens of the thirty-four populations when tested with the antisera. The results show that there is good correlation between the serological tests and the chromosome ploidy of the populations, and a lack of correlation with radular mesocones, inasmuch as *Bulinus natalensis* shows immunological affinities with the *tropicus* group rather than to the *truncatus* group.

It is concluded from these results that the subgenus *Bulinus* s.s. does comprise more than one species group, which can be identified immunologically, and that their serological groupings do not conflict with their ploidy or with groups based on host-parasite relationships. However, little reliance can be placed on radular characters now being used to assign the species to their groups.

INTRODUCTION

IN many groups of molluscs classical morphological studies at their current level of perfection have not been able to establish a satisfactory systematic arrangement of taxa in the lower taxonomic categories. The criteria considered significant in recognizing and distinguishing these systematic categories are, at present, often quite unreliable. The old taxonomic problem of what natural unit constitutes a population, or a sub-species, a species, or a group of species, has not been resolved for a surprising majority of molluscs.

In an effort to obtain a better taxonomic understanding of several groups of freshwater Mollusca' we have been employing an immunological method which is a modification of the Ouchterlony (1949) gel double diffusion technique. Most of our efforts so far have been directed to the gastropod genus *Bulinus* (Basommatophora: Planorbidae), a group of species found over most of the African continent, and additionally, found selectively in many Middle Eastern and Mediterranean countries.

---

[*] Sponsored by the Commission on Parasitic Diseases of the Armed Forces Epidemiological Board, and supported (in part) by the U.S. Army Medical Research and Development Command, and (in part) by a research grant (AI 07279) from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

[‡] Supported by a Research Career Program Award (No. 5-K3-AI-19, 451) from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

The African planorbid genus *Bulinus* is currently divided into three sub-genera (Walter, 1962), each with a number of species (Mandahl-Barth, 1957). Within the subgenera, the various species are very similar morphologically, although physiologically and cytologically some of them are quite distinct (Burch, 1964). This is especially true of the species of the subgenus *Bulinus* s.s., which comprises at least two, and perhaps more, species groups. Species are generally placed into these species groups according to the shapes of their radular mesocones or sometimes according to their chromosome numbers. However, these two sets of characters do not always show a correlation (Burch and Natarajan, 1966). In order to test which of these characters were the most reliable for placement of *Bulinus* s.s., specimens into their species groups (a placement which is of some practical importance because, of the two groups, only the *truncatus* species group is known to transmit urinary schistosomiasis) I was interested in studying the immunological relationships of the various species available to us. It is on the results of these studies that this paper is based.

TECHNIQUES AND MATERIALS

The immunological techniques used in this study are similar to those used by Davis (1968) with the snail genus *Oncomelania*. Antibodies against snail antigens were produced in virgin female rabbits by introducing intravenously into the external marginal vein of each rabbit's ear a series of ten one ml. injections of snail foot proteins in increasing concentrations (starting with 15 mg. and roughly doubling the dosage every other day until a final single dosage of 215 mg. was reached). Thirty days after the last injection a second series of injections using the same dosages of the first series was started. Three, five, and ten days after the last injection 50 ml. of whole blood were drawn from each rabbit from their external marginal ear veins. This blood was kept separate and allowed to stand at room temperature for 30 minutes and then cooled to 3° C. for another 30 minutes; this allowed the blood to clot. The clot and serum were then separated and placed into two different centrifuge tubes. These were spun at 3000 RPM for 30 minutes. The combined serum (from one rabbit) was then collected and pushed through a $0{\cdot}45\,\mu$ Gelman sterilization filter into a sterile container. Ten per cent of a 1 : 1000 merthiolate solution was then added to the container and the container sealed. This purified and sterile serum contained the antibody.

Micro-Ouchterlony plates were prepared by fastening a glass ring 21 mm. in inside diameter and 10 mm. in height to a microscope slide. The semi-solid medium used to fill the plates was a 1% agar gel with 0·4% salt concentration containing 10% of a 1 : 1000 solution of merthiolate.

The gel medium was prepared by combining 50 mg. of 2% deionized agar cubes, and 40 ml. of 1% NaCl solution. This was placed in an autoclave and heated at 10 lbs. pressure for 30 minutes. After the gel solution cooled to 40° C., 10 ml. of the 1 : 1000 merthiolate solution was added to the gel. The gel solution was then added to each plate, and after cooling and solidification, the desired pattern of wells was cut into the gel.

Four wells were cut in the gel in the pattern shown in Fig. 1. The procedure for filling the wells with antigen or antibody was as follows. Well 4 was filled with the antigen of population B, which was allowed to absorb into the gel around the well for 24 hours. At the end of that time any residual of this antigen was removed from the well. Well 1 was then filled with the antigen of population A, and wells 2 and 4 were filled with the antibodies of population A. Well 3 was filled with the antigen of population B. The gels were allowed to incubate for 3-5 days and then observed.

The antigen-antibody reactions between wells 1 and 2 are between the same population, and those between wells 2 and 3 are between different populations (Fig. 1 *b*). "Non-identity" reactions between the two populations occur between wells 1 and 4. The space between wells 3 and 4 served as a control to indicate when the system was overloaded with antigen or antibody. Precipitation should not occur in this area.

Antibodies were produced against three laboratory reared species, *Bulinus natalensis* ($n = 18$, Rhodesia), *B. coulboisi* ($n = 36$, Tanzania) and *B.* sp. ($n = 72$, Ethiopia). The snails used to supply antigens were *Bulinus natalensis* ($n = 18$) [four Rhodesian populations], *B. tropicus tropicus* ($n = 18$) [four Rhodesian populations and one from South Africa], *B. tropicus alluaudi* ($n = 18$) [Kenya], *B. "guernei"* ($n = 18$) [two Senegal populations], *B. "guernei"* ($n = 36$) [Gambia], *B. truncatus truncatus* ($n = 36$) [populations from Iran, Egypt (2) and Sudan], *B. truncatus rohlfsi* ($n = 36$) [Mauritania and Ghana], *B. truncatus* ssp. ($n = 36$) [Corsica], and *B. coulboisi* ($n = 36$) [three populations from Tanzania]. In addition, eleven populations of unnamed *Bulinus* s.s. species from Ethiopia ($n = 18$, 54, 72) and Western Aden Protectorate ($n = 36$) were also tested.

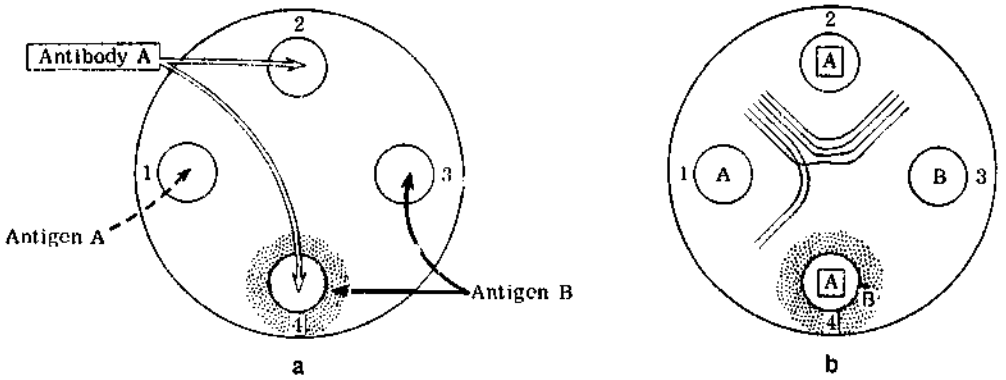


FIG. 1

RESULTS

Special attention was paid to those reactions indicating presence or absence of non-homologous proteins ("non-identity") between each of the two populations of any one test, because, for *Bulinus* s.s. species, "non-identity" reactions seem to occur only between species of different species groups and not between species of the same species group.

Table I shows the occurrence of "non-identity" bands between wells 1 and 4 of the micro-Ouchterlony plates. It is particularly significant that in no instance where tests were made did reactions of the "identity" type occur between populations of two different chromosome numbers, and that, but for one single exception, "non-identity" reactions occurred only between populations having different chromosome numbers, and populations of the same chromosome number showed only "identity". These are critical and conclusive tests for assessing the relative merits of the radular mesocones against chromosome numbers for the taxonomic placement of *Bulinus* s.s. species into their species groups. The crucial tests are those between *B. natalensis* ($n = 18$) antibodies and *B. tropicus* ($n = 18$) and *B. truncatus* ($n = 36$) antigens, and between *B. coulboisi* ($n = 36$) antibodies and *B. truncatus* ($n = 36$), *B. tropicus* ($n = 18$) and *B. natalensis* ($n = 18$) antigens.

The one exception mentioned above was *B.* sp. ($n = 18$) from near Asmara, Ethiopia, which exhibited a relatively strong non-homologous reaction with antisera for *B. natalensis* (as well as for the other two antisera). Asmara is very far north for a member of the *tropicus* ($n = 18$) species group to occur, so perhaps these specimens represent another subgroup within the subgenus *Bulinus*.

The occurrence of "non-identity" reactions between *B.* sp. ($n = 72$) antisera and those antigens of other chromosomal groups tested against it, may indicate yet another species group.

TABLE I

Occurrence of "non-identity" reactions between various populations of Bulinus *s.s.*

Species	Haploid chromosome number	Occurrence of "non-identity" reactions			Source
		B. natalensis (*n*=18) antisera	*B. coulboisi* (*n*=36) antisera	*B.* sp. (*n*=72) antisera	
Bulinus s.s.					
1. *B. natalensis*	18	–	+	+	Rhodesia
2. *B. natalensis*	18	–			Rhodesia
3. *B. natalensis*	18	–	+	+	Rhodesia
4. *B. natalensis*	18	–			Rhodesia
5. *B. t. tropicus*	18	–			Rhodesia
6. *B. t. tropicus*	18	–	+	+	Rhodesia
7. *B. t. tropicus*	18	–			Rhodesia
8. *B. t. tropicus*	18	–	+	+	Rhodesia
9. *B. t. tropicus*	18	–			S. Africa
10. *B. t. alluaudi*	18	–	+	+	Kenya
11. *B. "guernei"*	18	–		+	Senegal
12. *B. "guernei"*	18	–			Senegal
13. *B.* sp.	18	–	+		Ethiopia
14. *B.* sp.	18	–	+		Ethiopia
15. *B.* sp.	18			+	Ethiopia
16. *B.* sp.	18	+	+	+	Ethiopia (Asmara)
17. *B. t. truncatus*	36	+	–	+	Iran
18. *B. t. truncatus*	36		–		Egypt
19. *B. t. truncatus*	36	+			Egypt
20. *B. t. truncatus*	36	+			Sudan
21. *B. t. rohlfsi*	36	+	–		Mauritania
22. *B. t. rohlfsi*	36	+		+	Ghana
23. *B. t.* ssp.	36		–		Corsica
24. *B.* sp.	36	+			W. Aden
25. *B. "guernei"*	36	+	–		Gambia
26. *B. coulboisi*	36	+	–	+	Tanzania
27. *B. coulboisi*	36	+	–		Tanzania
28. *B. coulboisi*	36	+	–		Tanzania
29. *B.* sp.	54	+		+	Ethiopia
30. *B.* sp.	72	+	+	–	Ethiopia
31. *B.* sp.	72	+			Ethiopia
32. *B.* sp.	72	+			Ethiopia
33. *B.* sp.	72	+			Ethiopia
34. *B.* sp.	72	+			Ethiopia

* Blank spaces in the columns indicate that those particular antigen-antibody tests were not made.

DISCUSSION

The planorbid genus *Bulinus* is found over most of the African continent where habitats are suitable for freshwater pulmonate snails. The genus is also found on the East African islands and selectively in many Mediterranean and Middle Eastern countries. The medical importance of the genus lies in the fact that certain of its species are the intermediate hosts of human urinary schistosomiasis.

The various bulinine species traditionally have been grouped into three taxa (lately referred to as subgenera, formerly as genera): *Bulinus* s.s., *Physopsis*, and *Pyrgophysa*.§ It is the subgenus, *Bulinus* s.s., comprising the *tropicus* and *truncatus* species groups of Mandahl-Barth (1957), that is of special concern in the current study, because few of the taxa that have been established within these two species groups currently can be defined with any precision in terms of the limits of morphological variation and geographical distribution. Also, the validity of the two groups themselves has been questioned. Yet, on both parasitological and cytological grounds, there do seem indeed to be two distinct groups, that can be defined with some precision. The more northern *truncatus* group is polyploid and, as far as known, is susceptible to infection with *Schistosoma haematobium*, either under natural or experimental conditions. The more southern group is diploid and has not been found to be susceptible to human schistosome infection.

Assigning species to the two groups has proven difficult for malacologists. For example, species that were first placed with one group by Mandahl-Barth only to be shifted by him later to the other group are: *Bulinus guernei*, *B. natalensis*, and *B. sericinus*. Characters that are currently being used to assign species to one or the other of the two species groups in question are the shape of the mesocones of the first lateral teeth of the radula, the degree of presence or absence of a male copulatory organ, and the shape of the shell.

Recently, it has been reported that the *truncatus* group, previously thought not to occur south of the great African lakes, occurs as far south as South-West Africa and the Transvaal (Mandahl-Barth, 1965 ; Schutte, 1965, 1966). This information is based on the occurrence of *B. natalensis* and *B. depressus* (Haas) in these regions and the fact that these two species apparently have "arrow-head-shaped" mesocones on the first lateral teeth of the radula, thought to be characteristic of the *truncatus* species group (in contrast to the "triangular-shaped" mesocones thought to be characteristic of the *tropicus* species group). However, *B. natalensis* has 18 pairs of chromosomes, a characteristic of the *tropicus* group (some populations have one to several extra chromosomes), and, as shown by the present study, this species also shows immunological affinities with the *tropicus* group rather than the *truncatus* species group.

In the present study the use of an immunological technique employing the specific absorption technique enabled the observation of "identity" or "non-identity" among the thirty-four populations tested against each of the three species for which there was antisera. The results, as far as they go, show that there is good correlation between serological tests and the chromosomal ploidy of the populations, and a lack of complete correlation with characters of the radular mesocones, the single feature currently given the most importance for species group identification.

It is concluded from these results that (1) the subgenus *Bulinus* s.s. does indeed comprise more than one species group, which can be identified cytologically, parasitologically and immunologically, (2) little reliance can be placed on those morphological characters now being used to place a species into its species group, and (3) in face of the intensive but unrewarding morphological research already devoted to the genus, perhaps simple biochemical tests should be employed instead of morphological characters by field workers attempting to ascertain the potential of natural populations for transmitting urinary schistosomiasis.

---

§ Although there are certain nomenclatorial problems associated with this system (*see* Mandahl-Barth, 1957), it is nevertheless a traditional and convenient scheme which we hesitate to abandon until more critical taxonomic work has been undertaken.

ACKNOWLEDGEMENTS

The immunological work reported here was carried out with the technical assistance of Gene K. Lindsay of the Mollusk Division, Museum of Zoology, The University of Michigan, and special acknowledgement is herewith made for his conscientious and competent efforts. Appreciation is noted to the following individuals for their generosity in supplying snails used in this study: A. D. Berrie, E. G Berry, J. Bosch, D. S. Brown, K.-Y. Chu, V. de V. Clarke, A. Garnett, A. D. Harrison, E. A. Malek, J. McClelland, H. van der Schalie, C. H. J. Schutte, C. J. Shiff, Fikry el Tawil, F. Wickremasinghe, and C. A. Wright.

LITERATURE CITED

BURCH, J. B. 1964. Cytological studies of Planorbidae (Gastropoda: Basommatophora). I. The African subgenus *Bulinus* s.s. *Malacologia* **1** (3): 387–400.

—— AND R. NATARAJAN 1966. The species groups of African *Bulinus* s.s. *Amer. Malacol. Union Ann. Reps.* **33**: 39–40.

DAVIS, G. D. 1968. A systematic study on *Oncomelania hupensis chiui* (Gastropoda: Hydrobiidae). *Malacologia* (in press).

MANDAHL-BARTH, G. 1957. Intermediate hosts of *Schistosoma*. African *Biomphalaria* and *Bulinus*—II. *Bull. Wld. Hlth. Org.* **17**: 1–65.

——— 1965. The species of the genus *Bulinus*, intermediate hosts of *Schistosoma*. *Ibid.* **33**: 33–34.

OUCHTERLONY, O. 1949. Antigen-antibody reactions in gels. *Arch. Kem. Mineral. Geol.* **B (26)**: 1–9.

SCHUTTE, C. H. J. 1965. Notes on the radular mesocones as a criterion for distinguishing between the *tropicus* and *truncatus* groups of the genus *Bulinus* (Mollusca: Basommatophora). *Ann. Mag. Nat. Hist.* **8**: 409–419.

——— 1966. Observations on two South African bulinid species of the *truncatus* group (Gastropoda: Planorbidae). *Ann. Trop. Med. Parasit.* **60**: 106–113.

WALTER, H. J. 1962. Punctation of the embryonic shell of Bulininae (Planorbidae) and some other Basommatophora and its possible taxonomic-phylogenetic implications. *Malacologia* **1** (1): 115–137.

BIOSYSTEMATIC ANALYSIS OF *SEMISULCOSPIRA TRACHEA* (GASTROPODA: PLEUROCERIDAE)

GEORGE M. DAVIS

406th Medical Laboratory, U.S. Army Medical Command, Japan, APO San Fransisco, U.S.A.

ABSTRACT

Topotypes of the species of *Semisulcospira* from Japan and Korea have been studied to determine the criteria for defining species in adequate biosystematic terms. Burch and Davis (1967) found that cytological data clearly separate species groups in Japan and serve to characterize several species there.

Semisulcospira libertina (Gould) and *S. trachea* (Westerlund) are of the same species group where cytologically $n = 18$. The former is a river form with smoothish shell while the latter is lacustrine with prominent nodulate ribs on the shell. The question is asked, are they distinct species?

An analysis of the number of embryos per pallial brood pouch and their dimensions per whorl for each species revealed no significant differences. The embryos of *S. trachea* did have prominent nodes which were lacking in *S. libertina.*

Polyacrylamide electrophoresis of foot-muscle extract stained for proteins yielded similar densitometric profiles for the 24 components separated. *S. trachea* had 8 fractions which had higher R_F values than the corresponding fractions of *S. libertina* indicating the type of population difference discussed by Davis and Lindsay (1967).

Immunological studies using micro-Ouchterlony double diffusion tests with absorbed antiserum showed qualitative homology in antigen-antibody systems. Agar immunoelectrophoresis yielded the same general precipitin patterns for both species although slight quantitative differences were indicated.

As a result of these studies *S. trachea* is considered a synonym of *S. libertina* with a few accumulated genetic differences which are, however, insufficient to justify subspecific status.

INTRODUCTION

Semisulcospira is widely distributed in Japan, Korea, Taiwan, and China. The genus is, perhaps, the one most frequently encountered in rivers, streams, and lakes of Japan and Korea. An extremely wide range of variation in adult shell sculpture, shape, and coloration has made classification and recognition of taxa previously described in classical terms most difficult. As a result, historical aspects (classical descriptions from 1851 to 1929) involve a great body of tangled nomenclature. Current systematic studies of the genus are complicated both by the vast amount of phenotypic variation between populations and the noted historical aspects.

Over 32 names have been bestowed upon taxa ranked under *Semisulcospira* from Japan alone. Kuroda (1963) lists most of these; others are reviewed by Davis (1967). It is evident that adult shells alone will not serve to identify or define many species (Burch and Davis, 1967). One asks, what characters do serve to define objectively species and subspecies of *Semisulcospira*? Was Kuroda (1963) justified in listing 15 named taxa as subspecies or synonyms of *S. bensoni*?[1]

---

[1] *Semisulcospira libertina* was considered a subspecies of *S. bensoni* by Kuroda (1963) and a synonym of the latter by Habe (1965). Many of the taxa felt to be synonyms of *S. bensoni* by Kuroda were considered synonyms of *S. libertina* by Kobelt (1879). Until biosystematic studies prove otherwise, *S. bensoni* and *S. libertina* are to be treated as distinct, and Kuroda's list of synonyms is referred to *S. libertina.*

Parasitologists have repeatedly asked how to determine the limits of variation of *Semisulcospira libertina*, the species implicated as first intermediate host for the human lung fluke, *Paragonimus westermani* in Japan (Yokogawa *et al.*, 1960). Workers investigating this disease have asked for positive identification of snails found naturally infected and have desired to know if these snails belong to infraspecific groups of *S. libertina*, *S. libertina* s.s. or other species. It should be pointed out that the relationship of *S. libertina* to the maintenance of the life-cycle of *P. westermani* is obscure as evidenced, for example, by the fact that no person has succeeded in producing fully developed cercariae in *S. libertina* (Yokogawa, 1964).

Studies were initiated at the 406th Medical Laboratory aimed at blocking-out distinct subgeneric groups of *Semisulcospira*. Burch and Davis (1967) initiated a system of obtaining topotypes of species where locality data were adequate in the original descriptions, or where type localities were pointed out by the author of the species.[2] As a result of the initial study involving cytology, shell structure of embryos and adults, and patterns of embryo shell growth in the pallial brood pouch, ten distinct taxa were recognized and ranked as species or subspecies. These ten taxa were divided into two species complexes ; the *libertina* complex where the chromosome numbers were $n = 18$ to 20 ; the *niponica* complex where $n = 7$ to 14. Species belonging to the former are *S. libertina* s.s., *S. reiniana*, and *S. kurodai.*

This paper is concerned with the *libertina* complex. Patterson (1967) found that *S. trachea* (Westerlund) had a chromosome number of $2n = 36$, the same as that of *S. libertina* s.s. I investigated the relationship of *S. trachea* to *S. libertina* s.s. to determine if the two taxa were separate species, if *S. trachea* was a subspecies of *S. libertina* s.s. or if *S. trachea* was a synonym of *S. libertina* s.s. The purpose of this paper is to compare topotypes of both taxa in terms of the following : (1) embryo and adult shell morphology, (2) growth patterns of the embryos in the pallial brood pouch, (3) polyacrylamide electrophoretic profiles of proteins from foot muscle extract, and (4) immunological reactions using antigens extracted from foot muscle. Further, the purpose of this paper is to justify, on the basis of the data presented, placing *S. trachea* in synonymy with *S. libertina.*

Literature pertaining to the electrophoretic studies is reviewed by Davis (1967 *a*) and Davis and Lindsay (1967). References important for the immunological studies are those of Ouchterlony (1958), Morill *et al.* (1964), Schwick and Störiko (1965), Michelson (1966 *a, b*), Davis (1967 *b*), McKay (1967), and Wright and Klein (1967).

HISTORICAL

Topotypes of *Semisulcospira libertina* were obtained from : Japan, Honshu, Shizuoka Prefecture, Izu Peninsula, Shimoda Town, Inozawa River (Figs. 1, 2). Davis (1967 *c*) discussed the type locality.

A number of taxa placed in synonymy with *S. libertina* by Kobelt (1879), Kuroda (1963), and Habe (1965) were originally described in terms of variation in shell sculpture as observed in many populations of *S. libertina*. For example, von Martens (1877) discussed "*Melania libertina* var. *plicosa*," var. *decussata*, var. *tenuisulcata*[3] and var. *ambidextra*[4] which he noted could all be found in one population where the varieties graded into each other [*e.g.*, his population from Yokohama (next to Tokyo)]. von Martens (1877) stated that var. *decussata* (and thus *S. libertina*) was found in Lake Hakone (= Ashino Lake).

---

[2] Dr. T. Habe, National Science Museum, Tokyo, showed us type localities of species named by Kuroda (1929) and Kajiyama and Habe (1961).

[3] Originally described by Dunker (1859) as *Melania tenuisulcata*, Malac. Blätt, p. 229, Moll. Japon. (fide Brot, 1874; Kobelt, 1879).

[4] Originally described by von Martens (1860) as *Melania ambidextra.*

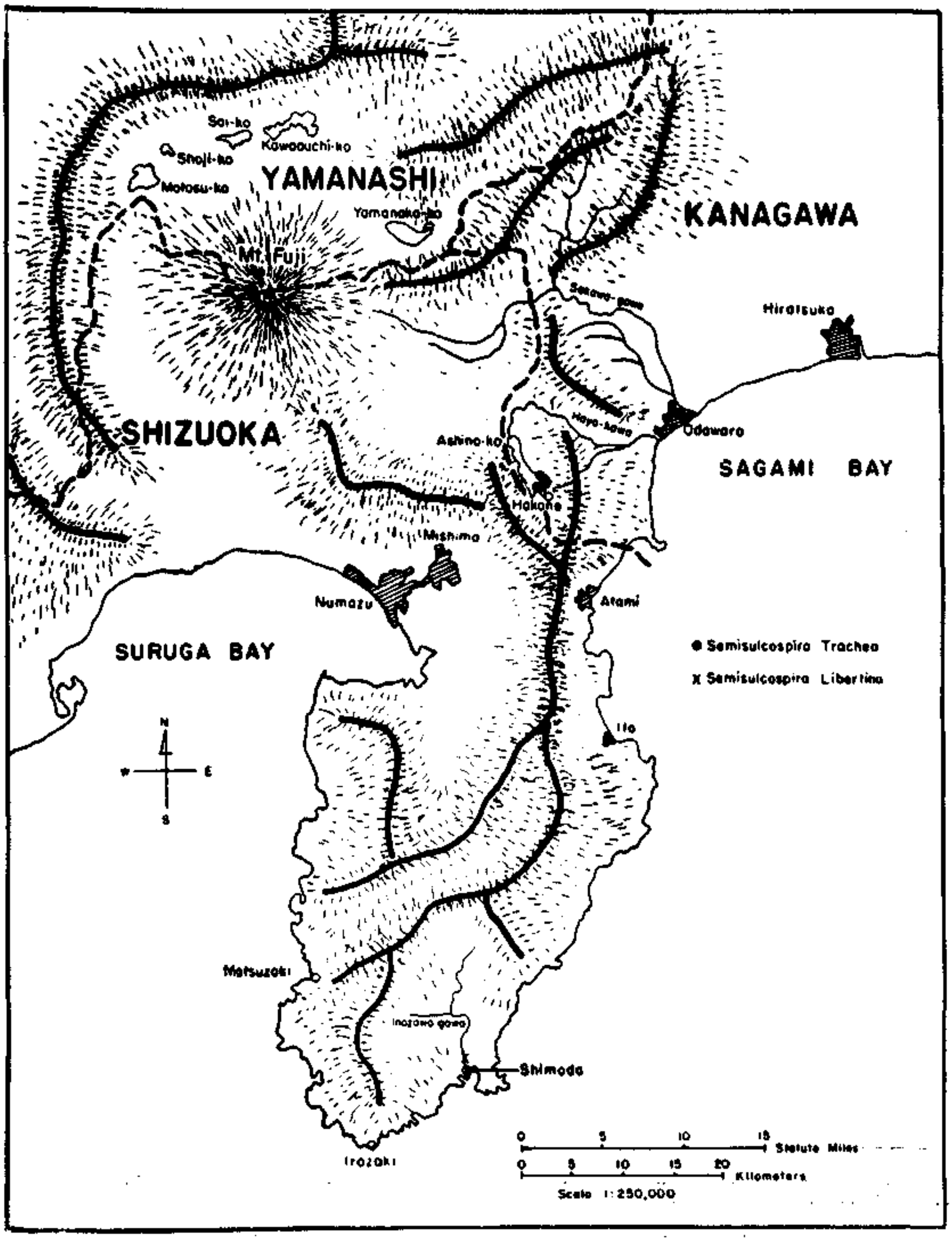


FIG. 1. Localities for *Semisulcospira libertina* s.s. and *Semisulcospira trachea*. The two localities are separated by high mountains. *S. trachea* was very common around the S.E. end of Ashino Lake.

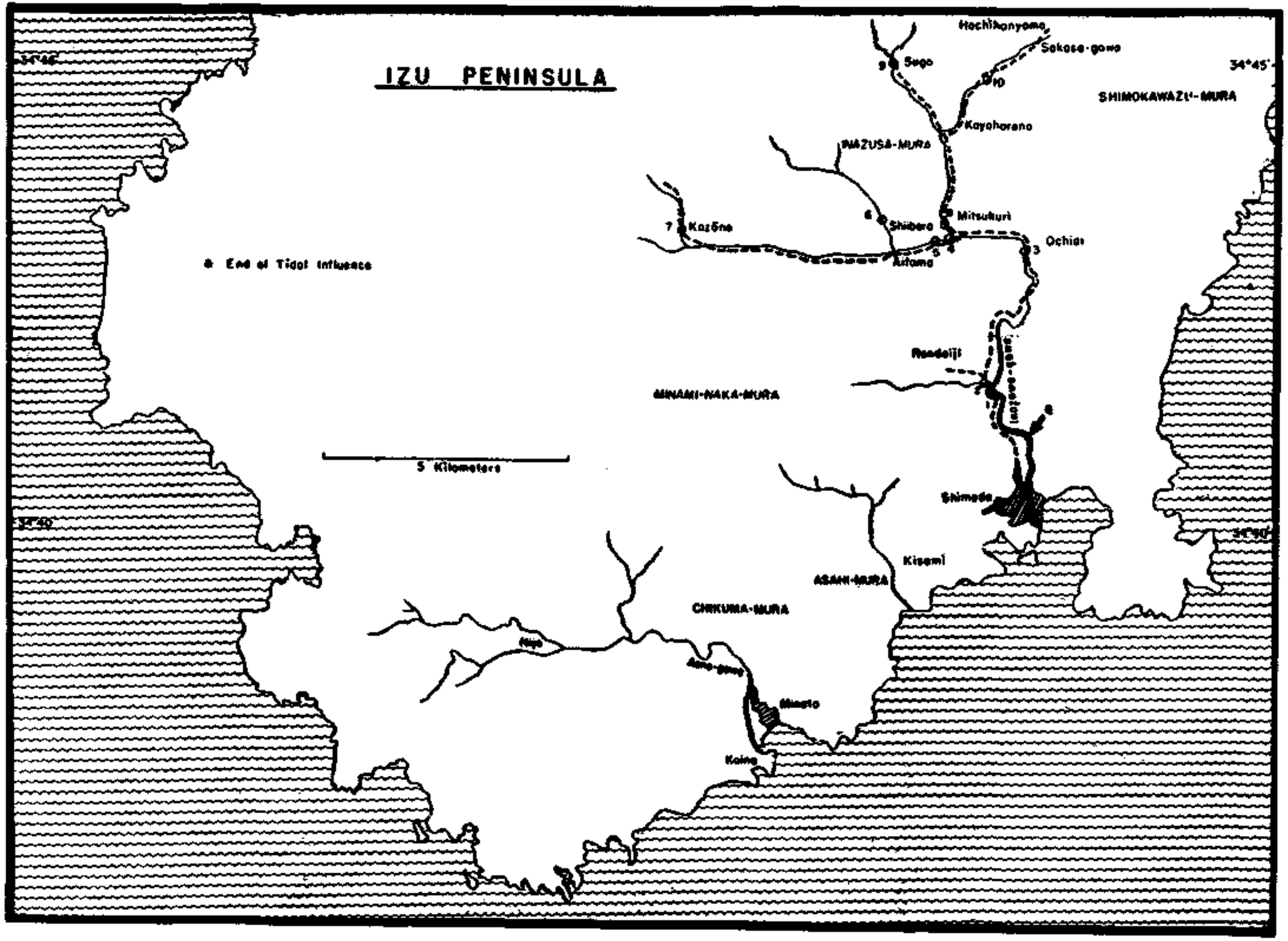


FIG. 2. Map of the Inozawa River with localities where populations of *S. libertina* were located. The area considered as the type locality was Station 1. * = point where tidal influence no longer was observed.

Donitz and Hilgendorf (fide von Martens, 1877) reported "*Melania niponica*" from Lake Hakone. Westerlund (1883) described "*Melania niponica* E. Smith var. *trachea*" from Lake Hakone. I have upon several occasions over a two-year period, studied the genus *Semisulcospira* in Ashino Lake and have found only one taxon pertaining to *Semisulcospira*, a population from which one finds numerous specimens fitting Westerlund's description. *Semisulcospira niponica* from Lake Biwa, Shiga Prefecture, is a distinct species not present in Kanagawa Prefecture. Specimens called var. *decussata* by von Martens were undoubtedly the same taxon which Westerlund later formally described.

S. trachea used in my studies were obtained from Japan, Honshu, Kanagawa Prefecture, Hakone Mts., Hakone Town, Ashino Lake, the swan breeding pond (Fig. 1).

MATERIALS AND METHODS

1. *Adults and Embryos*

Methods are those of Davis (1967 *c*). Data were recorded from the largest 10 per cent of the adults of the population. Size was based on length of body whorl. Spire angle, number of basal cords, number of ribs on the penultimate whorl, color patterns, shell length, and width were recorded. The following data were recorded for embryo shells : (1) total number per pallial brood pouch, (2) length and width of shell per whorl, (3) length of body whorl per whorl stage, (4) sculpture and color.

Data from *S. trachea* were compared with those compiled by Davis (1967 *c*) for *S. libertina*.

2. *Electrophoresis*

(*a*) *Foot Muscle Extract.*—Davis and Lindsay (1964, 1967) discussed using foot muscle as a source of protein for electrophoretic studies of molluscan individuals and populations. Foot muscle (epidermis removed as well as any dense green pigment) was homogenized (300 mg. blotted wet weight per 2·0 ml. saline) using a Sorvol microhomogenizer (50,000 rpm, 1 min.) as previously described (Davis and Lindsay, 1967). The homogenate was centrifuged at 3,000 rpm (1,500 g.) for 5 minutes and the supernatant decanted; the sediment was centrifuged again at 4000 rpm (2,600 g.) for 5 minutes. The supernatants were combined. All operations were carried out at 2–5° C. This extract was used for electrophoretic and immunological experiments.

Protein content of the extract was determined using the Biuret reaction (fide Kabat and Mayer, 1961). The standard curve was made using crystalline bovine albumen (clinical pathology standard). Carbohydrate content was determined using a phenol-sulfuric acid technique (Montgomery, 1957). The standard curve was established using purified dextrose. Determinations were made using a Shimadzu QR-50 spectrophotometer.

The dry weight of extract of *S. libertina* was determined (corrected for weight of salt in saline) and recorded as mg./ml. As shown in Table I, the average dry weight was 9·53 of which 5·27 were protein and 3·13 were carbohydrates. Extract was frequently prepared in bulk for lyophilization. As many as 20 to 25 units (1 unit = 300 mg. foot muscle per 2·0 ml. saline) were homogenized and the supernatants combined. The pooled extract yielded an average of 5·50 mg./ml. protein for *S. libertina*. There was no significant difference between the two taxa when weights of protein per ml. pooled extracts were compared (Table I).

(*b*) *Electrophoretic Procedures.*—Polyacrylamide electrophoresis was used as discussed by Davis (1967 *a*) and Davis and Lindsay (1964, 1967). The standard 7·5 per cent acrylamide gel was used. Potassium ferricyanide was not used to inhibit polymerization of the lower gel and accordingly the N, N, N, N, Tetramethylethylenediamine was reduced to 0·03 ml. per 100 ml.

mixed lower gel. A *tris*-glycine buffer was used (pH 8·2 to 8·4). Runs were made with 5 ma per tube (a run = experiment from the time current is switched on to current switched off). Runs were terminated when the brom phenol blue tracking dye had moved 32 mm. into the gel. Gels were stained for proteins in amidoschwartz for two hours and destained electrically in 8 per cent acetic acid. Gels were stored in tubes with 7·5 per cent acetic acid.

TABLE I

Dry weight, protein and carbohydrate contents (mg./ml.) of extracts of Semisulcospira libertina *s.s. and* S. trachea

Taxa Studied		*S. libertina*				*S. trachea*		
Statistic		$\bar{X}$	S	Se		$\bar{X}$	S	Se
Tests	No.				No.			
1. Dry weight	3	9·53	±0·66*	..	ND	..	—	—
2. Proteins	7	5·27	0·48	0·18	3	6·03	±0·39*	—
3. Carbohydrate	15	3·13	1·34	0·35	7	4·18	2·49	0·94
4. Protein (pooled ext.)	7	5·50	0·56	0·21	6	5·37	0·47	0·19

* = total variation.
ND = not determined.
$\bar{X}$ = mean.
S = standard deviation.
Se = standard error of the mean.
No. 1 to 3 = results testing 1 unit extract.

Experiments involved freshly prepared extract where the sample gel consisted of 2 parts upper gel to 1 part extract (an average of 182 μg. per tube). At least 15 experiments were conducted (each with fresh extract) with each taxon. Each experiment involved 10 to 12 tubes loaded with aliquots of the same extract. Human blood serum was routinely used as a control for gel conditions. In cases of poor gels yielding unfamiliar blood protein patterns, all gels in a run were discarded.

(*c*) *Analysis of Data.*—Densitometric tracings were made of the separated proteins using a Photovolt Densicord Densitometer. Emphasis was placed on the qualitative densitometric patterns. R_F values were calculated for each component as discussed by Davis and Lindsay (1967).

3. *Immunology*

(*a*) *Antigens.*—The extracts discussed under 2 (*a*) were the sources for antigens. Extracts used for immunological experiments were both fresh and lyophilized. Extracts from both taxa were adjusted in each experiment so that they contained equal concentrations of protein (5·0 to 6·0 mg./ml.).

(*b*) *Antiserum.*—Antisera against fresh extract of *S. libertina* s.s. were produced in eight rabbits (6–7 lb., albino, virgin female). Pre-injection control serum was obtained. Extracts were injected intravenously (IV) or subscapular (SS). As shown in Table II, two to four injection series were given. SS injections involved emulsification of extract with an equal volume of Freund's complete adjuvant. Rabbits were bled from the ear on the 5th or 7th day after the first series (Rabbits D, E, H), the second series (A–H), the 3rd series (H), and 4th series (B, E),

TABLE II

Mg. protein injected into eight rabbits each series

Series No.	Injection Day	Mg. Injected into Rabbits A to H							
		A	B	C	D	E	F	G	H
1	1	IV-6	IV-5	IV-5	IV-5	IV-5	IV-8	SS-60	SS-110
	3	6	5	7	10	10	12	Wait	Wait
	5	6	5	8	10	10	15	8	8
	7	6	5	8	12	12	20	Days	Days
	9	12	10	12	15	15	30		
	(No. Days Wait)	(8)	(20)	(8)	(20)	(20)	(8)		
2.	1	IV-6	IV-5	IV-5	IV-5	IV-5	IV-8	IV-7	SS-32
	3	6	6	7	10	10	12	13	Wait
	5	6	6	8	10	10	15	20	26
	7	6	10	8	12	12	20	20	Days
	9	12	10	12	15	15	30	30	
		(72T)	(67T)	(80T)	(104T)	(104T)	(170T)	(150T)	
	(No. Days Wait)		(229)			(240)			
3.	1		SS-30			SS-45			IV-5
	3		Wait			Wait			6
	5		19			8			12
	7		Days			Days			12
	9								12
									(189T)
4.	1		IV-7*			IV-7			
	3		(37ST)			9			
	5					12			
	7					15			
	9					15			
						(103ST)			

IV = intravenous.
SS = subscapular.
(—T) = total protein.
(—ST) = subtotal protein from series 3 and 4.
* = shock and death.

After clotting and centrifugation an estimate of the titer of the cell-free serum was made using the interfacial ring test and a twofold dilution series of antigen. A volume of antigen equal to that of antiserum was layered over the latter in a glass capillary tube (1·85 × 72·5 mm.). The tubes were maintained at 23° ± 2° C. and read for precipitin bands at 30 and 60 min. Titers thus determined are listed for each antiserum in Table III. Serum was frozen and stored at −15° C. until used.

(*c*) *Quality of Antiserum.*—The criterion for antiserum excellence was the number of discrete, clearly visible precipitin systems developed in gel diffusion experiments (micro-Ouchterlony and immunoelectrophoresis). It was found that antisera with titers of 1 : 128 or 1 : 256 at 30 min. generally yielded strong systems while those with titers below 1 : 128 were unusable. Antisera after the first injection series were poor. Not all antisera were suitable even with titers of 1 : 128 or 1 : 256. For this paper, excellent antisera yielded six or more systems, good yielded three to five, poor yielded two or less (Table III). Experiments were only carried out using good or excellent antisera.

TABLE III

Titer and quality of antisera produced in eight rabbits using injection series shown in Table II

Series	Time (min.) titer read	Rabbits A	B	C	D	E	F	G	H
1	30				1/64	1/64			1/32
	60				1/128	1/64			1/32
					P	P			P
2	30	1/128	1/128	1/128	1/128	1/128	1/128	1/256	1/128
	60	1/256	1/128	1/256	1/128	1/128	1/256	1/256	1/128
		P	E	P	G	E	G	G	P
3	30								1/256
	60								1/256
									G
4	30		1/128			1/128			
	60		1/256			1/256			
			P			G			

Quality of Antiserum (*see* text). E = excellent; G = Good; P = poor.

(*d*) *Micro-Ouchterlony Diffusion Experiments.*—Techniques involving micro-diffusion systems were previously discussed (Davis, 1967 *b*). Glass rings (22 mm. inside diameter) were cemented on microscope slides with a paraffin-wax mixture. Wells formed by the rings were washed with a 1 : 100 Siliclad solution, rinsed in distilled water, and dried. A 1 per cent solution of Special Agar Noble (0·45 per cent saline ; 1 : 10,000 merthiolate) was pipetted into the rings (2·5 ml./ring). The agar template used to cut three patterns was from a design of Dr. George Nace, University of Michigan, Ann Arbor, U.S.A.

In the five hole pattern (Pl. V, Fig. 10 A) each well has a 3 mm. diameter (volume 46 μl.). The six hole pattern (Fig. 10 E) has a center well of 4.5 mm. diameter and a capacity for 96 μl. The satellite wells are 3 mm. diameter. Wells of the diamond patterns (Fig. 10 B) are 4 mm. diameter and hold 82 μl.

Absorbed and unabsorbed antisera were used. Absorption was accomplished in two ways : (1) Heterologous extract was placed in one well of the diamond pattern (A_1, Fig. 10 F) for 24 to 30 hours and then the excess was removed. Anti-*S. libertina* serum was then placed in wells A_1 and A while extracts (homologous, L ; heterologous, T) were placed as shown. Antiserum in well A_1 must pass through a barrier of heterologous extract. (2) One ml. of antiserum was added to a tube with lyophilized heterologous antigen (5·0 to 6·0 mg.). The antigen was dissolved and the solution was left at room temperature for 30 min. ; then the solution was placed in the refrigerator (5° C.) for 24 hours. Subsequently, the serum was centrifuged ; the precipitate was thus packed and the absorbed serum was decanted. The process was repeated once again.

Gels, set up as shown in Fig. 10, were left at 23 ± 2° C. for two days after which they were removed from the glass rings, sliced in two, washed in 0·05 per cent cadmium sulfate for 5 minutes and subsequently washed in barbital buffer (pH 8·6) for two to three days (buffer changed thrice daily). Gels were then stained in amidoschwartz for two hours and destained in 8 per cent acetic acid. They were subsequently rinsed in water, mounted and dried on microscope slides, (*e*) *Immunoelectrophoresis*.—Microscope slides (75 × 25 mm.) were wiped with lens paper soaked in 0·5 per cent Siliclad, dried and evenly covered with 4·0 ml. of 2 per cent special Agar Noble [made with barbital buffer of pH 8·2, ionicity 0·1 (Crowle, 1961) and 1 : 10,000 merthiolate]. Wells cut into the agar were 4 mm. diameter (25 μl. capacity). The slot cut between the wells was 3 mm. from the edge of each well.

A voltage gradient of 6–7 v/cm. was maintained across each slide and icepacks served to maintain the temperature at 14 ± 2° C. The run time was 60 or 75 min. The buffer was that given above. Upon termination of the run the slots were cleared of agar and antiserum was added. Slides were kept in moist chambers at 23 ± 2° C. for 36 hours after which they were soaked in the 0·05 per cent cadmium solution, washed in buffer for two days, and dried at room temperature. Completely dried slides were stained in amidoschwartz for one hour, destained in 8 per cent acetic acid, rinsed in water, and dried again.

In all, 18 immunoelectrophoretic experiments were conducted using 10 to 12 slides each experiment.

RESULTS

1. *Adults and Embryos*

(*a*) *Adult Shells* (Pl. 1, Fig. 3, *a–l*).—A population of 200 *S. trachea* specimens was studied. Characteristic shell features are given in Table IV compared with those of topotype *S. libertina*. The whorls are flat-sided to slightly convex. The base is angular. Ribs are the most prominent feature of the shell of this taxon (18 ± 2 on the penultimate whorl). They are strong, opistocyrt, pass abapically over the periphery of the body whorl and become less prominent or fade out on the base. The ribs are characteristically nodulate, nodes corresponding to spiral cords which vary from prominent to obsolete. Intercord grooves are found.

TABLE IV

Comparison of adult shell features of 25 Semisulcospira libertina *s.s. and* 25 S. trachea

Taxa	*S. libertina*			*S. trachea*		
Statistic	$\bar{X}$	S	Se	$\bar{X}$	S	Se
Spire Angle	22	3·13	0·62	21	2·51	0·50
Basal Cords	9	1·56	0·31	9	1·22	0·24
Length B.W.	19·2	1·67	0·33	19·0	1·12	0·22
Ribs on P.W.				18·0	1·94	0·39
Nodes on R.P.W.				10·0*	1·49	0·32
No. Whorls	4 to 5			5	±1	..
Shell Length	28·6	+	—	31	1·59	0·32
Shell Width	13·0	+	—	13	0·74	0·15

* N = 22.
\+ = not calculated.
B.W. = body whorl.
P.W. = penultimate whorl.
R. = ribs.

At least ten color patterns were found (Table V). Of 65·5 per cent of the shells with uniform color, 41·4 were yellow and 24·1 were purple. Banding patterns were recorded from those observed on the body whorl. Bands in Fig. 6 are labelled with terminology used in Table V.

TABLE V

Color patterns on the adult shells of Semisulcospira trachea

Shell Background Yellow		Shell Background Purple	
Color Pattern	% of Population	Color Pattern	% of Population
1. Uniform Yellow ..	41·4	8. Uniform Purple ..	24·1
2. 2 bands; mid, adapical ..	10·3	9. 3 bands ..	6·0
3. 1 band; mid ..	7·8	10. 2 bands; mid, basal ..	3·4
4. 3 bands ..	4·3		
5. 2 bands; mid, basal ..	0·8		
6. 1 band; basal ..	0·8		
7. 1 band; adapical ..	0·8		

(*b*) *Embryo Shells* (Pl. III, Fig. 5, *a–f*).—An average 271 embryos per female was found (Table VI). The largest size attained in the brood pouch was 3·0 whorls but only 2·9 per cent of the embryos were this size. Statistics on embryo shell measurements are given in Table VII compared with those for *S. libertina* s.s. The relationships between taxa are graphically shown in Fig. 7.

TABLE VI

The number of embryo shells found per pallial brood pouch of Semisulcospira libertina *s.s. and* S. trachea

Taxa	*S. libertina*			*S. trachea*		
Statistic	$\bar{X}$	S	Se	$\bar{X}$	S	Se
No. embryos per female ..	352	234	74	271	104	23

$\bar{X}$ = mean; S = standard deviation; Se = standard error of mean.

Embryos of *S. trachea* are brown to yellow-brown. They have deep sutures and convex whorls. Two spiral cords cross the body whorl in 84 per cent of the shells of 2·0 whorls and one cord in 16 per cent. At 2·5 whorls or larger, 96 per cent of the shells have two cords. The cords terminate on the outer lip which bends outward at these points (Fig. 5 *b*, *c*, *f*). The outer lip appears grooved inside the aperture beneath the cords (Fig. 5, *c*, *f*).

The adapical cord is distinctly nodulate in 80 per cent of the 2·0 whorl shells and 100 per cent of those of 2·5 and 3·0 whorls. The nodes begin at 1·5 to 2·0 whorls from the apex Fig. 5, *b*, *c*, *d*). At 3·0 whorls the abapical cord is frequently nodulate (Fig. 5, *b*) and nodes between the cords are frequently connected with low ribs. The nodes may expand into faint ribs above and below the cords.

A distinct microsculpture is present represented by prominent spiral threads crossed by less pronounced growth lines.

TABLE VII

Comparison of embryo shell features of Semisulcospira libertina *s.s. and* S. trachea

Taxa	*S. libertina*				*S. trachea*			
Whorl size ..	< 2·	2·0	2·5	3·0	< 2·0	2·0	2·5	3·0
% embryos at each whorl size ..	47·6	35·6	16·1	0·7	47·5	30·9	18·7	2·9
Shell 1. $\bar{X}$ Length ..		0·95	1·15	1·35		0·96	1·20	1·39
2. $\bar{X}$ Width ..		0·74	0·84	0·93		0·70	0·86	0·93
3. L/W ..		1·28	1·37	1·45		1·37	1·40	1·49
4. $\bar{X}$ LBW ..		0·78	0·90	0·99		0·79	0·98	1·05

$\bar{X}$ = mean; L = length; W = width; BW = body whorl.

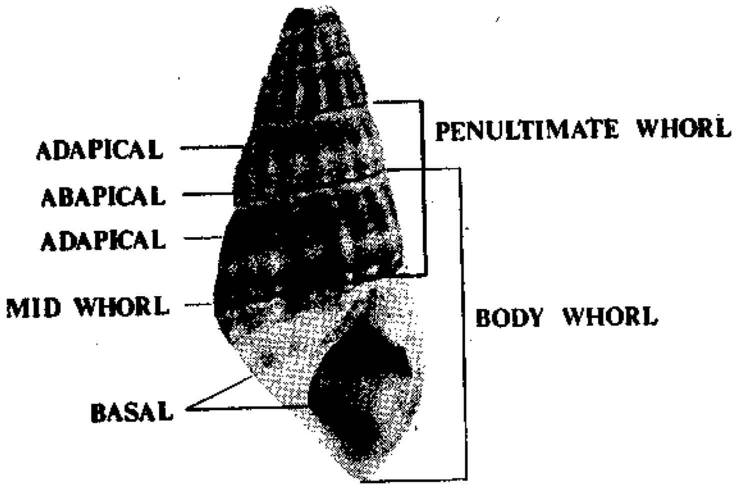


FIG. 6. A shell of *Semisulcospira trachea* with various color bands labeled.

(*c*) *Conchological Comparison of Taxa.*–Adult shells of *S. libertina* s.s. are shown in Pl. II, Fig. 4, *a–l*. They differ from those of *S. trachea* in that (1) ribs are found in only 3·0 per cent of the population (16–18 per penultimate whorl). The ribs are obsolete as are nodes on the ribs, with spiral grooves passing over the ribs (Fig. 4, *c*). (2) Spiral cords are in most cases obsolete except at the base of the shell (Fig. 4, *a*, *b*, *e–g*, *k*). However, specimens can be found with distinct cords (Fig. 4, *h–j*, *l*). (3) Shells of *S. libertina* s.s. are uniform yellow (60 per cent) or banded. One band (types 3 or 7, column 1, Table V) was found in 9·0 per cent; two bands (adapical and basal, not found for *S. trachea*) in 15·5 per cent; two bands (types 2 or 5, column 1, Table V) in 0·5 per cent; three bands (type 4, column 1, Table V) in 15·0 per cent.

Adult shells of the two taxa did not differ significantly in (1) spire angle, (2) number of basal cords, and (3) length of body whorl for shells of the largest 10 per cent of the population.

Embryo shells of both taxa are compared in Pl. III, Fig. 5. *S. trachea* has distinct nodes on the spiral cords, a condition not found for *S. libertina* s.s. *S. libertina* s.s. differs from *S. trachea* in

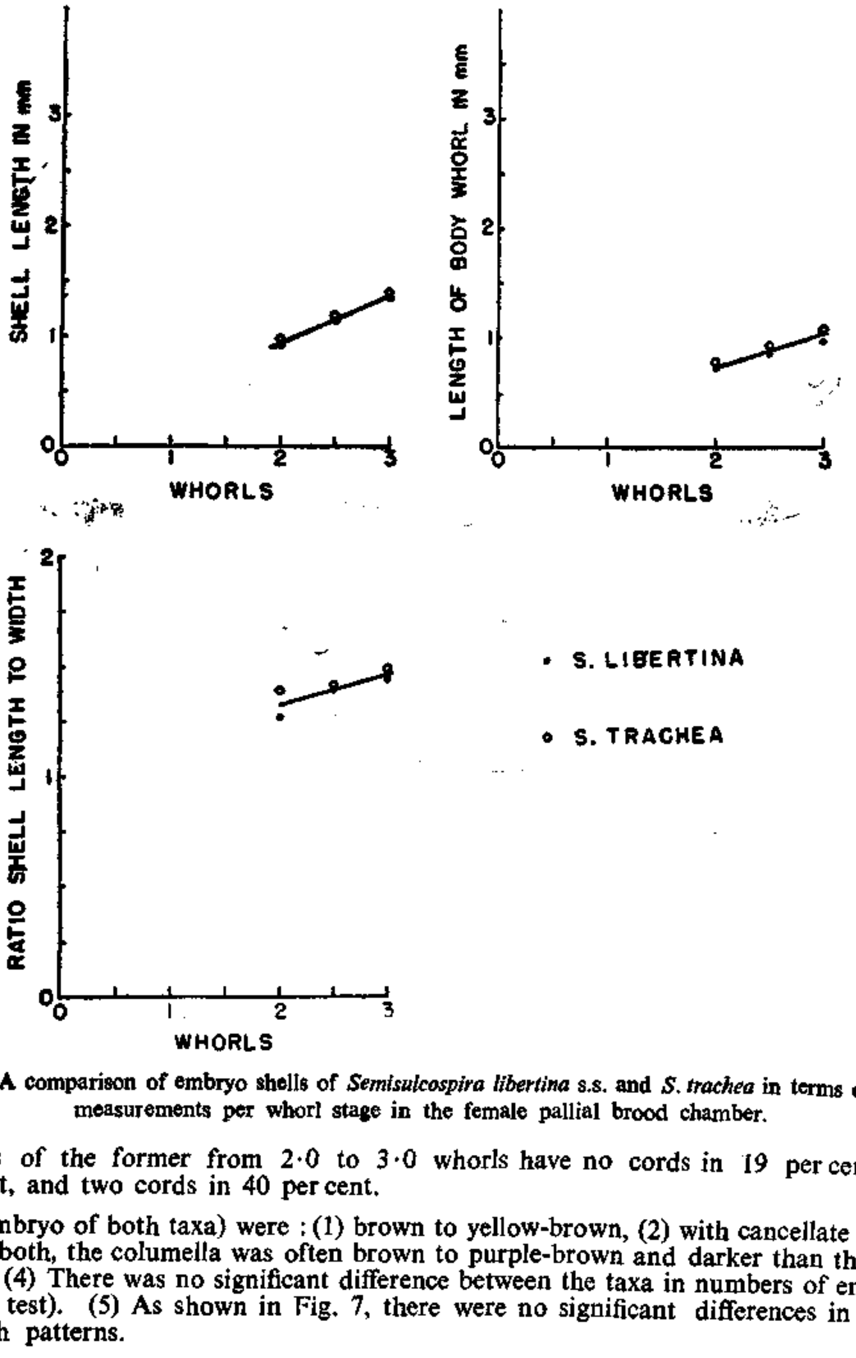


FIG. 7. A comparison of embryo shells of *Semisulcospira libertina* s.s. and *S. trachea* in terms of shell measurements per whorl stage in the female pallial brood chamber.

that embryos of the former from 2·0 to 3·0 whorls have no cords in 19 per cent, one cord in 41 per cent, and two cords in 40 per cent.

Shells (embryo of both taxa) were : (1) brown to yellow-brown, (2) with cancellate microsculpture. (3) In both, the columella was often brown to purple-brown and darker than the remainder of the shell. (4) There was no significant difference between the taxa in numbers of embryo shells per female (*t* test). (5) As shown in Fig. 7, there were no significant differences in intra-brood pouch growth patterns.

2. *Electrophoresis*

Stained gels were used as negatives under the photographic enlarger to make the prints shown in Pl. IV, Fig. 8. Densitometric patterns for these gels are shown in Fig. 9.

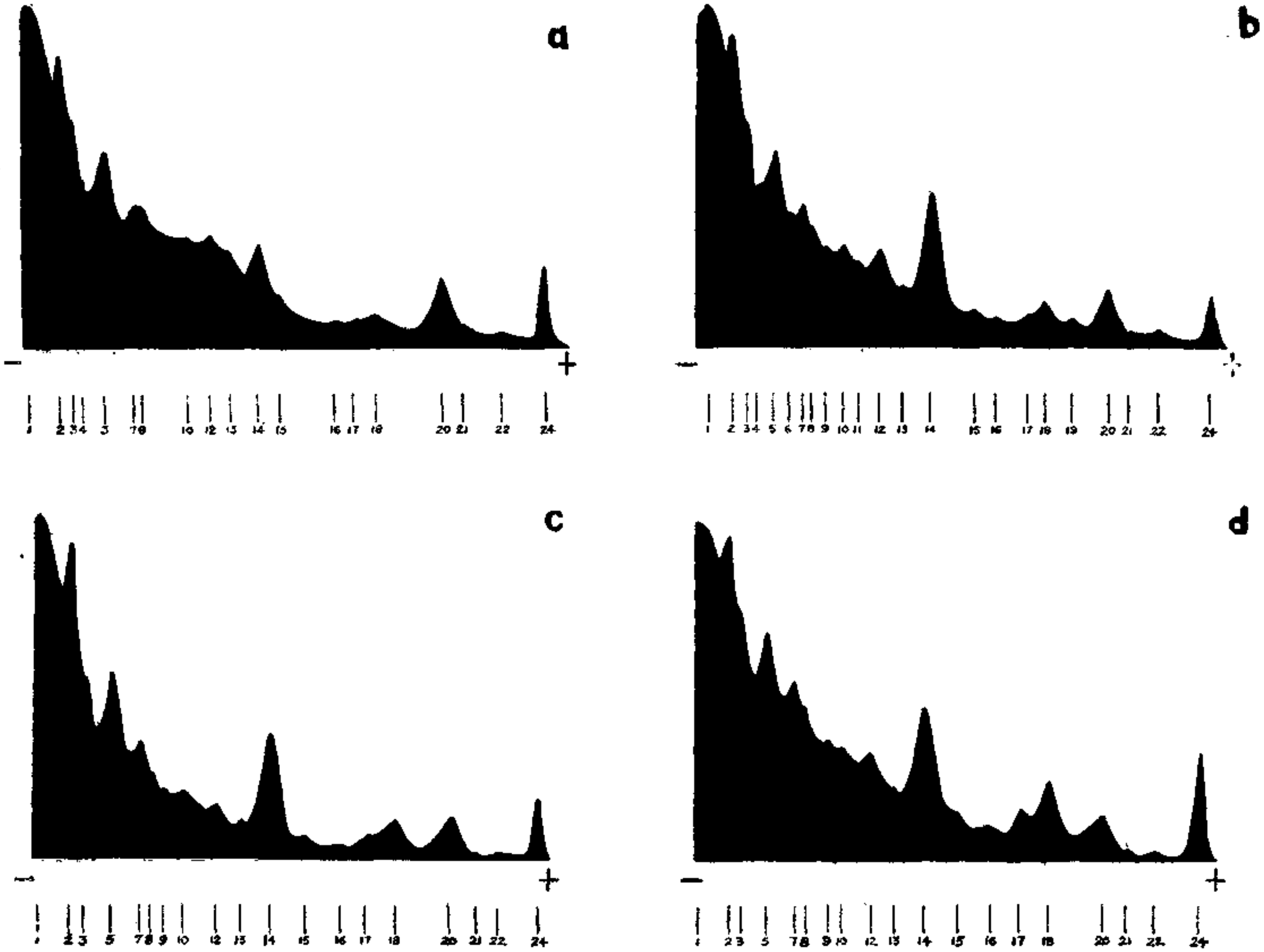


FIG. 9. Densitometric profiles for electrophoretically separated proteins of *Semisulcospira libertina* s.s. (*a*, *b*) and *S. trachea* (*c*, *d*). + = anode.

A total of 24 protein components was separated from extracts of *S. libertina* s.s. (Fig. 9 *a*, *b*). R_F values for these fractions are listed in Table VIII. Some fractions were not present in every run (*e.g.*, Nos. 3, 4, 6, etc.). These were generally faint or hazy when present. Fractions present in 100 per cent of the runs serve to define the taxon in terms of a specific densitometric profile.

TABLE VIII

Comparison of R_F values for fractions separated electrophoretically from extracts of Semisulcospira libertina *s.s. and* S. trachea

Band	*S. libertina*	12 % runs where present	*S. trachea*	9 % runs where present	SD
1	0·015	100	0·015	100	
2	0·067	100	0·072	100	
3	0·092	83	0·098	100	
4	0·110	92			
5*	0·144	100	0·148	100	
6	0·175	33			
7*	0·198	100	0·205	100	
8	0·215	100	0·225	67	
9	0·250	42	0·266	44	
10	0·285	100	0·298	89	
11	0·312	33			
12*	0·345	100	0·351	100	
13	0·391	100	0·403	100	
14*	0·448	100	0·465	100	SD
15	0·516	75	0·526	100	
16	0·578	92	0·592	100	
17	0·629	100	0·651	100	SD
18*	0·680	100	0·704	100	SD
19	0·725	67	0·776	44	SD
20*	0·794	100	0·813	100	SD
21	0·835	100	0·860	100	SD
22	0·890	92	0·913	100	SD
23	0·936	17			
24	1·000	100	1·000	100	

* = fractions of both taxa tested for significant difference (Table IX).

SD = Significant difference as R_F values differ by 0·017 or more; or were found different by *t* test (Table IX).

S. libertina s.s. is characterized by peaks 14, 18, 20, with 15 to 17 faint and variable in R_F; fraction 5, twin peaks 7, 8 and fraction 12. The drop in density between bands 2 and 5 is also characteristic.

The densitometric pattern for *S. trachea* was the same as that of *S. libertina* s.s. (Fig. 9, *c*, *d*). There were two groups of differences ; (1) fractions present in extract of *S. libertina* were missing in that of *S. trachea*, (2) differences in R_f values for some fractions contributing to the same densitometric profile seen for *S. libertina* s.s.

(1) *S. trachea* did not have fraction 4, 6, 11, and 23. The last three were not frequently encountered in *S. libertina* s.s. (Table VIII). Fraction 4 of *S. libertina* s.s. is very faint and does not contribute to the taxon-specific densitometric profile. Differences in this category are accordingly considered small in significance.

(2) Fractions marked SD (Table VIII) have R_f values significantly different than corresponding fractions of *S. libertina* s.s. The asterisk (column 1, Table VIII) marks key fractions for both taxa tested for significant difference (Table IX). Fractions other than key ones which had R_f differences of 0·017 or greater were considered significantly different (Davis and Lindsay, 1967).

TABLE IX

Pronounced fractions of the densitometric profiles of Semisulcospira libertina *s.s. and* S. trachea tested for significant *difference* (t *test*)

Taxon	Band No.	Statistic			P
		$\bar{X}$	S	Se	
S. libertina ..	5	·144	·009	·0026	·10
	7	·198	·011	·0032	·10
	12	·345	·008	·0023	·10
	14	·448	·015	·0043	SD ·01
	18	·680	·009	·0026	SD ·01
	20	·794	·015	·0043	SD ·01
S. trachea ..	5	·148	·006	·0020	
	7	·205	·008	·0027	
	12	·351	·009	·0030	
	14	·465	·010	·0033	
	18	·704	·009	·0030	
	20	·813	·009	·0030	

$\bar{X}$ = mean.
S = standard deviation.
Se = standard error of mean.
SD = *significant difference when fractions of the two taxa are compared.*

As previously found (Davis and Lindsay, 1967) fractions of two taxa yielding the same densitometric profile yet differing slightly in R_f value are indicative of population differences within the same species.

3. *Immunology*

When immunodiffusion tests were conducted with unabsorbed antisera using full strength antisera and extract (Pl. V, Fig. 10, A–D) all precipitin systems appeared homologous (no spurs or unique systems). With full strength antiserum and extract at 100 per cent (full strength) (Fig. 10, E, 1, 2) 50 per cent (3, 4) and 25 per cent (5, 6) only homologous reactions resulted. No systems appeared between A_1 and L (Fig. 10, F) in experiments with absorbed antisera.

A summary of immunoelectrophoretic tests is given inPl. VI, Fig. 11, *a–j*. Runs were stained for proteins after 45 min. (*a*), 60 min. (*b*) and 75 min. (*c*) thus showing the degree of migration from the wells of protein from the extracts of each taxon. Two types of immunoelectrophoretic patterns developed. Type 1 (Fig. 11, *g–j*; 12 A) resulted when antiserum from one rabbit was used, all other antisera yielded the Type 2 pattern (Fig. 11, *d–f*; 12 B, C). In all cases the precipitin patterns resulting from the use of Type 2 sera were the same for both taxa (Fig. 12, B, C).

Precipitin patterns with Type 1 antiserum appeared qualitatively similar, but possible quantitative differences were indicated. These can be more readily discussed by studying Fig. 12, A. When full strength extracts of both taxa were used (5·0 to 6·0 mg./ml. protein) system 1 for *S. libertina* s.s. was clearly observable; 4 and 5 crowded against the slot and were elongate as shown. Considering systems pertaining to *S. trachea*, 4 and 5 bent away from the slot (anodal end) tending to make system 1 obscure. Systems 4 and 5 were not elongate (comparatively). The greater distance of 4 and 5 from the slot made 7 appear more pronounced (*S. trachea*).

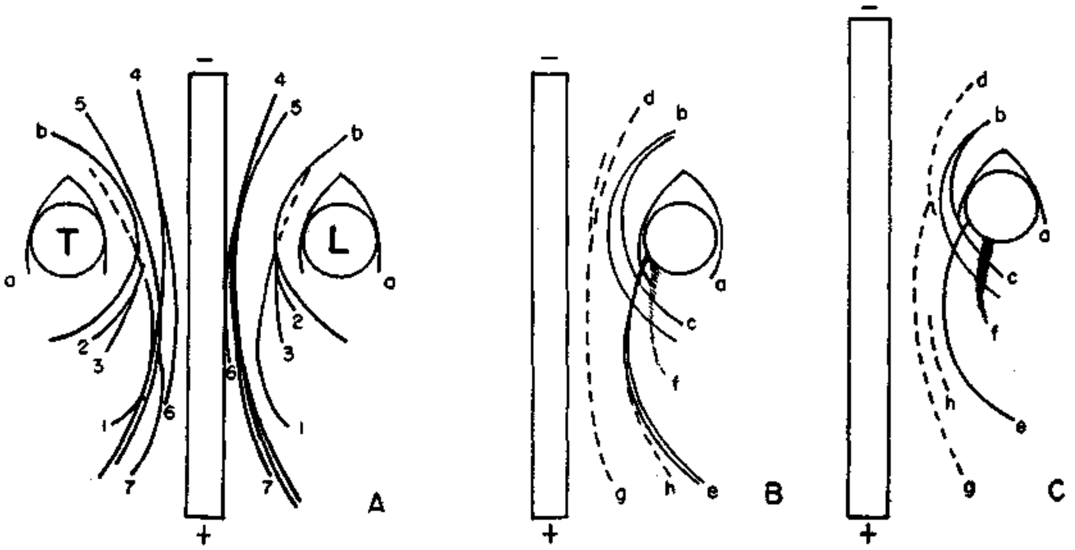


Fig. 12. Tracings of immunoelectrophoretic results with Type 1 antiserum (A) and Type 2 antisera (B, C). Patterns in B and C were the same using L or T extract. Systems *a* and *b* seemed clearly in common between Type 1 pattern (A) and Type 2 pattern (B, C). Differences seen in A are discussed in the text. L = extract of *Semisulcospira libertina* s.s., T = extract of *S. trachea*. + = anode.

When antigens were diluted with L (Fig. 11, *j*) 75 per cent concentration and T, 60 per cent, system 1 became more pronounced in *S. trachea*. With both extracts (L and T) at 25 per cent, system 1 was not observed for *S. libertina* s.s. but was very strong for *S. trachea*.

DISCUSSION

1. *The* libertina *Complex*

S. trachea clearly belongs to the *S. libertina* complex. The chromosome number is the same as that of *S. libertina* s.s., the adult shell has 9 ± 1 basal cords, there are numerous embryos per female. Westerlund (1883) considered the taxon to be a variety of *S. niponica*. However, *S. niponica* is a representative of the *niponica* complex which is characterized by (1) a chromosome number where $n = 7$ to 14 (*S. niponica*, $n = 12$), (2) adult shells with 3 ± 1 basal cords, (3) few young per female (mean of 5 to 25 depending on the taxon).

2. *Relationship of* S. trachea *to* S. libertina *s.s.*

A summary of shell differences between the taxa is given in Table X. Differences in color patterns on adult shells in the *libertina* complex are not reliable for assessing the degree of relationship between taxa. Patterns are highly variable between young and adult shells of the same population and between various populations of the same river drainage system. Banding patterns should not be used to justify specific or subspecific rank in the *libertina* complex.

TABLE X

Summary of differences between S. trachea *and* S. libertina *s.s.*

Feature Compared	*S. trachea*	*S. libertina*
Habitat		
1.	Lake Dwelling	River Dwelling
Adult Shell		
2. Ribs	Noded Ribs	Ribs Obsolete
3. Color Background	Purple or Yellow	Only Yellow
4. Banding Patterns	More diverse	Less Diverse
Embryo Shells		
5. Nodes	+	–
6. Spiral Cords (presence of 1 or 2 from 2·0 to 3·0 whorls)	100%	81%

The presence of ribs and rib nodulation on the adult shell coupled with nodes on embryo shells appears to yield characters more meaningful for comparison of taxa (also *see* Davis, 1967 *c*). These characters are more stable within a population than patterns of coloration. Only 3 per cent *S. libertina* s.s. had a trace of ribs. The question of environmental influence on rib presence or absence arises. Shells of *S. libertina* s.s. are more eroded than those of *S. trachea* (4–5 whorls remaining in adults of the former, 5–6 common in the latter). Ribs when observed on *S. libertina* s.s. appear eroded and pitted. However, it is noted that taxa with pronounced ribs in their post-embryonic ontogeny [*e.g.*, *S. trachea* this paper; *S. kurodai*; *S. niponica*, *S. reiniana*, etc. (Davis, 1967 *c*)], have embryos with distinct nodes or ribs. These nodes or ribs develop when the embryo shell is contained in the egg membrane within the pallial brood pouch, an environment considered the most stable the snail will experience and within which the most uniform growth processes will occur.

Ribs do appear in the early post-embryonic ontogeny of some *S. libertina* s.s. (Fig. 4, *c*) which indicates that genes governing this phenomenon *are* present at a low frequency in the population. However, embryos have not been observed from these few adult *S. libertina* s.s. which have ribs to verify presence of nodes on the embryo (the presence of ribs has only been discovered after the shells were cleaned of encrusting black deposits).

The two taxa are extremely similar in terms of color of embryonic shell, spiral cords being present, microsculpture, and growth patterns (size per whorl) in the female brood pouch.

The similarity of electrophoretic profiles implies close genetic alliance of the taxa. The few differences documented for *S. trachea* did not interrupt the taxon-specific densitometric pattern for *S. libertina* s.s. and were considered as population difference as discussed by Davis and Lindsay (1967). The antigen-antibody systems studied qualitatively were homologous thus tending to confirm the close genetic alliance of the taxa. However, several provisions must be made.

(1) Electrophoretic results involving taxon-specific densitometric profiles resulted from proteins not entering into the immunological reactions. Antigens separated in polyacrylamide electrophoresis did not migrate beyond the spacer gel or initial lower gel. This phenomenon was previously mentioned (Davis, 1967 *b*). Therefore different genetic systems were tested. The proteins yielding the taxon-specific densitometric patterns are not tested for homogeneity in the immunological tests.

(2) Homogeneity of the antigens tested was demonstrated using several antisera. However, the degree of antigen heterogeneity between distinct species (especially those with pronounced cytological differences) has yet to be demonstrated. I have noticed (unpublished data) that specificity of reactions is great when species of other families or genera are compared with *Semisulcospira*. Davis (1967 *b*), using the same techniques, found that three taxa defined as subspecies of *Oncomelania hupensis* (Hydrobiidae) did not have one or more antigen-antibody system present in the homologous reactions with foot muscle extract from *O. h. formosana*. This heterogeneity was present at a level defined as infraspecific. It is expected, but must be proved, that distinct species of *Semisulcospira* will have unique antigens and some of partial identity with antigens of *S. libertina* s.s.

3. *Conclusion*

Semisulcospira trachea has accumulated a few characteristics which superficially seem to separate this taxon from *S. libertina* s.s. However, upon close examination of numerous characters which represent a large number of genetic systems it is evident that *S. trachea* is a variant population of *S. libertina*, a race which cannot be considered distinct enough to be ranked as a subspecies. I consider *S. trachea* to be a synonym of *S. libertina*. The population in Ashino Lake serves to demonstrate some of the variability of the species *S. libertina*.

SUMMARY

Topotypes of the lacustrine snail *Semisulcospira trachea* were compared with topotypes of the river snail *Semisulcospira libertina*.

There were no significant differences between the taxa when numbers of embryos per pallial brood chamber were compared. The dimensions of embryo shell length, width and length of body whorl per whorl stage were similar.

Embryos of *S. trachea* had prominent nodes which were lacking in *S. libertina*. Adult *S. trachea* had pronounced nodulate ribs lacking on the shells of *S. libertina*.

Polyacrylamide electrophoresis of foot-muscle extract stained for protein yielded similar densitometric profiles for the 24 components separated. *S. trachea* had 8 fractions with higher R_f values than the corresponding fractions of *S. libertina* indicating the type of population difference discussed by Davis and Lindsay (1967).

Immunological studies using micro-Ouchterlony double diffusion tests with absorbed antiserum as well as immunoelectrophoretic experiments showed no qualitative differences between the taxa.

As a result of this investigation *S. trachea* is considered a synonym of *S. libertina* where a few accumulated genetic differences are not sufficient enough to even justify subspecific status.

ACKNOWLEDGEMENTS

I am extremely grateful for the assistance of Mr. Shohei Yamaguchi, Mrs. Setsuko Suzuki, and Mr. Tsuguo Takada who worked on various aspects of electrophoresis and immunology. Photo-

graphs of the shells were taken by Captain R. J. Garcia and the staff of the 628th Medical Illustration Detachment at the 406th Medical Laboratory.

LITERATURE CITED

BORT, A. 1874. Die Melaniaceen (Melanidae) in Abbildungen nach der Natur mit Beschreibungen, in: *Systematisches Conchylien—Cabinet* von Martini und Chemnitz, Bauer and Raspe, Nurnberg, pp. 1–488, 49 pl.

BURCH, J. B. AND G. M. DAVIS 1967. A taxonomic study of some species of the freshwater snail genus *Semisulcospira* in Japan (Gastropoda: Mesogastropoda: Pleuroceridae. *Amer. malacol. Union ann. Reps.* **34**: 36–38.

CROWLE, A. J. 1961. *Immunodiffusion*, Academic Press, N.Y., i–ix, 1–333.

DAVIS, G. M. 1967 *a*. The systematic relationship of *Pomatiopsis lapidaria* and *Oncomelania hupensis formosana*. *Malacologia*, **6** (1–2): 1–143.

——— 1967 *b*. A systematic study of *Oncomelania hupensis chiui*. (Gastropoda: Hydrobiidae). *Ibid.* (in press).

——— 1967 c. A taxonomic study of some species of *Semisulcospira* in Japan (Mesogastropoda: Pleuroceridae). (MS).

——— AND G. K. LINDSAY 1964. Disc electrophoresis in the study of molluscan systematics. *Ann. Rept. Amer. Malacol. Union*, **31**: 20–21.

——— 1967. Disc electrophoretic analysis of molluscan individuals and populations. *Malacologia*, **5** (2): 311–334.

HABE, T. 1965. Gastropoda, in the *New Illustrated Encyclopedia of the Fauna of Japan.* Hokuryu-Kan Pub. Co., Ltd., Tokyo, Japan, pp. 14–208.

KABAT, E. A. AND M. M. MAYER 1961. *Experimental Immuno-chemistry*, C. C. Thomas, 2nd ed., Springfield, Ill., i–xii, 1–905.

KAJIYAMA, A. AND T. HABE 1961. Two new forms of Japanese melanians, *Semisulcospira. Venus, Jap. J. Malacology,* **21** (2): 167–176.

KOBELT, W. 1879. *Fauna Molluscorum Extramarinorum Japoniae,* Christian Winter, Faukfurt am Main, pp. 1–171, 23 pl.

KURODA, T. 1929. On the species of Japanese Kawanina. *Venus, Jap. J. Malacology,* **1** (5): 179–193, pls. 4, 5 (in Jap.).

——— 1963. *A Catalogue of the Non-marine Mollusks of Japon, Including the Okinawa and Ogasawara Islands.* Malacological Soc. Japan, Tokyo, pp. i–v, 6–71.

MCKAY, G. G. 1967. Practical application of immunoelectrophoresis. *Lab. Synopsis,* **2**: 1–8. Hoechst Pharm., Inc., Kansas City, Missouri.

MICHELSON, E. H. 1966 *a*. Specificity of hemolymph antigens in taxonomic discrimination of medically important snails. *J. Parasit.,* **52** (3): 466–472.

——— 1966 *b*. Characterization of the haemolymph antigens of *Australorbis glabratus* by disc electrophoresis and immuno-electrophoresis. *Ann. Trop. Med. and Parasit.,* **60** (3): 280–287.

MONTGOMERY, R. 1957. Determination of Glycogen. *Archiv. Biochem. Biophys,* **67**: 378–386.

MORRILL, J. B., E. NORRIS AND S. D. SMITH 1964. Electro- and immunoelectrophoretic patterns of egg albumen of the pond snail *Limnaea palustris. Acta Embry. Morph. Exp.,* **7**: 155–166.

OUCHTERLONY, O. 1958. Diffusion-in-gel methods for immunological analysis. *Prog. in Allergy,* **5**: 1–78.

PATTERSON, C. M. 1967. Chromosome numbers of some Japanese freshwater snails. *Venus, Jap. J. Malacology,* **25** (2): 69–71.

SCHWICK, G. AND K. STORIKO 1965. Qualitative and quantitative determination of plasma proteins by immunoprecipitation. *Lab. Synopsis,* **1**: 1–69. Hoechst Pharm., Inc., Cincinnati, Ohio.

VON MARTENS, E. 1860. Die Japanesischen Binnenschnecken im Leidner Museum. *Malak. Blatter,* **7**: 32–61.

——— 1877. *Sitzungs — Bericht der Gesellschaft naturforschender Freunde zu* Berlin. pp. 114–116.

WESTERLUND, C. A. 1883. Von Der Vega—Expedition in Asien gesammelte Binnenmollusken. *Nachrichtsblett der Deut. Malak. Ges.,* **15**: 48–64.

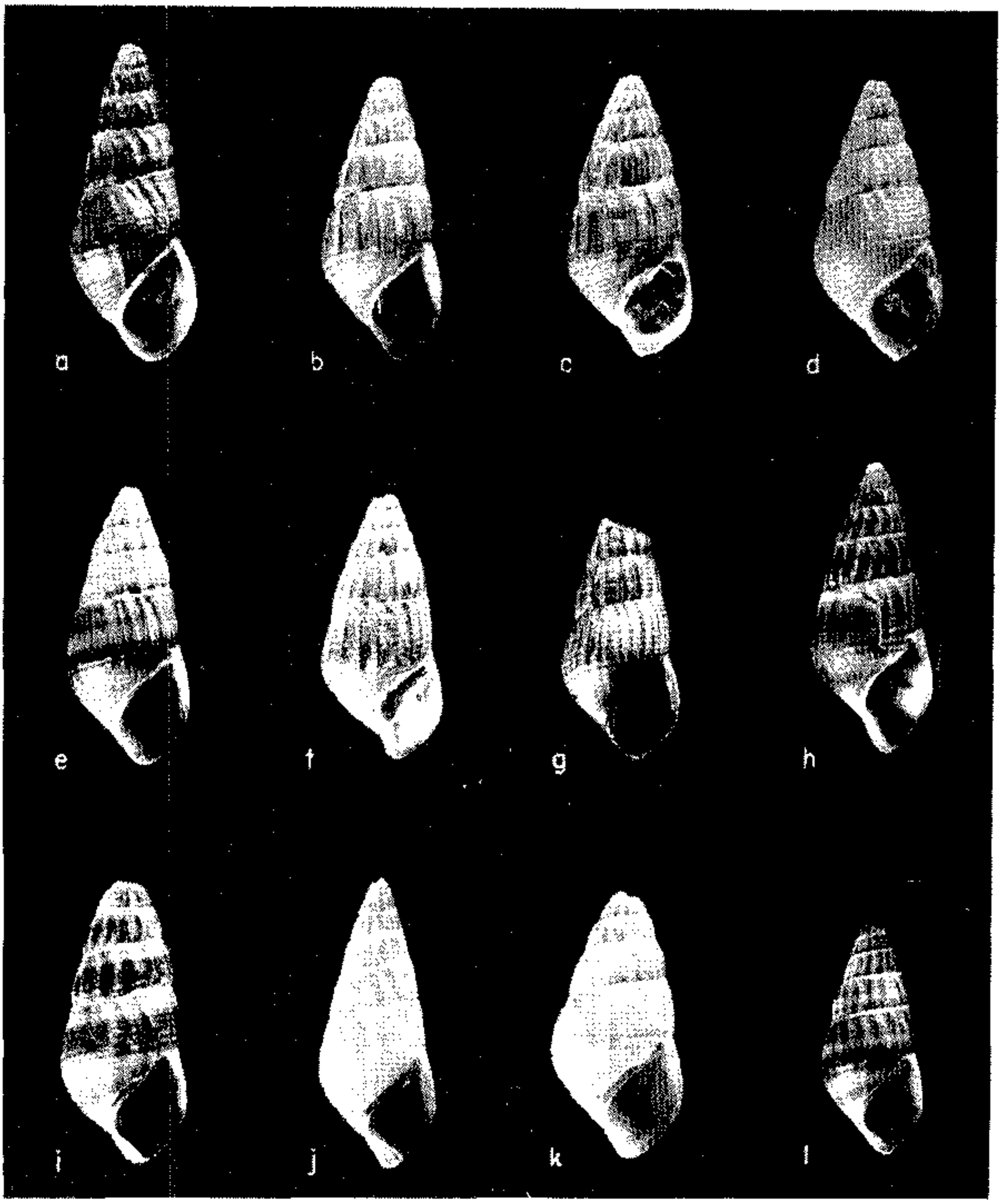


Fig. 3. Shells from the largest 10 per cent of the population of *S. trachea*. Shell a is 37 mm. long. Shells *e*, *g-l* were cleaned in Clorox. Note the wide range of variation in shell shape, color patterns, sculpture.

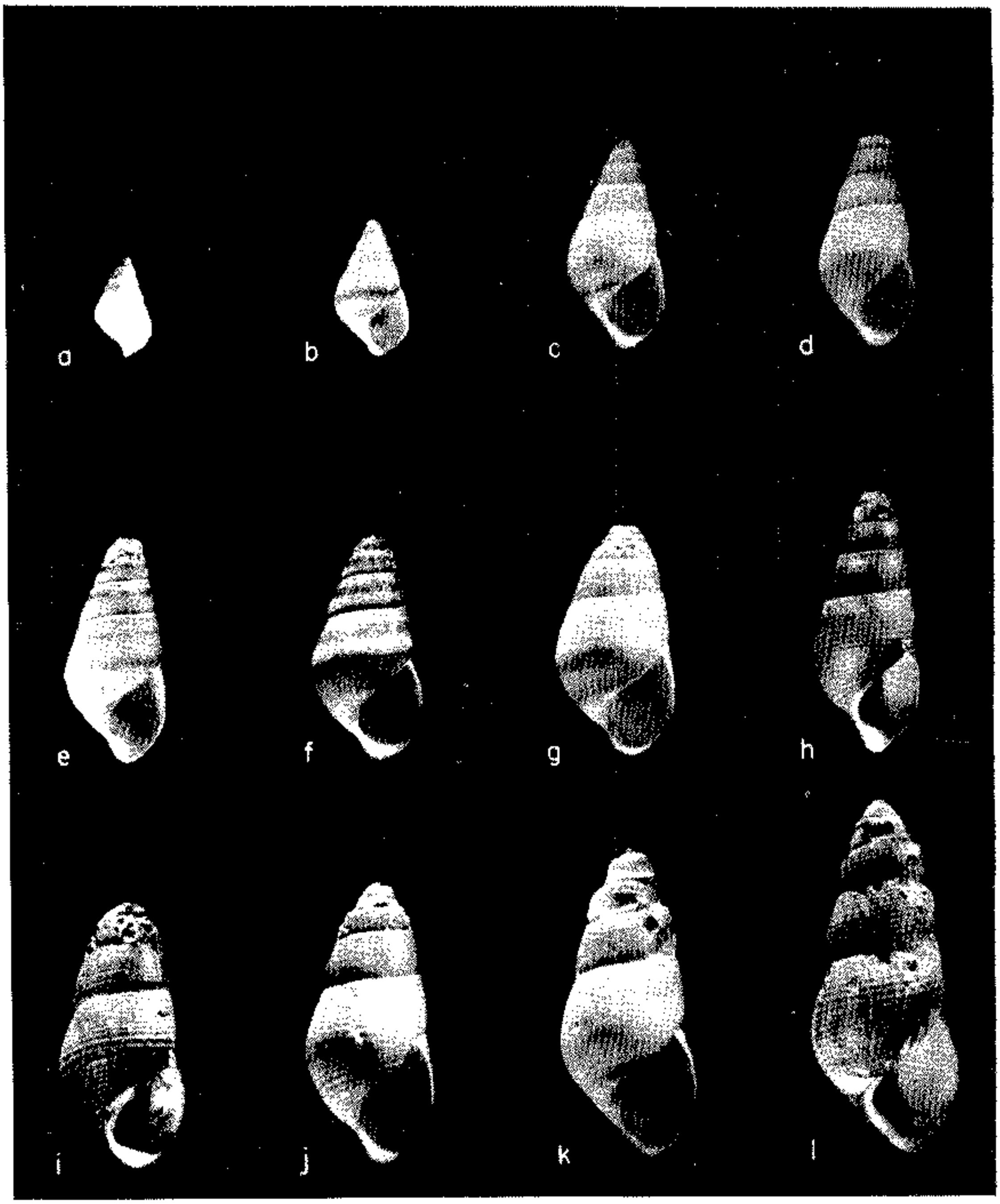


FIG. 4. Topotype *S. libertina* showing a size gradient in shells. Shell l is 39 mm. long. Note the variation in shape and strength of spiral cords.

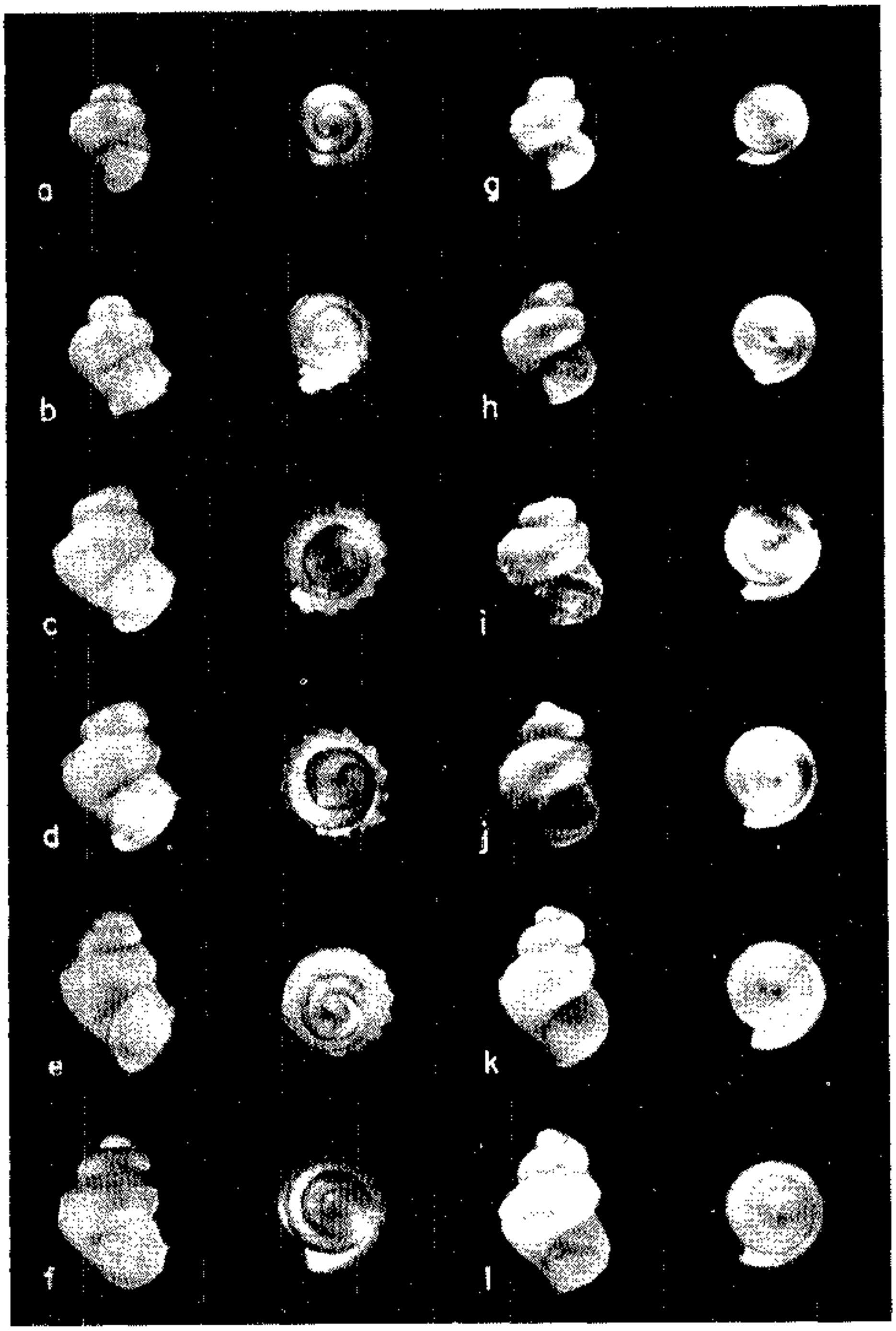


Fig. 5. A comparison of embryo shells of *Semisulcospira trachea* (*a–f*) and *S. libertina* s.s. (*g–l*). Apertural and apical views are shown.

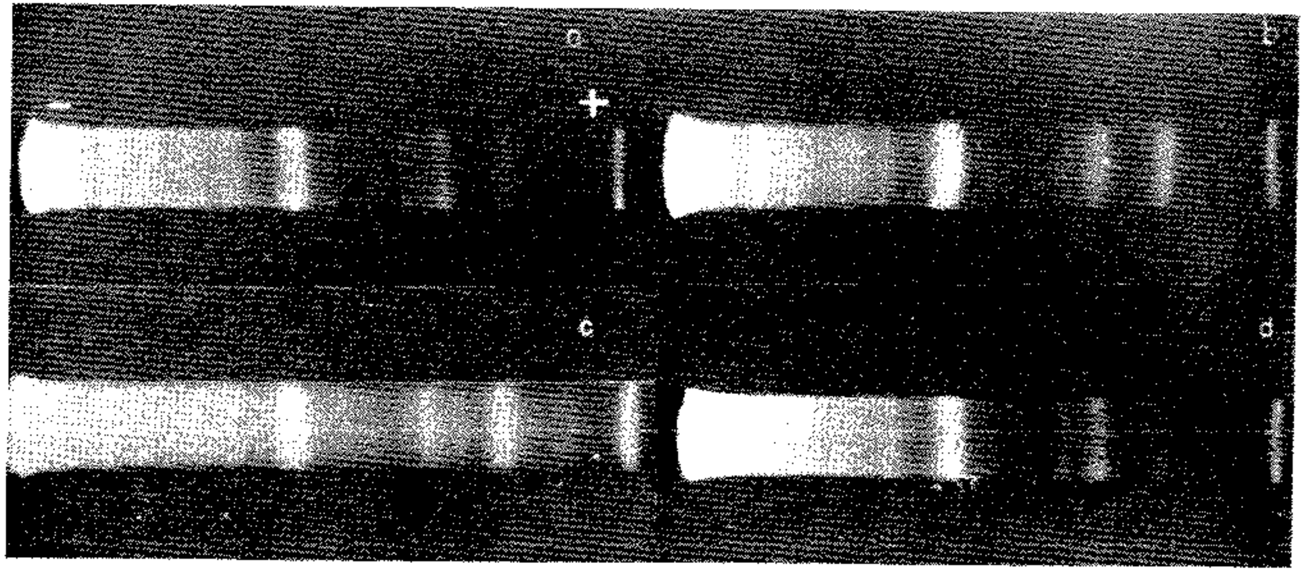


FIG. 8. Prints of gels showing protein fractions isolated from foot muscle extract of *Semisulcospira libertina* s.s. (*a, b*) and *S. trachea* (*c, d*). + anode.

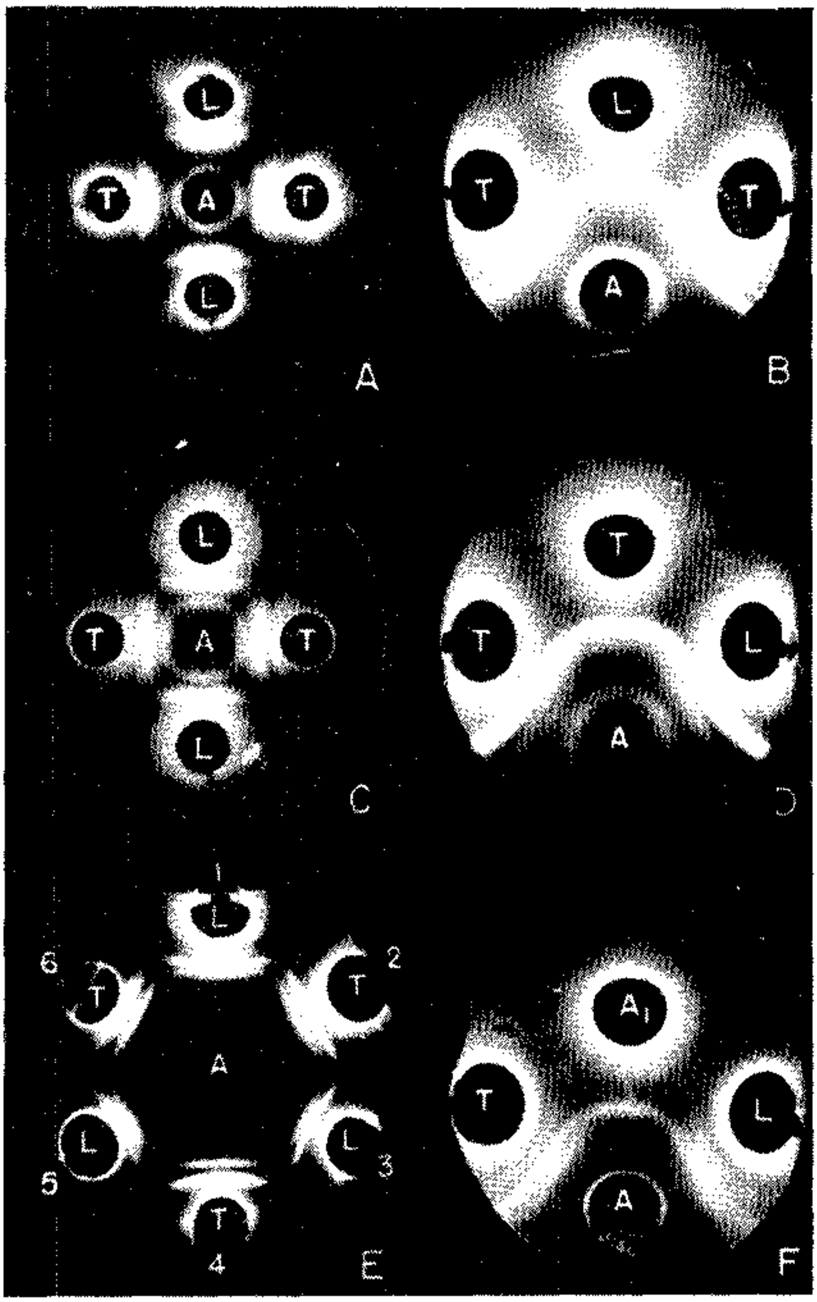


FIG. 10. Examples of results with micro-Ouchterlony gel diffusion tests. A = antiserum, L = extract of *S. libertina* s.s., T = extract of *S. trachea*. Gels A–D involved unabsorbed antisera full strength and extracts full strength (5·0 to 6·0 mg/ml). Extracts were diluted in gel E; 1–2 (100%), 3–4 (50%), 5–6 (25%). A test with absorbed antiserum (A_1) is shown in gel F.

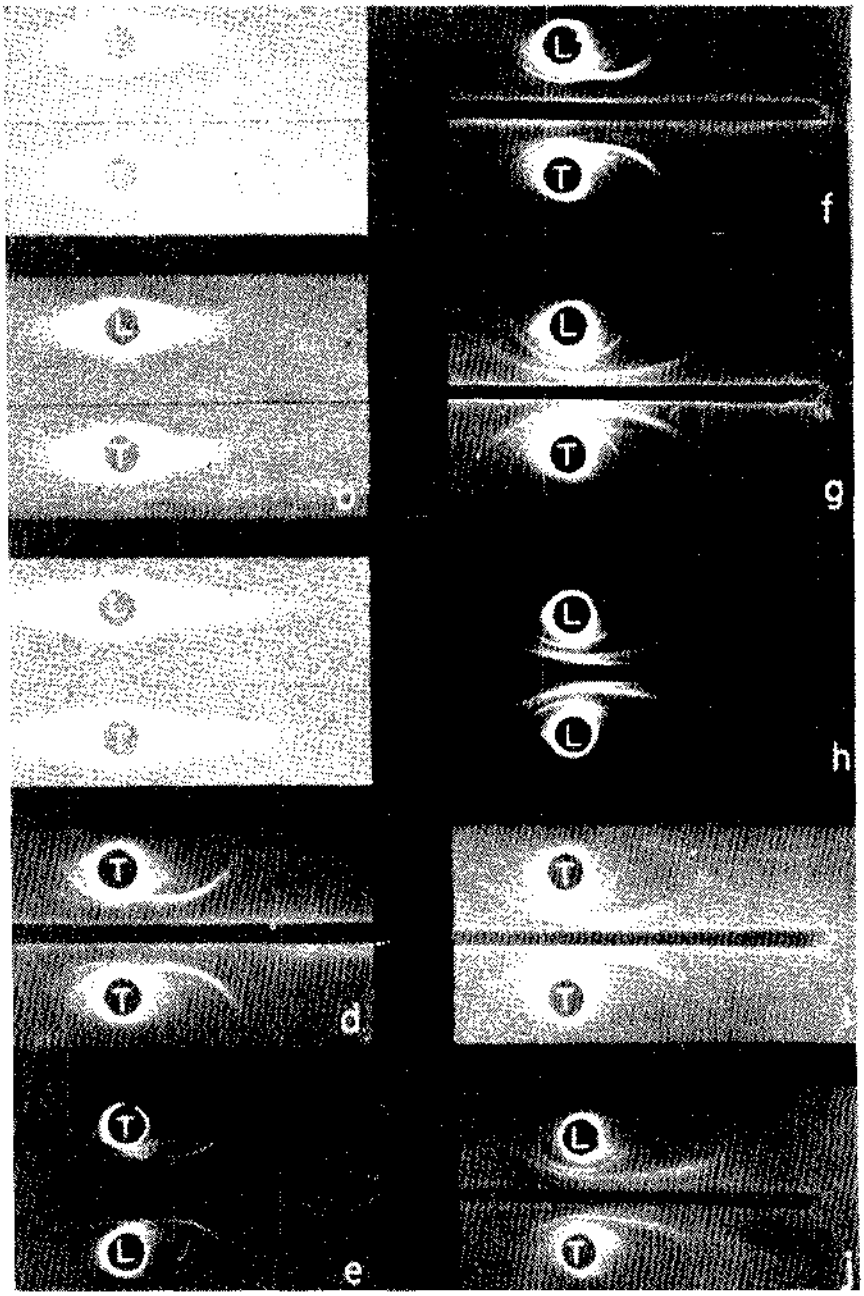


FIG. 11. Examples of results with immunoelectrophoretic tests. Slides *a*–*c* were stained for proteins; the runs were terminated at 45 min. (*a*), 60 min. (*b*), 75 min. (*c*). Slides *d*–*f* involved Type 2 antisera (see text); *g*–*j* involved Type 1. In *j*, L (extract from *S. libertina*) was 75% concentration, T was 66%.

WRIGHT, C. A. AND J. KLEIN 1967. Serological studies on the taxonomy of planorbid snails. *J. Zool., Lond.*, **151**: 489–495.

YOKOGAWA, M. 1964. *Paragonimus* and paragonimiasis, in *Progress of Medical Parasitology*, **1**: 61–156. Meguro Parasitological Museum, Tokyo.

YOKOGAWA, S., W. W. CORT AND M. YOKOGAWA 1960. *Paragonimus* and Paragonimiasis. *Exper. Parasit.*, **10** (1): 81–137.

DISCUSSION

Dr. A. J. Kohn: Have you determined whether the two taxa can interbreed?

Dr. G. M. Davis: Experiments are in progress where I hope to interbreed *S. libertina* and so-called *S. trachea*. These snails, liberated from the female brood pouch at 3 whorls, grow very slowly and I do not have, at this time, sufficient sexually mature individuals, grown in isolation, to attempt carrying on experiments.

Dr. M. Anantaraman: Would the two taxa be equally susceptible to infection with the same species of trematodes?

Dr. G. M. Davis: I would predict that the two taxa under discussion could be infected with the same species of trematodes if given the opportunity.

CHECK-LIST OF RECENTLY COLLECTED CYPRAEIDAE FROM CEYLON WATERS

RODNEY JONKLAAS

No. 18, Tudella-Kurunduwatte, Ja-Ela, Ceylon

ABSTRACT

It is of regret that there have been no recent papers or publications on the Cypraeidae of Ceylon, a Family which is perhaps the most popular of all marine Gastropoda to both collectors and scientists alike. The author attempts to present as comprehensive and accurate a Check-list of all Cypraeidae collected by him and fellow-workers in Ceylon during the past 10 years without additions from older works.

Precise location data giving time, place, depth, and date of each live specimen collected form part of the paper.

It has been observed that many former workers have obtained shells from local inhabitants of the coastal area and took it for granted that these had been found alive in Ceylon waters but recent observations have revealed that many of these were of Maldivian origin brought here by traders.

Wherever possible information on mantle colouration and sex is given and also any peculiarities regarding distribution.

More than 40 species are listed and described.

INTRODUCTION

The steadily increasing interest in conchology coupled with the growth and popularity of skin-diving has resulted in a greater accumulation of accurate locality data than ever before for the marine Mollusca. Of these, the most popular and sought-after Family is that of the Cypraeidae and in recent years both malacologists and conchologists have been able to record hitherto unknown data, a fair amount of which is incorporated in this paper.

Earlier workers were obviously not equipped and trained to dive as in modern times and in several cases it is suspected that specimens of cypraeid shells obtained in Ceylon and presumed collected in these territorial waters might well have originally come from elsewhere, most probably the Maldive Islands, and India.

In Colonial times there was considerable trade in cowries and literally tons of them, comprising in the main *Monetaria moneta moneta* Linné and *Cypraea tigris* Linné. These came into local circulation in Ceylon and as a result were often supposed to have been collected in Ceylon waters. In more recent times (1958) the writer was given specimens of *Ornamentaria annulus annulus* Linné in Galle, Ceylon, which had been washed up on the beach in the harbour. Subsequent investigation revealed that sacks of Maldivian cowries unloaded from a schooner on to a local craft had fallen into the sea and burst and the contents had then been washed ashore in choppy weather.

Since 1960, several skilled divers and workers have hunted for marine Gastropoda in many places along Ceylon's coastline and certainly more expertly than ever before. At no time were specimens of *Palmadusta ziczac undata* Lamarck or *Gratiadusta pyriformis pyriformis* Gray found dead or alive, yet these are recorded from Ceylon in earlier works. Only one good specimen of *Mystaponda nivosa* Broderip has been seen by the writer. The owner states that it was live-collected in "South Ceylon", but is unwilling to supply more accurate data presumably because of the extreme rarity and value of the shell. Although this is included in the Check-list, from the writer's point of view it is classified as "doubtful".

P. ziczac undata Lamarck was collected alive in the Maldive Islands by the writer in 1961 where it is fairly plentiful, but by no means common. *G. pyriformis pyriformis* Gray has not been seen or found in India or Ceylon or the Maldive Islands by the writer. The closest authentic source of this cypraeid is Singapore.

Therefore, only live-collected shells of Cypraeidae within Ceylon territorial waters are listed here and of these all but three have actually been taken alive by the writer using skin-diving techniques. The three which have not been seen alive were collected by reliable workers who have the shells in their own collections and who loaned them to the writer for purposes of identification.

In most cases the most typical habitat is given which would enable the average worker using basic skin-diving gear to collect specimens without unnecessary waste of time. Very rare species are, of course, found with a fair margin of luck. The areas most systematically hunted are indicated in a sketch map and in the text. It is quite obvious that the greater part of Ceylon's coastline remains virtually untouched and unexplored for Cypraeas and that this paper is more of a guide than a comprehensive report.

THE HABITAT OF CYPRAEIDAE IN CEYLON

Although earlier workers took it for granted that Cypraeas are found in coral reefs, this is not strictly correct. The Cypraeas of Ceylon are found in 6 main habitats, *viz.*,

1. Shallow coral reefs up to 2 fathoms.
2. Deeper coral reefs up to 6 fathoms.
3. Shallow rock or sandstone reefs up to 2 fathoms.
4. Deeper rock on sandstone reefs up to 10 fathoms.
5. Sheltered coastal water and harbours up to 10 fathoms.
6. In association with gorgonids and alcyonarians.

All Cypraeidae appear to be nocturnal in habit and prefer to remain in shady areas under rocks or coral and protected by their mantles by day. It has been observed that by late evening many species, for example, *C. tigris* Linné, retract their mantles and come out into the open presumably to feed.

Most collectors operate by day and after some practice are able to locate most of the commoner Cypraeidae infallibly. By night, using water-proof flashlights, Cypraeas are often found in the open but the smaller species are not so easily detected as by day where they live under rocks or corals.

The relatively small difference between high and low tides in Ceylon is not so important a factor in locating living Cypraeidae as in countries with much greater tide intervals, *viz.*, Singapore and Bombay, where many Cypraeas are often left almost out of the water at low tide.

Dredging is done only occasionally in Ceylon and only by the Department of Fisheries. Only one species has been collected in large quantities by this method which was utilised in 1959 for the Survey of the Pearl Oyster Beds in Mannar.

CHECK-LIST OF CYPRAEIDAE COLLECTED IN CEYLON AFTER 1958

1. *Pustularia globulus brevirostris* Schilder and Schilder, 1938

This Cypraea was discovered in fair numbers only recently and up-to-date the only infallible location is Pigeon Island, about a mile out at sea off Nilaveli, North-East Ceylon, where it is washed up in great numbers on the beach. The only other location is off Galle, where only beach-worn specimens are found.

Live *P. globulus brevirostris* are extremely difficult to find as they live in between the branches of living corals which must be broken off, washed in a bucket and the washings carefully examined for specimens. It does not appear to live in water deeper than 2 fathoms.

2. *Purperosa limacina limacina* Lamarck, 1810

This is a scarce shell so far located only off Trincomalee under rocks in water 3–5 fathoms deep. The few specimens in collections were all taken after 1966 and less than 25 have so far been collected since 1958.

3. *Nuclearia nucleus sturangi* Schilder and Schilder, 1939

This Cypraea is almost as uncommon in Ceylon as the former and only after 1966 has it been taken in small numbers in the same area.

4. *Staphylaea staphylaea laevigata* Dautzenberg, 1932

This is fairly common off Trincomalee in the same habitat as the former, if not shallower and has also been collected off Colombo reef and in Tangalle in deeper water up to 6 fathoms. The shell of the Ceylonese race of *Staphylaea staphylaea laevigata* Dautzenberg is very dark purplish-gray in colour.

5. *Talparia talpa imperialis* Schilder and Schilder, 1939

This is an uncommon but fairly widespread Cypraea which has been live-collected in Trincomalee, Colombo, Hikkaduwa, Kalkudah, and off Pigeon Island in Nilaveli. It is usually found in pairs and under coral boulders on rocks up to a depth of 6 fathoms.

6. *Basilitrona isabella rumphii* Schilder and Schilder, 1939

This occurs in limited numbers in almost the same habitat as the former and the Ceylonese variety is exceptionally well marked, unlike shells from the Maldive Islands. Most of the *B. isabella rumphii* collected have been from Trincomalee but this is no indication that it is commonest in this area since skin-diving activity (mainly for live tropical fishes) is concentrated in Trincomalee from April till October and collectors have access to locations here more than anywhere else in Ceylon.

7. *Arestorides argus argus* Linné, 1758

As is to be expected this is widespread but uncommon in Ceylon and finding live specimens depends to a great extent on luck. Specimens have been collected in Negombo, Colombo, Hikkaduwa, Kalkudah, Trincomalee, and Pigeon Island, Nilaveli, but nowhere is it so numerous as to be found in a few hours with certainty. The number of dead shells washed ashore at Pigeon Island and Kalkudah beach suggest that it is plentiful in these spots and it is possible that the dense coral growths here prevent collectors from locating more live specimens than they have. This Cypraea lives under flat coral boulders in water from 3 to 6 fathoms deep and seems to prefer dead to living coral. It is also found most often in pairs.

8. *Erronea errones errones* Linné, 1758

So far the only location data for this species comes from in and around Trincomalee where it is abundant. However, it would appear that it occurs also in good numbers in the North, off Jaffna and adjacent islands where conditions are similar. Very large numbers are collected off Rameswaram Island in South India. This species prefers sheltered shallow water of harbours where there is often a drop in salinity caused by excessive rainfall. It occurs to a depth of 4 fathoms but is commonest at one fathom under rocks.

9. *Ovatipsa coloba coloba* Melvill, 1888

This is an uncommon species which has been taken in very limited numbers off Trincomalee, Colombo, Galle, and Tangalle. In 1967 the writer discovered a certain location for them in water 6-8 fathoms deep off Tangalle where several were collected from under rocks and corals off rocky islets in the open sea. The mantle is a delicate shade of coral pink.

10. *Ovatipsa caurica dracaena* Born, 1778

A very plentiful species, found most abundantly off Trincomalee in water from 2-5 fathoms deep under rocks and coral. Other locations are Colombo, Galle, and Tangalle. Off Tangalle the specimens are found in deeper water and are less numerous than at Trincomalee but larger in size.

11. *Talostolida teres subfasciata* Link, 1807

This species was found only in very recent years, but in 1967 the writer discovered a very reliable location for them off Tangalle in precisely the same area as that recorded for *C. coloba coloba*. *T. teres subfasciata* has a pinkish mantle and is thus readily distinguished from *O. caurica dracaena* which has a gray speckled one. The shells of these two species have some superficial resemblance especially in the younger post-bulla stages.

12. *Bistolida stolida enthracensis* Sowerby, 1870

Although Ceylon is given as the type locality for this species it is by no means common. Less than 30 live specimens have been collected in recent years in such widespread locations as Trincomalee, Colombo, Mount Lavina (South Colombo), and Kudawella (close to Tangalle). It lives under rocks and corals up to a depth of 6 fathoms and most specimens taken were at 3 fathoms or so off Trincomalee.

13. *Adusta onyx adusta* Lamarck, 1880

This is one of the scarcer species so far but may be fairly abundant off Jaffna and adjacent islands in the North where the habitat closely resembles the extreme South of India. The few specimens taken by the writer some years ago came from Trincomalee harbour where they were found on the hull of a sunken launch and on wooden stakes erected for fish-traps. This indicates that it probably feeds on an alga living on water-logged wood. In Singapore, an allied subspecies occurs in good numbers on the wooden stakes of "kelongs" or fish-traps. Fair numbers of the Ceylonese/Indian type are offered for sale at Rameswaram and it is stated that they are collected by divers from close by and off Dhanushkodi. The mantle is black and the shell very dark brown with two faint transverse bands.

14. *Palmadusta clandestina clandestina* Linné, 1767

This species is fairly uncommon and seems to have diminished in numbers in recent years probably through over-collecting. The typical location is off Trincomalee where the writer collected several in 1–2 fathoms under rocks in Back Bay near Fort Frederick. It has also been found in small numbers on Colombo reef and in Tangalle in deeper water up to 7 fathoms.

15. *Cribraria cribraria comma* Ferry, 1811

The greatest numbers of this species are collected off Colombo reef where there is considerable collecting activity by divers from November till April. It is also found off Trincomalee, Galle, and Tangalle in water up to 4 fathoms deep. The mantle is a brilliant vermilion-red and shells of Ceylonese specimens are unusually richly marked and dark coloured. This species lives under rocks but has often been taken sheltering under small sandstone ledges in the company of sea-urchins.

16. *Paulonaria fimbriata fimbriata* Gmelin, 1791

This species has been collected in Trincomalee and off Colombo in similar locations to *Cribraria cribraria* Linné, *viz*., under rocks in shallow water from 1–3 fathoms. Not over-plentiful, probably due to the small size of shell, it escapes detection from most but the very discriminating diver-collector. It is most probably found in many other similar locations round Ceylon not as carefully exploited and worked over as Trincomalee and Colombo.

17. *Paulonaria gracilis notata* Gill, 1858

This is most commonly found off Trincomalee but is also to be met with off Colombo and Tangalle.

18. *Evenaria asellus asellus* Linné, 1758

An extremely uncommon species for Ceylon with only a few specimens collected off Colombo and one in Tangalle by the writer. It is abundant in the Maldive Islands and probably requires almost pure coral reefs to live in, uncontaminated by lagoons, rivers, and human influence.

19. *Evenaria punctata punctata* Linné, 1758

This species is almost as rare as the former in Ceylon and very few specimens, probably less than 20 in all, have been taken in recent years. The greatest number have come from Trincomalee from under rocks in water 2–4 fathoms deep and others have been live-collected off Colombo, Tangalle, and Galle.

20. *Evenaria hirundo hirundo* Linné, 1758

Fairly common and widespread and washed ashore in great numbers off Hikkaduwa and Galle, this species is live-collected in Trincomalee, Colombo, Galle, and Tangalle in fair numbers. It always occurs under rocks and corals.

21. *Melicerona felina listeri* Gray, 1824

This species occurs in the same location as the former and is more abundant especially off Trincomalee, Colombo.

22. *Mauritia mauritiana mauritiana* Linné, 1758

This species appears to be getting scarcer probably due to over-collecting. Formerly found in great abundance from Negombo down to Hambantota, it is now very seldom collected. In 1962 several dozens were obtained by the writer from a fisherman who dived for them in shallow sandstone and rock reefs off Beruwala. A good many were taken under ledges and in crevices off Fort Frederick, Trincomalee. Good specimens are taken off Pallikuda (Tangalle) almost at tide-level on sheltered rocks. Its preference for extremely shallow water and its large size make it readily accessible to all, not only divers. The writer has collected them in Negombo, Colombo (especially round the harbour), Mount Lavinia, Beruwala, Ambalangoda, Galle, Ahangama, Tangalle, the Great Basses, and Trincomalee.

23. *Arabica arabica asiatica* Schilder and Schilder, 1939

Emphatically the commonest and most widespread of the larger Ceylon Cypraeidae, this species occurs in considerable concentrations off Trincomalee, Nilaveli, Kalkudah, Negombo, the Arippu Reef, Talaimannar, Colombo and right down to Hambantota wherever there are rocks and reefs. It lives in water from 1 to 10 fathoms deep and beach specimens washed ashore indicate that it is found right round Ceylon wherever there are rocks and reefs except in very close proximity to river mouths.

Probably the greatest concentration of them is in Trincomalee Harbour amongst the rocks and boulders dumped into the sea around piers and jetties and by night, as many as a hundred can be collected alive by a diver in less than 5 minutes.

This species has an affinity for sheltering in sunken ships and launches and after some months in such places the shell takes on a reddish tinge from the rusty iron.

24. *Arabica histrio* Gmelin, 1791

This is a very uncommon species for Ceylon, but is very abundant in the Maldive Islands. The few Ceylon specimens taken were from off Tangalle and the Great Basses reef in water 5–6 fathoms deep under rocks.

25. *Arabica scurra argiolus* Bolton, 1799

The only two specimens positively collected alive off Ceylon are in the collection of Dr. G. H. P. de Bruin of the Government Fisheries Corporation who informs the writer that they were taken in a dredge off the Pearl Banks of Mannar when surveying for pearl-oysters, in 1963.

Dead specimens have been taken on the beach off Pigeon Island, Nilaveli, and it is possible that live ones will soon be taken from there by skilled divers.

26. *Arabica depressa dispersa* Schilder and Schilder, 1939

The only authentic live-collected specimens of this species is in the collection of Mr. Cedric Martenstyn of Colombo who informs the writer that a diver friend of his collected it alive in Trincomalee in July, 1967, in 3 fathoms of water under a rock in Dutch Bay.

Many specimens come from the Maldive Islands mixed up with *R. caputserpentis caputserpentis* which it superficially resembles in size and colouration of shell.

27. *Erosaria erosa phagedaina* Kelwill, 1888

This is a fairly widespread and common species but is not abundant. It occurs all over Ceylon and has been collected in Trincomalee, Negombo, Colombo, Beruwala, Ambalangoda, Galle, Dodanduwa, Tangalle, and Dickwella. It lives under rocks and corals in from 3 to 8 fathoms.

28. *Erosaria ocellata* Linné, 1758

This is one of the commonest of Ceylonese Cypraea and is found right around Ceylon in coastal waters from 1 to 10 fathoms deep in reefs and even amongst sedentary bivalve Mollusca

(Pinna). Specimens have been collected from Jaffna, Nilaveli, Trincomalee, Kalkudah, Arugam Bay, the Great Basses, Hambantota and in fact almost everywhere where shell-collecting has been done.

It is particularly abundant in the Pearl Banks where during dredging operations for pearl-oysters in 1957 and 1958, hundreds were collected with dead and living Pinna shells. The writer was able to purchase by the pound, a pure culture of *E. ocellata* shells from one dealer who had at least one full gunnybag of them.

From this location, the species seems to have two distinct varieties judging from the colour of the shells. Var. "rubra" has a distinct reddish colouration with less distinct spots and markings than the familiar subspecies. Approximately 50% of those specimens dredged off the Pearl Banks are of the "rubra" variety and nowhere else in Ceylon has the writer seen them.

The specimens from North Ceylon and South India are somewhat paler and larger in size than those from the South and Trincomalee.

29. *Ravitrona caputserpentis caputserpentis* Linné, 1758

This is also a very common and widespread species in Ceylon, but has a distinct preference for very shallow rough water and is not found deeper than 3 fathoms. It seems to like being exposed to surf and a little light and a favourite hiding-place is inside the dead shells of *Balanus*. This species is most abundant off Trincomalee, Colombo, and Tangalle and seldom, if ever, occurs in sheltered water like *E. errones errones*.

30. *Ravitrona gangranosa reentsi* Dunker, 1852

A rather rare and scarce species with specimens coming up from Trincomalee, Colombo, and Tangalle. Less than 40 have been taken and most of these came from Trincomalee in recent years, in from 2 to 4 fathoms of water under rocks and corals.

31. *Ravitrona helvola argella* Melvill, 1888

This species is also uncommon in Ceylon in its live condition and only a few specimens have been taken in the same location as the former. However, judging from several hundred of beach-collected Cypraeidae from the Galle area, this species forms more than 50% of the total which indicates that its most typical hiding-place may be in the depths of coral growths which divers are usually unable to get at. The few live specimens examined by the writer were collected in Colombo and Trincomalee.

32. *Ravitrona poraria poraria* Linné, 1758

A very scarce species of which only a few live specimens have recently been collected in Trincomalee from under rocks and corals in 2–4 fathoms. One or two have also been taken in Colombo and one only, by the writer, off Tangalle.

33. *Monetaria moneta moneta* Linné, 1758

A quite common species taken in fair numbers in very shallow water under rocks in crevices and hollows in Trincomalee and Colombo. It occurs in many other places no doubt but most collectors are not interested in collecting it and so data are meagre. It is always found in water from 1 to 3 fathoms deep and somewhat exposed to the surf.

34. *Monetaria annulus annulus* Linné, 1758

This is found in the same locations as the former but is much less common. Most of the specimens collected by the writer came from under and amongst living corals in Tangalle reef,

35. *Cypraea tigris* Linné, 1758

Due to over-collecting this species is now uncommon in the more dived-in areas like Colombo and Trincomalee. The writer has taken them in depths of from 2 to 9 fathoms off Trincomalee, the Arippu reef, Kalkudah, the Great Basses, Tangalle, Beruwala, Galle, Hikkaduwa, Colombo, and Negombo. The best location at the time of writing (1968) appears to be under the corals of Arippu reef in North-West Ceylon where conditions are very similar to the pure coral reefs of the Maldive Islands.

36. *Lincina lynx lynx* Linné, 1758

This is a widespread and common species but is most common in shallow and sheltered waters of Trincomalee. Live specimens have been taken off Kalkudah, Colombo, Negombo, Beruwala, Hikkaduwa, Tangalle, and the Arippu reef.

37. *Mystaponda vitellus vitellus* Linné, 1758

This species is located in the same manner as the former but seems to be commonest in Trincomalee in water from 1 to 4 fathoms deep and under rocks. The fresh-collected live specimens from Trincomalee are often coloured and attractively pinkish-mauve on the ventral surface, but this fades away after a few weeks of storage.

38. *Mystaponda nivosa* Broderip, 1877

Although the type locality for this very rare species is said to be Ceylon, recent reports from collectors indicate that most of the specimens are coming from Arakan in Burma. The single specimen seen by the author is in the collection of Mr. Ranil Senanayake of Colombo who states that it was collected "down South" in Ceylon. The collector is apparently unwilling to divulge the real location.

39. *Ponda carneola carneola* Linné, 1758

This is a very familiar and widespread species but is not over-numerous in its many locations which extend from Trincomalee to Arippu reef, Negombo, Colombo, Galle, Hikkaduwa, Tangalle, and Beruwala. It is found under rocks in shallow water from 1 to 3 fathoms deep and reasonably sheltered.

Allied Cowry Groups.—Five positive and one probable species of allied cowry groups are included in this Check-list as they are of as great interest to malacologists and conchologists as the true cowries.

40. *Amphiperas ovum* Linné, 1758

This species is quite common in Ceylon wherever colonies of Alcyonarian corals are present with which it lives. Many specimens are collected off Trincomalee and from Dondra to Tangalle in from 4 to 10 fathoms of water over rock or coral bottoms on which grow the leathery forms of alcyonarians resembling convoluted thalli of a fungoid. This species is almost always found in pairs and by day the greater part of its white shell is covered by the black mantle spotted with yellow/gold. This mantle is retracted towards evening, or when water transparency is poor and also in rough water.

41. *Calpurnus verrucosus* Linné, 1758

This species also lives with alcyonarians but only in the branched species, sheltering in the folds and seldom, if ever seen by day. The mantle is attractively semi-transparent white with tiny black spots. *Calpurnus* is abundant in the alcyonarian colonies off Trincomalee, Kuchchaveli, and Galle and it has also been collected off Nilwella, close to Tangalle.

42. *Calpurnus lacteus* Lamarck, 1810

This very small species is much scarcer than the former and lives in the same habitat. It was discovered in recent years by Mr. Cedric Martenstyn who brought it to the notice of the writer in 1967. Subsequently several more specimens were collected, all of them in Trincomalee.

43. *Trivirostra oryza* Lamarck, 1810

This very small species is quite abundant off Colombo and is probably also common elsewhere. It appears to prefer shaded over-hanging ledges on the sandstone reef off Colombo and in the company of sea-urchins in quite exposed and rough conditions less than 2 fathoms deep. The mantle is pure black in colour.

44. *Volva volva* Linné, 1758

This is a "probable" species on account of its abundance in the shell shops of Rameswaram Island, South India, and whence it is said to be collected in the Gulf of Mannar between India and Ceylon. It lives on gorgonians and is often taken in dredges. Since the territorial waters of Ceylon extend well beyond the usual 3-mile limit in the Pearl Banks, the writer includes this species as probably Ceylonese although to his knowledge no live specimens have been collected by Ceylonese divers and on Ceylon shores.

45. *Volva brevirostris* Schum., 1817

A fairly rare species occasionally collected on a species of golden gorgonian found off Trincomalee and Colombo. Not every gorgonian growth has its attendant *V. brevirostris* and it is still regarded as one of the rarer shells from Ceylon. The gorgonian colonies live in waters from 10 to 50 ft. and are more abundant off the West coast of Ceylon.

CONCLUSIONS

The writer lists a total of 45 species of Cypraeidae and closely allied groups and has personally examined and identified each of these with at least one specimen. It is possible that some species not listed here and recorded as from Ceylon by earlier workers who did not employ divers or dive themselves with modern equipment could have come into Ceylon from India, the Maldive Islands, the Andaman Group, and Singapore and found their way into local collections which former workers had access to.

At the same time it is readily admitted that only very small areas of Ceylon's territorial waters have been carefully worked by collectors and that dredging has been almost negligible and only in water less than 20 fathoms deep.

It is also observed that the more numerous and common species are also very adaptable in actual habitat whereas the very rare ones are obviously very localised. In many cases the writer and other collectors have failed to locate the best locations for some species, but in a few, such as *Ovula ovum* Linné an infallible method has been found since they are associated only with a particular species of alcyonarian.

Very little work has been done in recent times on gastropod Mollusca of Ceylon, much less the Cypraeidae, and it is hoped that the many gaps and defects in this paper will be revealed in the near future.

ACKNOWLEDGEMENTS

The writer is indebted to Messrs. Cedric Martenstyn, Trevor Ferdinands, Ranil Senanayake, P. Kirthisinghe, Ranjith Perera, Miss M. de Silva, Mr. Langston Pereira, and Dr, G. H. P. de Bruin for information and access to specimens for examination and identification. Also to Messrs. J. Johnson and J. Fisher of Singapore for information relating to Cypraeas.

LITERATURE CITED

ALLAN, JOYCE 1956. *Cowry Shells of World Seas.*

HORNELL, JAMES 1951. Indian Mollusca. *Bombay nat. Hist. Soc.*, p. 96.

SCHILDER, F. A. The geographical distribution of cowries. *The Veliger* 7 (3).

TAXONOMIC STUDIES OF THE SUCCINEIDAE (GASTROPODA, STYLOMMATOPHORA)

C. M. Patterson[1]

Museum and Department of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A.

Abstract

The pulmonate land snail family Succineidae is the only familial member of Pilsbry's (1900) order Heterurethra. Snails of this group differ from other Stylommatophora by characters of the pallial organs, principally the renal organs and ducts.

The Succineidae were divided into two subfamilies by Odhner (1950), the Succineinae and the Catinellinae, on the basis of presence or absence of a penial sheath covering the terminal male reproductive organ. According to Zilch (1959-60), the subfamily Succineinae (penial sheath present) contains nine genera and fifteen subgenera, and the subfamily Catinellinae (without penial sheath) contains five genera and three subgenera. However, much of this system is still based largely on characters of the shell, which give little or unreliable aid in systematic analyses because there is little diversity and considerable convergence of shell characters. Several aspects of the male and female reproductive tracts and features of the radula and jaw currently are used to characterize several of the genera and species, but the anatomy of the majority of the species has not yet been critically studied.

Species of the Succineinae are known to occur in North America, Europe, Asia, North Africa, the Orient (including India) and on various Pacific Islands. Members of the Catinellinae occur in North Central and South America, Europe, Africa, the Orient (including India) and Hawaii.

Our laboratory is currently engaged in taxonomic studies of the Succineidae, which in addition to conchology and comparative anatomy, embrace chromosome cytology, comparative protein analyses and immunological tests.

Haploid chromosome numbers in the Succineidae range from five to twenty-five. Four species of the genus *Catinella* have six pairs of chromosomes and one species has only five pairs. These are the lowest chromosome numbers known to occur in the Mollusca. Haploid chromosome numbers of twenty-nine species of the genera *Succinea*, *Succinella*, *Omalonyx* and *Oxyloma* range from eleven to twenty-five. Thus the more "primitive" subfamily Catinellinae has the lower number of chromosomes.

Comparative studies of electrophoretically separated foot muscle esterases and other proteins show that these are additional characters that can be used for taxon discrimination at various taxonomic levels. Immunological studies are proving of considerable value in showing relationships between taxa.

THE pulmonate land snail family Succineidae is a morphologically diverse group of great antiquity. As the predominant members of the stylommatophoran order Heterurethra, the succineids differ from most other land snails in the organization of their pallial organs (Pilsbry, 1900). There is a short lung with a transverse kidney extending from the pericardium to the rectum with the ureter passing along its front border and bending forward beside the rectum. However, in some of the more slug-like forms such as *Aillya* and *Omalonyx* (*see* Baker, 1955), a rotation has occurred so that the kidney lies nearly longitudinal with the body axis. The present classification of the Succineidae is still based largely on shell characters, which because of little diversity and considerable convergence, give only fragmentary or unreliable aid in systematic analyses. Currently, features of the male and female reproductive tracts, the radula and jaw, and to some extent, patterns of pigmentation, are used to characterise some genera and species. However, to date, only a very few species have been studied with regard to such morphological characters, which leaves the systematics of the Succineidae in an inadequate and confused state.

---

[1] Supported (in part) by grants GB-5601 from the National Science Foundation, Washington, D.C., and 5 T1 AI-41 (Training Grant) from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service, and (in part) by grant SFC-7-0067 from the Foreign Currency Program, Office of International Activities, Smithsonian Institution, Washington, D.C., U.S.A.

The Succineidae are especially interesting cytologically because of the wide variation in chromosome numbers among the species (Burch, Patterson and Natarajan, 1966; Natarajan, Hubricht and Burch, 1966) and because the lowest haploid numbers known in the Mollusca occur in several species of the subfamily Catinellinae (Burch, 1964 *a*, *b*; Patterson and Burch, 1966). The Succineidae also have gained special attention because the family has been considered to be the most primitive land pulmonate snail group (Cook, 1966; Van Mol, 1967), and Rigby (1965) considered the family to be a terrestrial opisthobranch group. The succineids possess features common to other stylommatophoran representatives, *e.g.*, eyes located at the tips of dorsal, inversible tentacles, an aulacopod foot with one or two pedal grooves, and the possession of a cerebral ganglion composed of a procerebrum and metacerebrum which closely resembles that of the typical stylommatophoran, *Helix pomatia* (Cook, 1966). Some basommatophoran-like characters of the Succineidae include the possession of lateral cerebral lobes, which characterize few stylommatophoran representatives but all basommatophorans (Cook, 1966); a discrete prostate gland situated along the vas deferens; a posterior gastric caecum similar to that found in the higher Basommatophora and aplysiomorph opisthobranchs; and for most species, the deposition of eggs bound together in a mass. Rigby (1965) contends that the Succineidae should more correctly be regarded as terrestrial opisthobranchs because of several common features shared with some of the opisthobranchiate members. These features include the functional division of the pallial reproductive tract into three channels for separate passage of departing sperm, outgoing eggs and sperm received during copulation; separation of the albumen gland from the main reproductive tract by a short duct; a distended post-esophagus used for initial breakdown of food; a reduced stomach with the portions linking with the digestive gland separated by sphincter muscles from the axial tract of the stomach and the posterior excretory caecum which arises from the style sac region of the stomach; the mode of feeding; and the relatively low chromosome numbers in both groups. However, Cook (1966) and Van Mol (1967) recognize certain features pointed out by Rigby as being similar to those of opisthobranchs, but contend that the succineids are true stylommatophoran land snails and they should not be regarded as opisthobranchs. In addition, it should be pointed out that the occurrence of low chromosome numbers in the two groups does not indicate *per se* their close systematic relationship (*see* Patterson, 1968).

The Succineidae have generally been considered a rather primitive land snail group due to the lack of structural complexity of the species. Recent anatomical studies include those of Rao (1927), Quick (1933, 1934, 1936, 1939 *a*, *b*), Boettger (1939), Pilsbry (1948), Odhner (1950), Franzen (1959, 1963, 1964, 1966), Rigby (1965), Cook (1966), and Van Mol (1967). Baker (1955) postulated that the ancestral stylommatophoran possessed heterurethrous pallial organs and an aulacopod foot. Van Mol (1967), on the basis of the structure of the cerebral ganglion, considers the Succineidae to be the most primitive stylommatophoran group. Recent morphological observations from our laboratory indicate that all other stylommatophoran groups, including the aberrant Athoracophoridae, can be derived from the Succineidae. The unique anatomical and cytological features of the Succineidae and the need for a systematic study of the family on a worldwide basis led to the initiation of the current study, an investigation of all available species using modern techniques of electrophoresis, immunology, and cytology in conjunction with anatomy and shell morphology.

The Succineidae were divided into two subfamilies by Odhner (1950), on the basis of presence or absence of a penial sheath. According to Zilch (1959–60) and more recently compiled data, the subfamily Succineinae (penial sheath present) contains nine genera and fifteen subgenera occurring in North and South America, Europe, Asia, Africa, India, the Orient, and on various Pacific Islands, while the Catinellinae, which lacks a penial sheath, is composed of five genera and three subgenera that occur in North, Central and South America, Europe, Africa, India, the Orient, and Hawaii.

Haploid chromosome numbers range from $n=5$–25 in the Succineidae (Table 1). The genus *Catinella* (subfamily Catinellinae) is characterized by the absence of a penial sheath and the

TABLE I

Haploid chromosome numbers of Succineidae

Species	Haploid No.	Source	Reference
Subfamily CATINELLINAE			
Catinella rotundata	5	Hawaii	Burch, 1964 *a*
C. cf. *gabbi*	6	U.S.A.	Burch, Patterson and Natarajan, 1966
C. texana	6	U.S.A.	Natarajan, Hubricht and Burch, 1966
C. vermeta	6	U.S.A.	Burch, 1964 *b*
C. arenaria	6	England	Butot and Kiauta, 1967
Subfamily SUCCININAE			
Succinella oblonga	11, 12	Europe	Rainer, 1967; Butot and Kiauta, 1967
Oxyloma japonica	15	Japan	Burch, 1965
O. hirasei	17	Japan	Koyama, 1955
O. kwansae	17	Japan	Koyama, 1955
O. elegans	17	Europe	Butot and Kiauta, 1964
O. sarsi	17	Europe	Butot and Kiauta, 1964
O. cleopatraea	18	Egypt	Patterson (unpublished)
O. haydeni	19	U.S.A.	Franzen, 1966
O. salleana	19	U.S.A.	Natarajan, Hubricht and Burch, 1966
O. retusa	19	U.S.A.	Burch, Patterson and Natarajan, 1966
Omalonyx felina	21	Antigua	Patterson (unpublished)
Succinea sp.	11	Tanzania	Patterson (unpublished)
S. horticola	17	Japan	Inaba, 1945
S. girata	17	Curacao	Butot and Kiauta (pers. comm.)
S. concordialis	18	U.S.A.	Natarajan, Hubricht and Burch, 1966
S. sanibelensis	18	U.S.A.	Patterson (unpublished)
S. greeri	18	U.S.A.	Natarajan, Hubricht and Burch, 1966
S. urbana	18	U.S.A.	Natarajan, Hubricht and Burch, 1966
S. campestris	18	U.S.A.	Burch, Patterson and Natarajan, 1966
S. luteola	18	U.S.A.	Natarajan, Hubricht and Burch, 1966
S. sp.	18	U.S.A.	Patterson (unpublished)
S. cf. *strubelli*	18	Papua	Patterson (unpublished)
S. kuntziana	18	New Hebrides	Patterson (unpublished)
S. grosvenori	19	U.S.A.	Natarajan, Hubricht and Burch, 1966
S. ovalis	21	U.S.A.	Husted and Burch, 1946; Burch, Patterson and Natarajan, 1966
S. putris	22	Europe	Perrot, 1938; Butot and Kiauta, 1964
S. lauta	22	Japan	Burch, 1965
S. l. sphaerica	22	Japan	Burch, 1965
S. gravelyi	25	India	Patterson (unpublished)

presence of a large penial appendix and has cytological information for five of its species: *C. rotundata* from Hawaii has five pairs of chromosomes which are metacentric or very nearly so; *C. vermeta*, *C. gabbi* and *C. texana*, all from the United States, have six pairs of metacentric or nearly metacentric chromosomes; *C. arenaria* from England also has a chromosome number of $n = 6$ but is distinct from the other *Catinella* species in having two pairs of subterminally constricted chromosomes. Twenty-nine species and subspecies of the Succininae have haploid chromosome numbers ranging from $n = 11$ to $n = 25$. *Succinella oblonga* possesses a penial sheath within which is a non-convoluted epiphallus, the upper portion protruding through the sheath; there is no penial appendix. Butot and Kiauta (1964) reported *S. oblonga* from two European populations to have 12 pairs of chromosomes, but Rainer (1967) reported individuals with $n = 11$ and $n = 12$ from two other European populations. Nine species of the genus *Oxyloma* from Japan, Africa, Europe, and North America have haploid chromosome numbers ranging from $n = 15$ to $n = 19$. Members of this genus possess a penial sheath, a small penial appendix, and a convoluted epiphallus. *Succinea*, a genus characterized by the presence of a penial sheath, a non-convoluted epiphallus and absence of a penial appendix, has haploid chromosome numbers that range from $n = 11$ to $n = 25$ among the eighteen species and subspecies investigated. The presence of a penial sheath and a highly elongated, convoluted penis and absence of a penial appendix has been observed in *Omalonyx felina*. This species also shows a conspicuous bulbous enlargement of the epiphallus at the junction with the vas deferens. The haploid chromosome number of *O. felina* is $n = 21$ with four of the bivalents being considerably larger than the others. In light of the available data on chromosome numbers, the Catinellinae and Succininae appear to be cytologically distinct; haploid chromosome numbers $n = 5$ and $n = 6$ characteristic of the former subfamily, and eleven or more pairs of chromosomes are found in members of the latter. It will be interesting to note if this distinction is borne out with subsequent chromosome number determinations of various other species.

Fifteen to eighteen proteins can be separated from succineid foot muscle tissue using Canalco acrylamide gel disc electrophoresis and napthol blue-black stain. Five to ten bands are evident when the gels are stained with fast blue RR salt using alpha napthol acetate as a substrate. This latter method detects the presence of esterases. The electrophoretically separated foot muscle proteins appear to be clearly distinct for each of the six species studied to date.

I recently initiated an immunological study of the Succineidae, using the Ouchterlony double diffusion technique as adapted for molluscan studies (*see* Davis, 1968). Antisera have been developed for *Catinella vermeta*, *Succinea ovalis*, and *Oxyloma retusa* from Michigan, U.S.A., and for *S. putris* of France. Antigens of these four species each have been tested against the antisera developed. All of these tests showed "identity" reactions, but also a significant number of "non-identity" reactions. Similar results were obtained when the North American *S. ovalis* was tested against the European *S. putris*, indicating that these two species are probably rather distantly related.

LITERATURE CITED

BAKER, H. B. 1955. Heterurethrous and aulacopod. *Nautilus*, **68** (4): 109–112.

BOETTGER, C. R. 1939. Bemerkungen über die in Deutschland vorkommenden Bernsteinschnecken (Fam. Succineidae). *Zool. Anz.*, **127** (3/4): 49–64.

BURCH, J. B. 1964 *a*. Chromosomes of the succineid snail *Catinella rotundata*. *Occ. Paps. Mus. Zool., Univ. Michigan*, No. 638: 1–8.

——— 1964 *b*. The chromosomes of *Catinella vermeta* (Mollusca, Euthyneura, Succineidae). *Acta biol. Acad. Sci. Hung.*, **15** (1): 87–94.

——— 1965. Chromosome numbers and systematics in euthyneuran snails. *Proc. first Europ. malacol. Congr.*, 1962, pp. 215–241.

———, C. M. PATTERSON AND R. NATARAJAN 1966. Chromosomes of four species of North American Succineidae. *Venus, Jap. J. Malacol.*, **24** (4): 342–353.

BUTOT, L. J. M. AND B. KIAUTA 1964. Voorlopig rapport over de chromosomen van vier Nederlandse succineiden. *Corresp. Ned. malacol. Ver.*, **111**: 1163–1164.

——— 1967. The chromosomes of *Catinella arenaria* (Bouchard-Chantereaux, 1837) with a review of the cytological conditions within the genus *Catinella* and considerations of the phylogenetic position of the Succineoidea ord. nov. (Gastropoda: Euthyneura). *Beaufortia*, Zool. Mus. Univ. Amsterdam, **14** (174): 157–164.

Cook, H. 1966. Morphology and histology of the central nervous system of *Succinea putris* (L.). *Arch. Neerland. d. Zool.*, **17** (1): 1–72.

Davis, G. M. 1968. A systematic analysis of *Oncomelania hupensis chiui* (Gastropoda: Hydrobiidae). *Malacologia* (in press).

Franzen, D. S. 1959. Anatomy of *Succinea ovalis* Say. *Proc. malacol. Soc. Lond.*, **33** (5): 193–199.

——— 1963. Variations in the anatomy of the succineid gastropod *Oxyloma retusa*. *Nautilus*, **76** (3): 82–95.

——— 1964. Anatomy of the succineid gastropod *Oxyloma haydeni*. *Ibid.*, **77** (3) : 73–81.

——— 1966. Anatomy of the succineid gastropod *Oxyloma salleana* (Pfeiffer). *Ibid.*, **80** (2): 59–69.

Husted, L. and P. R. Burch 1946. The chromosomes of the polygyrid snail *Allogona profunda*. *Amer. Natur.*, **80**: 410–429.

Inaba, A. 1945. Chromosome numbers in some land snails. *Venus, Jap. J. Malacol.*, **14**: 97–102.

Koyama, T. 1955. Studies on the chromosome numbers of two species of *Succinea* in Japan. *Ibid.*, **18**: 259–265.

Natarajan, R., L. Hubricht and J. B. Burch 1966. Chromosomes of eight species of Succineidae (Gastropoda, Stylommatophora) from southern United States. *Acta Biol. Hung.*, **17** (1): 105–120.

Odhner, N. 1950. Succineid studies: genera and species of subfamily Catinellinae nov. *Proc. malacol. Soc. Lond.*, **28**: 200–210.

Patterson, C. M. 1968. Chromosomes of mollusks. *J. Mar. biol. Ass. India* (in press).

—— and J. B. Burch 1966. The chromosome cycle in the land snail *Catinella vermeta* (Stylommatophora: Succineidae). *Malacologia*, **3** (3): 309–325.

Perrot, M. 1938. Étude de cytologie comparée chez les gastéropodes pulmonées. *Rev. suisse Zool.*, **45** (20): 487–566.

Pilsbry, H. A. 1900. On the zoological position of *Partula* and *Achatinella*. *Proc. Acad. nat. Sci. Philad.*, **1900** (3): 561–567.

——— 1948. Land Mollusca of North America (North of Mexico). *Acad. nat. Sci. Philad.*, Monogr. No. 3: 1–1113.

Quick, H. E. 1933. The anatomy of British Succineae. *Proc. malacol. Soc. Lond.*, **20** (6): 295–318, pls. 1–2.

——— 1934. The development of radula and jaw, and the specific differences in young *Succinea pfeifferi* Rossm. and *Succinea putris* (L.). *Ibid.*, **21**: 96–103.

——— 1936. The anatomy of some African Succineae, and of *Succinea hungarica* Hazay and *S. australis* Ferussac for comparison. *Ann. Natal Mus.*, **8**: 19–45, pls. 1–4.

——— 1939 *a*. Some particulars of four Indopacific *Succinea*. *Proc. malacol. Soc. Lond.*, **23**: 298–302.

——— 1939 *b*. On *Succinea andecola*. *Ibid.*, **23**: 333–335.

Rainer, M. 1967. Chromosomenuntersuchengen an Gastropoden (Stylommatophora). *Malacologia*, **5** (3): 341–373.

Rao, H. S. 1927. *Anatomical and Taxonomic Studies of Some Indian Freshwater and Amphibious Gastropods.* Univ. Madras Gov. Press, Madras, p. 181.

Rigby, J. 1965. *Succinea putris*: A terrestrial opisthobranch mollusc. *Proc. zool. Soc. Lond.* **144** (4): 445–486.

Van Mol, J.-J. 1967. Étude morphologie et phylogénétique de ganglion cerebroide des gastéropodes pulmonés. (Mollusques). *Mem. Acad. roy. Belg.*, **37** (5): 1–168, pls. 1–3.

Zilch, A. 1959–60. Gastropoda, Teil 2, Euthyneura *In*: Schindewolf, *Handbuch der Palaozoologie*, v. 6, Borntraeger, Berlin, xii + 834 p.

ON A NEW GENUS AND SOME NEW SPECIES OF OPISTHOBRANCHIATE GASTROPODS OF THE FAMILY EUBRANCHIDAE FROM THE GULF OF MANNAR[1]

K. Prabhakara Rao[2]

Central Marine Fisheries Research Institute, Mandapam Camp, India

Abstract

A new genus *Annulorhina* based on the type species *A. mandapamensis* and three new species namely *Eubranchus mannarensis*, *Capellinia fuscannulata*, and *Eubranchopsis indicus* of the family Eubranchidae are described from the Indian Ocean. The present record of the genera *Capellinia* and *Eubranchopsis* extend their distribution to the Indian Ocean.

The detailed structure and specific characters of each species have been given and their affinities discussed.

The family Eubranchidae, according to Baba (1960), consists of six genera namely, *Eubranchus* Forbes, 1838; *Capellinia* Trinchese, 1929; *Eubranchopsis* Baba, 1929; *Galvinella* Eliot, 1907; *Egalvina* Odhner, 1929, and *Cumanotus* Odhner, 1907. During the course of study of the nudibranch fauna of Gulf of Mannar and Palk Bay around Mandapam from the intertidal region near the jetty of Central Marine Fisheries Research Institute, certain specimens representing three new species under the known genera *Eubranchus*, *Capellinia*, and *Eubranchopsis* and a fourth one under a genus not hitherto known have been collected and described in the present communication.

1. Genus *Eubranchus* Forbes (1838)

Synonyms : *Amphorina* Quatrefages (1844), *Galvina* Alder and Hancock (1855)

Acleioproct Eolidacea with triseriate radula; a single row of denticles on the masticatory borders; anal opening about the middle of the body, in front of the right post-anal row; rhinophores smooth; cerata simple; foot corners round, angulate or tentaculiform; ptyaline glands present; penis unarmed with a separate preputial sac.

Eubranchus mannarensis **sp. nov.**

Locality.—Gulf of Mannar, near the jetty of the Central Marine Fisheries Research Institute, Mandapam Camp.

Five specimens collected during December, 1963 to March, 1964. The type specimens are deposited in the Reference Collection Museum of the Central Marine Fisheries Research Institute, Mandapam Camp. Holotype registered No. CMFRI/82.

The largest specimen (Fig. 1, *a*) is about 5 mm. in length, slender and elongated in appearance. The specimens are translucent white, mottled with orange and grey patches all over the body except on the sole of the foot. The oral tentacles and rhinophores have dark brown bands with white, shining granules distributed all over the body.

---

[1] Published with the permission of the Director, Central Marine Fisheries Research Institute.

[2] Present Address: Lecturer in Zoology, Stewart Science College, Cuttack, Orissa, India.

The head bears two pairs of smooth and bluntly pointed tentacles. There are five-paired rows of cerata, which are arched and situated opposite one another. The first row of each side is deeply arched with five to six cerata arranged in a line. There are four cerata in the second row, three in the third, two in the fourth, and one in the last. The largest cerata (Fig. 1, *b*) is about 1 mm. in length, fusiform and slender with a constriction below the tip. The hepatic diverticulum in the cerata (Fig. 1, *dg*) is yellowish-brown, but deep red at its base. Tail is long and tapering. The pericardial prominence is situated between the first and second rows of cerata.

The anus (Fig. 1, *an*) is behind the pericardial prominence, median in position, inclined to the right and situated on a low papilla in front of the right post-anal row. The renal opening is close to the anal opening. The genital openings (Fig. 1, *go*) are on the right lateral side below the first arch of the cerata. The foot is narrower than the back extending up to the tip of the tail. The anterolateral corners of the foot are produced into short horn-like processes. The eyes are black, situated below the rhinophores.

The jaws (Fig. 1, *c*) are colourless, with a row of pointed denticles (Fig. 1, *d*) along the delicate masticatory border. The radula is triseriate, with 56 to 62 teeth which gradually narrow down posteriorly. The young median tooth (Fig. 1, *e*) is 17μ in width, horseshoe-shaped with three denticles on either side of the median spine. The lateral teeth (Fig. 1, *h*) are thin, smooth, and plate-like with triangular spine. The ptyaline glands extend posteriorly up to the middle of the body.

The hermaphrodite gland consists of two groups of follicles. The hermaphrodite duct dialates into a sausage-shaped ampulla. The male duct slender and muscular continuing into the muscular unarmed penis (Fig. 1, *i*). The preputial sac is fairly large and attached to the posterior end of the penis. The oviduct is short, passes through the female gland mass, and opens into the female atrium by nidamental duct. The vagina is short and leads into the club-shaped spermatheca.

The specific characters of *Eubranchus mannarensis* sp. nov. are as follows: Body translucent white, mottled with orange and grey-coloured patches; cephalic tentacles with brown-coloured bands, smooth and bluntly pointed; cerata caducous, simple, fusiform with constriction below the tip; foot narrower than the dorsum with anterolateral corners produced into short horns; anus acleioprotic median; masticatory border with a row of denticles; radula triseriate, median tooth with two to three lateral denticles on either side of the sharp median spine, lateral teeth thin plate-like with triangular spines; ptyaline glands present; penis unarmed with a separate preputial gland.

Discussion.—The genus *Eubranchus* is so far known to include *E. productus* (Farran, 1905); *E. horii* Baba (1960); *E. masakiensis* Baba (1960) and *E. rubeolus* Burn (1964) all from the Indo-Pacific region. All the above species are characterised by the branching of the right and left livers. The genital openings are on the right and lateral side below the first arch in all the forms. Except that of *E. rubeolus* the descriptions of the morphological and anatomical characters of the other three species were incompletely reported.

Eubranchus horii, reported by Baba (1960) from Sagami Bay, Japan, is typical of the genus *Eubranchns*. It differs from *E. mannarensis* described above in (1) the general colouration of the body, (2) the arrangement of rows of cerata, (3) the nature of the foot, and (4) the shape and size of the teeth of radula.

Eubranchus misakiensis, described by Baba (1960) from Sagami Bay, Japan, like *E. mannarensis* has produced foot corners, but differs from it in (1) the general colouration of the body, (2) in the absence of chocolate brown ring in the sub-apical region of the cerata, and (3) the presence of a large boss in the middle of the hepatic diverticulum of the cerata.

Eubranchus rubeolus described by Burn (1964) from Victoria, Australia, is characterised by the dark red patches on the notum. In both *E. rubeolus* and *E. mannarensis* the posterior part of

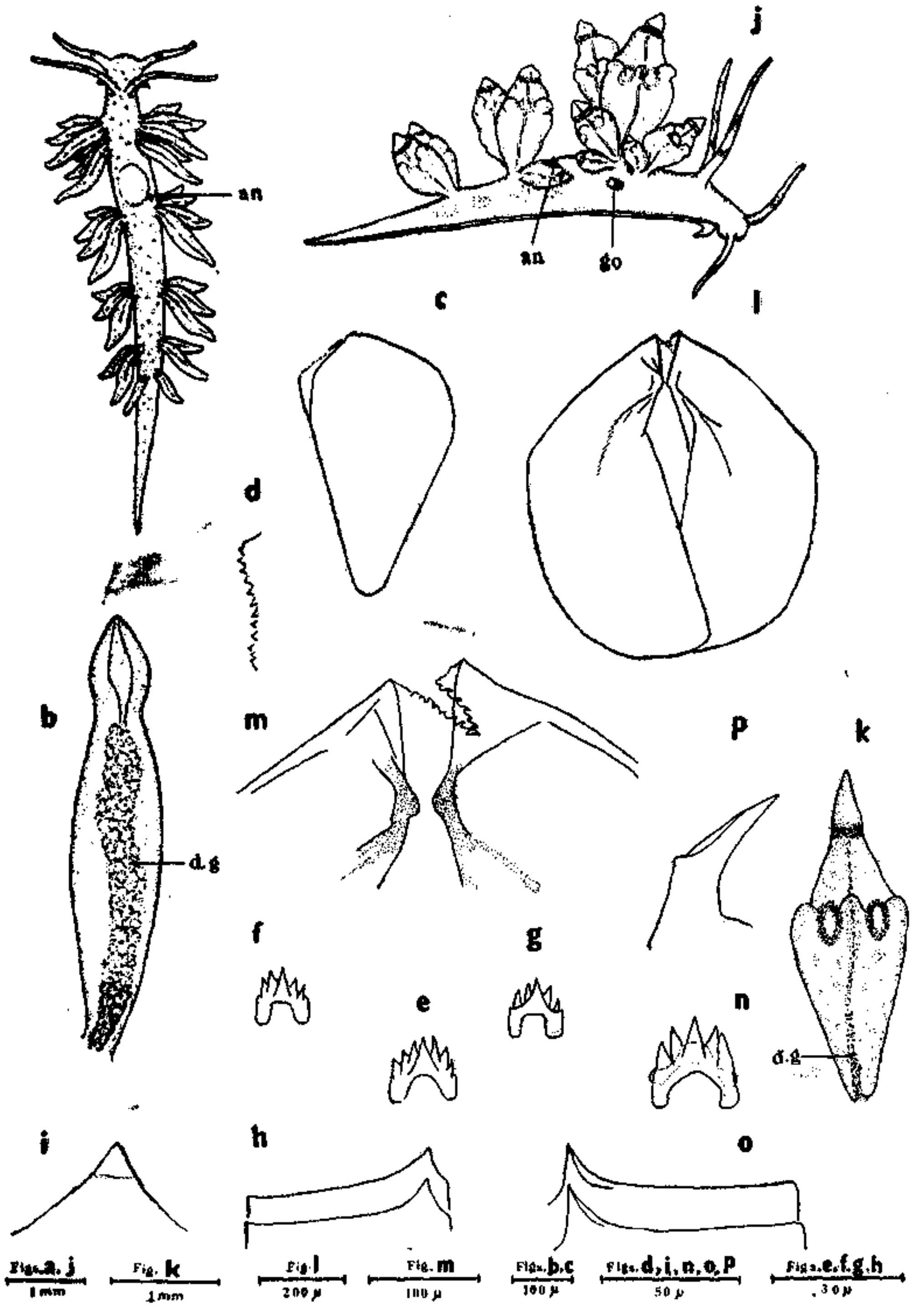


FIG. 1. (*a–i*) *Eubranchus mannarensis* sp. nov. (*a*) Dorsal view of the entire animal; (*b*) Cerata; (*c*) Jaw; (*d*) Masticatory border; (*e*) Median tooth; (*f*, *g*) Dorsal and ventral views of the older teeth; (*h*) Lateral teeth; (*i*) Tip of the penis. (*j–p*). *Capellinia fuscannulata* sp. nov. (*j*) Lateral view of the entire animal; (*k*) Cerata; (*l*) Jaws; (*m*) Masticatory border; (*n*) Median tooth; (*o*) Lateral teeth; (*p*) Penial stylet. *an* anus; *dg* digestive gland; *go* genital openings.

the hepatic diverticulum of the cerata is red in colour. The presence of (1) coloured patches on the notum, (2) rounded corners of the foot, (3) notch on the lateral tooth and the overlapping denticles on the masticatory border, distinguish *E. rubeolus* from *E. mannarensis*.

Eubranchus productus, described by Farran (1905) from the Gulf of Mannar, Ceylon, resembles *E. mannarensis* in (1) the general contour of the body, (2) the shape of the cerata, and (3) the nature of the foot.

In *E. productus* the radula has only nine teeth, the median teeth robust with short median spine and five to six lateral denticles. The lateral teeth are triangular in shape whereas in *E. mannarensis* the radula has a large number (56–62) of minute teeth, each with a large median spine with two to three lateral denticles. The lateral teeth are rectangular in shape.

In view of the above, although *E. mannarensis* resembles other species known so far in certain characters, it is strikingly different from them in certain other characters. It is therefore described here as a new species after the place of its occurrence.

2. Genus *Capellinia* Trinchese (1874)

Acleioproct Eolidacea with triseriate radula; masticatory border with a single row of denticles; foot corners round or angulate; cerata with knobs or tubercles; ptyaline glands present; separate preputial sac exists; penis armed with obliquely cut stylet.

Capellinia fuscannulata sp. nov.

Locality.—Gulf of Mannar, near the jetty of the Central Marine Fisheries Research Institute, Mandapam Camp.

Five specimens collected during February and March, 1964. The type specimens are deposited in the Reference Collection Museum of the Central Marine Fisheries Research Institute, Mandapam Camp. Holotype registered No. CMFRI/83.

The specimens are long and slender and the largest of them (Fig. 1, *j*) is about 5 mm. in length. The body is translucent and milky-white in colour. The paired tentacles of the head are marked with deep brown bands. Prominent brown rings in between the tubercles of the cerata and deep brown bands in the sub-apical regions of the cerata are present.

The head bears two pairs of long slender and smooth tentacles, which are bluntly terminated. The dark-pigmented eyes are situated below the rhinophores. The dorsum has three paired rows of cerata.

The first row is deeply arched with three to five cerata arranged in a line. The second row has two and the third row a solitary cerata. The inner cerata of each row are larger than the others and inflated. The cerata (Fig. 1, *k*) are caducous with a row of tubercles in the anterior one-third of its length. The hepatic diverticulum (Fig. 1, *dg*) in the cerata is a simple stem, without any boss-like projections and terminates by a cnidosac. The pericardial prominence is situated in between the first and second rows of cerata. The foot is less wider than the dorsum, extending to the tip of the pointed tail. The anterolateral corners of the foot have short horn-like projections.

The anus (Fig. 1, *an*) is situated on a low papilla, median in position, in front of the right second row of cerata. The genital openings (Fig. 1, *go*) are on the right lateral side, just below the posterior end of the first arched row, The jaws (Fig. 1, *l*) are straw-coloured with a row of pointed denticles (Fig. 1, *m*), on the masticatory borders. The radula is a long ribbon with 35 to 101 rows of teeth. The older teeth are in line with the younger ones. The median tooth (Fig. 1, *n*) is 34μ in height and 28μ in width, with two denticles on either side of the sharp median spine. The smooth, thin and plate-like lateral teeth (Fig. 1, *o*) are longer than broad with sharp triangular spines. The paired ptyaline glands extend up to the base of the first liver arch. The male follicles of the hermaphrodite gland are dark grey in colour. The club-shaped preputial sac is attached at the base of the penis. The muscular penis is armed with an obliquely cut stylet (Fig. 1, *p*). The spermatheca is club-shaped attached to the vagina by a short thick stalk.

The specific characters of *Capellinia fuscannulata* sp. nov. are as follows: Body translucent, milky white, with brown bands on the tentacles and on the cerata; cephalic tentacles smooth and bluntly pointed, cerata inflated with a single row of tubercle-like projections; hepatic diverticulum in the cerata simple, terminating by a cnidosac; foot narrow, anterolateral corners produced into short processes; anus median, radula triseriate, median tooth with two denticles on either side of the median spine, lateral teeth plate-like, longer than broad with spines; masticatory border with a row of denticles; ptyaline glands present; penis armed with an obliquely cut stylet and a separate preputial sac.

Discussion.—Marcus (1958) has discussed the value of the penial stylet in classifying the various species of the genus *Eubranchus* and provisionally included *Eubranchus*-like species with armed penis in the genus *Capellinia* Trinchese (1874).

Eubranchus montraveli (Risbec, 1937) is the only species from the Pacific Ocean with an armed penis. *E. montraveli* differs from *Capellinia fuscannulata*, in having the anus almost at the base of the cerata.

Capillinia conicla described by Marcus (1958) from the Brazilian coast of South America resembles *C. fuscannulata* in certain characters. Both have ptyaline glands, preputial sac, and an obliquely cut stylet. However, *C. conicla* differs from *C. fuscannulata* in having hollow bosses of hepatic diverticulum in the cerata, the presence of finest spines on the posterior rows of the denticles of the masticatory borders.

Marcus (1961) reported *Capellinia rustya* from Monterey Bay. It is white to translucent with pink colour. *C. fuscannulata* resembles *C. rustya* in the colour of the body, shape of the cerata, presence of ptyaline glands, preputial sac, and the penial stylet. *C. rustya* differs from *C. fuscannulata* in not having circular coloured patches on the cerata, the presence of rounded foot corners, in the nature of the masticatory border of the jaws, and in having four denticles on either side of the median spine of the median tooth.

The author, therefore, considers that *Capellinia fuscannulata* is a new species of the genus *Capellinia* and names it after the characteristic dominant brown rings on the cerata.

3. Genus *Eubranchopsis* Baba (1940)

Acleioproct Eolidacea with triseriate radula; cephalic tentacles smooth; foot corners tentaculiform; cerata in oblique rows, caducous and with acutely conical tubercles in about three circlets; genital orifice below the second row; anus median, above the inner corner of the third right branchial row; nephroproct in front of the anus; masticatory edge either smooth or denticulate; median teeth with three to six lateral denticles on either side of the median spine, lateral teeth broad, long, and plate-like; ptylaline glands present; penis unarmed; separate preputial sac absent.

***Eubranchopsis indicus* sp. nov.**

Locality.—Gulf of Mannar near jetty of the Central Marine Fisheries Research Institute, Mandapam Camp.

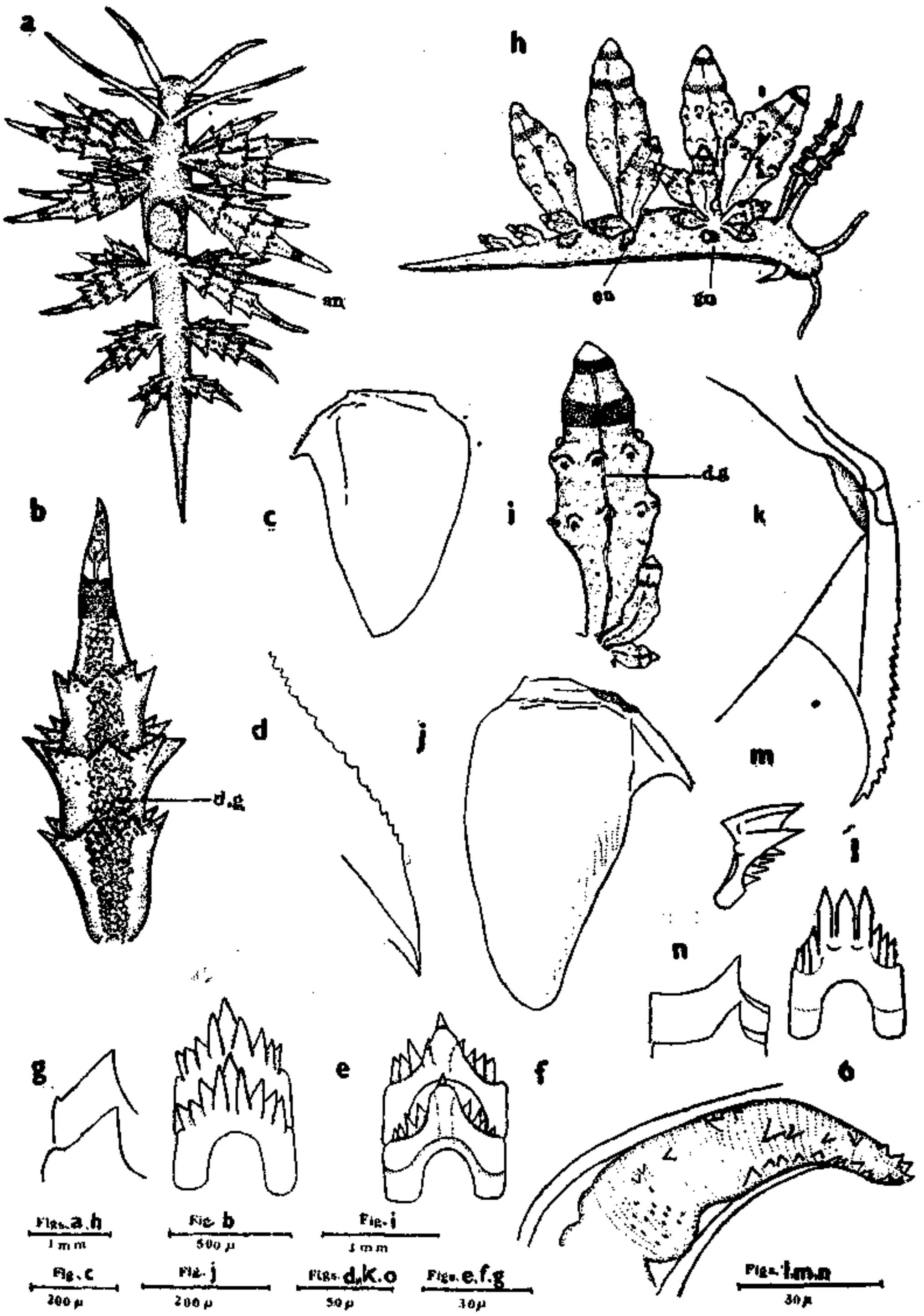


FIG. 2. (*a–g*) *Eubranchopsis indicus* sp. nov. (*a*) Dorsal view of the entire animal; (*b*) Cerata; (*c*) Jaws; (*d*) Masticatory border; (*e, g*) Median teeth, dorsal and ventral views; (*g*) Lateral teeth. (*h–o*). *Annulorhina mandapamensis* gen. nov. sp. et (*h*) Lateral view of the entire animal; (*i*) Cerata; (*j*) Jaw; (*k*) Masticatory border; (*l, m*) Dorsal and lateral views of the median teeth; (*n*) Lateral teeth; (*o*) Penis showing the spines, *an* anus; *dg* digestive gland; *go* genital openings.

Seven specimens were collected from April, 1963 to March, 1964.

The type specimens are deposited in the Reference Collection Museum of the Central Marine Fisheries Research Institute, Mandapam Camp. Holotype registered No. CMFRI/84.

The largest specimen (Fig. 2, *a*) is about 6 mm. in length, speckled light brown. Deep violet or blue-coloured bands are present on the cephalic tentacles and on the sub-apical region of the cerata. The extremities of the cephalic tentacles, foot prolongations, and conical tubercles of the cerata are covered with white shining granules.

The head is somewhat narrower than the body with paired tentacles, which are long, smooth and bluntly pointed. The cerata are arranged in vertical rows on either side of the body. The inner cerata (Fig. 2, *b*) has three circlets of eight to ten conical tubercles. The hepatic diverticulum (Fig. 2, *dg*) in the cerata is a single stem, yellowish-brown in colour, terminating by a cnidosac. The arrangement of the cerata is as follows: First row three, second row three or four, third row four, fourth row three, and the last row two. The tail is long and tapers to a fine point. The foot is narrower than the body with the anterolateral corners produced into tentacular processes.

The jaws (Fig. 2, *c*) are well developed with a denticulate masticatory border (Fig. 2, *d*) The radula is triseriate with 50 to 60 teeth arranged in a row. The median teeth (Fig. 2, *e*, *f*) are horseshoe-shaped about 35 μ wide and 38 μ long with four denticles on either side of the median spines. The lateral teeth (Fig. 2, *g*) are thin more or less triangular in shape with sharp conical spines. The ptyaline glands are paired and fairly big in size. Penis is simple without armature. Preputial sac absent and a portion of the vas deferens modified into a thick prostate. Spermatheca is short and club-shaped.

The specific characters of *Eubranchopsis indicus* sp. nov. are as follows: Body light brown with deep violet or blue bands on the cephalic tentacles and cerata; cephalic tentacles smooth; foot corners tentaculiform; cerata long with acutely conical tubercles arranged in three circlets; hepatic diverticulum in the cerata simple, terminating by a cnidosac; anus located in the inner corner of the third right branchial row; nephroproct close and in front of the anal opening; masticatory edge of the jaw denticulated; radula triseriate, median teeth horseshoe-shaped with four lateral denticles on either side of the median cusp; lateral teeth triangular, higher than broad with a triangular spine; ptyaline glands present, preputial sac absent, vas deferens modified into glandular prostate; penis unarmed.

Remarks.—*Eubranchopsis virginalis* described by Baba (1940) from Sagami Bay was 12 mm. long, olive-yellow in colour, ornamented with deep blue spots. *E. indicus* differs from it in the general colour of the body and in having a row of denticles on the masticatory border.

The author, therefore, considers *Eubranchopsis indicus* a new species under the genus and it is named after the region of its occurrence.

4. Genus *Annulorhina*

Acleioproct Eolidacea with triseriate radula; single row of denticles on the masticatory border; rhinophores cylindrical, annulate ; foot corners angulate or tentaculiform; cerata inflated and with two circlets of tubercles on the surface; ptyaline glands present; penis covered with triangular spines; without preputial sac, vas deferens with a thick prostatic portion.

***Annulorhina mandapamensis* gen. *et* sp. nov.**

Locality.—Gulf of Mannar, near the jetty of the Central Marine Fisheries Research Institute, Mandapam Camp, Five specimens were collected from June, 1963 to February, 1964. The type specimens are deposited in the Reference Collection Museum of the Central Marine Fisheries Research Institute, Mandapam Camp. Holotype registered No. CMFRI/85.

The specimen is yellowish-brown with grey spots all over the body and with orange-coloured patches on the cerata. A bright yellowish orange band is present on the sub-apical region of the cerata, and another pink or purple-coloured band just below the sub-apical region. Prominent dark patches are visible through the integument at the bases of the first circlet of tubercles. The apex and the tubercles of the cerata are covered with white shining granules.

The largest specimen (Fig. 2, *h*) is 7 mm. in length and 1·5 mm. in width near the widest part of the body. The head bears two pairs of tentacles. The first pair, or the oral tentacles, is smooth, directed forwards and backwards. The posterior pair, or rhinophores, is longer than the oral tentacles placed close to one another. Each rhinophore has three to five annulations at equal distance. The dark pigmented eyes seen through the integument are at the base of the rhinophores. The cerata are arranged in three to five paired rows on either side of the dorsum. The first row is deeply arched with three to five cerata arranged in a row. The second and third rows have three cerata each and the last two rows have a single cerata in each. The inner cerata (Fig. 2, *i*) of each row is about three to four times larger than the outer cerata, inflated in the middle with two circlets of tubercle-like projections. The hepatic diverticulum (Fig 2, *dg*) in the cerata is brown in colour, and it is narrow without any lateral projections and terminates by a cnidosac. The pericardial prominence is in between the first two anterior rows of cerata. The anal opening is on a low papilla, median in position, in front of the

TABLE I

Distinguishing characters of the seven genera of the family Eubranchidae

S. No	Characters	*Eubranchus*	*Capellinia*	*Galvinella*	*Cumanotus*	*Egalvina*	*Eubranchopsis*	*Annulorhina* gen. nov.
1	Rhinophores ..	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Annulated
2	Liver branching	Retained by the anterior liver	Retained by the anterior liver	Retained by the anterior liver	Retained by the anterior liver	Retained by the anterior and posterior livers, papillae multiplying laterally	Retained in the anterior liver	Retained in the anterior liver
3	Cerata ..	Smooth and simple	Inflated with row of knobs or tubercles	Inflated at the tips	Simple, situated on elevate pedaments	Simple	With circlet of acute projections	Inflated with rows of tubercles
4	Preputial sac ..	Present	Present	Present	Not known	Absent	Absent	Absent
5	Vas deferens ..	Simple	Simple	Simple	,,	With a thick prostatic part	With a thick prostatic part	With a thick prostatic part
6	Penis ..	Simple unarmed	Armed with a stylet	Simple unarmed	,,	Simple unarmed	Simple unarmed	Armed with short spines
7	Female aperture	Not known	Not known	Not known	Armed with hooks	Simple	Simple	Simple

right second row of the cerata. The genital openings are on the right lateral side below the posterior end of the first arch. The foot is narrower than the dorsum extending to the tip of the tail. The anterolateral corners of the foot are produced into short tentacular prolongations.

The jaws (Fig. 2, *j*) are straw-coloured. The masticatory border (Fig. 2, *k*) of it has a row of pointed denticles. The radula is triseriate with 49 rows of teeth arranged in a long ribbon. The median tooth (Fig. 2, *l*) is horseshoe-shaped, 34 μ in height and 27 μ in width. The median spine is sharply pointed with four to five lateral denticles. The first pair of lateral denticles of both sides is slightly longer than the median spine. The other lateral denticles are smaller than the first laterals and are of uniform size. The lateral teeth (Fig. 2, *n*) are thin and plate-like, elongated and with a single spine. The paired ptyaline glands extend to the anterior half-length of the animal. The pedal glands are densely distributed over the foot. The renopericardial syrinx is a pyriform body without any longitudinal muscular bands. Its inner layer is lined by long cilia. The renal opening is close to and in front of the anal opening. The hermaphrodite follicles are well differentiated into male and female acini. The hermaphrodite duct dilates into the sausage-shaped ampulla.

The posterior part of the vas deferens is thick and corresponds to the prostate part. Separate preputial sac is absent. The penis (Fig. 2, *o*) is cylindrical, muscular, and covered with short triangular spines all over its surface. The oviduct is short, and is continued through the muco-albumen gland complex and opens into the female atrium by nidamental openings. The vagina is short and leads into the voluminous spermatheca by a thick duct.

The specific characters of *Annulorhina mandapamensis* sp. nov. are as follows: Body yellowish-brown mottled with grey; cerata with yellowish-orange and purple-coloured bands; rhinophores annulated; radula triseriate; masticatory border denticulate; ptyaline glands present; preputial sac absent; vas deferens with glandular prostate, penis armed with short triangular spines.

The distinguishing features of the seven genera including *Annulorhina* are given in Table I.

CONCLUSIONS

The author's observations on the family Eubranchidae comprising four genera and four species indicate that besides the common characters like the variations in the number of branchial rows of the right liver, the nature of the cerata, the position of the genital openings, the presence or absence of salivary glands or ptyaline glands, the presence of preputial sac, and the nature of the penis recognised by the earlier workers (Odhner, 1939; Baba, 1949; Pruvot-Fol, 1954; Marcus, 1958), the following characters are noteworthy in distinguishing the members of this group: (1) presence or absence of annulations on the rhinophores and (2) armed or unarmed nature of the penis and if armed, whether with a single stylet or with a number of small spines.

While the seven known genera including the new genus *Annulorhina* resemble each other in (1) having smooth oral tentacles, (2) triseriate radula, (3) rounded, angulate or tentaculiform foot corners, (4) in the positions of the anal and genital openings, and (5) in having denticulated masticatory borders and (6) ptyaline glands, they differ from one another in several other characters as shown in Table I. It may be seen from this that the new genus can easily be distinguished externally by its annulated rhinophores.

ACKNOWLEDGEMENTS

The author is thankful to Dr. H. Lemche of Copenhagen, for helpful suggestions and to Mr. K. Virabhadra Rao, Dr. P. S. B. R. James, Dr. M. Umamaheswara Rao, for going through the manuscript. He is also thankful to the Government of India, Ministry of Education, for the award of

a Senior Research Training Scholarship during the tenure of which this work was carried out at the Central Marine Fisheries Research Institute.

LITERATURE CITED

ALDER, J. AND A. HANCOCK 1845–1855. *A Monograph of the British Nudibranchiate Mollusca,* Ray Society, London, Parts 1–7.

BABA, K. 1949. *Opisthobranchia of Sagami Bay.* Iwanami Shoten, Tokyo, pp. 194–197.

——— 1960. Two new species of the genus *Eubranchus* from Japan (Nudibranchia-Eolidacea). *Publ. Seto Mar. Biol. Lab.,* **8**: 229–302.

BURN, R. 1964. Descriptions of Australian Eolidacea (Mollusca Opisthobranchia). *J. Malac. Soc. Aust.,* **8**: 10–22.

ELIOT, C. 1907. Nudibranchiata. *Nat. Antarct. Exped. Nat. Hist.,* **2**: 1–28.

——— 1910. *A Monograph of the British Nudibranchiate Mollusca,* 8 (Supplement), Ray Society, London, pp. 1–198.

FARRAN, G. P. 1905. Report on the opisthobranchiate Mollusca. *Rep. Pearl Fish. Mannar,* **3**: 329–364.

LEMCHE, H. 1935. On some nudibranchiate gastropods from the Northern Atlantic. *Vidensk. Medd. fra. Danisk Naturh. Foren.,* **99**: 131–148.

——— 1964. *Eubranchus* Forbes, 1938 (Gastropoda). Proposed designation under the Plenary powers of a type-species, etc., Z.N. (S), 11027. *Bull. Zool. Nom.,* **21**: 40–44.

MARCUS, E. 1958. On Western Atlantic opisthobranchiate gastropods. *Amer. Mus. Novit.,* **1906**: 1–82.

——— 1959. Lamellariacea and Opisthobranchia. *Lunds Univ. Arsskr.,* **55**: 1–135.

——— 1960. Opisthobranchs from American Atlantic warm waters. *Bull. Mar. Sci. Gulf and Caribb.,* **10**: 129–203.

——— 1961. Opisthobranch Mollusks from California. *Veliger,* **3**: 1–84.

ODHNER, N. HJ. 1907. Northern and Arctic Invertebrates in the Collection of the Swedish State Museum. III. Opisthobranchia and Pteropoda. *K. Svenska vetensk. Akad. Handl.,* **144**: 1–112.

——— 1939. Opisthobranchiate Mollusca from the Western and Northern coasts of Norway. *K. Norske Vidensk. Selsk. Skr.,* **1**: 1–93.

*PRUVOT-FOL, A. 1954. Mollusques Opisthobranches. *Faune de France,* **58**: 1–460.

*RISBEC, J. 1937. Note preliminaire au sujet de nudibranches Neo-Calédoniens. *Bull. Mus. Natl. Hist. Nat. Paris,* **9**: 159–164.

THIELE, J. 1931. *Handbuch der Systematischen Weichtierkunde.* Gustav Fischer, Jena, **1**: 451–453.

* Not referred to in original.

A RE-APPRAISAL ON THE SUBGENERA OF *ANADARA*

C. F. LIM[1]

Department of Physiology, University of Singapore, Singapore

ABSTRACT

A systematic re-appraisal of the genus *Anadara* is conducted. Using information from studies on its form, ligament, distribution and so on the division of the genus into five phylogenetic subgenera is proposed. The five subgenera are *Anadara* s.s., *Scapharca*, *Senilia*, *Tegillarca*, and *Argina*. The most primitive is *Anadara* s.s. and it is most likely that the other four subgenera evolved independently of each other from *Anadara* s.s.

INTRODUCTION

NYST (1836) described the earliest species of *Anadara* which existed in the Tongrian Stage (Schenck and Reinhart, 1938) of the Oligocene period. He called it *Arca sulcicosta*. It was not until eleven years later when Gray (1847) proposed the name *Anadara* that the species could be placed in its proper genus.

The genus *Anadara* is geologically fairly young compared to many other genera of the Arcidae which have forms like *Barbatia* that originated in the Triassic period. *Anadara* is not the youngest, however, since *Bantharca* Verrill and Bush, *Noetiella* Thiele and Jaeckel, *Scaphula* Benson, and others evolved only recently (Reinhart, 1935). Nevertheless, *Anadara* began with a few Oligocene species, such as *A. invidiosa* (Cassy), *A. sulcicosta* (Nyst), *A. waylandi* Cox, and *A. daitokudoensis* (Makiyama), which were widely distributed in North America, Europe, Africa, and Japan respectively. The genus became abundant in species and in number in the Miocene and younger strata (Schenck and Reinhart, 1938; Kotaka, 1953). The recent genus which has about sixty valid species is distributed as far south as Southern Australia and in the north as far as the islands of Japan and the Mediterranean Sea (Figs. 7, 8 and 9). Its bathymetric range is from intertidal zones to infratidal depths of 80 to 100 fathoms (Rost, 1955). The species of *Anadara* may be attached to rocks and other supports by byssus or burrow freely in sand or mud. The group still retains some primitive characters [external ligament of chevron-type (Owen, 1959) and taxodont hinge (Purchon, 1958) present in all, and byssus (Yonge, 1962 *a*) in some species]. It is specialized with the invariable occurrence of *haemoglobin* in the blood of all its species (Sato, 1931; Sullivan, 1961; others) and the possession of an inhalant aperture in the posterior region of some members (Yonge, 1955).

The group is important economically. The species *Anadara granosa* (L.) has been cultured for food in Malaya (Pathansali and Soong, 1958) and possibly sold in markets of India (Hornell, 1951), China (Grabau and King, 1928), and Japan (Yoshida, 1957). In the Philippines *A. inaequivalvis* (Brug.) is collected commercially as food (Faustino, 1932). Yonge (1955) has remarked that *A. senilis* (L.) was an important source of food in West Africa.

A number of genera have been assigned to the *Anadara* group or series (Adams and Adams, 1858; Iredale, 1939). The group or series has also been divided into subgenera (Thiele, 1935; Reinhart, 1935; Schenck and Reinhart, 1938). An attempt is made here to re-appraise the genus

---

[1] Present Address: Department of Zoology, University of Singapore.

Anadara systematically. A scheme of classification employing phylogenetic subgenera based on the knowledge of past and present studies is as follows:—

THE SUBGENERA OF *ANADARA*

Subgenus *Anadara* sensu stricto

1847 *Anadara* Gray, *Proc. Zool. Soc., Lond.*, p. 198.

Type species: *Arca antiquata* Linnaeus, 1758, *Syst. Nat.*, ed. **10**: p. 694.

Recent; probably from Ceylon.

1857 *Rasia* Gray, *Ann. Mag. Nat. Hist.*, ser. 2, **19**: p. 371.

Type species: *Arca formosa* Sowerby, 1833, *Proc. Zool. Soc., Lond.*, pt. 1: p. 20.

Recent; from Gulf of Tehuantepec, Mexico.

1925 *Diluvarca* Woodring, *Carn. Inst., Washington, Pub.* **366**: p. 40.

Type species: *Arca diluvii* Lamarck, 1805, *Ann. Mus. Hist Nat., Paris*, **6**: p. 219.

Recent; from the Mediterranean Sea.

Subgenus *Scapharca* Gray, 1847

1847 *Scapharca* (written *Scapharea*) Gray, *Proc. Zool. Soc., Lond.*, p. 198.

Type species: *Arca inaequivalvis* Bruguiere, 1789, *Encycl. Meth., Hist. Nat. Vers.*, **1**: 106–107.

Recent; from Tranquebar, India.

1857 *Cara* Gray, *Ann. Mag. Nat. Hist.*, ser 2, **19**: p. 371.

Type species: *Arca aviculoides* Reeve, 1844, *Conch. Icon.*, **2**: *Arca*, pl. 10, fig. 63.

Recent; from Santa Elena, Ecuador. Renamed *Arca aviculiformis* Nyst.

1898 *Cunearca* Dall, *Trans Wagner Free Inst. Sci.*, **3**, pt. 4: p. 618.

Type species: *Arca incongrua* Say, 1822, *Jour. Acad. Nat. Sci., Philadelphia*, **2** (2): 268–269.

Recent; from South-Eastern United States.

1929 *Imparilarca* Iredale, *Mem. Queensland Mus.*, **9**, pt. 3: p. 263.

Type species: *I. hubbardi* Iredale, 1929 (*op. cit.*, p. 263, pl. 30, figs. 1 and 2).

Recent; from Queensland, Australia.

1939 *Potiarca* Iredale, Mollusca, pt. 1. *Sci. Rep. Gr. Barrier Reef Exped.*, **5**: p. 284.

Type species: *P. (pilula) saccula* Iredale, 1939 (*op. cit.*, pp. 284–285, pl. 3, fig. 17).

Recent; from Low Isles, Australia.

Subgenus *Tegillarca* Iredale, 1939

1939 *Tegillarca* Iredale, Mollusca, pt. 1. *Sci Rep. Gr. Barrier Reef Exped.*, **5**: p. 281.

Type species: *T. (granosa) bessalis* Iredale, 1939 (*op. cit.*, pp. 281–282; not figured).

Recent; from Queensland, Australia.

1853 *Anomalocardia* (Klein) Morch (*non* Schumacher, 1817), *Catalogue Conchylicrum quae reliquit D. Alphonso d'Aguirra and Gadea Comes de Yoldi, Fasc* **2**: Acephala, etc., p. 41.

Type species (by monotypy): *Arca granosa* Linneaus, 1758, *Syst. Nat.*, ed. **10**: p. 694.

Subgenus *Larkinia* Reinhart, 1935

1935 *Larkinia* Reinhart, *Mus. Roy. d'Hist. Nat. Bull.*, Brussels, **11** (13): 41–42, pl. 4, fig. 1.

Type species: *Anadara larkinii* (Nelson), Olsson, 1932, *Bull. Amer. Paleo.*, **19**: 75–76, pl. 2, figs. 1, 4 and 5.

Fossil; from the Tumbez formation, Miocene, of Peru.

Subgenus *Senilia* Gray, 1842

1842 *Senilia* Gray, *Syn. Cont. British Mus.*, ed. **44**: pl. 81.

Type species: *Arca senilis* Linneaus, 1758, *Syst. Nat.*, ed. **10**: p. 694.

Recent; from West Africa.

KEY TO THE SUBGENERA OF *ANADARA*

(applicable to adult specimens only)

1.	Shell equivalve	2
	Shell inequivalve	*Scapharca*
2.	Radial ribs smooth; byssus present or absent	3
	Radial ribs nodulated; byssus absent	*Tegillarca*
3.	Ventral margin of shell crenulated; byssus present or absent	4
	Ventral margin of shell smooth; byssus absent	*Senilia*
4.	Shell trigonal with umbos elevated; byssus absent	*Larkinia*
	Shell not trigonal and umbos not elevated; byssus present or absent	*Anadara* s.s.

FORM

Cuvier (1836), Vaillant (1865), Jackson (1890), Yonge (1952, 1953, 1958, 1962 *b*), and Stasek (1963) have regarded the Bivalvia as consisting of the body and mantle/shell, the two distinct but interacting components. Stasek (1963) in his course of investigations on the comparative anatomy of bivalves has illustrated this "correspondence of mantle/shell and body" as he (p. 200) calls it with the genera *Clinocardium*, *Venericardia*, *Chlamys*, *Tridacna*, and *Solen* using the principle of 'transformation' diagrams of the latter four with a basic grid of *Clinocardium*. The theory of 'transformations' was demonstrated by Thompson (1942) for organisms that were relisted but differed in body proportions. The theory employs graphical use of grids or systems of crossing co-ordinates to correlate two or more forms that are different in body proportions but believed to be derived from a basic one. The deformation diagrams thus obtained according to Thompson (1942) can be classified under four basic types. They are, as summarized by Stasek (1963, p. 203),

(1) "a grid in which one of the two series of co-ordinates is extended or contracted with respect to the other, all lines of each series being equidistant."

(2) "a grid in which the co-ordinates of one series are not equidistant but increase or decrease their separation in some particular ratio."

(3) "a grid in which the parallel equidistant co-ordinates of one series are at a constant angle to the parallel co-ordinates of the second series." This is the simple shear type of deformation.

(4) "a grid in which the co-ordinates of one series emanate from a point within or without the figure while those of the second series are formed into parallel circular arcs." This is the complex shear type of deformation.

Graham (1949) applied the above principle to bivalves when he compared a hypothetical dimyarian with *Pecten*, but Stasek (1963) used it for various bivalve forms at the generic level. Aiattempt is made here to apply the theory of transformations at the subgeneric level on the genus *Anadara*. The species experimented are (1) *A.* (*Anadara*) *antiquata*, (2) *A.* (*Scapharca*) *inaequivalvis*, (3) *A.* (*Scapharca*) *anomala*, (4) *A.* (*Tegillarca*) *granosa*, and (5) *A.* (*Tegillarca*) *cuneata*. (2) and (4) were observed to give identical diagrams with those of (3) and (5) respectively. The results of (1), (3) and (5) are given in Figs. 1, 2 and 3 for the subgenera *Anadara* s.s., *Scapharca*, and *Tegillarca* respectively. Using *Anadara* s.s. on a basic grid, the transformations of *Scapharca* and *Tegillarca* are concluded to be basically of Type Four with *Tegillarca* having 2 points or nodes (X_1 and Y_1) and *Scapharca* having one (X_1).

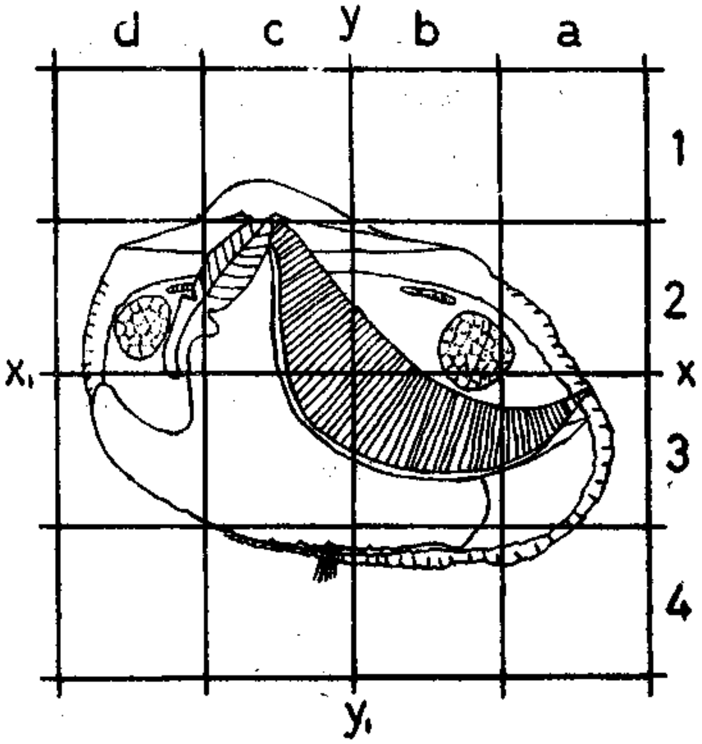


FIG. 1. *Anadara* (*Anadara*) *antiquata* (L.) Basic grid.

THE LIGAMENT

Owen (1959) has given a possible explanation to the origin and structure of the arcid ligament and figured its form in a hypothetical member. From his studies of the ligamental area in *Anadara granosa* and species of *Arca* he believed that the ligament consisted of an outer continuous

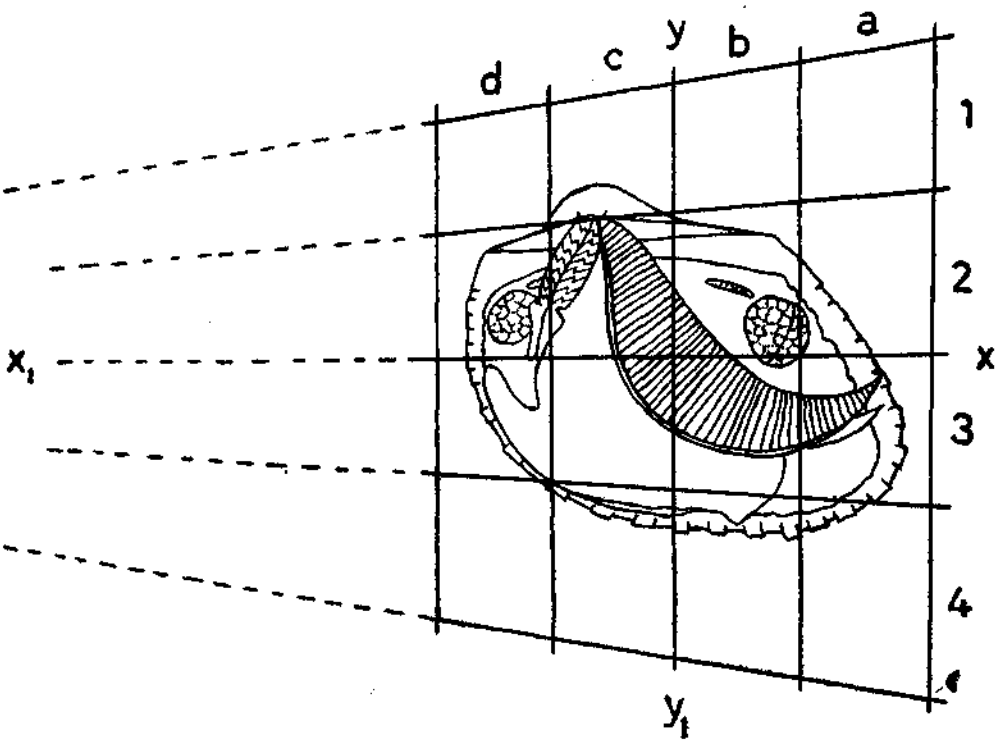


FIG. 2. *Anadara* (*Scapharca*) *anomala* (Rve.). "Transformation" based on *A. antiquata.*

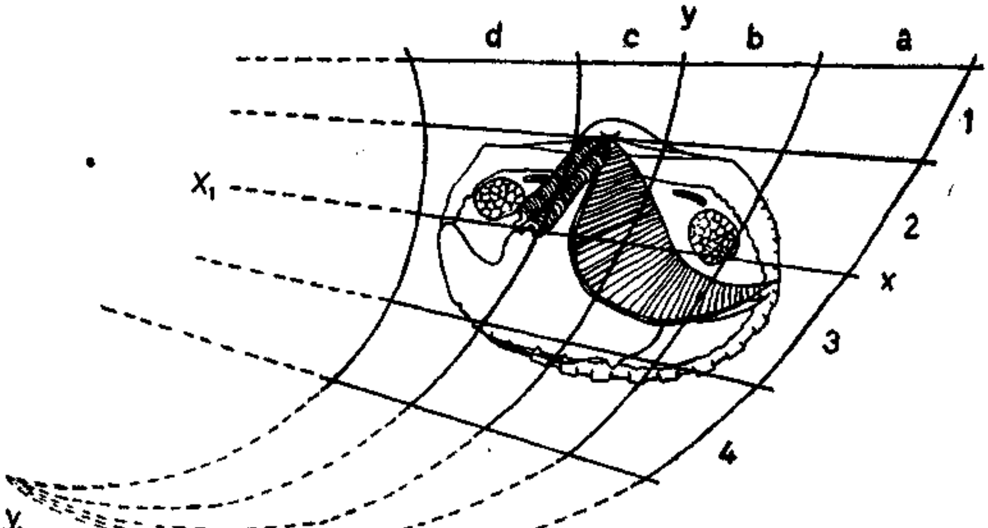


FIG. 3. *Anadara* (*Tegillarca*) *cuneata* (Rve.). "Transformation" based on *A. antiquata.*

nuous layer with chevrons appearing as the thickened regions and an inner (? discontinuous) layer for two portions, one on each side of the hinge mid-line. He further stated that unlike the majority of bivalves the arcid mantle isthmus was divided during ontogeny into two with the outer marginal folds of the left and right mantle lobes running across in the middle. According to Owen, the outer and inner layers of the ligament resulted, presumably, from an increase and decrease in the rate of secretion.

The anatomy of the ligament in the subgenera *Anadara* s.s., *Scapharca*, and *Tegillarca* was investigated here. Nine species of Malayan *Anadara* belonging to these 3 subgenera were studied. The anatomy of their ligaments is represented in Figs. 4, 5 and 6. The chevrons are obliquely arranged and are invariably present in all the species studied. However, they vary in number and development with different species (variations occur at the intra- and inter-subgeneric levels). The simplest, with one complete marginal chevron, is seen in *A. pilula* (Fig. 5C). *A. antiquata* and *A. secticostata* each of which has one complete and three incomplete chevrons (Figs. 4 A and 4 B). Two completely developed chevrons occur in *A. oblonga* (Fig. 6 B), and two complete *plus*

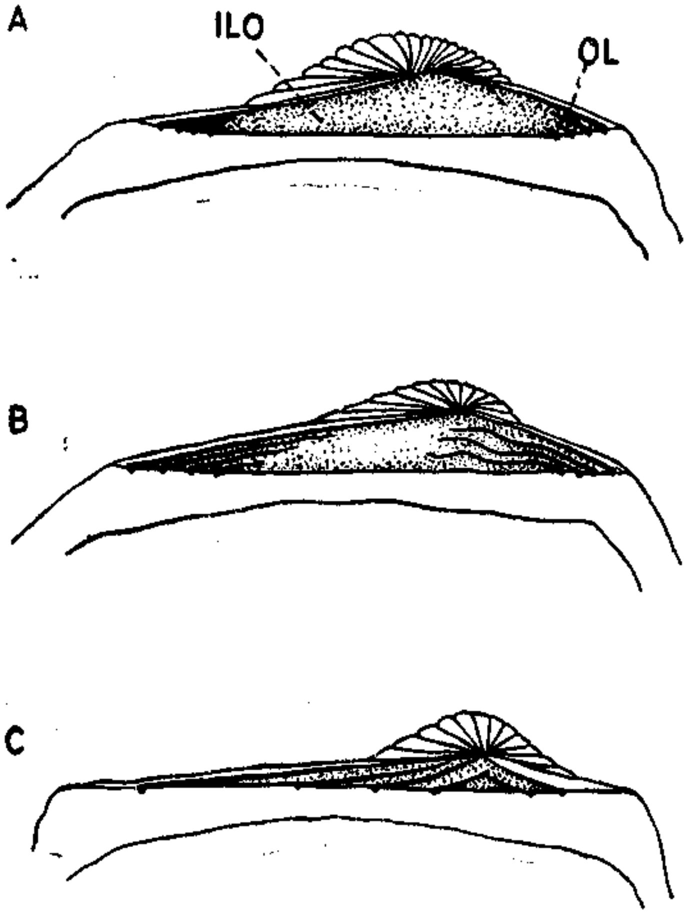


FIG. 4. A. *Anadara (Anadara) antiquata* (L.). The ligament in the left shell valve. B. *Anadara (Anadara) secticostata* (Rve.). The ligament in the left shell valve. C. *Anadara (Anadara) auriculata* (Lam.). The ligament in the left shell valve. OL, chevron (thickened regions of the outer layer); ILO, inner layer covered by a thin sheet of outer layer.

two incomplete ones occur in *A. auriculata* (Fig. 4 C). *A. anomala* has three complete chevrons and an incomplete one (Fig. 5 C). Four complete and one incomplete chevrons occur in *A. granosa* (Fig. 6 A) and four complete and two incomplete ones are found in *A. inaequivalvis* (Fig. 5 B). The species *A. cuneata* (Fig. 6 C) has the greatest number of chevrons (8 complete ones) among all the species investigated.

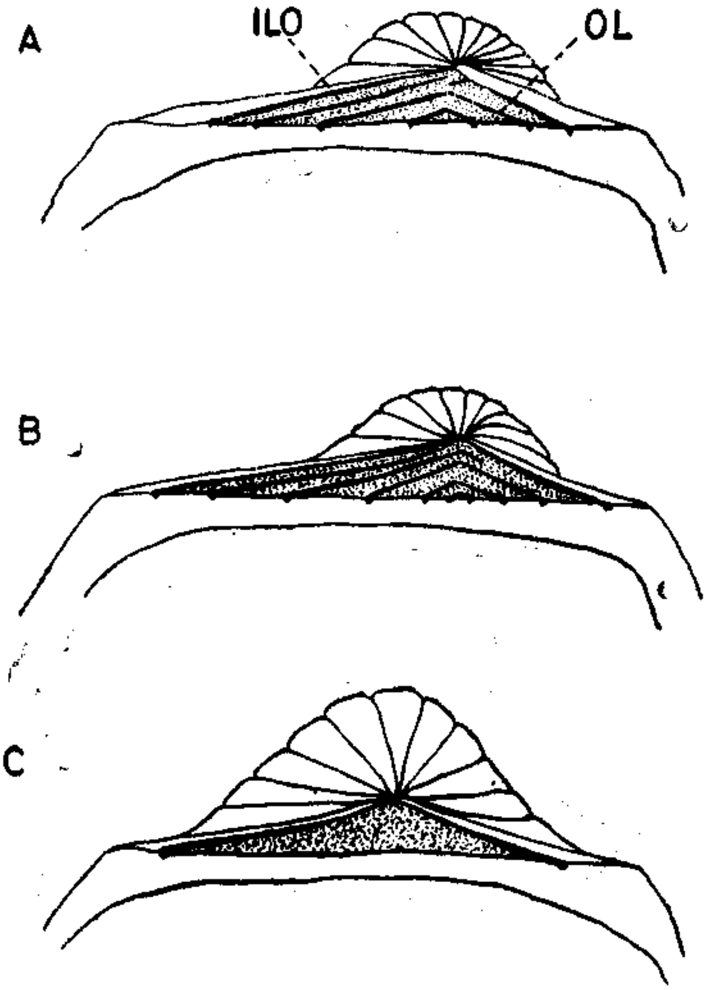


FIG. 5. A. *Anadara* (*Scapharca*) *anomala* (Rve.). The ligament in the left shell valve. B. *Anadara* (*Scapharca*) *inaequivalvis* (Brug.). The ligament in the left shell valve. C. *Anadara* (*Scapharca*) *pilula* (Rve.). The ligament in the left shell valve. OL, chevron (thickened regions of the outer layer); ILO, inner layer covered by a thin sheet of outer layer.

Figures 4, 5 and 6 are all of fully grown adult specimens. The juveniles or young adults show gradual development of the number of chevrons with age, with the older ones lying towards the outer margins of the ligament. Schenck and Reinhart (1938, p. 16) were in error when they reported that "(*Anadara*) *antiquata* is shown to have no true 'chevrons' but only a groove bounding the outer side of the ligamental area". This observation was possibly made on juvenile or young adult shells, in which full development of the chevrons has not occurred, and the first complete chevron was formed but abraded or torn away, thus leaving a "groove" (as described by Schenck and Reinhart) along the outer margins of the ligament in *A. antiquata.*

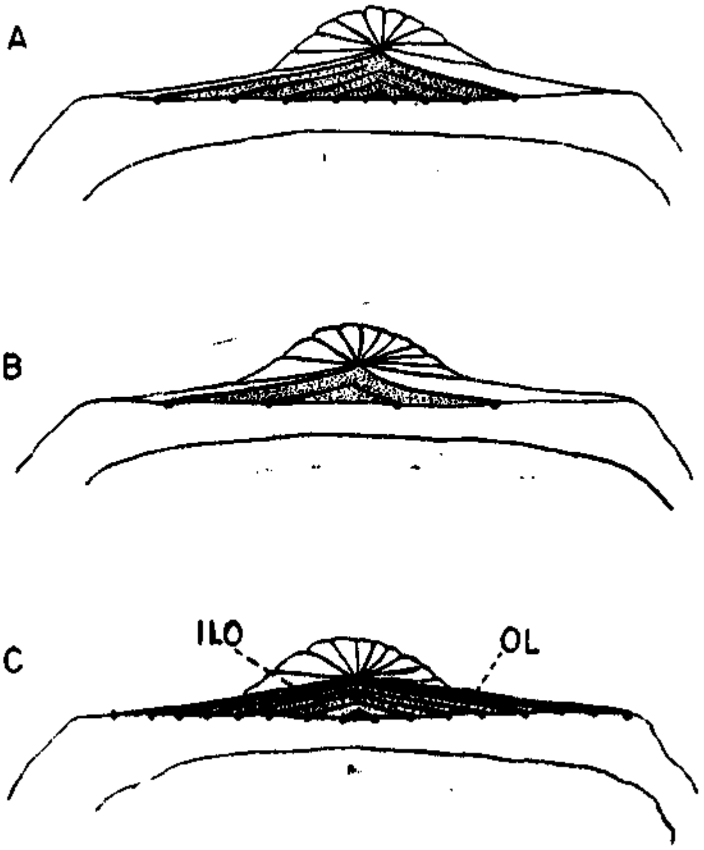


Fig. 6. A. *Anadara (Tegillarca) granosa* (L.). The ligament in the left shell valve. B. *Anadara (Tegillarca) oblonga* (Phil). The ligament in the left shell valve. C. *Anadara (Tegillarca) cuneata* (Rve.). The ligament in the left shell valve. OL, chevron (thickened regions of the outer layer); ILO, inner layer covered by a thin sheet of outer layer.

GEOLOGIC DISTRIBUTION

The geologic distribution of the subgenera of *Anadara* has been well studied by Schenck and Reinhart (1938) and may be summarised as follows:

Subgenus	*Range*
Anadara s.s.	Oligocene (early Tongrian) to Recent.
Scapharca	Oligocene to Recent.
Tegillarca	Miocene (Vigo) to Recent.
Larkinia	Oligocene (Vaqueros) to Recent.
Senilia	Miocene (?) to Recent.

The origin of *Senilia* is uncertain but it probably arose in the Miocene or Pliocene as reported by Dreger (1895).

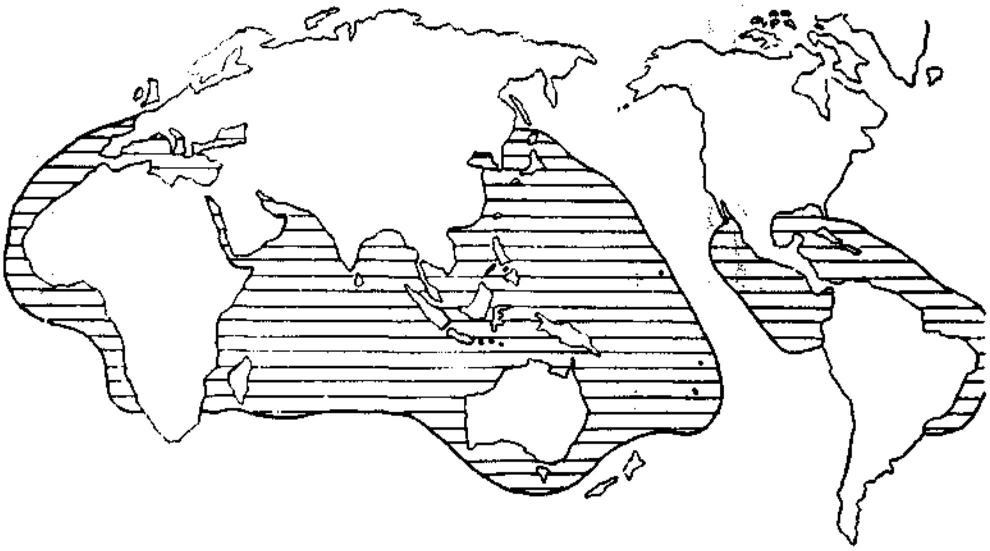


FIG. 7. Geographic distribution of the recent subgenus *Anadara* s.s.

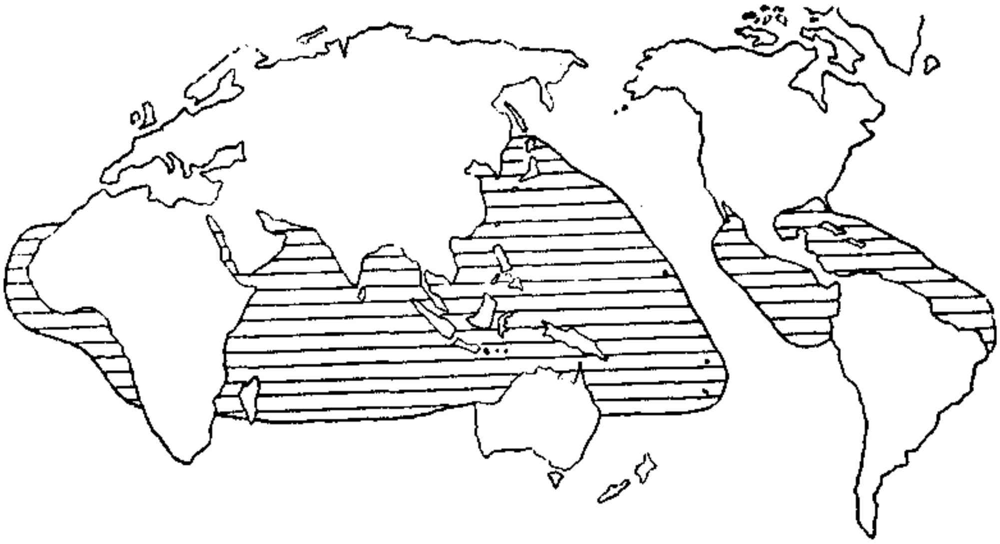


FIG. 8. Geographic distribution of the recent subgenus *Scapharca*.

GEOGRAPHIC DISTRIBUTION

Schenck and Reinhart (1938) have studied the geographic distribution of the fossil and recent *Anadara* s.s. (*see* Fig. 7 for distribution of recent *Anadara* s.s.). The recent distribution of *Scapharca, Tegillarca, Larkinia,* and *Senilia* is investigated in this study and reproduced in Figs. 8

and 9. It is found that *Scapharca* is world-wide in distribution but more restricted in latitude than *Anadara* s.s. The subgenera *Tegillarca, Larkinia,* and *Senilia* tend to be restricted to the Indo-West Pacific (Hornell, 1951; Lynge, 1909; Lim, 1963; Suvatti, 1938; Serene, 1937; Kuroda and Habe, 1951; Annandale and Prashad, 1924; Faustino, 1928; Iredale, 1939), Tropical America (Abbott, 1954; Rost, 1955), and West Africa (Nickles, 1950) respectively. The subgenus *Tegillarca* may possibly have a more limited distribution, namely, only west of India as the record of *A.* (*Tegillarca*) *cuneata* for East Africa given by Reeve (1844) is rather dubious.

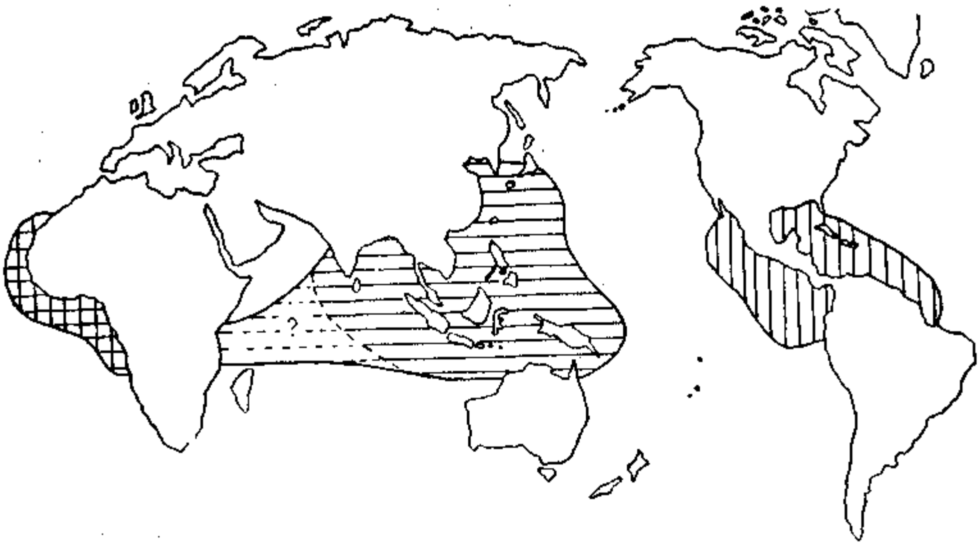


FIG. 9. Geographic distribution of the recent subgenera *Tegillarca, Larkinia,* and *Senilia.* Horizontal lines—*Tegillarca*, Vertical lines—*Larkinia*; Checked lines—*Senilia.*

DISCUSSION

The generic definition of *Anadara* by Gray (1847) has been recognised by Reinhart (1935). The confusion of its type species has been cleared with the ruling of the International Commission on Zoological Nomenclature in 1944 in favour of *A. antiquata* (L.). Hence Thiele's (1935) classification of *Anadara,* which he placed as a synonym of *Arca* s.s. becomes invalid.

Subgeneric proposals for the genus *Anadara,* based mainly on shell characters, have been made by Thiele (1935), Reinhart (1935), and Schenck and Reinhart (1938). They recognised five, six and four subgenera respectively (Table I). The last was reduced to four as a result of two subgenera (*Argina* and *Senilia*) being raised to generic level. The splitting of the *Anadara* series into distinct genera as done by Adams and Adams (1858) and Iredale (1939) is not a desirable solution as they only examined shell features. Information gathered from the past makes it possible to show phylogenetic relationships within the group by erecting five subgenera as laid out in Table I. My proposal of the subgenera of *Anadara* is similar to that of Schenck and Reinhart (1938) except that I have (*a*) combined *Scapharca* and *Cunearca,* (*b*) split up *Anadara* s.s. into *Anadara* s.s. and *Tegillarca,* and (*c*) retained *Senilia* as a subgenus while they have raised it to a genus. The reasons for these changes are as follows ;

TABLE I

Classification of Anadara, *sensu lato, according to various authors*

Adams and Adams (1858)	Thiele (1935)	Reinhart (1935)	Schenck and Reinhart (1938)	Iredale (1939)	Lim
Anomalocardia	*Arca* (*Arca*)	*Anadara* (*Anadara*)	*Anadara* (*Anadara*)	*Anadara*	*Anadara* (*Anadara*)
Scapharca	*Arca* (*Scapharca*)	*Anadara* (*Scapharca*)	*Anadara* (*Scapharca*)	*Scapharca*	
Lunarca	*Arca* (*Cunearca*)	*Anadara* (*Cunearca*)	*Anadara* (*Cunearca*)	*Potiarca*	*Anadara* (*Scapharca*)
	Arca (*Imparilarca*)			*Imparilarca*	
Senilia	*Arca* (*Senilia*)	*Anadara* (*Senilia*)	*Senilia*		*Anadara* (*Senilia*)
				Tegillarca	*Anadara* (*Tegillarca*)
		Anadara (*Larkinia*)	*Anadara* (*Larkinia*)		*Anadara* (*Larkinia*)
Argina	*Argina*	*Anadara* (*Argina*)	*Argina*		*Argina*

Subgenus = in brackets Genus = not in brackets

(*a*) *Dismissal of* Cunearca

The only significa character for separation of *Scapharca* and *Cunearca* was the discrepant sculpture of the shelll surface in the latter and not in the former (Reinhart, Iredale, 1939; others). This is only one external feailure when there are numerous similar characters such as from (mantle/shell and body), organs (labial palps), and geographic distribution of both the forms. In addition, there is the absence of gigantism (species of over 9 to 10 cm. in length) in *Cunearca* when compared to the other subgenera. Schenck and Reinhart (1938) stated that the "increase in size is doubtless too indefinite to have exact time value, but a trend from small to large species is nevertheless an hypothesis worth testing". This statement may suggest that a subgenus of *Anadara* must undergo a sufficient period of time to establish and stabilize itself as a group and eventually evolve a giant species. Reported maximum lengths of a giant species in the subgenera proposed are:

Species	Subgenus	Length (cm.)	Author
A. formosa (Sow.)	*Anadara* s.s.	12	Schenck and Reinhart (1938)
A. inaequivalvis (Brug.)	*Scapharca*	9·5	
A. cuneata (Rve.)	*Tegillarca*	10·5	
A. grandis (Brod. & Sow.)	*Larkinia*	?	
A. senilis (L.)	*Senilia*	13·5	Yonge (1955)

No specimens of *Cunearca* have been recorded to exceed 4 or 5 centimetres. The species *A. anomala* (Rve.) classified as a *Cunearca* with the definitions of Reinhart (1935) or Iredale (1939) showed no difference in form as indicated by transformation diagrams. Hence, in conclusion it is well to let *Scapharca* include all forms previously called *Cunearca.*

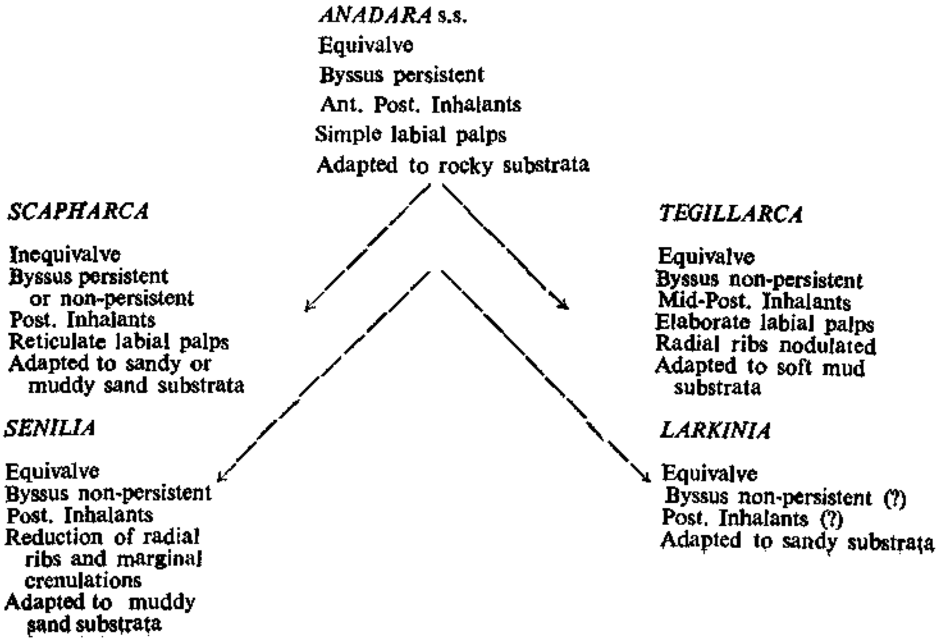
(*b*) *Acceptance of* Tegillarca

Iredale (1939) proposed the genus *Tegillarca.* His description for such a group can be accepted as a subgenus of *Anadara.* The key character is the presence of strong nodules or knobs on the radial ribs of both the left and the right shell valves. This is an adaptive structure as its typical members (*e.g.*, *A. granosa* and *A. cuneata*) are shallow burrowers in soft mud. The absence of any siphon required the animal to remain near the surface for survival. The numerous well-developed protruding rib nodules like those of *A. cuneata* serve to give an increased area of contact with the surrounding soft mud and subsequently assist in keeping the animal, which is rather large and heavy, from sinking too deep. The large species of other subgenera of *Anadara* do not have this problem since *A.* (*Senilia*) *senilis* lives in muddy sand (Yonge, 1955) and both *A.* (*Larkinia*) *grandis* and *A.* (*Scapharca*) *inaequivalvis* burrow into sand (Rost, 1955). The sand particles give a better resistance to sinking than soft mud.

The body of *Tegillarca* is appreciably transformed from *Anadara* s.s. as the transformation Figures 1 and 3 illustrate. Geologically, *Tegillarca* is younger than *Anadara* s.s. as they possibly originated in the Oligocene and Miocene respectively (Schenck and Reinhart, 1938). Thus, the former may have evolved from the latter. The geographic distribution differences as illustrated in Figs. 7 and 9, total absence of a byssus, and the labial palps (Lim, 1966) add further evidence in favour of the acceptance of *Tegillarca* as a subgenus. The shell of *Tegillarca* is highly variable in shape (Kotaka, 1953) but the nodule is an invariable character in all the species.

TABLE II

Possible evolution of the subgenera of Anadara



ANADARA s.s.
Equivalve
Byssus persistent
Ant. Post. Inhalants
Simple labial palps
Adapted to rocky substrata

SCAPHARCA

Inequivalve
Byssus persistent
or non-persistent
Post. Inhalants
Reticulate labial palps
Adapted to sandy or
muddy sand substrata

TEGILLARCA

Equivalve
Byssus non-persistent
Mid-Post. Inhalants
Elaborate labial palps
Radial ribs nodulated
Adapted to soft mud
substrata

SENILIA

Equivalve
Byssus non-persistent
Post. Inhalants
Reduction of radial
ribs and marginal
crenulations
Adapted to muddy
sand substrata

LARKINIA

Equivalve
Byssus non-persistent (?)
Post. Inhalants (?)
Adapted to sandy substrata

(*c*) *Retention of* Senilia

Schenck and Reinhart (1938) have raised *Senilia* to a genus on the grounds of shell characters. The use of shell characters are unreliable, as stated previously, if they are used solely. *Senilia* has only one species, *A. senilia*, which still exists in some areas of West Africa (Nickles, 1950). Yonge (1955) studied this species to some extent. Until more information on its internal organs (labial palps, etc.) becomes available, it is preferable to retain *Senilia* as a subgenus of *Anadara*.

The genus *Argina* Gray was at one time placed as a subgenus of *Anadara* (Reinhart, 1935). A generic status for *Argina* is more appropriate since the group was likely to have originated in late Eocene (Olsson, 1929), which is an earlier period than Oligocene, during which *Anadara* s.s. evolved.

A possible trend of the evolution of the subgenera of the genus *Anadara* is proposed in Table II.

Literature Cited

Abbott, R. T. 1954. *American Seashells.* D. van Nostrand Co. Inc., New York.

Adams, H. and A. Adams 1858. *The Genera of Recent Mollusca,* 2. J. van Voorst, London.

Annandale, T. N. and B. Prashad 1924. Report on a small collection of molluscs from the Chekiang Province of China. *Proc. Malac. Soc., London,* **16**: 27–49.

Cuvier, G. 1836. *Le regne animal,* 2, 3rd ed., Bruxelles.

Dreger, J. 1895. Vorkommen der Senilia senilia senilis Linne als Fossil. *Verhandlungun der k.k. geologischen Reichsanstalt, Jahrg., No.* 4, *Sitzung vom Maorz,* pp. 129–130.

Faustino, L. A. 1928. Summary of Philippine marine and freshwater mollusks. *Bur. Sci. Mon., Manila,* **25**: 1–384.

——— 1932. Recent and fossil shells from the Philippine Islands. *Philippines J. Sc., Manila,* **49**: 543–549.

Grabau, A. W. and S. G. King 1928. Shells of Peitaiho. *Handbook Soc. Nat. Hist., Peking,* **2**: 1–280.

Graham, A. 1949. The molluscan stomach. *Trans. Roy. Soc., Edinb.,* **61**: 737–776.

Gray, J. E. 1847. List of the genera of recent Mollusca, their synonyms and types. *Proc. Zool. Soc. London.* pp. 129–206.

Hornell, J. 1951. *Indian molluscs.* Bombay Nat. Hist. Soc. publication.

Iredale, T. 1939. Mollusca, Part 1. *Gt. Barrier Reef Exped.* 1928–29 *Scient. Reps.,* **5**: 209–425.

Jackson, R. T. 1890. Phylogeny of the Pelecypoda. *Mem. Bost. Soc. Nat. Hist.,* **4**: 277–400.

Kotaka, T. 1953. Variation of Japanese *Anadara granosa. Trans. Paleont. Soc., Japan,* **10**: 31–36.

Kuroda, T. and T. Habe 1952. *Check List and Bibliography of the Recent Marine Mollusca of Japan.* Hosokawa Printers, Tokyo.

Lim, C. F. 1963. A preliminary illustrated account of mangrove molluscs from Singapore and South-West Malaya. *Malayan Nature J.,* **17**: 235–240.

——— 1966. A comparative study on the ciliary feeding mechanisms of *Anadara* species from different habitats *Biol. Bull.,* **130**: 106–117.

Lynge, H. 1909. *The Danish Expedition to Siam.* 4. *Marine Lamellibranchia.* Bianco Lunos Bogtrykkeri, Copenhagen.

Nickles, M. 1950. Mollusqucs testaces marine de la Cote occidentale d'Afrique. *Manuels Ouest-Africains, Bd.* 2, *Paris.*

Nyst, P. H. 1836. *Recherches sur les Coquilles fossiles de Housselt et de Kleyn-Spauwen.* Gand.

Olsson, A. 1929. Contributions to the Tertiary paleontology of Northern Peru. *Bull. Amer. Paleont.,* **15**: No. 57.

Owen, G. 1959. The ligament and digestive system in the taxodont bivalves. *Proc. Malac. Soc. London,* **33**; 215–223.

Pathansali, D. and M. K. Soong 1958. Some aspects of cockle (*Anadara granosa* L.) culture in Malaya. *Proc. Indo-Pacific Fish. Council*, **8** (2): 26–31.

Purchon, R. D. 1958. Phylogeny in the Lamellibranchia. *Proc. Centenary and Bicentenary Congr. of Biol., Singapore*, pp. 69–82.

Reeve, L. 1844. Monograph of the genus *Arca*. *Conchologica Iconica*, **2**.

Reinhart, P. W. 1935. Classification of the pelecypod family Arcidae. *Bull. Mus. Hist. Nat. Belg.*, **11** (13): 1–68.

Rost, H. 1955. A report on the family Arcidae (Pelecypoda). *Allan Hancock Pacific Exped.*, **20** (2): 175–248.

Sato, T. 1931. Untersuchungen am Blut der gemeinen japanischen Archemuschel (*Arca inflata* Rve.). *Z. vergl. Physiol.*, **14**: 763–783.

Schenck, H. G. and P. W. Reinhart 1938. Oligocene arcid pelecypods of the genus *Anadara*. *Mem. Mus. Hist. Nat. Belg.*, **14** (2) : 1–73.

Serene, R. 1937. Inventaire des invertebres marine de l'Indochine (1 liste). *Inst. Oceanographique de l'Indochine*, **30**: 1–83.

Stasek, C. R. 1963. Orientation and form in the bivalved Mollusca. *J. Morph.*, **112**: 195–214.

Sullivan, G. E. 1961. Functional morphology, micro-anatomy, and histology of the 'Sydney Cockle', *Anadara trapezia* (Deshayes). *Aust. J. Zool.*, **9**: 219–257.

Suvatti, C. 1938. *Molluscs of Siam*. Bureau of Fisheries, Bangkok.

Thiele, J. 1935. *Handbuch der Weichtierkunde*, 3 teil, Jena.

Thompson, D. W. 1942. *On Growth and Form*. Cambridge.

Vaillant, L. 1865. Recherches sur la famille des Tridacnides. *Ann. Sci. Nat. Zool.*, **4**: 65–172.

Yonge, C. M. 1952. The protobranchiate Mollusca, a functional interpretation of their structure and evolution. *Phil. Trans. (B)*, **230**: 79–147.

——— 1953. The monomyarian condition in the Lamellibranchia. *Trans. Roy. Soc., Edin.*, **62**: 443–478.

——— 1955. A note on *Arca (Senilia) senilis* Lam. *Proc. Malac. Soc., London*, **31**: 202–208.

——— 1958. Evolution within the bivalve Mollusca. *Proc. 15th Intern. Congr. Zool. Sect.* 4, Paper 26.

——— 1962 *a*. On the primitive significance of the byssus in the Bivalvia and its effects in evolution. *J. Mar. Biol. Ass., U.K.*, **42**: 113–125.

——— 1962 *b*. On *Etheria elliptica* Lam. *Phil. Trans. (B)*, **244**: 423–458.

Yoshida, H. 1957. Early life-history of useful bivalves in the Areake Sea. 2. (*Anadara granosa bisinensis* and *Simonovacula constricta*). *J. Shimonoseki Coll. Fish.*, **6**: 347–352.

CYTOTAXONOMY OF SPECIES OF CLAMS (*MERCENARIA*) AND OYSTERS (*CRASSOSTREA*)[1]

R. W. MENZEL

Department of Oceanography, Florida State University, U.S.A.

ABSTRACT

The northern quahog clam (*Mercenaria mercenaria*) and the southern quahog (*M. campechiensis*) occurring along the eastern coasts of North America are sympatric in part of their ranges. *M. mercenaria* is usually confined to the more saline bays and inlets whereas *M. campechiensis* is restricted to the outer coastal waters in the more northern part of the range but occurs in both habitats in the southern part. The two species hybridize readily in the laboratory and the F_1's are fertile; the four F_2 combinations have been growing over two years. Attempts will be made to spawn these clams during the spring of 1968. Collections made, where the two species occur together, indicate, based on shell morphology, that some hybridization is occurring in nature. Chromosome studies of the species and hybrids have been made at meiosis and mitosis and the chromosomal behaviour of the hybrids appears normal.

The economic importance of oysters has resulted in widespread introduction of species to many areas. Species determination, based on shell morphology, may be confusing because the shape of the shell is determined partly by the substrate and the ecological conditions. Attempts are being made to cross species from as many areas as possible. It has been known for some time that crosses between *C. virginica* and *C. gigas* will cause cleavage but it has been reported that the embryos die within several days at the straight line stage. All species crosses made so far have caused cleavage with limited success in rearing the hybrids, except crosses with *C. commercialis*, from Australia. This species differs morphologically from the other species seen by having denticles and depressions along the anterior margins of the shell, similar to *Ostrea*. Chromosome studies have shown that all species of oysters examined have a 2 *n* number of 20. Preliminary analyses of mitosis in the F_1's show no apparent abnormalities.

INTRODUCTION

FOR the past several years, the cytotaxonomic relationships between species of quahog clams, *Mercenaria mercenaria* (L.) and *M. campechiensis*(Say), and more recently between species of oysters of the genus *Crassostrea* have been studied. For both groups of pelecypods, the work involved laboratory and field rearing of laboratory spawned mollusks and chromosome analyses.

These investigations have been conducted at the Marine Laboratory, Department of Oceanography, Florida State University (Fig. 1, M.L.) and the campus of the Florida State University, and have included both laboratory and field experiments. This work is supported by the National Science Foundation, Grant Number GB-5034, entitled "Cytotaxonomy of Related Species of Pelecypod Mollusks" awarded to the writer. Mr. Theodore P. Ritchie and Mr. Harold Sims very ably assisted in the spawning and rearing of the mollusks.

Quahog Clams (*Mercenaria* Spp.)

Abbott (1954) separates the northern quahog (*M. mercenaria* L.) and southern (*M. campechiensis* Gmelin) on shell morphology. The northern species has a characteristic smoothish, glossy area on the exterior centre of the valves, whose interiors are white and commonly have purple stains. The

---

[1] Contribution No. 222, Department of Oceanography, Florida State University, Tallahassee, Florida 32306, U.S.A.

entire lunule is three-fourths as wide as long. He recognizes two subspecies ; *M. m. texana* (Dall) originally described by Dall (1902) as *M. campechiensis texana*, with large irregular coalescing flat-topped concentric ribs and *M. m. notata* (Say) with external zigzag brown mottlings which were shown by Chanley (1959) to be inherited in *M. mercenaria* in a Mendelian ratio. The southern quahog lacks the smooth central area on the exterior of the shells and has persistent raised growth

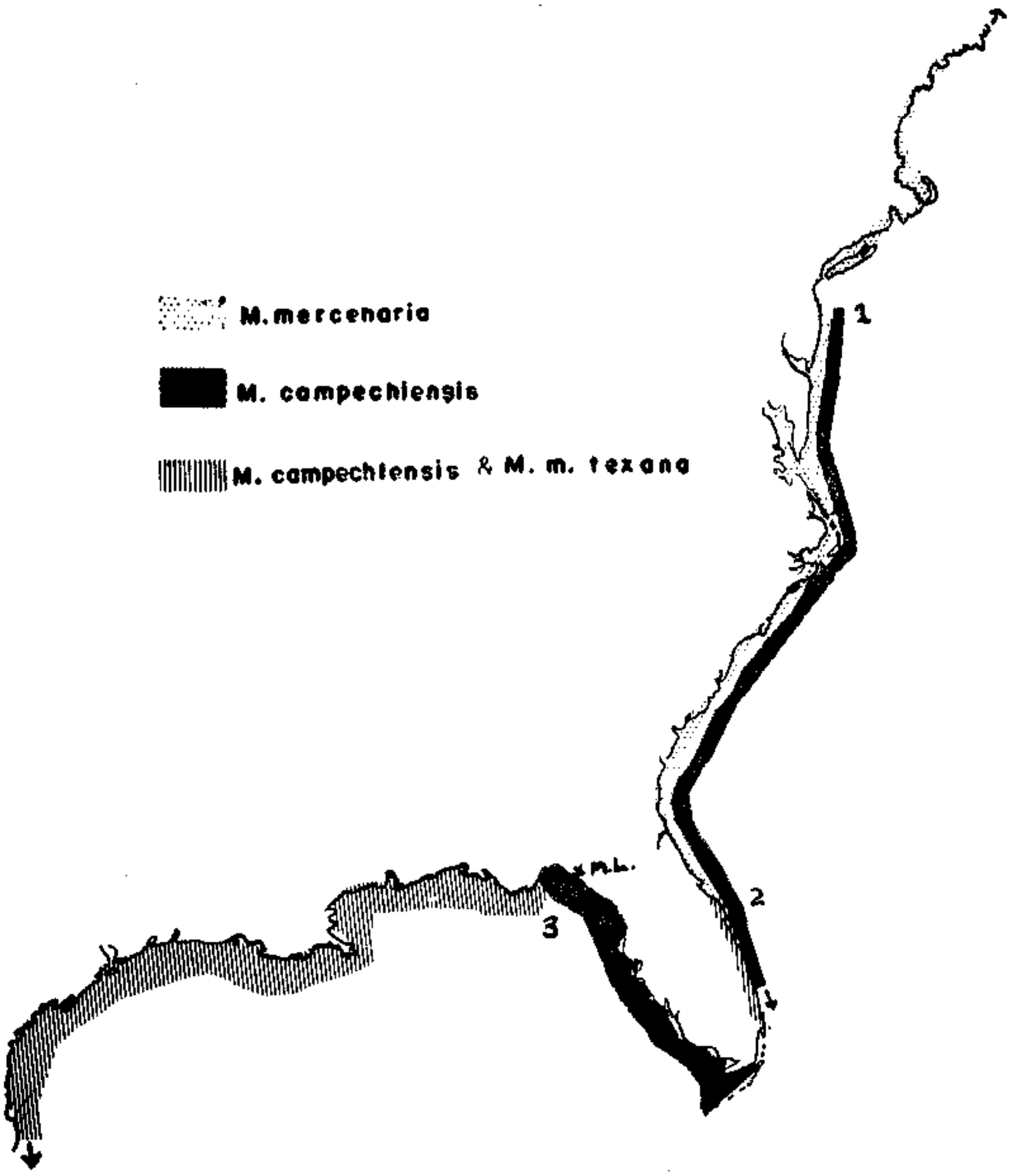


FIG. 1. Distribution map of *Mercenaria mercenaria*, *M. m. texana* and *M. campechiensis*. (1) Northern limit of *M. campechiensis*. (2) Beginning of *M. m. texana* and where *M. campechiensis* occurs inshore. (3) Beginning of *M. m. texana* along with *M. campechiensis*. M. L. = Marine Laboratory (Alligator Harbor) of Florida State University.

ridges and more obese shells. The interiors of the valves are white with no purple stains and the entire lunule is usually as wide as long.

Menzel and Menzel (1965) observed that : (1) fast growing specimens of northern quahogs, less than 25-35 mm. long, lack the characteristic glossy, smooth area on the exterior of the valves; (2) when grown under the same conditions, small specimens of *M. mercenaria* have heavier shells than specimens of *M. campechiensis* of the same length ; (3) otherwise typical individuals of the southern quahog occur with internal purple stains; (4) the characteristic brown mottlings of the subspecies *M. m. notata* are often found in typical *M. campechiensis*. Meiosis and mitosis in the F_1 hybrids between the two species appeared perfectly normal (both species of clams have $2n = 38$).

When laboratory-spawned progenies of the two species of clams and their F_1 hybrids were grown under the same conditions (Menzel, 1961, 1962) the southern species had a much greater annual shell growth than the northern. The period of greatest shell increase for both species and hybrids was in the spring and fall ; the northern species had less growth in the winter and a cessation during the warmest months of the summer ; the southern species continued good shell growth during the warmest period but stopped during the coldest. The F_1 hybrids had a growth rate intermediate between those of the parents, but closer to that of the southern parent, during the first two years of observation. The strain of *M. mercenaria* used was native to Long Island Sound, New York, and that of *M. campechiensis* was native to Alligator Harbor, Florida. Further observations (unpublished) showed that later the hybrids surpassed in shell size the originally faster growing southern parent.

The northern quahog is of considerable economic importance. Those of the most valuable size, "cherrystones" and "littlenecks" (55-80 mm. long), are used for the half-shell trade, either eaten raw or steamed. This species will remain tightly closed out of the water up to two weeks especially under refrigeration. The southern species, on the other hand, will gape, lose its shell liquor, and spoil within several days, even under refrigeration (Menzel and Sims, 1961).

METHODS

Dr. V. L. Loosanoff supplied the first laboratory-reared specimens of both species as well as laboratory-reared F_1 hybrids between the two species. Subsequent progenies were reared in Florida. Living specimens of *M. mercenaria* were obtained from Clifford Varin, Great South Bay, New York ; Theodore P. Ritchie, Delaware Bay ; Jay D. Andrews, lower Chesapeake Bay ; Hugh Porter, North Carolina ; Robert Luntz, South Carolina. *M. campechiensis* were obtained from Hugh Porter, North Carolina, and from Jack Taylor and Harold Sims from the Tampa Bay area of Florida on the Gulf of Mexico side. I have collected both species of clams from both the east and west coasts of Florida and examined shell collections at the Gulf Coast Research Laboratory (Mississippi) and Harvard University.

The two species and the hybrids were crossed in various combinations and when the progeny reached a suitable size (Menzel, 1961), they were planted in the adjacent water for further observations.

OBSERVATIONS AND DISCUSSION

Reciprocal F_1 hybrids between *M. campechiensis* and *M. mercenaria* are fertile and the four possible types of F_2 hybrids have been reared in our laboratory using techniques modified from those of Loosanoff and Davis (1963). After planting, monthly observations were made on growth and shell morphology. The growth of the F_2's compared very favorably with those of the parent species and also the F_1 hybrids (Menzel, 1961, 1962). Shell length increase is shown in Table I for the F_2 hybrids.

TABLE I

Growth (length in mm.) of F_2 clams

Spawned	23 March, 1965	23 March, 1965	21 March, 1965	24 Feb. 1966
Date—Measured	(♀X) (♂X)	(♀$\bar{X}$) (♂$\bar{X}$)	(♀$\bar{X}$) (♂X)	(♀X) (♂$\bar{X}$)
15 Oct. 1965	5·0	5·0	5·0	
15 Nov. 1965	6·7	6·7	7·0	..
15 Dec. 1965	8·3	8·3	8·9	..
15 Jan. 1966	9·7	9·7	10·7	..
15 Feb. 1966	11·2	11·2	12·6	..
15 March 1966	12·8	12·7	13·9	..
15 April 1966	17·8	18·9	15·9	..
15 May 1966	21·1	23·0	21·0	5·0
15 June 1966	25·6	26·3	26·0	7·6
15 July 1966	29·5	30·3	30·6	14·0
15 Aug. 1966	33·5	36·0	32·5	17·0
15 Sep. 1966	34·5	39·4	35·3	20·5
15 Oct. 1966	36·8	40·1	38·9	24·9
15 Nov. 1966	39·7	42·1	42·4	28·2
15 Dec. 1966	41·2	45·6	44·2	30·2
15 Jan. 1967	43·4	46·0	44·2	30·3
15 Feb. 1967	43·4	47·6	46·0	31·8
15 March 1967	43·4	47·8	46·0	32·5
15 Apr. 1967	44·6	49·3	48·4	34·3
15 May 1967	47·0	52·6	49·5	36·4
15 June 1967	50·0	55·5	52·0	39·3
15 July 1967	52·5	56·3	54·0	44·7
15 Aug. 1967	54·6	59·4	59·8	48·1
15 Sep. 1967	56·5	60·4	60·9	51·1
15 Oct. 1967	59·2	62·8	61·0	52·4

X = ♀ *M. campechiensis* × ♂ *M. mercenaria* $\bar{X}$ = ♀ *M. mercenaria* × ♂ *M. campechiensis*

Monthly examination of the external shell morphology revealed that when the clams were 35-45 mm. long, some of the clams began to have smooth central areas (Figs. 2, 3, 4, No. 4) characteristic of *M. mercenaria*. Smaller clams had the persistent growth ridges typical of the southern quahog and found in small specimens of the northern species. By the time the F_2's were two years old and averaged at least 50 mm. long, almost seventy-five per cent had the smooth area ; the rest had the more or less typical shell morphology of *M. campechiensis*. Those F_2's (Figs. 2, 3, 4, No. 4) with the smooth area were compared with the parent species and other collections. Their shell morphology most resembled those clams that have been designated as subspecies *M. m. texana* (Figs. 2, 3, 4, Nos. 5, 6).

The ranges reported for species of clams along the Atlantic and Gulf Coasts of the United States have been compiled from Abbott (1954), Cummings (1966), Merrill and Ropes (1967), Porter and Chestnut (1960), collections of the Harvard Museum, (M.C.Z.), and personal observations (Fig. 1). Typical *M. mercenaria* (Figs. 2, 3, 4, No. 2) occurs only inshore on the Atlantic Coast (Fig. 1). Many of the *M. mercenaria* found south of St. Augustine, Florida (Fig. 1, No. 2), especially those from the area two-thirds down the Florida Coast, would be classified as the subspecies *M. m. texana* (Figs. 2, 3, 4, Nos. 5, 6). Judging from specimens in the Harvard Museum (M.C.Z.) and limited first-hand observations, only the subspecies *M. m. texana* is found in the Gulf of Mexico from Apalachicola Bay and Panama City, Florida, (Fig. 1, No. 3) westward and southward to Texas. (A single specimen of *M. m. texana* in the Harvard Museum was collected at Campeche, Mexico.)

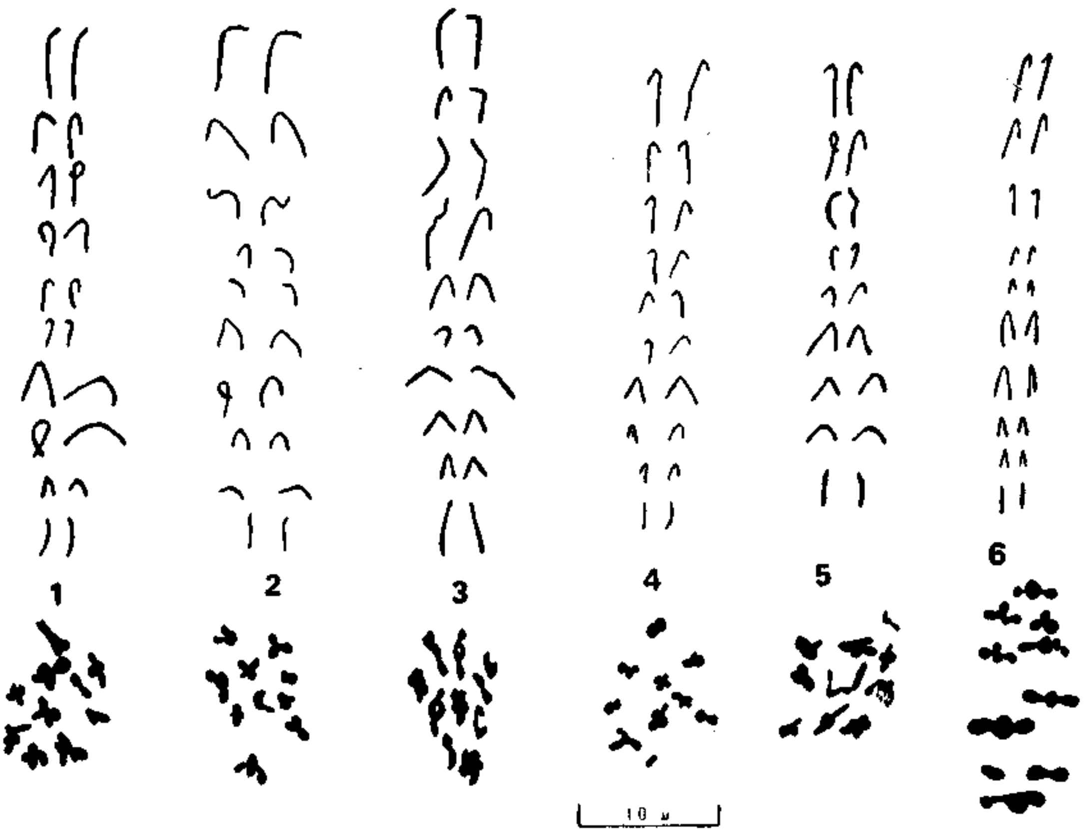


FIG. 5. Mitotic (upper ideograms) and meiotic (lower) chromosomes of six species of *Crassostrea*.
(1) *C. angulata*, (2) *C. commercialis*; (3) *C. gigas*; (4) *C. iredalei*; (5) *C. rhizophorae*; (6) *C. virginica*.

In the more northern part of its range, southward to about the middle of the Atlantic Coast of Florida, *M. campechiensis* occurs only offshore. From the vicinity of Cape Kennedy southward it is also found inshore, growing in juxtaposition with more or less typical *M. mercenaria* and *M. m. texana*. *M. campechiensis* occurs both inshore and offshore in the Gulf of Mexico.

Porter and Chestnut (1960) suggest that salinity tolerance may separate the northern and southern clams in the region of North Carolina, restricting *M. campechiensis* to the offshore more saline area, but this would not seem to be the case as *M. campechiensis* occurs in both habitats in the Gulf of Mexico area as well as the lower Atlantic Coast of Florida. It seems more likely that temperature is a factor and that the southern form cannot withstand the extreme winter temperatures in the more northern inshore area. The ability of stenohaline animals to adjust better osmotically to lowered salinities in warmer waters may be a factor also.

It is puzzling that *M. m. texana* has not been seen in the area from Key-West to Apalachicola Bay, Florida, when it has been collected in the same latitude from the Atlantic Coast of Florida and the Western Gulf of Mexico.

The juxtaposition of the southern and northern forms along the lower east coast of Florida allows ample opportunity for hybridization. The resemblance of the laboratory-reared F_2 hybrids

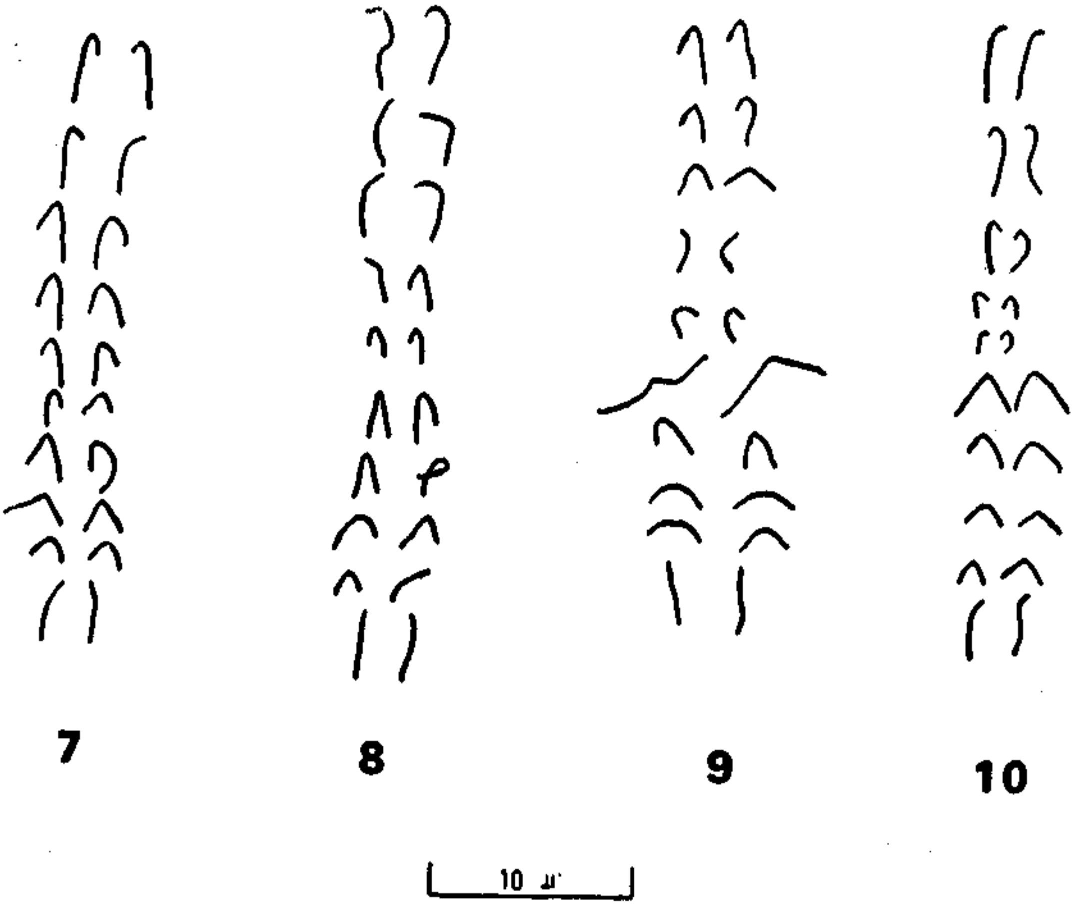


FIG. 6. Mitotic chromosomes (ideograms) of four hybrids of *Crassostrea*; (7) ♀ *C. angulata* × ♂ *C. gigas*; (8) ♀ *C. angulata* × ♂ *C. virginica*; (9) ♀ *C. gigas* × ♂ *C. virginica*; (10) ♀ *C. virginica* × *C. rhizophorae*.

M. m. texana suggests that the latter may be of hybrid origin. However, typical northern forms have not been seen from the Gulf of Mexico. An attempt to rear progeny from *M. m. texana* was unsuccessful (technical difficulties were experienced during the season of 1967). If the subspecies is really a naturally occurring hybrid population there might be some segregation toward the parent types. (Laboratory-reared F_2's have shown some segregation). It may take several generations of selective breeding to obtain the parent types.

The subspecies *M. m. notata* has no validity. Chanley (1959) showed that he could increase shell coloration by selective breeding. In some areas this character occurs very frequently in *M. campechiensis*. F_1 hybrids between the species, when one of the parents had this character, also have the coloration to some degree.

If one accepts the criterion of a species, that breeding will produce fertile offspring, then the northern and southern clams are conspecific. No chromosome aberrations occurred when the two forms were crossed. The morphological characters used to separate the two overlap in some instances. There is a strong indication that hybridization is occurring, based on the similar morphology of the subspecies *M. m. texana* with the laboratory-reared F_2 hybrids.

Oysters (*Crassostrea* Spp.)

It is generally accepted that the family Ostreidae contains only three living genera *Crassostrea*, *Ostrea*, and *Pycnodonta* (Gunter, 1945 ; Thomson, 1954). My studies are confined to the genus *Crassostrea* because of its wide distribution and because it lends itself to laboratory culture involving hybridization.

Species of *Crassostrea* are often very difficult to determine from their shell morphology in that the same species will have varied shell shapes according to the ecological conditions of substrate, salinity, etc. Species of oysters have been widely disseminated by man. There are good records of some introductions of exotic species in modern times, but undoubtedly many have been lost in antiquity. This may further confound the species determination.

One method to help resolve some of the taxonomic difficulties is to rear hybrids of the several species and determine the characteristics of these hybrids from a cytotaxonomic standpoint. Living collections of *Crassostrea* were obtained through the kindness of the following individuals :

C. angulata (Lam.) from England, Peter Walne ; *C. commercialis* (Iredale and Roughly) from Australia, Peter Wolf ; *C. gigas* (Thunberg) from the State of Washington (originally from Japan), Kenneth Chew and Ronald Westley ; *C. iredalei* (Faustino) from the Philippines, Narcisso Ligeralde; *C. rhizophorae* (Guilding) from Canal Zone and Puerto Rico, Horace Loften and Luis Almodovar. *C. virginica* (Gmelin) were collected locally. R. Tucker Abbott kindly identified *C. iredalei.*

METHODS

All possible reciprocal crosses were attempted among the six species. The oysters were spawned using heat treatment (Loosanoff and Davis, 1963), or the gametes were removed ("stripped") and mixed in sea-water. The latter method proved more satisfactory, especially in the hybridization attempts. At the time of crossing each species was selfed to serve as controls. The larvae were cultured in five gallon containers to which filtered water and algal food were added. The water was changed and new food added every second day. Strings of clean shells were suspended in the containers as cultch when the larvae reached the late umbo stage. If attachment occurred the oyster spat were suspended in aquaria with running sea-water. The species of oysters were kept in tanks with running sea-water and the outlets from these as well as from the laboratory reared spat were connected to a pit in the ground to prevent the introduction of exotic species and possible disease organisms into nearby waters.

At the time of attempted crossing, eggs and zygotes were preserved in acetic-ethanol and later stained with aceto-carmine in squash preparations and examined under a Zeiss phase contrast microscope. The procedure was similar to that employed for clams (Menzel and Menzel, 1965). Drawings were made of the chromosomes with aid of a camera lucida.

OBSERVATIONS AND DISCUSSION

All the reciprocal crosses of the species of oysters caused cell cleavage, presumably fertilization, except the crosses with *C. commercialis* whose gametes were incompatible with those of all other species. All of the hybrids lived to the umbo stage and some went through metamorphosis and attached. The failure of others to attach, in most instances, was probably due to technical difficulties rather than something inherent in the cross ; often the controls, *i.e.*, the selfed species, perished before attachment.

Growth rates of the hybrids and some of the controls are given in Table II. The growth of the oyster spat in the laboratory is not as great as it would be in open water. Selfed *C. virginica*, grown outside in adjacent water, are almost twice as large during the same period.

TABLE II

Growth (length in mm.) of oyster species and their hybrids during 1967, Temperature range 25–30° C.

Type*	V × V		G × V		A × V		A × G		G × A		R × R		R × A		R × V	
Date—Attached	6/5		5/15		7/1		8/5		8/18		8/3		8/28		8/28	
Date Measured	Size	#	Size	#	Size	#	Size	#	Size	#	Size	#	Size	#	Size	#
6/22	—	—	9·7	58	—		—		—		—		—		—	
7/5	8·5	50	20·9	56	—		—		—		—		—		—	
7/31	18·8	43	33·5	45	17·8	3	—		—		—		—		—	
8/9	20·0	42	34·8	43	18·8	3	—		—		6·4	20	—		—	
9/8	21·8	39	36·7	42	22·8	3	4·1	100+	4·5	17	12·7	17	3·0	100+	2·5	100+
10/5	27·3	39	36·8	33[l]	27·5	3	11·9	75[n]	11·9	16	18·0	16	8·1	90[n]	6·5	100[n]

* V × V = *C. virginica* × *C. virginica*
G × A = ♀ *C. gigas* × ♂ *C. virginica*
A × V = ♀ *C. angulata* × ♂ *C. virginica*
A × G = ♀ *C. angulata* × ♂ *C. gigas*
G × A = ♀ *C. gigas* × ♂ *C. angulata*
R × R = *C. rhizophorae* × *C. rhizophorae*
R × A = ♀ *C. rhizophorae* × ♂ *C. angulata*
R × V = ♀ *C. rhizophorae* × ♂ *C. virginica*

l Larger oysters used for fertilization attempt.
n Culled to fewer numbers.

The cross *C. gigas* × *C. virginica* was the first attempted and the first successful one made. This is the first time this hybrid has been reported ; Davis (1950) and Imai, Sato, Saki, and Yuki (1950) were unsuccessful in obtaining it. (I understand that the hybrid between *C. angulata* and *C. gigas* has been made in Japan, but I have not seen the published report.)

All six species had a diploid number of 20 chromosomes (Fig. 5). Galtsoff (1964) and several workers whose observations he summarized reported diploid numbers ranging from 8 to 24. Kobayashi (1954) reported $2n = 24$ for two Japanese species. These workers used sections which do not always give an accurate analysis. All of the species have morphologically similar mitotic chromosomes (Fig. 5). Mitosis in the hybrids (Fig. 6) appeared normal except when C. *iredalei* was used as one of the parents, especially as the female parent (Fig. 7). With *C. iredalei* as one of the parents, mitotic figures with haploid, triploid, and hexaploid numbers were seen ; sometimes up to 90% of the cells examined were anomalous. In one mitotic anaphase only five chromosomes were seen at each pole (Fig. 7, No. 16).

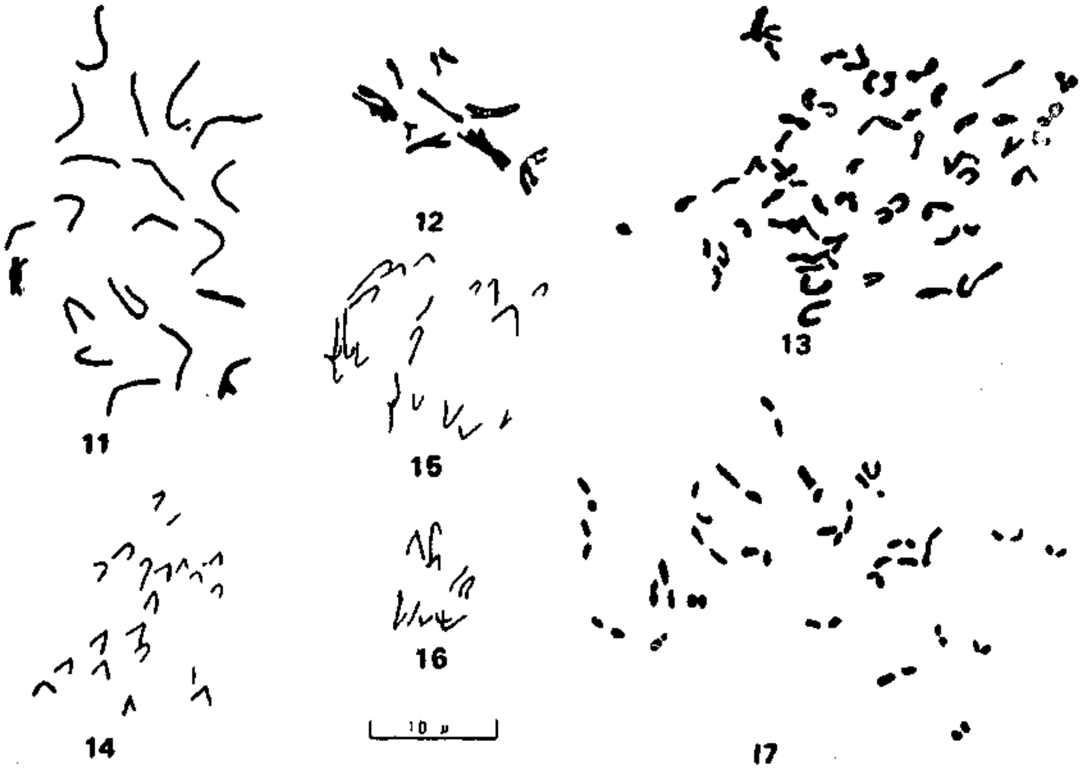


FIG. 7. Mitotic chromosomes occurring when *C. iredalei* was used as one of the parents in crosses. (11) ♀ *C. gigas* × ♂ *C. iredalei*. Showing some abnormality; from a four-cell embryo in which two were haploid. (12) ♀ *C. iredalei* × ♂ *C. gigas*. Abnormal from a two-cell embryo; other was diploid and more or less normal. (13) ♀ *C. iredalei* × ♂ *C. angulata*. Hexaploid; other zygotes from this cross were about 75% haploid, triploid of hexaploid. (14) ♀ *C. iredalei* × ♀ *C. virginica*. Seemingly "normal" anaphase. (15) ♀ *C. iredalei* × ♂ *C. virginica*. Haploid anaphase. (16) ♀ *C. iredalei* × ♂ *C. virginica*. Sub-haploid, *i.e.*, five chromosomes to each pole in anaphase. (17) ♀ *C. iredalei* × ♂ *C. virginica*. Triploid from four-cell zygote; other three haploid.

The F_1 hybrids of *C. gigas* × *C. virginica*, have become sexually mature and on September 26, 1967, six of these were sacrificed and stripped. The gametes were used for selfing to make F_2 zygotes and back-crossed reciprocally to *C. virginica*. Meiosis in the F_1's and mitosis in the F_2's and back-crosses appeared normal.

The incompatibility of the gametes of *C. commercialis* with those of the other species is interesting. This is the only species of *Crassostrea* I have studied that has denticles along the anterior margins of the shell. Ranson (1948) and Thomson (1954) list a total of seven species of *Crassostrea*[2] with denticles, but this condition is more typical of the genus *Ostrea.* (There are three species of *Ostrea* in our area, all with denticles.)

The fertilization, cell cleavage, larval development, metamorphosis and attachment of the hybrids, with apparently normal mitosis and meiosis in the F_1 and mitosis in the F_2 (*C. gigas* × *C. virginica*) would suggest that the species *C. angulata*, *C. gigas*, *C. rhizophorae* and *C. virginica* are fairly closely related. The anomalies found in the chromosome analyses in which *C. iredalei* was used as one of the parents, suggest that this species is more distantly related to the above four species than they are to each other. The imcompatibility of the gametes of *C. commercialis* with the other species and the presence of shell denticles suggests that this species and others in the same group may constitute a distinct taxon, possibly of generic rank.

LITERATURE CITED

ABBOTT, R. T. 1954. *American Seashells.* D. Van Nostrand Co., Inc., New York, 541 pp.

CHANLEY, P. E. 1959. Inheritance of shell markings and growth in the hard clam, *Venus mercenaria. Proc. Nat'l. Shellf. Assoc.*, **50**: 163–169.

CUMMINGS, R. JR. 1966. Hard clam explorations of south-eastern United States. *Comm. Fish. Rev.*, **28** (12): 33–42.

DALL, W. H. 1902. Synopsis of the family Veneridae and of the North American recent species. *Proc. U.S. Nat'l. Mus.*, **26** (1312): 335–412.

DAVIS, H. C. 1950. On interspecific hybridization in *Ostrea. Science*, **111** (2889): 522.

GALTSOFF, P. S. 1964. The American oyster, *Crassostrea virginica* Gmelin., *U.S. Bur. Comm. Fish. Bull.*, **64**: 480 pp.

GUNTER, G. 1950. The generic status of living oysters and the scientific name of the common American species. *Amer. Midl. Nat.*, **43** (2): 438–449.

IMAI, R., R. SATO, S. SAHI AND R. YUKI 1950. Artificial breeding of oysters in tanks. *Tohoku Jour. Agric. Res.*, **1**: 69–86.

KOBAYASHI, H. 1954. Überdie Chromomenzahl der zwei Arten von japanischen Austern. *Cytologia*, **10**: 371–376.

LOOSANOFF, V. L. AND H. C. DAVIS 1963. *Rearing of Bivalve Larvae. Recent Advances in Marine Biology.* Academic Press, Inc., London, 1: 1–136.

MENZEL, R. W. 1961. Seasonal growth of the northern quahog, *Mercenaria mercenaria*, and the southern quahog *M. campechiensis*, in Alligator Harbor, Florida. *Proc. Nat'l. Shellf. Assoc.*, **52**: 37–46.

——— 1962. Seasonal growth of the northern and southern quahogs, *Mercenaria mercenaria* and *M. campechiensis* and their hybrids in Florida. *Ibid.*, **53**: 103–109.

—— AND M. Y. MENZEL 1965. Chromosome of the species quahog clams and their hybrids. *Biol. Bull.*, **129** (1): 181–188.

—— AND H. W. SIMS 1962. Experimental farming of hard clams in Florida. *Proc. Nat'l. Shellf. Assoc.*, **53**: 103–109.

MERRILL, A. S. AND J. W. ROPES 1967. Distribution of southern quahogs off the middle Atlantic Coast. *Comm. Fish. Rev.*, **29** (4): 62–64.

PORTER, H. M. AND A. CHESTNUT 1960. The offshore clam fishery of North Carolina. *Proc. Nat'l. Shellf. Assoc.*, **51**: 67–73.

RANSON, G. 1948. Prodissoconques et classification des ostreides vivants. *Bull. Nat. Hist. Nat. Belg.*, **24** (42): 1–12.

THOMSON, J. M. 1954. The genera of oysters and the Australian species. *Australian Journ. Mar. and Freshwater Res.*, **8** (1): 132–160.

---

[2] *C. amasa* (Iredale), *C. cucullata* (Born), *C. commercialis*, *C. denticulata* (Born), *C. echinata* (Quoy and Gaimard), *C. margaritacea* (Lam.), *C. tuberculata* (Lam.).

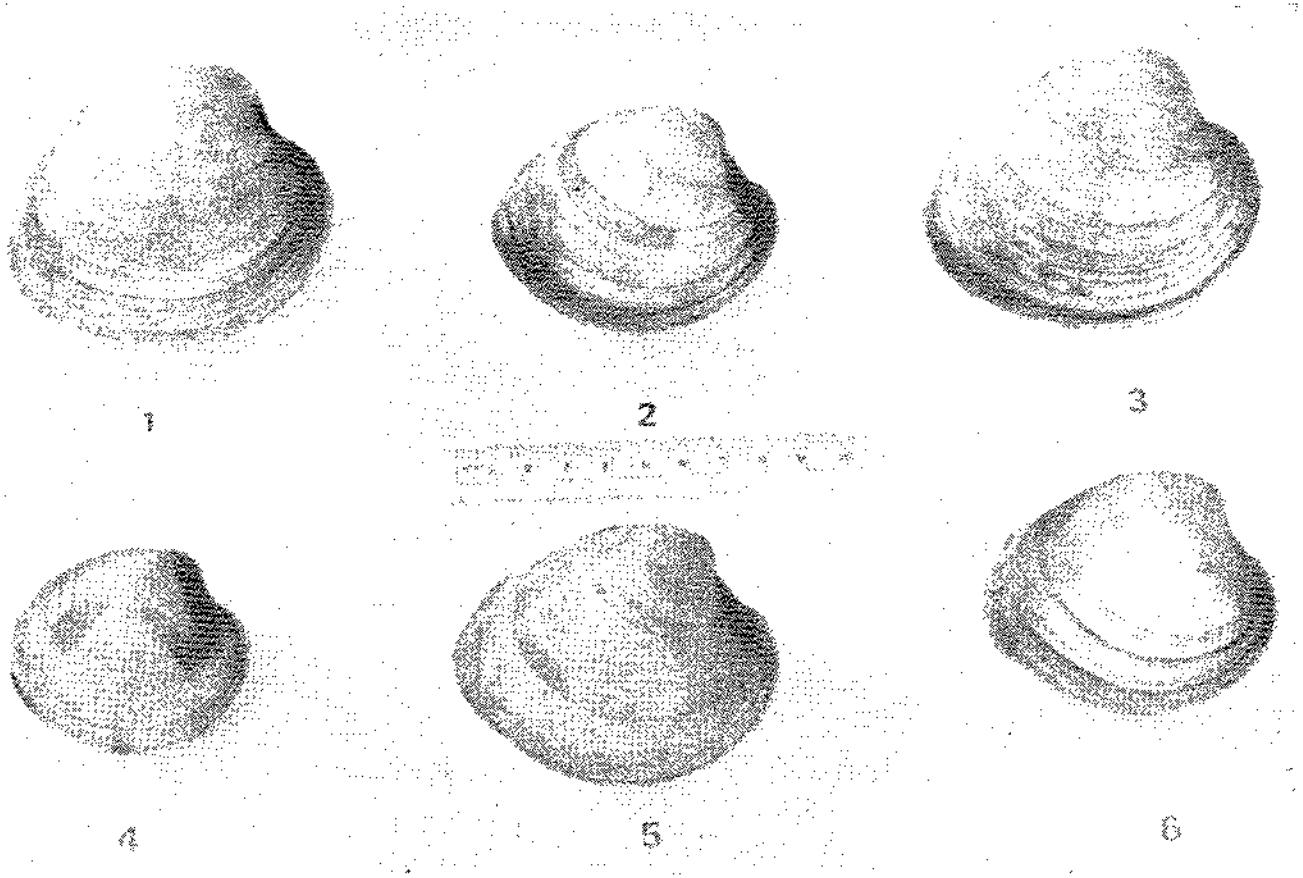


FIG. 2. Types of quahog clams. (1) Typical *M. campechiensis* from near Marine Laboratory. (2) Typical *M. mercenaria* from Great South Bay, New York. (3) F_1 hybrid of *M. campechiensis* ♀ ♂ *M. mercenaria*. (4) F_2 hybrid of number 3. (5) *M. m. texana* from just below St. Augustine, Florida. (6) *M. m. texana* from Stuart, Florida.

Plate II

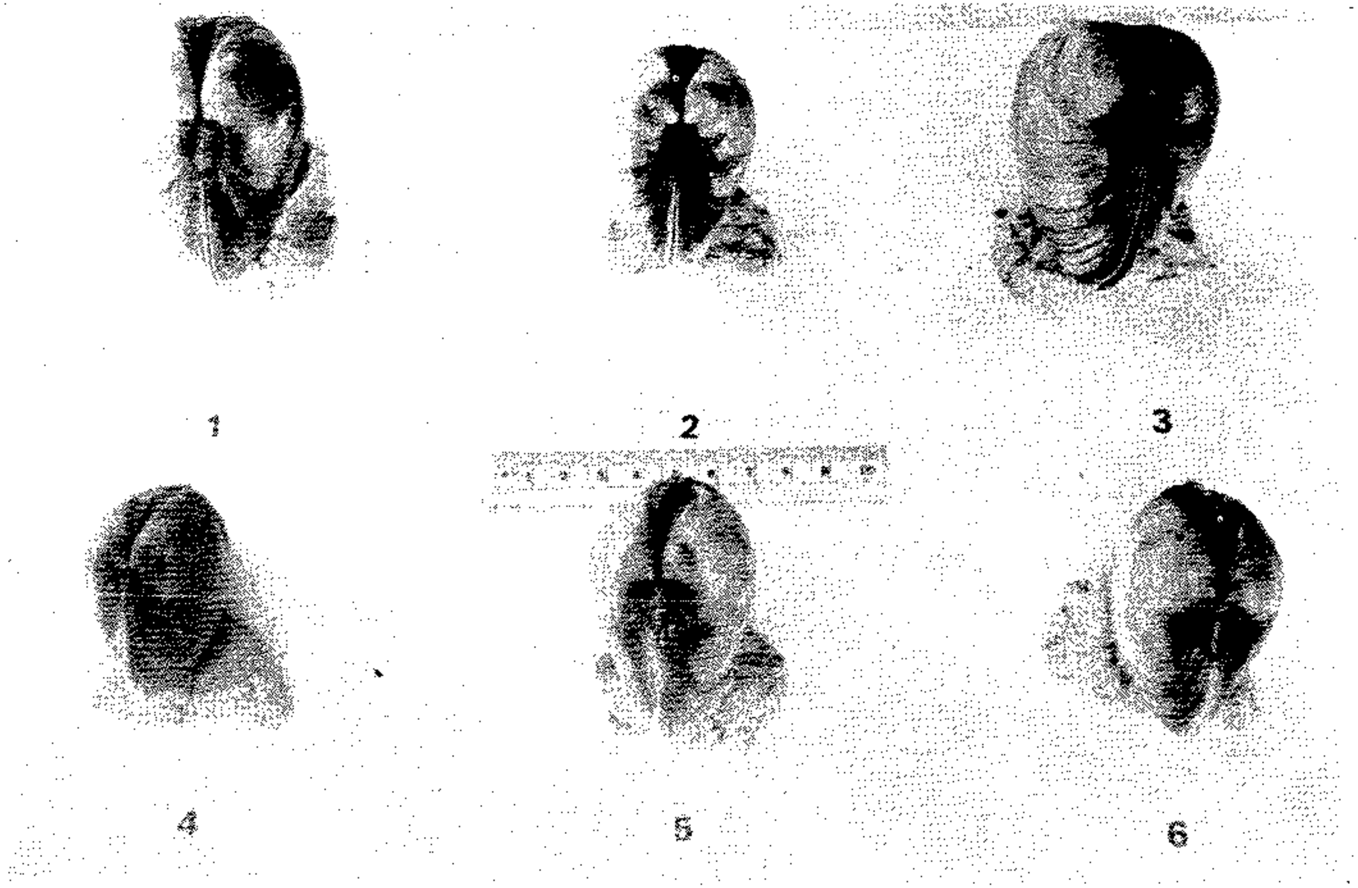


FIG. 3. Types of quahog clams. (1) Typical *M. campechiensis* from near Marine Laboratory. (2) Typical *M. mercenaria* from Great South Bay, New York. (3) F_1 hybrid of ♀ *M. campechiensis* ♂ *M. mercenaria*. (4) F_2 hybrid of number 3. (5) *M. m. texana* from just below St. Augustine, Florida. (6) *M. m. texana* from Stuart, Florida.

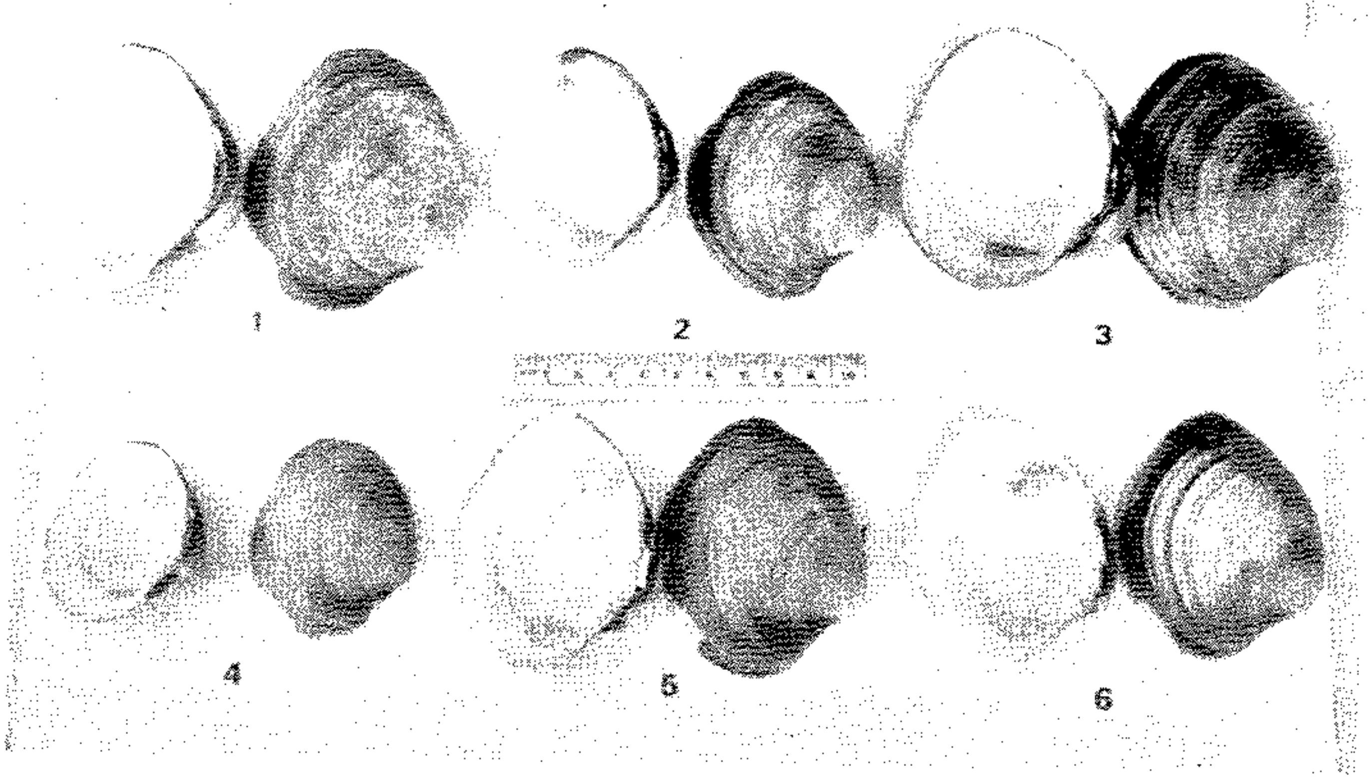


FIG. 4. Types of quahog clams. (1) Typical *M. campechiensis* from near Marine Laboratory. (2) Typical *M. mercenaria* from Great South Bay, New York. (3) F_1 hybrid of ♀ *M. campechiensis* × ♂ *M. mercenaria.* (4) F_2 hybrid of number 3. (5) *M. m. texana* from just below St. Augustine, Florida. (6) *M. m. texana* from Stuart, Florida.

Plate III

REPORT ON A COLLECTION OF WOOD-BORING MOLLUSCS FROM MAHANADI ESTUARY, ORISSA, INDIA

N. V. SUBBA RAO

Zoological Survey of India, Calcutta, India

ABSTRACT

In recent years much attention has been paid to the study of marine wood-boring molluscs of India. Several workers have contributed to the knowledge of these forms. But most of the earlier studies were based on collections made from test panels, catamarans, etc.

The taxonomical studies of the borers in the estuaries have not been paid much attention to. Hence a survey was conducted in the mangroves of Mahanadi Estuary, and the results are presented in this paper. About 700 examples belonging to 13 species were collected. The synonymy, ecology and distribution for each species are given. Descriptions of the pallets are included for certain species.

Three species, *viz.*, *Bankia fimbriatula* Moll & Roch, *Nototeredo knoxi* (Bartsch), and *Nausitora fusticula* (Jeffreys) are recorded for the first time from Indian seas.

INTRODUCTION

In recent years much attention has been paid to the study of marine wood-boring molluscs of India. Several workers have contributed to the knowledge of these forms. Nair (1954–1956, 1961, 1963, 1965) and Nair and Gurumani (1957) reported 27 species from Madras coast. Nagabhushanam (1955, 1960) noted the occurrence of 23 species from Visakhapatnam Harbour. Palekar and Bal (1955) recorded 7 species from Bombay Harbour. But all these reports are based on the collections made from test panels, catamarans, driftwood, etc. The mangrove forests which form the natural abodes of these wood-boring molluscs are not thoroughly explored. Roonwal (1954) made some observations of their attack on the living mangrove trees in the Sunderbans. Rajagopal (1961–as Rajagopalaiengar, 1964) also surveyed the Sunderban area and reported 6 species from there (Roonwal, 1966). Turner (1966) in her excellent treatise on the family Teredinidae surveyed the work that had been done on the systematics, biology, and distribution of this group. She listed only 18 species from India and Indian Ocean Islands.

Earlier studies on the east coast of India were confined mainly to the borers of Madras coast, Godavary Estuary (Ganapati and Rao, 1959), Visakhapatnam, and Sunderbans thus leaving a large area of Mahanadi Estuary in Orissa and Krishna Estuary in Andhra Pradesh unsurveyed. The present paper is an attempt to fill this gap in our knowledge of the borers of Mahanadi Estuary. About 700 examples belonging to 13 species were collected from live trees and dead stumps of mangroves. Three species, *viz.*, *Bankia fimbriatula*, *Nototeredo knoxi*, and *Nausitora fusticula* are recorded for the first time from Indian seas.

The borers were collected mostly from the dead stems, and the infestations of live trees were noticed only in a few instances.

Investigation has revealed the presence of more than one species of borer in a single piece of wood.

The borers were extracted from the following trees, either living or dead:

Vernacular name (Oriya)	Scientific name	Family
" Rai "	*Dillenia* sp.	Dilleniaceae
" Sundari "	*Heritiera minor* Roxb.	Sterculiaceae
" Bania "	*Clerodendron viscosum* Vent.	Verbenaceae
" Goan "	*Excoecaria agallocha* Linnaeus	Euphorbiaceae
" Kherua "	*Sonneratia apetala* Bucha-Hamilton	Sonneratiaceae
" Bamboo " " (Bhansa) "	*Bamboosa* sp.	Graminae
" Karanja "	*Pongamia pinnata* (Linn.)	Papilionaceae

SYSTEMATIC ACCOUNT

Family TEREDINIDAE

Turner (1966), while redefining the genera, recognized 14 genera, but no subgenera were used. The system adopted by her is generally followed here with a few exceptions at specific level.

Genus *Bactronophorus* Tapparone-Canefri, 1877

1. ***Bactronophorus thoracites*** **(Gould, 1859)**

1859. *Teredo thoracites* Gould, *Pro. Boston Soc. Nat. Hist.*, 6 : 15.

1966. *Bactronophorus thoracites* Roonwal, *Proc. Dacca Sympos.*, 1964, Paris (UNESCO) : 279.

Material : Coll. N. V. Subba Rao : (1) 6 examples, N. Bank of Madeli creek, Khira Gachha Madeli, 4. iii. 1964, ext. from "Sundari" wood. (2) 2 examples, W. bank of canal S. of Light House, False point, 12. iii. 1964, ext. from "Rai" wood. (3) 9 examples, jetty near Light House, 13 and 15. iii. 1964, ext. from "Rai" wood. (4) 22 examples, a small creek on the N. of jetty near Light House, 14. iii. 1964, ext. from "Sundari" wood. (5) 5 examples, *C* 3 km. N. E. of Light House, 16. iii. 1964, ext. from "Gamma" and " Kherua" woods. (6) 3 examples, N. Bank of Madeli creek, *C* 3 km. W. of Fishery jetty, Khira Gachha Madeli, 22. iii. 1964, ext. from " Sundari " wood. (7) 5 examples, S. Bank of Mahanadi R., Khira Gachha Madeli, 23. iii. 1964, ext. from "Sundari" wood.

Distribution. India : Sunderbans, Visakhapatnam, and Bombay ; Burma ; Tavoy ; Cochinchina ; Singapore ; Indonesia : Sumatra, Borneo, Moluccas ; New Guinea ; the Philippines ; North Australia : Queensland ; West Australia.

Remarks : This species was found to attack only dead wood. A few examples were collected from dead stumps lying even above high tide level and not submerged under water except during monsoon. The largest live example measured about 44 cm. in length.

Genus *Dicyathifer* Iredale, 1932

2. ***Dicyathifer manni*** **(Wright, 1866)**

1866. *Kuphus*? *mannii* Wright, *Trans. Linn. Soc. London*, **25** (3) : 565, pl. 65, figs. 1–6.

Material : Lot A. Coll. N. V. Subba Rao, Paradip, Cuttack Distt. (1) 2 examples, Fishery ghat, Khira Gachha Madeli, 26–11–1964, ext. a piece of unidentified wood. (2) 1 example, N.-W. of Nehru Sabha, V-point, 21. iii. 1964, ext. a piece of "Rai" wood. Lot. B. Coll. N. V. Subba Rao, False Point, Cuttack Distt. (3) 12 examples, W. bank of the canal S. of Light House, 12. iii.1964, ext. a piece of "Rai" wood. (4) 1 example, a creek on the N.-E. of jetty opp. Light House, 14. iii. 1964, ext. a piece of "Kherua" wood. (5) 2 examples, a creek on the N.-E. of jetty opp. Light House, 14. iii. 1964, ext. a piece of "Sundari" wood. (6) 12 examples, jetty opp. Light House, 15. iii. 1964, ext. a piece of "Rai" wood. (7) 6 examples *C* 2·5 km. N.-E. of Light House, 16. iii. 1964, ext. a piece of "Gamma" wood. (8) 8 examples, *C* 2·5 km. N.-E. of Light House, 16. iii. 1964, ext. a piece of "Kherua" wood. (9) 4 examples, a small creek on the N. of Jetty opp. Light House, 16. iii. 1964, ext. a piece of "Rai" wood. (10) 5 examples, *C.* 4 km. S.-E. of Light House, 18. iii. 1964, ext. a piece of "Kherua" wood.

Distribution : India : Sunderbans, Visakhapatnam, Madras Harbour, Pulicat Lake, Keelak-Karai, Cochin, Karwar, Bombay ; Indian Ocean : East African coast, Kerinba Islands, Madagascar, Reunion, Comoro Island ; Burma : Tavoy; Malaysia; Singapore; Cochinchina; Tonkin; Indonesia; Sumatra; Babalan, Belawan Deli, Fantai Tjermin, Soeng Sang, Langsa River; Borneo : Kota Baru ; Java : Surabaja ; South Celebes : Moena ; Amboina : Moluccas ; Rhiow-Archipelago : Tandjoeng Babi, Tandjoeng Penang ; New Guinea ; Bismarck Archipelago ; the Philippines ; Australia : Brisbane.

Remarks : This is generally found to attack "Rai" and "Kherua" woods. The anterior part of the borer when alive is always of dull-bluish colour. A good account of its field ecology is given by Rajagopal (1965, in press).

Genus *Teredora* Bartsch, 1921

3. ***Teredora princesae*** **(Sivicks, 1928)**

1928. *Teredo princesae* Sivicks, *Philippine J. Sci.*, **37** : 291, pl. 2, fig. II.

Material : Coll. N. V. Subba Rao : 17 exs., Khira Gachha Madeli opp. P. W. D. Bungalow, 1. iii. 1964, ext. a piece of Bamboo washed ashore.

Distribution : India : Madras ; Philippine Islands ; North Pacific Ocean : Hawaii, Johnston and Wake Islands.

Remarks : This borer was found to attack bamboo. However, Nair (1956) reported its attack on *Cedrela tonna, Terminalia* sp., and *Aegele* sp. He (1954) collected specimens measuring 29cm. in length, but in the present collection even a full-grown specimen does not attain more than 32 mm. in length.

The borer secretes a very thin tube of calcareous matter and when freshly extracted it appears dull white in colour. It can easily be recognised by its spoon-shaped pallets and a ring-like prominence at the junction of the blade and the stalk.

Genus *Lyrodus* Gould, 1870

4. ***Lyrodus pedicellatus*** **(Quatrefages, 1849)**

1849. *Teredo pedicellatus* Quatrefages, *Ann. Sci. Nat. Zool.*, **2** (3) : 26, pl. 1, fig. 2.

1941. *Teredo pedicellatus*, Moll, *Sitzungsber. Ges. Naturforsch. Fr.*, Berlin, 1941 : 183.

Material : Lot. A : Coll. G. Ramakrishna : (1) 2 pairs of pallets, Khira Gachha Madeli, 10. xi. 1962, ext. from a piece of "Karanja" wood. Lot. B : Coll. N. V. Subba Rao : (2) 3 examples, Lion's Rump, near mouth of Mahanadi River, 4. iii. 1964. ext. from a piece of "Sundari" wood.

Distribution : India : Madras, Tondi, Adirampatnam and Kayankulam, world-wide in tropical and warm temperate seas.

Remarks: The specimens were very short (25 mm. in length) and collected from a piece of "Sundari" wood which was infested in large numbers by *Bankia campanellata*.

Genus *Nototeredo* Bartsch, 1923

5. *Nototeredo knoxi* (Bartsch, 1917)

1922. *Teredo* (*Psiloteredo*) *knoxi*, Bartsch. *Bull. U.S. Nat. Mus.*, **122** : 51, pl. 29, fig. 2; pl. 34, fig. 2.

Material : Coll. N. V. Subba Rao : 2 exs., Lion's Rump, mouth of Mahanadi River, 4. iii. 1964, ext. from "Sundari" wood.

Distribution : Africa : West Coast ; North America : East Coast ; South America : East Coast ; Gulf of Mexico.

Remarks : The specimens are found in a piece of "Sundari" wood infested by a large number of *Bankia campanellata*.

The species can readily be recognised by its leaf-shaped pallets. There is a small depression at the tip of the blade. The stalk is short and slender and extends through the centre of the blade just like the median rib of a leaf.

Nagabhushanam's (1955, Text-fig. I S, t.) figure of *Teredo* (*Teredora*) *thomsoni* appears to resemble very closely the pallets of this species. So the author presumes that the pallets figured by Nagabhusanam may belong to the present species rather than *T. thomsoni*, in which case its distribution extends to Visakhapatnam also. Anyway without examining the material studied by him no conclusion can be arrived at and until then this is considered as a first record from Indian seas.

The genus *Nototeredo* is thought to be occurring in fully marine conditions, but here it is collected from brackish waters.

Genus *Nausitora* Wright, 1864

6. *Nausitora fusticula* (Jeffreys, 1860)

1860. *Teredo fusticulus* Jeffreys, *Ann. Mag. Nat. Hist.*, **6** (3): 125.

1922. *Bankia* (*Nausitora*) *fusticula*, Bartsch, *Bull. U.S. Nat. Mus.*, **122**: 16, pl. 20, fig. 2; pl. 31, fig. 2.

Material : Coll. N. V. Subba Rao : 1 ex., 2·5 km. North-east of Light House, False point, 16. iii. 1964, ext. from "Kherua" wood.

Distribution : Europe : Scotland ; South America : Brazil.

This is the first record of occurrence of this species in the Indian seas.

Remarks : The specimen agrees well with the description and figures given by Bartsch (1922), This is characterised by its shell having widely spaced dental ridges on the anterior part, which is separated from the anterior median portion by a straight line. Pallets have a stalk twice as long as the blade. The stalk is rounded and gently sinuously curved. The blade is oval, half of its length solid, and the distal part marked by grooves which denote corresponding segments on the inside. The outside is covered by a thick solid periostracum.

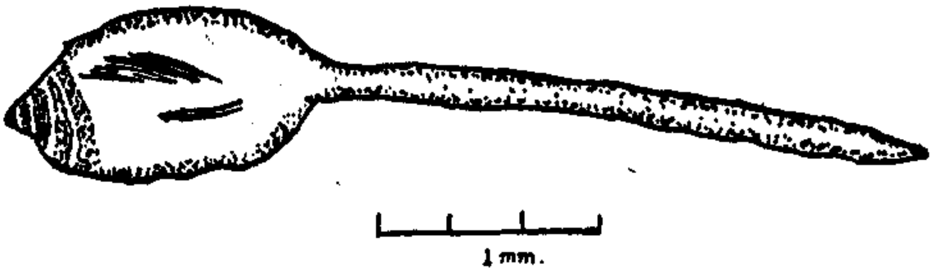


FIG. 1. Pallet of *Nausitora fusticula* Jeffreys.

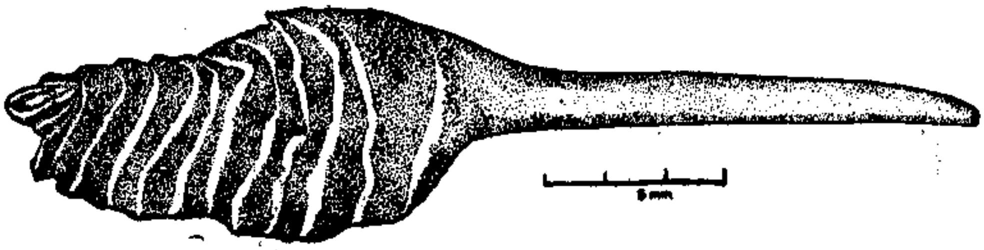


FIG. 2. Pallet of *Nausitora hedleyi* Schepman.

7. *Nausitora hedleyi* Schepman, 1918

1918. *Nausitora hedleyi* Schepman, *Nova Guinea Res. Exped. Scient.*, 13, Zoologie : 195, pl. 7, fig. 3.

1955. *Nausitora hedleyi*, Roch, *Zool. Meded.*, 34 (8) : 139, fig. 7, *f*, *g*.

1955. *Bankia* (*Nausitora*) *gabrieli* Nair, *Rec. Indian Mus*, 53 (1–2) : 262, text-fig. 1 *a–d*.

Material : Coll. N. V. Subba Rao : 10 exs. Hukitola beach, 17. iii. 1964, ext. from "Kherua" stamps.

Distribution : India : Ernakulam ; Borneo ; Sumatra ; Java ; New Guinea ; Philippines ; New Caledonia.

Remarks : A few examples were collected from the dead stumps of "Kherua" tree lying on the sea beach at Hukitola. All the four trunks lying in this area were affected by the same species.

Pallets are of brown colour with a rather long and pointed stalk. The basal portion of the blade is covered with golden brown periostracum. In many cases the burrow is not lined with any shelly tube.

8. *Nausitora lanceolata* Rajagopal, 1964

1964. *Nausitora lanceolata* Rajagopal, *J. Bombay Nat. Hist. Soc.*, 67 (1) ; 109, pl. figs. 1-3, text-fig. 1.

Material : Lot A. Coll. N. V. Subba Rao, Paradip, Cuttack Distt. (1) 1 example, Fishery ghat, Khira Gachha Madeli, 26. ii. 1964, ext. from "Kherua" wood. (2) 24 examples, Badpadia, 7–8. ii. 1964, ext. from "Kherua" wood. (3) 1 example, Badpadia, nr. Nehru Sabha, 1. iii. 1964, ext. from unidentified wood. (4) 11 examples, N. of Nehru Sabha, Badpadia, 20–21 iii. 1964 ext. from "Rai" wood. (5) 1 example, S. bank of Mahanadi R., *C* 3 km. W. of Fishery jetty, Khira Gachha Madeli, 23. iii. 1964, ext. from "Sundari" wood.

Lot. B. Coll. N. V. Subba Rao, False Point. (6) 1 example, W. bank of the Canal S. of Light House, 12. iii. 1964, ext. from "Ragi" tree. (7) 7 examples, W. bank of the "Katai" canal S. of Light House, 13. iii. 1964, ext. from "Kherua" tree. (8) 7 examples, jetty near Light House, 13–14. iii. 1964, ext. from "Rai" wood. (9) 1 example, jetty near Light House, 14. iii. 1964, ext. from "Kherua" wood. (10) 1 example, a small creek on the N. of jetty near Light House, 16. iii. 1964, ext. from "Rai" wood. (11) 1 example, 2·5 km. N.-E. of Light House, 16. iii. 1964, ext. from "Gamma" wood. (12) 3 examples, 3 km. S.-E. of Light House, 18. iii. 1964, ext. from "Kherua" wood. (13) 13 examples, 3 km. N.-E. of Light House, 19. iii. 1964, ext. from Bania tree.

Distribution : India : Port Canning, Kidderpore docks, and Sunderbans.

Remarks : This species is very common in the estuary and generally attains large size. The largest example in the living condition measured about 84 cm. in length. This is the largest species so far known in the estuary.

The burrow is lined with a very thick secretion of shelly matter.

Turner (1966) has merged this species with *Nausitora dunlopei* Wright as a synonym. But the collection before me agrees in all respects with the Holotype of *N. lanceolata* Rajagopal present in the Zoological Survey of India and for the present they are treated under this species.

Genus *Bankia* Gray, 1842

9. *Bankia carinata* (Gray, 1827)

1827. *Teredo carinata* Gray, *Phil. Mag.* (N.S.), **2** : 411.

1954. *Bankia* (*Bankiella*) *indica* Nair, *Rec. Indian Mus.*, **52** (2-4) : 393, fig. 3 *a–d*.

Material : Coll. G. Ramakrishna : 10 exs., Khira Gachha Madeli, 10. xi. 1962, ext. from a piece of "Karanja" wood.

Distribution : India : Calcutta, Visakhapatnam, Madras, Adirampatnam, Cochin, Bombay ; Mediterranean ; Philippine Islands ; Japan ; Reunion Island ; Indonesia ; Malacca ; Caribbean Sea.

Remarks : All the specimens are uniformly small. In some specimens the rims of the cups of the pallets are covered by brown periostracum.

10. *Bankia campanellata* Moll and Roch, 1931

1931. *Bankia campanellata* Moll and Roch, *Proc. Malac. Soc. London*, **19** (4) : 215, pl. 25.

1954. *Bankia* (*Bankia*) *bengalensis* Nair, *Rec. Indian Mus.*, **52** (2–4) : 411, fig. 10 *a–c*.

Material : Lot. A : Col. G. Ramakrishna : (1) 26 exs., Khira Gachha Madeli, 10. xi. 1962, ext. from a piece of "Karanja" wood.

Lot. B : Coll. N. V. Subba Rao : (2) 6 exs., Fishery Ghat, Khira Gachha Madeli, 26. ii. 1964, ext. from "Goan" tree ; (3) 38 exs., mouth of Mahanadi River, Lion's Rump, 2-5. iii. 1964, ext. from a piece of "Sundari" wood.

Distribution : India : Sunderbans, Diamond Harbour, Visakhapatnam, Godavary Estuary, Masulipatam, Nizampatnam, Madras ; Reunion Island ; Malay Archipelago ; Sumatra ; South America : East Coast.

Remarks : The presence of this borer inside the wood can readily be detected by the pallets protruding on its surface.

11. *Bankia fimbriatula* Moll and Roch, 1931

(Plate I)

1931. *Bankia fimbriatula* Moll and Roch, *Proc. Malc. Soc. London*, **19** : 213, pl. 25, fig. 37.

1946. *Bankia (Plumulella) fimbriatula* Clench and Turner, *Johnsonia*, **2** (19) : 22, pl. 14.

Material : Coll. N. V. Subba Rao : (1) 19 examples, Badpadia, near Nehru Sabha, Paradip Port, 8. iii. 1964, ext. from "Kherua" wood. (2) 5 examples, jetty near Light House, False Point, 15. iii. 1964, ext. from "Rai" wood.

Distribution : Atlantic Ocean ; Eastern Pacific.

It is interesting to record for the first time the occurrence of this species from Indian waters.

Remarks : The species is characterised by its dark brown pallets with a series of moderately spaced cones and the calcareous portion of each cone deeply notched. Outer margin of periostracum is wide and U-shaped, with fine pectinate processes and with faint indications of vertical ribs extending below the union of pectinations. Inner margin is also U-shaped and possessing long pectinate processes. Lateral borders of each cone are produced into greatly extended awns which also bear pectinate process.

The specimen whose pallets are shown in the photograph measures about 21·5 cm. in length and the pallets themselves measuring 3·4 cm. in length.

12. *Bankia roonwali* Rajagopalaiengar, 1961

1961. *Bankia (Neobankia) roonwali* Rajagopalaiengar, *Sci. and Cult.*, **27** (11) : 550.

Material : Coll. N. V. Subba Rao : (1) 14 examples, W. bank of the canal S. of Light House, False Point, 12. iii. 1964, ext. from "Ragi" tree. (2) 25 examples, a small creek on N. of jetty near Light House, 14. iii. 1964, ext. from "Sundari" and Kherua" woods. (3) 15 examples, jetty near Light House, 15. iii. 1964, ext. from "Rai" wood. (4) 21 examples, a small channel on the N. of jetty near Light House, 16. iii. 1964, ext. from "Rai" wood. (5) 60 examples *Ca*, 2·5 km. N.-E. of Light House, 16. iii. 1964, ext. from "Gamma" wood. (6) 9 examples, 4 km. S.-E. of Light House, 16. iii. 1964, ext. from "Gamma" wood. (7) 9 examples, 4 km. S.-E. of Light House, 15. iii. 1964, ext. from "Kherua" wood. (8) 1 example N. of Nehru Sabha, V. point, Paradip Port, 20. iii. 1964, ext. from "Rai" wood. (9) 2 examples, S. bank of Mahanadi R., *Ca* 3 km. W. of Fishery Jetty, Khira Gachha Madeli, 23. iii. 1964, ext. from "Sundari" wood.

Distribution : India : Sunderbans.

Remarks : This is another common species in the estuary. The largest live example measured about 21 cm. in length.

The burrow is lined by a calcareous tube and the species can be recognised by its brown-coloured pallets with compactly arranged cones.

This species is merged with *Bankia rochi* Moll (Turner, 1966) as a synonym.

Family PHOLADIDAE

Genus *Martesia* Sowerby

13. *Martesia* (*Martesia*) *striata* (Linnaeus, 1758)

1758. *Pholas striata* Linnaeus, *Syst. Nat.*, ed. **10**: 669.

1959. *Martesia* (*Martesia*) *striata* Srinivasan, *Proc. Indian Acad. Sci.*, **50 B** (2): 105, text-fiig. 1,

Material: Coll. N. V. Subba Rao: (1) 53 examples, a wood washed ashore, Khira Gachha Madeli, 1. iii. 1964, (2) 35 examples, S. bank of Mahanadi R., Lion's rump, 2. iii. 1964. (3) 92 examples, mouth of Mahanadi R., Lion's Rump, 3, 5. iii. 1964. (4) 5 examples, W. bank of the canal S. of Light House, False Point, 13. iii. 1964. (5) 12 examples, jetty near Light House, False Point, 15. iii. 1964. (6) 10 examples, a small creek near Light House, False Point, 16. iii. 1964.

Distribution: India: Port Canning, Kidderpore docks, Visakhapatnam Godavary Estuary, Krishna Estuary, Nizampatnam, Madras, Porto-Novo, Tuticorin, Krusadi Islands, Kayankulam, Cochin Harbour, Mangalore and Bombay; Eastern Pacific; Indo-Pacific; Western Atlantic.

Remarks: This is a common borer in the estuary, but not specific to any particular species of wood. The animal bores vertically and makes a neat and cylindrical burrow into the wood.

ACKNOWLEDGEMENTS

The author is grateful to the Director, Zoological Survey of India, for giving him an opportunity to survey the area, and to Shri A. S. Rajagopal for his guidance and helpful suggestions. Thanks are also due to Dr. H. C. Ray for critically going through the manuscript, and Dr. R. D. Turner for identifying *Nausitora hedleyi*.

LITERATURE CITED

BARTSCH, P. 1922. A monograph of the American shipworms. *Bull. U.S. Nat. Mus.*, **122**: 1–48, 37 pls.

GANAPATI, P. N. AND M. V. LAKSHMANA RAO 1959. Incidence of marine borers in mangroves of Godavary Estuary. *Curr. Sci.*, **28**: 332.

NAGABHUSHANAM, R. 1955. A systematic account of the molluscan wood-borers of Visakhapatnam Harbour. *Rec. Indian Mus.*, **53** (1 & 2): 1–11. 1 text-fig. and 1 pl. (1958).

——— 1960. Notes on shipworms from Visakhapatnam Harbour. *J. Bombay Nat. Hist. Soc.*, **57** (2): 362–370.

NAIR, N. B. 1954. Shipworms from India. I. Report on ten species of shipworms from the Madras coast. *Rec. Indian Mus.*, **52**: (2–4): 387–414.

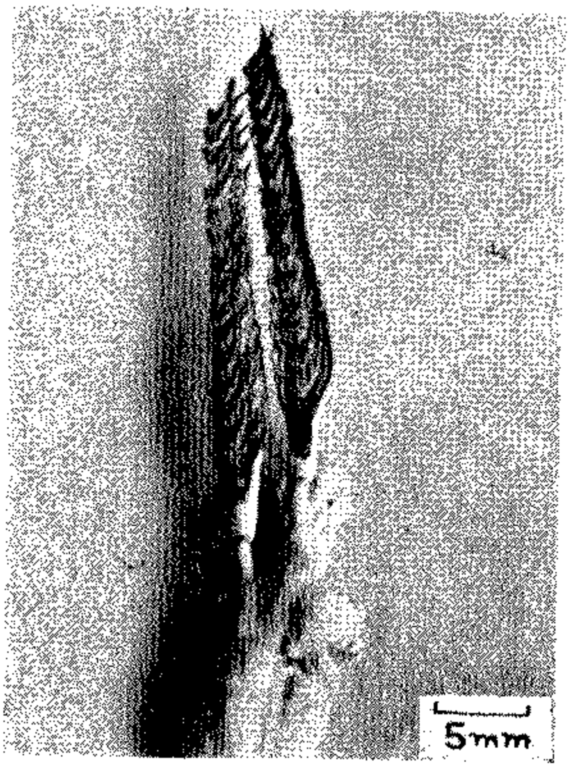
——— 1955. Shipworms of India. II. Seven more shipworms from South India. *Ibid.*, **53** (1 & 2): 261–278.

——— 1956. Destruction of timber structures by shipworms in Madras waters. *J. Sci. industr. Res.*, **15 C** (3): 81–82.

——— 1961. Some aspects of the marine borer problem in India. *Ibid.*, **20 A** (10): 584–591.

——— 1963. Shipworms from the Pulicat Lake, East Coast, Madras State. *Curr. Sci.*, **32** (5): 215–216.

——— 1965. Marine timber-boring organisms of the Indian coast, Report on a collection from the south-east coast of India with notes on distribution in the Indo-Pacific area, *J. Bombay Nat. Hist. Soc.*, **62** (1): 120–131, 2 tables.



Pallets of *Bankia fimbriatula* Moll & Roch.

Nair, N. B. and O. N. Gurumani 1957. Timber boring molluscs of the Indian coast. I. Report on a collection from Tondi, and Adirampatnam, East coast. *J. Bombay Nat. Hist. Soc.*, **54** (3): 663–673, 8 figs.

Palekar, V. C. and D. V. Bal 1955. Marine organisms injurious to submerged timber in the Bombay Harbour. *Ibid.*, **53** (2): 201–204, 1 pl. 12 figs., 1 map.

Rajagopalaiengar, A. S. 1961. A new species of the marine borer, *Bankia* (*Neobankia*) *roonwali* (Mollusca: Teredinidae), from India. *Sci. and Cult.*, **27** (11): 550.

Rajagopal, A. S. 1964. Two new species of marine borers of genus *Nausitora* (Mollusca: Teredinidae) from West Bengal, India. *J. Bombay Nat. Hist. Soc.*, **61** (1): 108–118, 1 pl. and 2 text-figs.

——— (in press). Field ecology of some marine borers (Mollusca: Teredinidae) on mangroves in Sunderbans, India. *Rec. Indian Mus.*

Roonwal, M. L. 1954. The marine borer, *Bactronophorus thoracites* (Gould), as a pest of living trees in the mangrove forests of the Sunderbans, Bengal, India. *Proc. Zool. Soc.*, Calcutta, **7**: 91–100, 3 pls. and 2 figs.

——— 1966. Wood-boring teredinid shipworms (Mollusca) of mangroves in the Sunderbans (West Bengal). Sci. Problems Humid Trop. Zone Deltas, *Proc. Dacca Sympos.*, 1964, Paris (UNESCO): 277–283, 2 pls.

Turner, R. D. 1966. *A Survey and Illustrated Catalogue of the Teredinidae* (*Mollusca: Bivalvia*). Museum of Comparative Zoology, Harvard University, Cambridge, Mass., pp. 1–265, 25 figures and 64 plates.

ABBREVIATIONS USED

Coll. = Collector; ex (s) = example(s); ext. = extracted; S = South; S.-E. = South-East; S.-W. = South-West; N = North; E = East; W = West.

AQUATIC AND AMPHIBIOUS MOLLUSCS OF THE KASHMIR VALLEY, INDIA[1]

A. S. Rajagopal and N. V. Subba Rao

Zoological Survey of India, Calcutta, India

Abstract

The paper is on a systematic study of all the unidentified collections of the Kashmir Valley present in the Zoological Survey of India, those particularly, of two successive faunistic surveys of the Valley in 1954 and 1955 constituting the bulk of the material for study. Altogether 12 genera and 18 species are dealt with. These represent a further augmentation in the number of genera and species of aquatic and amphibious molluscs known so far from the valley. Of these one genus namely, *Hippeutis* with the species *fontanus*, and two more species, *i.e.*, *Viviparus variatus* Frauenfeld and *Planorbis rotundatus* Poiret, are recorded from the area for the first time. Brief field ecological observations, wherever possible, are included under respective species. Note on distribution of each species is made as complete as possible.

A short note on the zoogeographical significance of the aquatic and amphibious molluscs of Kashmir is also appended.

I. INTRODUCTION

This paper presents a systematic account of the collections made mainly in two successive faunistic surveys of the Kashmir Valley in 1954 and 1955. In 1954, the late Dr. S. L. Hora placed at the disposal of the senior author a collection of molluscs made in the Valley during May–June of that year. A second survey specially for the collection of aquatic and terrestrial molluscs was made during June–August, 1955. Further, this paper also includes all the previous collections, both named and unnamed, present in the Zoological Survey of India.

Brief Review of Earlier Literature

Woodward's (1856) short paper based on the collection of Thomson which, probably, is the earliest work in this respect, gives a list of land and freshwater shells of Kashmir and Tibet comprising 12 genera and 22 species. Theobald (1878) who made "a hasty traverse of the ground" from Murree to Srinagar and thence *via* the Mohu Pass to Jammu, in 1877, has listed 32 genera and 64 species of land and freshwater forms from Kashmir and its vicinity. Nevill's (1878) work based upon the molluscs of Central Asia and Ladak obtained by Dr. F. Stoliczka includes 4 genera and 7 species of amphibious and land molluscs strictly within the confines of Kashmir. Weber (1910) reporting on Zugmayer's collection from Eastern Turkestan, Kashmir, and Western Tibet deals with 8 genera and 9 species. Prashad (1937) in his valuable contribution on the aquatic molluscan fauna of Kashmir has reported 9 genera and 15 species from G. E. Hutchinson's collection of the Yale North India Expedition. Hora *et al.* (1955) dealing with aquatic fauna in general have discussed briefly the zoogeographical significance of aquatic molluscs with other aquatic animals.

Material and Methods

Besides the collections mentioned above, all the identified material and type specimens available in the collections in respect to the species studied have also been carefully checked.

---

[1] Published with the permission of the Director, Zoological Survey of India, Calcutta.

Collections of aquatic gastropods of the families Viviparidae, Valvatidae, Amnicolidae, Lymnaeidae and Planorbidae were made mostly by hand or hand-net from submerged aquatic vegetation, edges of ponds, lakes, streams, and paddy fields. Bivalves of the families Corbiculidae and Sphaeriidae were collected by scraping superficial layers of soft mud from paddy fields and beds of streams and washing them repeatedly in water. Specimens of *Pisidium*, in particular, were collected by washing tufts of roots of weeds from swamps and floating aquatic algae. Amphibious forms like succineids were collected by sweeping with hand-net the thick and luxuriant vegetation lining irrigation channels besides paddy fields.

ABBREVIATIONS USED

Coll.—Collector; ex(s).—example(s); Reg. No.—Register Number; Sta.—Station; Z.S.I.—Zoological Survey of India.

ACKNOWLEDGEMENTS

We express our thanks to the Director, Zoological Survey of India, Calcutta, for necessary facilities. Our thanks are also due to Dr. H. C. Ray, Superintending Zoologist, for going through the manuscript. We are obliged to Dr. K. C. Jayaramakrishnan, Superintending Zoologist, for offering many useful suggestions and criticisms.

II. COMPLETE LIST OF AQUATIC AND AMPHIBIOUS MOLLUSCS SO FAR KNOWN FROM KASHMIR VALLEY

Class **GASTROPODA**

Order MESOGASTROPODA

Family VIVIPARIDAE

1. *Viviparus variatus* Frauenfeld.
*2. „ *bengalensis* (Lamarck).
*3. „ *dissimilis* (Müller).

Family VALVATIDAE

4. *Valvata piscinalis* (Müller).
*5. „ *stoliczkana* Nevill.

Family AMNICOLIDAE

6. *Bulimus tentaculatus* (Linnaeus) var. *kashmirensis* Nevill.
*7. „ *troscheli* (Paasch).
*8. *Digoniostoma pulchella* (Benson).

Family MELANIIDAE

*9. *Melanoides* (*Melanoides*) *tuberculatus* (Müller).
*10. *Acrostoma variabilis* (Benson).
*11. *Paludomus tanschaurica* Gmelin.

---

* No specimens of these species from Kashmir have been examined by us but they have been listed from literature.

Order BASOMMATOPHORA

Family LYMNAEIDAE

12. *Lymnaea* (*Lymnaea*) *stagnalis* (Linnaeus)
13. „ (*Radix*) *auricularia* (Linnaeus)
14. „ „ *brevicauda* Sowerby.
15. „ „ *lagotis* f. *striata* Andreae.
16. „ „ „ f. *costulata* von Martens.
17. „ „ „ f. *solidissima* Kobelt.
18. „ „ „ f. *defilippii* Issel.
*19. „ „ *pereger* (Müller).
20. „ (*Galba*) *truncatula* (Müller).
21. „ (*Pseudosuccinea*) *luteola* f. *typica* (Lamarck).
22. „ „ „ f. *succinea* Deshayes.

Family PLANORBIDAE

23. *Planorbis planorbis* (Linnaeus) var. *tangitarensis* Germain.
24. „ *rotundatus* Poiret.
*25. „ *carinatus* Müller
26. *Indoplanorbis exustus* (Deshayes).
27. *Gyraulus pankongensis* (von Martens).
*28. „ *convexiusculus* (Hutton)
29. *Hippeutis fontanus* (Lightfoot)
*30. *Segmentina calatha* Benson.

Order STYLOMMATOPHORA

Family SUCCINEIDAE

31. *Succinea indica* Pfeiffer.
*32. *Succinea pfeifferi* Ross.
*33. „ *putris* Linnaeus.
*34. „ *stoliczkana* Rao.
35. „ sp. prox *daucina* Pfeiffer.

Class BIVALVIA

Order EULAMELLIBRANCHIATA

Family CORBICULIDAE

36. *Corbicula cashmiriensis* Deshayes.
*37. „ *striatella* Deshayes.

Family SPHAERIIDAE

38. *Sphaerium kashmirensis* Prashad.
*39. „ *indicum* Deshayes.
40. *Pisidium hydaspicloa* Theobald.
*41. „ *mitchelli* Prashad.

---

* No specimens of these species from Kashmir have been examined by us but they have been listed from literature.

III. KEY TO THE IDENTIFICATION OF KASHMIR MOLLUSCS TO FAMILIES

Class **GASTROPODA**

1.	Shell operculate	2
	Shell non-operculate	4
2.	Shell of fairly large size, turbinate, subperforate or imperforate, whorls more or less convex, operculum horny, concentric with excentric sublateral nucleus placed near the inner margin	VIVIPARIDAE
	Shell small in size, ovately fusiform or subdiscoidal depressed, labrum continuous, aperture oval or round, operculum testaceous and multispiral ..	3
3.	Shell ovately fusiform, not widely umbilicate, sometimes with a closed umbilicus, with more or less convex whorls, aperture oval, operculum testaceous and multispiral	AMNICOLIDAE
	Shell turbinate or subdiscoidal depressed, umbilicate, few whorls, aperture circular, operculum multispiral	VALVATIDAE
4.	Shell normally dextral, spiral, usually oval	5
	Shell sinistral, flat and discoidal	PLANORBIDAE
5.	Shell thin, spiral with exerted or more or less contracted spire, more or less ovate, always less than 50 mm. and almost always more than 5 mm. long, always aquatic in habit	LYMNAEIDAE
	Shell imperforate, usually oval, rarely cap-like, relatively thin and translucent, never smooth but rarely with prominent sculpture, spire much shorter than the last whorl, never sharply conical, whorls rapidly increasing, aperture oval or oblong with a thin columellar fold, not reflexed beyond the columellar margin of the aperture, shell always less than 20 mm., either amphibious or terrestrial in habit	SUCCINEIDAE

Class **BIVALVIA** (=*Pelecypoda*)

Shell fairly large, subtrigonal or cordiform, subequilateral, prominent and centrally placed umbones, concentrically grooved	CORBICULIDAE
Shell generally smaller, ovate or trigonal, umbones not very prominent and not centrally placed but either towards the anterior or the posterior side	SPHAERIIDAE

IV. SYSTEMATIC ACCOUNT

Class **GASTROPODA**

Order MESOGASTROPODA

Family VIVIPARIDAE

Genus *Viviparus* Montfort, 1810

Viviparus variatus **Frauenfeld, 1862**

1862. *Vivipara variata* Frauenfeld, *Verhandl. Zool. bot. Ges. Wien*, **12**, p. 1163. (Type-locality: Pondicherry, S. India).

1915. *Vivipara variata*: Preston, *Fauna Brit. India*, Mollusca (*Freshwater Gastropoda and Pelecypoda*), p. 89.

Material.—No. of examples studied: 26.

Lot. A: Coll. S. L. Hora: (1) 8 exs., Sta. 3—Stagnant water by the road side near Dal Gate, Srinagar, 24-5-1954; (2) 1 ex., Sta. 6—Along the east bank of Dal Lake for 3-8 Km. from Dal Gate, 25-5-1954; (3) 2 exs., Sta. 7—By boat from Dal Gate to Shalimar Garden *via* Char Chinari (West), 26-5-1954; (4) 9 exs., Sta. 8—First terrace tank, Shalimar Garden, 26-5-1954.

Lot. B: coll. A. S. Rajagopalaiengar: (5) 6 exs., Sta. 25—Dal Lake from Nishat Bagh to Char Chinari (East), 11-7-1955.

Distribution: India: Punjab: Ferozepore, Gurdaspur, Hissar; Uttar Pradesh: Kumaon; Bihar: Dinapore, Patna, River Ganga; West Bengal: Darjeeling, Sheoraphuli; Orissa: Ganjam, Rambha, Sur Lake (Puri Dist.); Andhra Pradesh: Eluru, Nellore, Secunderabad, Vijayawada, Visakhapatnam; Madras: Tiruchirapalli; Mysore: Bangalore, Shimoga Dist., Srirangapatnam Fort; Kerala: Quilon, Trivandrum; Rajasthan: Bharatpur Town; Pakistan: Dera Ghazi Khan Dist., East Pakistan: Jessore; Ceylon; Burma: Mandalay.

Remarks: Shells are well developed and of large size. Most of them are of an olive green colour, with the rim of aperture being typically black.

This is the first record of this species from Kashmir.

Family VALVATIDAE

Genus *Valvata* O. F. Müller, 1774

***Valvata piscinalis* Müller, 1774**

1774. *Nerita piscinalis* Müller, *Verm. Terr. Fluv. Hist.*, **2**, p. 172 (Type-locality: Europe).

1878. *Valvata piscinalis:* Nevill, *Sci. Res. Second Yarkand Mission*, Mollusca, p. 12.

1937. *Valvata piscinalis:* Prashad, *Rec. Indian Mus.*, **39** (3), p. 262.

Material: Total No. of examples studied: 1035.

Lot. A: Coll. ? (1) 3 exs., Kashmir.

Lot. B: Coll. B. Prashad: (2) 160 exs., Sta. 1—Chenar Bagh Nullah (a very shallow, slow running stream with a sandy and muddy bottom), Srinagar, 6-8-6-1921; (3) 153 exs., Sta. 14—Wular Lake and streams flowing into it, 1-7-1921; (4) 17 exs., Sta. 20—Nalmar, a slow running nullah from the Dal Lake into the Jhelum River.

Lot. C: Coll. S. L. Hora: (5) 6 exs., Sta. 7—By Boat from Dal Gate to Shalimar Garden *via* Char Chinari (West), 26-5-1954; (6) 3 exs., Sta. 8—First terrace tank, Shalimar Garden, 26-5-1954; (7) 6 exs., Sta. 9—Marginal area of Eastern side of Dal Lake about 1·5 km. away from Nishat Garden, 27-5-1954; (8) 1 ex., Sta. 12—Junction of Tel-bal stream with Dal Lake, 30-5-1954; (9) 4 exs., Sta. 13—Tel-bal nullah near Lower Telbal village, 30-5-1954; (10) 35 exs., Sta. 15—Channels of the Harawan Hatchery, 30-5-1954; (11) 1 ex., Sta. 18—Acchabal Hatchery, 31-5-1954; (12) 9 exs., Sta. 24—Wular Lake side near Forest Rest House, Ningli, 3-6-1954; (13) 4 exs., Sta. 25—Wular Lake collection with boats and fishermen, Ningli, 4-6-1954; (14) 27 exs., Sta. 68—The Sind River at Shalboog, 29-6-1954; (15) 5 exs., Sta. 69—A small stream flowing into the Sind River above the junction of the Jhelum and Sind Rivers, 29-6-1954; (16) 4 exs., Sta. 72—Manasbal Lake marginal area on the Tourist Hut side, 29-6-1954.

Lot. D: Coll. A. S. Rajagopalaiengar: (17) 15 exs., Sta. 5—Nasim Bagh side of Dal Lake, Srinagar, 22-6-1955; (18) 12 exs., Sta. 10—A slow moving stream between paddy fields at the edge of Dal Lake, at Bareen, 27-6-1955; (19) 170 exs., Sta. 25—In the Dal Lake from Nishat Bagh to

Char Chinari along the Eastern border, 11-7-1955; (20) 33 exs., Sta. 30—A marshy area by the road side about 400 m. from Thajiwara near Acchabal Garden, 15-7-1955; (21) 14 exs., Sta. 34—From the terraced tanks of the Acchabal Garden, 17-7-1955; (22) 300 exs., Sta. 36—By boat along the Wular Lake border near Ningli, 22-7-1955; (23) 22 exs., Sta. 38—By boat in the Dal Lake around Char Chinari (West), 26-7-1955; (24) 17 exs., Sta. 39—By boat in the Tel-bal stream near Dal Lake, 26-7-1955.

Lot. E: Coll. K. S. Pradhan: (25) 9 exs., Sta. 48—Gandarbal, collected from a slow running nullah near Forest Rest House, Fatehpur, 3-8-1955; (26) 5 exs., Sta. 64—A number of deep pools about 1·5 km. from Kokarnag.

Distribution: India: Kashmir; Northern Asia; Asia Minor; Europe.

Remarks: Specimens ranging in size from 0·35 mm. to 5·8 mm. are represented in the collection. They agree generally in their characters with Mozley's (1935) description. But the spire appears to be somewhat suppressed and not so sharp. They are mostly greenish, but a few full-grown ones are, however, quite dark in colour and most of them, excepting the small sized, are covered with some encrustations.

Family AMNICOLIDAE

We have followed Pilsbry and Bequaert (1927) in adopting the family name Amnicolidae in place of Hydrobiidae and Paludestrinidae of older authors.

Genus *Bulimus* Scopoli, 1777

Prashad (1937) traces briefly the history of this generic name and refers to the decision of the International Commission of Zoological Nomenclature in its opinion 116, that *Bulimus* Scopoli with its type species *Helix tentaculata* Linnaeus would replace *Bithynia* Leach, 1818, with the same type species.

This genus is represented in the collection by a single species only.

***Bulimus tentaculatus* (Linnaeus) var. *kashmirensis* (Nevill, 1885)**

1885. *Bithynia tentaculata* var. *kashmirensis* Nevill, *Hand List Moll. Indian Mus.*, **2**, p. 39 (Type-locality: Srinagar, Kashmir).

1925. *Bithynia tentaculata* var. *kashmirensis*: Prashad, *Rec. Geol. Surv. India*, **56**, p. 358, pl. 29, figs. 2-5 (1926).

1937. *Bulimus tentaculatus* var. *kashmirensis*: Prashad, *Rec. Indian Mus.*, **39** (3), pp. 263-264.

Material: No. of examples studied: 813.

Lot. A: Coll. ? (1) 29 exs., Z.S.I., Reg. No. 2236, Kashmir.

Lot. B: Coll. S. L. Hora: (2) 1 ex., Sta. 8—First terrace tank Shalimar Garden, 26-5-1954; (3) 5 exs., Sta. 24—Wular Lake side nearest Forest Rest House, 3-6-1954; (4) 1 ex., Sta. 25—Wular Lake collection with boats and fishermen, Ningli, 4-6-1954; (5) 131 exs., Sta. 34—Around Acchabal paddy fields, 11 and 14-6-1954; (6) 1 ex., Sta. 35—A channel of Acchabal stream at Thajiwara, 13-6-1954; (7) 26 exs., Sta. 38—Streams and paddy fields along the road between Acchabal and Kokarnag, 15-5-1954; (8) 50 exs., Sta. ?—Paddy fields below the channel at Pingwana, near Acchabal, 16-6-1954; (9) 25 exs., Sta. 60—Paddy fields at Silunda village about 3 km. from Yarikha Rest House, 24-6-1954; (10) 1 ex., Sta. 61—Roadside about 8 km. from Tangmarg on way to Srinagar (*ca.* 1820 M.) paddy fields, 26-6-1954; (11) 1 ex., Sta. 64—Paddy fields about 27 km. from Tangmarg on way to Srinagar (*ca.* 1575 M.), 26-6-1954.

Lot. C: Coll. K. K. Tiwari: (12) 90 exs., Rice fields at Bareen (Nishat), 10–6–1955; (12 *a*) 65 exs., Paddy fields at Banihal.

Lot. D: Coll. A. S. Rajagopalaiengar: (13) 200 exs., Sta. 7—Paddy fields at Bareen 10 km. from Srinagar, 24–6–1955; (14) 36 exs., Sta. 8—Stagnant water in the lowest tank in Shalimar Garden, 25–6–1955; (15) 20 exs., Sta. 11—Lowest tank in Shalimar Garden, 27–6–1955; (16) 67 exs., Sta. 28—Rice fields at Pingwana about 2·5 km. from Acchabal, 14–7–1955; (17) 51 exs., Sta. 32—Rice fields round about Kokarnag, 16–7–1955; (18) 7 exs., Sta. 33 *a*—Paddy fields near Kalhar village, on the bank of Bhring river about 5 km. from Acchabal, 16–7–1955; (19) 2 exs., Sta. 36—By boat along Wular Lake border near Ningli, 22–7–1955; (20) 4 exs., Sta. 44—Stagnant water in lowest tank in Shalimar, 31–7–1955.

Distribution: India: Kashmir; Punjab: Salt Range.

Remarks: Nevill (1885) merely gave the above name to his new variety based on two lots of collections respectively, from Kashmir (exact locality not stated) and Srinagar and measurements of a single specimen. Later on, Prashad (1925 *b*) stated briefly its diagnostic characters and figured the type shells.

The specimens before us exhibit individual variations in their shell characters, such as, whorls more or less tumid, sutures more or less deeply impressed, etc. Moreover, these variations are not found to be confined to any particular locality or indicative of any significant correlation to an ecological niche to which a lot may be referred. So, it is rather difficult to attribute any systematic importance to these variations.

This is very common in the paddy fields.

Order BASOMMATOPHORA

Family LYMNAEIDAE

A noteworthy contribution to the study of this family is a monograph recently brought out by Hubendick (1951) wherein the author has made a thorough revision and has reduced the multitude of species in the family to approximately forty. Among the earlier works of revision of the family mention may be made of that of Baker (1911) and Annandale and Rao (1925). The last named authors have contributed much to our knowledge of Indian Lymnaeidae. We have followed the classification and nomenclature adopted by them.

Genus *Lymnaea* Lamarck, 1799

Type-species: *Helix stagnalis* Linnaeus.

The diagnostic characters of the genus are described in detail by Baker (1911) and Annandale and Rao (1925). For a detailed synonymy and discussion on the correct spelling of the genus Baker's work cited above may be consulted.

This genus is represented by six species in the collection.

Subgenus *Lymnaea* S.S.

***Lymnaea stagnalis* (Linnaeus, 1758)**

1758. *Helix stagnalis* Linnaeus, *Syst. Nat.* (Ed. X), p. 774 (Type-locality: Sweden).

1799. *Limnaea stagnalis:* Lamarck, *Prodr. Nouv. Clas. Coq.*, p. 75.

1925. *Limnaea stagnalis:* Annandale and Rao, *Rec. Indian Mus.*, **27** (3), p. 147.

1925. *Limnaea stagnalis* form *Kashmiriensis*: Prashad in Annandale & Rao, *Rec. Indian Mus.*, **27** (3), pp. 148, 149.

1925. *Limnaea stagnalis* form *minor*: Prashad in Annandale and Rao, *Rec. Indian Mus.*, **27** (3): p. 150.

Material: No. of examples studied: 634.

Lot. A: coll. ? (1) 8 exs., Srinagar; (2) 10 exs., Kashmir; (3) 1 ex., Rampur, Kashmir, 10–4–1916.

Lot. B: Coll. B. Prashad: (4) 77 exs., Sta. 3—A pond about 1 metre deep on roadside near Missionary Hospital, Srinagar, 10–6–1921; (5) 17 exs., Z.S.I., Reg. No. M 12507/2, Sta. 4—Gandarbal, ponds in the course of a shallow streamlet, *ca*, 1,820 M.; (6) 24 exs., Z.S.I, Reg. No. M 15107/2, Sta. 4—Gandarbal, ponds in the course of a shallow streamlet, *ca.* 1,820 M.; (7) 28 exs., Z.S.I., Reg. No. M 15109/2; Sta. 21—An artificial tank in the pleasure garden, Shalimar; (8) 14 exs., Z.S.I., Reg. No. M 12506/2, Sta. 25—Ponds on the Ichabal-Martand Road.

Lot. C: Coll. G. E. Hutchinson: (9) 4 exs., Z.S.I., Reg. No. M 15108/2, Sta. K 19—Gagribal (closed swamp).

Lot. D: Coll. S. L. Hora: (10) 20 exs., Sta. 8—First terrace tank, Shalimar Garden, 26–5–1954; (11) 12 exs., Sta. 23—Stagnant water near Forest Rest House, Ningli, 3–6–1954; (12) 2 exs., Sta. 35—A channel of Acchabal stream at Thajiwara, 13–6–1954.

Lot. E: Coll. A. S. Rajagopalaiengar: (13) 5 exs., Sta. 7—Channels of paddy fields at Bareen near Srinagar, 24–6–1955; (14) 70 exs., Sta. 8—Stagnant water in the lowest terrace tank in Shalimar Garden, 25–6–1955; (15) 145 ex., Sta. 11 (*a*)—Lowest terrace tank in Shalimar Garden, 27–6–1955; (16) 35 exs., Sta. 28 (*a*)—Channel between rice fields at Pingwana about 2·5 km. from Acchabal, 14–7–1955; (17) 13 exs., Sta. 31—A channel of rice fields by the roadside about 1·6 km. from Acchabal on Acchabal–Thajiwara Road, 15–7–1955; (18) 29 exs., Sta. 36—By boat along the border of Wular Lake to the east of Ningli nullah, 22–7–1955; (19) 53 exs., Sta. 37—Stagnant water pools about 1·6 km. from Ningli Forest Rest House, on the road to Sopur, 23–7–1955; (20) 1 ex., Sta. 40—By boat from Nishat Bagh to Dal Gate (near Gagribal) along the eastern border, 28–7–1955; (21) 25 exs., Sta. 41—Stagnant pools by the roadside opposite the Dal Gate (near Gagribal), 28–7–1955; (22) 2 exs., Sta. 42—Stagnant water from a nullah between paddy fields near Bareen village and bordering the Dal Lake, 29–7–1955; (23) 34 exs., Sta. 44—Stagnant water in the lowest terrace tank in Shalimar Garden, 31–7–1955.

Lot. F: Coll. H. D. Srivastava: (24) 5 exs., Z.S.I., Reg. No. M 16329/2, Srinagar.

Distribution: In India the species is confined to Kashmir only. But regarding its wide range Hubendick (1951) states: "The geographical range of *L. stagnalis* extends over almost the whole of Europe, and the western part of North Africa. The species inhabits all Asia with the exception of the most southern regions, and probably also the extreme north-eastern region. The range extends from Asia Minor, Syria, and Iran in the south, to Obdorsk in the north and Kamchatka in the east. The species is widely distributed in North America, where it inhabits the region of the great lakes. According to Baker (1911) the range extends from the lake basins in a north-westerly direction to the Yukon River in Alaska. In the western states the species occurs to the north of the 37th parallel. It is particularly important to notice that the species inhabits the Alaska Peninsula but is absent along the east coast of America as well as on Newfoundland. Furthermore, the species is absent on Greenland and Iceland. The species is secondarily introduced in some areas, for instance New Zealand."

Remarks: After a critical examination of all the specimens of *L. stagnalis* collected from different localities of Kashmir and also those available in the collection of Zoological Survey of India, it is found that the individual variations amongst them are such that they gradually intergrade with one another and thereby making it rather difficult to distinguish the two forms described from Kashmir, namely, *kashmiriensis* Prashad and *minor* Kobelt from *stagnalis* proper. In this connection the statement of Hubendick (1951) appears interesting: "A great many forms of *L. stagnalis* have been described and named. Only those forms, which represent geographical races, have any systematic importance. Many names only refer to phenotypes, eco-phenotypes or microgeographical races, *i.e.*, single populations, and must be rejected.

In the valley these snails were found, apart from lakes and streams, quite commonly in channels draining paddy fields rather than in the fields themselves. These are the largest among the lymnaeids found in Kashmir.

Subgenus *Radix* Montfort, 1810

Type-species—*Helix auricularia* Linnaeus.

Baker (1911) has given the synonymy and diagnostic characters of *Radix* treating it as a genus, while Annandale and Rao (1925) have subordinated it to *Lymnaea* and recognized the following four Indian species:

1. *L. auricularia* (Linnaeus)
2. *L. brevicauda* Sowerby
3. *L. lagotis* (Schrank)
4. *L. persica* Issel.

In the collection before us only the first three species are represented.

***Lymnaea auricularia* (Linnaeus, 1758)**

1758. *Helix auricularia* Linnaeus, *Syst. Nat.* (Ed. X), p. 774 (Type-locality: Sweden).

1925. *Limnaea auricularia:* Annandale and Rao, *Rec. Indian Mus.*, **27** (3), p. 158, figs. 1–2 and 4

1937. *Lymnaea auricularia:* Prashad, *Rec. Indian Mus.*, **39** (3), pp. 266–267.

1951. *Lymnaea auricularia:* Hubendick, *Kungl. Vetensk. Handl.*, 3 (1), pp. 151–153, figs. 336—*b*.

Material: No. of examples studied: 600.

Lot. A: Coll. ? (1) 7 exs., Kashmir.

Lot. B: Coll. B. Prashad: (2) 24 exs., Z.S.I., Reg. No. M 15006/2—Chinarbagh nullah—a very slow-running shallow stream with a sandy and muddy bottom; (3) 33 exs., Z.S.I. Reg. No. M. 15007/2, Sta. 14—Wular Lake and the streams flowing into it, alt. *ca.* 1,575 M., 1–7–1921; (4) 42 exs., Z.S.I. Reg. No. M 15008/2, Sta. 16—Dal Lake—eastern corner near Gagribal; (5) 8 exs., Z.S.I., Reg. No. M 15009/2, Sta. 20—Nan Mar, a slow-running nullah or streamlet from the Dal Lake into the Jhelum river.

Lot. C: Coll. S. L. Hora: (6) 8 exs., Sta. 7—By boat from Dal Gate to Shalimar Garden *via* Char Chinari (West), 26–5–1954; (7) 50 exs., Sta. 8—First terrace tank, Shalimar Garden, 26–5–1954; (8) 2 exs., Sta. 25 *a*—Wular Lake collection with boats and fishermen, Ningli, 5–6–1954; (9) 11 exs., Sta. 72—Mansabal Lake Marginal area on the tourist hut side, 29–6–1954.

Lot. D: Coll. A.S. Rajagopalaiengar: (10) 20 exs., Sta. 2—Nagin Bagh, edge of Dal Lake, 18–6–1955; (11) 250 exs., Sta. 25—Dal Lake from Nishat Bagh to Char Chinari (East) along the eastern border of the lake, 11–7–1955; (12) 58 exs., Sta. 36—By boat along the border of Wular Lake by the Sopur bund for 4 km. to the east of Ningli nullah, 22–7–1955; (13) 45 exs., Sta. 40—By boat from Nishat Bagh to Dal Gate (near Gagribal) along the eastern border, 28–7–1955, Lot. E: Coll. K. K. Tiwari: (14) 3 exs., Paddy fields, Banihal, 15-7-1955; (15) 9 exs., Paddy fields near Banihal, 17-7-1955; (16) 30 exs., Banihal, in the stream, 17-7-1955.

Distribution: Hubendick (1951) considers *L. auricularia* as a superspecies complex in which he includes the Indian form *rufescens* Gray along with many other Asiatic species. According to this interpretation, the geographical range of *auricularia* would extend over a much wider area than the species in *sensu stricto*. However, since we are treating the species here in *sensu stricto*, it appears more appropriate to follow the distribution as summed up by Mozley (1935): "Europe, as far south as Spain and Italy; Northern Asia; Afghanistan and Kashmir."

Remarks: Though a great deal of variations are found to occur in the specimens studied, yet there is very little doubt as to their close identity with *L. auricularia*. The shell is thin and highly fragile with a bulging body whorl and short but pointed spire. The colour of the periostracum is shining light brown to light olive green. Sometimes shells with a light pinkish hue are also met with. The greatly twisted columella distinguishes it from *L. brevicauda*.

The animals are light coloured. They were found in paddy fields crawling on the mud.

Lymnaea brevicauda Sowerby, 1873

1873. *Limnaea brevicauda* Sowerby, in Reeve's *Conch. Icon.*, **18**, p. 105, pl. xv (Type-locality—Kashmir).

1925. *Limnaea brevicauda:* Annandale and Rao, *Rec. Indian Mus.*, **27** (3), pp. 157-158, figs. 1-6.

1937. *Lymnaea brevicauda:* Prashad, *Rec. Indian Mus.*, **39** (3), p. 270.

Material: No. of examples studied: 225.

Lot. A: Coll. B. Prashad: (1) 3 exs., Sta. 22—Ichabal stream flowing from the spring.

Lot. B: Coll. S. L. Hora: (2) 30 exs., Sta. 18—Channels of the Acchabal Hatchery, 31-5-1954.

Lot. C: Coll. A. S. Rajagopalaiengar: (3) 150 exs., Sta. 26—A pond full of floating vegetation by the side of Naghdandi Ashram, Acchabal, 13-7-1955; (4) 42 exs., Sta. 34—Terraced tanks of the Acchabal gardens, 17-7-1955.

Distribution: This species seems to be confined to Kashmir only; commonly found around Acchabal.

Remarks: The species is characterised by having a thick and hard shell. When fresh, it is dark brown in colour. In living condition the animal including its mantle is of a dull yellow colour. When a crawling snail is lifted up, its mantle can be seen as a thick fold lining the rim of the aperture till the animal slowly withdraws it inside the shell.

The senior author observed these animals having a preference to crawl on stones and cemented side-walls of tanks and other surfaces over which water flows, thus confirming the observation of Annandale and Rao (1925).

Lymnaea lagotis (Schrank, 1803)

1803. *Buccinum lagotis* Schrank, *Fauna Boica*, **3**, p. 290 (Type-locality: River Donau).

1874. *Limnaea lagotis:* von Martens, in Fedtschenko's *Reise in Turkestan, Mollusca*, **2**, p. 26, pl. ii, fig. 22.

1925. *Limnaea lagotis:* Annandale and Rao, *Rec. Indian Mus.*, **27** (3), pp. 151-153.

1937. *Lymnaea lagotis:* Prashad, *Rec. Indian Mus.*, **39** (3), p. 267.

L. lagotis proper is not known to have been recorded so far from Indian limits. But four forms of it, *viz.*, *striata* Andreae, *costulata* Martens, *solidissima* Kobelt, and *defilippii* Issel, are recorded from Kashmir. All the four are represented in the collection.

Form *striata* Andreae, 1911

1911. *Limnaea* (*Gulnaria*) *lagotis* var. *striata* Andreae, in Futterer: *Durch Asien*, **3**, p. 75, fig. (Type-locality: Central Asia).

1925. *Limnaea* (*Radix*) *lagotis* f. *striata*: Annandale and Rao, *Rec. Indian Mus*, **27** (3), p. 153, figs. I—1.

1937. *Lymnaea lagotis* f. *striata*: Prashad, *Rec. Indian Mus.*, **39** (3), p. 267.

Material: No. of examples studied: 589.

Lot. A: Coll. ? (1) 2 exs., Gandarbal; (2) 13 exs., Sta. 25—Ponds on the Ichabal-Martand road; (3) 48 exs., Sta. ?—Swamps 11·2 km. from Gandarbal on the road to Sonamarg; (4) 24 exs., Sta. K. 17—Streams from the water works reservoir leading to the Trout farm at Harawan.

Lot. B: Coll. S. L. Hora: (5) 12 exs., Sta. 3—Stagnant water by the roadside near Dal Lake Gate, Srinagar, 24-5-1954; (6) 20 exs., Sta. 6—Along the east bank of Dal Lake for 3-8 km. from Dal Gate, 25-5-1954; (7) 2 exs., Sta. 14—Irrigation Channel behind Harawan Hatchery, 30-5-1954; (8) 8 exs., Sta. 18—Channels of the Acchabal Hatchery, 31-5-1954; (9) 1 ex., Sta. 30—Streams in front of Chowalgam Rest House (Tehsil branch of the Vishoo River), 10-6-1954; (10) 15 exs., Sta. 34 *b*—A stream below Acchabal Hatchery spring, 13-6-1954; (11) 10 exs., Sta. 35—A channel of Acchabal stream at Thajiwara about 3 km. from Acchabal, 13-6-1954; (12) 30 exs., Sta. 41—Arpat stream about 3 km. from Acchabal on way to Martand temple, 17-6-1954.

Lot. C: Coll. K. K. Tiwari: (13) 30 exs., Acchabal, in the Hatchery, 6-6-1955.

Lot. D: Coll. A. S. Rajagopalaiengar: (14) 35 exs., Sta. 7—Paddy fields at Bareen near Srinagar, 24-6-1955; (15) 45 exs., Sta. 29—Malu stream by the side of Akhran village about 4 km. from Acchabal, 14-7-1955; (16) 148 exs., Sta. 30—A swampy area by the roadside about ½ km. from Thajiwara, 15-7-1955; (17) 5 exs., Sta. 31—Thajiwara above the junction of Arpat stream and Acchabal stream, 15-7-1955; (18) 100 exs., Sta. 34—A channel of the Acchabal Trout Hatchery, 17-7-1955; (19) 36 exs., Sta. 38—By boat in Dal Lake around Char Chinari (West), 26-7-1955; (20) 1 ex., Sta. 41—Stagnant pools by the roadside opposite the Dal Gate (near Gagribal), 28-7-1955.

Lot. E: Coll. K. S. Pradhan: (21) 4 exs., Sta. 52—A pool of water by the side of paddy fields, Ganderbal, 5-8-1955.

Distribution: Central Asia: Gobi desert: Sulai-ho; Tibet: Gyantse (3980 M.), Lhasa (3580 M.) Mangtsa (4398 M.), Somada (4246 M.); India: Kashmir.

Remarks: The large collection studied contains specimens in all stages of growth. It is noticed that the spire in the younger stages is longer than in the adults. Moreover, the aperture of the shell is ovoid in the earlier stages and gradually becomes semicircular or auriculate in the adult. Fine longitudinal striae can also be seen in some cases. In these respects, our observations agree with those of Prashad (1937). The shell is rather thin and fragile.

In living condition, the animal with fine dark spots on the body, except on the ventral side of the foot, can be seen through the almost transparent body whorl. Occasionally, some shells are rosy or pinkish in fresh condition somewhat similar to *L. auricularia* (Linn.).

Form *costulata* von Martens, 1874

1874. *Limnaea lagotis* var. *costulata* von Martens, in Fedtschenko's *Reise in Turkestan, Mollusca*, **2**, p. 26, pl. ii, fig. 24. (Type-locality: Tashkent).

1925. *Limnaea lagotis* form *costulata*: Annandale and Rao, *Rec. Indian Mus.*, **27** (3), pp. 153–154, figs. 1–7.

1937. *Limnaea lagotis* form *costulata*; Prashad, *Rec. Indian Mus.*, **39** (3), p. 268.

Material: No. of examples studied: 357.

Lot. A: Coll. H. S. Pruthi: (1) 23 exs., Srinagar, Kashmir, N.-W. Himalayas, 8–9–1932.

Lot. B: Coll. S. L. Hora: (2) 1 ex., Sta. 3—Stagnant water by the roadside near Dal Lake Gate, Srinagar, 4–5–1954; (3) 3 exs., Sta. 25 *a*—Wular Lake collection with boats and fishermen, Ningli, 5–6–1954; (4) 4 exs., Sta. 67—Anchar Lake from off Anchar village, 29–6–1954.

Lot. C: Coll. A. S. Rajagopalaiengar: (5) 10 exs., Sta. 2—Nagin Bagh side of Dal Lake, 18–6–1955; (6) 28 exs., Sta. 7—Paddy fields near Bareen at the edge of Dal Lake, 24–6–1955; (7) 250 exs., Sta. 26—A pond full of floating vegetation by the side of Nagdandi Ashram about 1·5 km. from Acchabal 13–7–1955; (8) 25 exs., Sta. 34—A channel of the Acchabal Trout Hatchery, 17–7–1955; (9) 1 ex., Sticking to a stone in the nullah in front of the Bareen Substation of Z.S.I., near Srinagar, 31–7–1955.

Lot. D: Coll. K. K. Tiwari: (10) 9 exs., Banihal, in the stream by the town, 13–7–1955; (11), 3 exs., Paddy fields, Banihal, 15–7–1955.

Distribution: Asia: Turkestan: Tashkent; Tibet: Chusol (4155 M.), Gyantse, Mugleb (4155 M.); India: Kashmir, Ladakh: Leh.

Remarks: We find that the spire of the shell here is larger and the aperture is less expanded than in *striata*, and shape of aperture being more or less constant. But in the collection from Acchabal, this form occurs along with *striata* and also specimens with intermediate characters appear to be quite common.

Form *solidissima* Kobelt, 1872

1872. *Limnaea lagotis* var. *solidissima* Kobelt, *Malakozool. Blätt.*, 19, p. 77, pl. ii, figs. 17–18 (Type-locality: Himalayas).

1925. *Limnaea lagotis* f. *solidissima*: Annandale and Rao, *Rec. Indian Mus.*, **27** (3), pp. 154–155, figs. 1–3 and 5.

1937. *Lymnaea lagotis* f. *solidissima*: Prashad, *Rec. Indian Mus.*, **39** (3), pp. 268–269.

Material: No. of examples studied: 3.

Lot. Coll: A. S. Rajagopalaiengar: (1) 2 exs., Sta. 30—A swampy area by the roadside about ¼ km. from Thajiwara near Acchabal, 15–7–1955; (2) 1 ex., Sta. 35—Terraced tanks of the Acchabal Garden, 17–7–1955.

Distribution: Tibet: Chusol (4315 M.), Panggong Tso (Pankong Lake) (4220 M.), Tsar Tso (4231 M.) India: Kashmir.

Remarks: The limited collection that we have in hand shows the characteristic solid nature of the shell, but its thickness is not to such an extent as observed in Stoliczka's collection studied by Nevill (1878). The columella also shows the thickening, but to a lesser degree. The peristome agrees with Annandale and Rao's (1925), fig. 1, No. 3.

Form *defilippii* Issel, 1865

1865. *Limnaea defilippii* Issel, *Catalog. Moll. Miss. Ital. in Persia*, p. 45, pl. iii, figs. 62–63. (Type-locality: Lake Goktscha, Armenia).

1925. *Limnaea lagotis* f. *defilippii*: Annandale and Rao; *Rec. Indian Mus.*, **27** (3), pp. 156–157, figs. 1–9.

1937. *Lymnaea lagotis* f. *defilippii*: Prashad, *Rec. Indian Mus.*, **39** (3), pp. 269–270.

Material: No. of examples studied: 33.

Lot. A: Coll. ? (1) 5 exs., Kashmir.

Lot. B: Coll. S. L. Hora: (2) 6 exs., Sta. 41—Arpat stream about 3 km. from Acchabal on way to Martan temple, *17–6–1954*; (3) 14 exs., Sta. 42—Martan temple, 17–6–1954.

Lot. C: Coll. A. S. Rajagopalaiengar: (4) 1 ex., Sta. 31 *a*—A channel of the rice fields by the roadside about 1·6 km. from Acchābal, 15–7–1955.

Lot. D: Coll. K. K. Tiwari: (5) 5 exs., Paddy fields, Banihal, 15–7–1955.

Distribution: USSR: Armenia: Lake Goktscha; India: Kashmir.

Remarks: Annandale and Rao (1925) and Prashad (1937) have discussed at some length the affinities of this species to *L. lagotis* and *L. auricularia* on the one hand and with *L. stagnalis* on the other.

The shells are extremely fragile.

Subgenus *Pseudosuccinea* Baker, 1908

Type species: *Lymnaea columella* Say, 1817 (Type-locality: U.S.A.).

Baker (1908) erected *Pseudosuccinea* as a genus for the reception of Succinea-like forms, but Annandale and Rao (1925) made it a subgenus of *Lymnaea*.

Lymnaea luteola f. *typica* Lamarck, 1822

1838. *Limnaea luteola* Lamarck, *Hist. Nat. Anim. Sans Vert.*, 8, p. 411. (Type-locality: Bengal).

1925. *Limnaea luteola*: Annandale and Rao, *Rec. Indian Mus.*, **27** (2), pp. 106–107.

Material: No. of examples studied: 13.

Lot. A: Coll. F. J. Mitchell: (1) 2 exs., Z.S.I., Reg. No. M 15043/2, Srinagar, Kashmir.

Lot. B: Coll. S. L. Hora: (2) 3 exs., Sta. 61—Roadside about 8 Km. from Tangmarg on way to Srinagar (*ca.* 1,820 M.), paddy fields, 26–6–1954; (3) 8 exs., Sta. 62—Roadside about 14·4 Km. from Tangmarg on way to Srinagar, near Chichilura village, 26–6–1954.

Distribution: India: Kashmir; Punjab: Salt Range; Himachal Pradesh: Kulu; Delhi; Uttar Pradesh: Aligarh, Bikapur, Faizabad, Mussoorie, Nainital, Roorkee; Bihar: Manbhum, Rajmahal, Ranchi; West Bengal: Calcutta, Ranigunge; Manipur; Orissa: Barkuda Island, Kallikote; Andhra Pradesh: Godavari Town, Golconda, Hyderabad, Kurnool, Nizamsagar Project area, Secunderabad, Tungabhadra Project area; Madras: Kallar (Nilgiri District), Saidapet (Madras Town), Tiruchirapalli; Mysore: Bangalore, Mandya, Mysore;

Kerala; Goa: Salsettee; Maharashtra: Bombay, Nagpur; Poona; Gujarat: Kutch; Madhya Pradesh: Itarsi, Kamptee, Pachmarhi, Raipur; Andamans; Pakistan: Rawalpindi; Nepal: Pharping; Burma; Siam; Ceylon.

Remarks: The characters of this species and the forms recognised under it are described in detail by Annandale and Rao (1925). Hubendick (1951), however, does not recognise any form under this species.

These were found to occur generally in paddy fields proper.

Lymnaea luteola f. *succinea* Deshayes, 1834

1834. *Limnaea succinea* Deshayes, *Voy. dans. Ind. Belanger, Zool.*, p. 418, pl. ii, figs. 13, 14. (Type-locality: Malabar Coast, S. India).

1925. *Limnaea luteola* f. *succinea*: Annandale and Rao, *Rec. Indian Mus.*, **27** (3), p. 185, text-figs. IV-4.

Material: No. of examples studied: 176.

Lot. A: Coll. B. Prashad: (1) 23 exs., Z.S.I., Reg. No. M 15076/2, Sta. 18—A rice field along the bank of the hill-stream leading to the front farm at Harwan; (2) 34 exs., Z.S.I., Reg. No. M 15077/2, Sta. 27—Rice fields at Kukarnag.

Lot. B: Coll. S. L. Hora: (3) 2 exs., Sta. 27—Sangram, about 5 km. from Sopore, paddy fields, 4-6-1954; (4) 1 ex., Sta. 40—Paddy fields below the channel near Acchabal, 16-6-1954.

Lot. C: Coll. A. S. Rajagopalaiengar: (5) 2 exs., Sta. 1—Batakoot, Paddy fields, 16-6-1955; (6) 4 exs., Sta. 3—Paddy fields at Bareen (Nishat) near Srinagar, 19-6-1955; (7) 19 exs., paddy fields at Bareen, 9·5 km. from Srinagar, 23-6-1955; (8) 36 exs., Sta. 7—Paddy fields near Bareen at the edge of Dal Lake, 24-6-1955; (9) 12 exs., Sta. 28—Rice fields at Pingwana, about 2·5 km. from Acchabal, 14-7-1955; (10) 11 exs., Sta. 33—Rice fields round about Kokarnag, 16-7-1955; (11) 3 exs., Sta. 33 *a*—Paddy fields near Kalhar village, on the bank of Bhring river, about 5 km. from Acchabal, 16-7-1955.

Lot. D: Coll. K. K. Tiwari: (12) 3 exs., Banihal, in the stream by the town, 13-7-1955; (13) 22 exs., Paddy fields near Banihal, 17 and 20-7-1955.

Lot. E: Coll. K. S. Pradhan: (14) 3 exs., Sta. 50—Manasbal Lake, 4-8-1955.

Lot. F: Coll. V. P. Rao: (15) 1 ex., Z.S.I., Reg. No. M 17229/2, Srinagar.

Distribution: India: Kashmir: Harawan, Kokarnag, Srinagar; Punjab; Uttar Pradesh: Baijnath, Saranath; Bihar: Hazaribagh, Ranchi; Andhra Pradesh: Godavari Town, Husainsagar, Kurnool, Secunderabad; Madras: Coonoor (Nilgiri Hills), Palni Hills; Maharashtra: Andheri (Bombay); Rajasthan: Udaipur.

Remarks: The collection is of uniform nature and does not exhibit much individual variation. The shells are mostly large and narrow with large tapering spire. They are generally glossy and thin.

The specimens from the rice fields round about Kokarnag are especially much larger than usual. The animals when alive were black in colour and commonly seen floating with the foot turned upwards.

Subgenus *Galba* Schrank, 1803

Type-species: *Buccinum truncatalum* Müller

1803. *Galba* Schrank, *Fauna Boica*, **3** (2), pp. 262, 285.

1925. *Galba*: Annandale and Rao, *Rec. Indian Mus.*, **27** (3), p. 161.

Annandale and Rao (1925) used this subgenus in a restricted sense to include the type-species *L. truncatula* and its allies.

In the present collection this subgenus is represented by only one species, *viz.*, *truncatula.*

Lymnaea truncatula (Müller, 1774)

1774. *Buccinum truncatulum* Müller, *Verm. Terr. Fluv. Hist.*, **2**, p. 130 (Type-locality: Denmark).

1925. *L'mnaea truncatula*: Annandale and Rao, *Rec. Indian Mus.*, **27** (3), pp. 161–162, figs. V—3 to 5.

1937. *Lymnaea truncatula*: Prashad, *Rec. Indian Mus.*, **39** (3), p. 271.

1951. *Lymnaea truncatula*: Hubendick, *Kungl. Vitensk. Handl.*, **3** (1), pp. 122–124.

Material: No. of examples studied: 48.

Lot. A: Coll. S. L. Hora: (1) 30 exs., Sta. 43—Stagnant water near Pahalgam, 12–14–6–1954; (2) 1 ex., Sta. 39—A small channel at Naghdandi, about 1·6 km. from Acchabal, 16–6–1954.

Lot. B: Coll. A. S. Rajagopalaiengar: (3) 17 exs., Sta. 22—Stagnant pools by the side of the canal of Lidar river, Pahalgam on the road to Chandanwari, 8–7–1955.

Distribution: India: Kashmir: Chitral (2,730 M.), Chushod (3,213 M.), Dras (3,075 M.), Kangral (3,365 M.) and Spitok (3,253 M.); Ladakh; Leh.

Hubendick (1951) states: "*L. truncatula* is distributed all over Europe including Iceland, the Faeroe Islands and Madeira. The species inhabits North-Western Africa and Egypt. Its range extends through Asia from Iran and northernmost Russia to Camchatka. Within Asia the southern limit of the range is obscure particularly because of confusion with the similar East Asiatic species *L. viridis.* The Asiatic range is connected with the North American one through occurrences on the Aleutian Islands. Finally, the species occurs in East Africa, Cameron, and South Africa. In East Africa the species is found in Ethiopia, one find is coming from the eastern slope of Mount Elgon at about 2,300 m. altitude above sea-level, another find originating from north of Mount Kenya in Tropical Africa. The distribution of *L. truncatula* in Africa seems in all probability to be the result of transportation by migrating birds."

Remarks: The shells which are rather small in size are with strongly impressed sutures. The columellar fold is broad and forms a flat projection over the umbilicus.

Several live specimens were found sticking to stones, while others to blades of grass, leaves and stems of plants in water.

Family PLANORBIDAE

Genus *Planorbis* Geoffroy, 1767

1767. *Planorbis* Geoffroy, *Traite, Coq.*, p. 12.

1921. *Planorbis*: Germain, *Rec. Indian Mus.*, **21** (1), p. 1.

1937. *Planorbis*: Prashad, *Rec. Indian Mus.*, **39** (3), p. 271.

Prashad (1937) has pointed out clearly the difference of opinion existing among authors regarding the authorship of this genus and its type-species. We follow Prashad in this respect.

Planorbis planorbis (Linnaeus) var. *tangitarensis* Germain 1918

1918. *Planorbis* (*Tropidiscus*) *planorbis* var. *tangitarensis* Germain, *Bull. Mus. Hist. nat. Paris*, **24** (4), p. 276 (Type-locality: North Tangitar).

1921. *Planorbis* (*Tropidiscus*) *planorbis* var. *tangitarensis*: Germain, *Rec. Indian Mus.*, **21** (1), pp. 77–78, pl. iv, figs. 3–4 & 8.

1937. *Planorbis planorbis* var. *tangitarensis*: Prashad, *Rec. Indian Mus.*, **39** (3), p. 272.

Material: No. of examples studied: 70.

Lot. A: Coll. ? (1) 22 exs., Marshes near Dal Lake, 30–3–1916.

Lot. B: Coll. H. Khajuria: (2) 9 exs., Sta. 6—Along the east bank of Dal Lake for 3–8 km. from Dal Gate, 25–5–1954; (3) 1 ex., Sta. 7—By boat from Dal Gate to Shalimar Garden *via* Char Chinari (West), 26–5–1954.

Lot. C: Coll. A. S. Rajagopalaiengar: (4) 15 exs., Sta. 41—Stagnant pools by the roadside opposite the Dal Gate (near Gagribal), 28–7–1955; (5) 22 exs., Sta. 43—Stagnant pools by the roadside opposite Dal Gate (near Gagribal), 30–7–1955.

Lot. D: Coll. K. S. Pradhan: (6) 1 ex., Sta. 83—Pools about 5 km. south of the base camp at Bareen, 22–8–1955.

Distribution: India: Kashmir; Central Asia: (China): North Tangitar.

Remarks: It was Nevill (1878) who commented briefly on the collection from Tangitar and noticed that it was a remarkable one and may prove to be new to science, but he did not proceed further. It was left to Germain (1918) to designate this new variety as *tangitarensis* and later (1921) to figure it.

In Kashmir, it seems to thrive well in stagnant pools with highly decomposing organic matter in preference to lakes and ponds with comparatively fresh and clear water. In the light of this observation the localities (2) and (3) under Lot. B. above appear to be peculiar. During an intensive search, in June–August 1955, in Dal Lake in the same localities it has not been possible to obtain even a single specimen. But in any case the specimens collected by Shri Khajuria and other parties as stated above appear identical.

Planorbis rotundatus Poiret, 1801

(Pl. I, Figs, 2, 3 & 4)

1801. *Planorbis rotundatus* Poiret, *Coq. Aisne, environs de Paris*, Prodrome, p. 93 (non.: *Planorbis rotundatus* Brongniart).

1875. *Planorbis rotundatus*: Westerlund, *Malakozool. Blätt.*, **22**, p. 108, No. 10, pl. iii, figs. 40 and 42.

1913. *Planorbis* (*Paraspira*) *rotundatus*: Germain, *Mollusques France et regions voisines*, p. 225, fig. 301.

Material: No. of examples studied: 156.

Lot.: Coll. A. S. Rajagopalaiengar: (1) 10 exs., Sta. 8—Stagnant water in the lowest terraced tank in Shalimar Garden, 25–6–1955; (2) 2 exs., Sta. 11—Lowest terraced tank in Shalimar Garden, 27-6-1955; (3) 50 exs., Sta. 26—A pond full of floating vegetation by the side of Naghdandi Ashram about 1·5 km. from Acchabal, 13-7-1955; (4) 85 exs., Sta. 30—A swampy area by the roadside about ½ km. from Thajiwara near Acchabal, 15-7-1955; (5) 9 exs., Sta. 44—Stagnant water in the lowest terraced tank in Shalimar Garden, 31-7-1955.

Distribution: Europe: Norway; Sweden; Spain; Protugal; Asia: Siberia; Africa: Algeria; Morocco; Tunisia.

Remarks: The collection agrees well with specimens of *P. rotundatus* available in Z.S.I. obtained from different localities in England. But some of the shells from locality (3) as noted above show some concavity on the ventral side.

This is the first record of the species from Kashmir.

Genus *Indoplanorbis* Annandale and Prashad, 1921

Type-species: *Planorbis exustus* Deshayes

1921. *Indoplanorbis* Annandale and Prashad, *Rec. Indian Mus.*, **22** (4), pp. 578–580.

1923. *Indoplanorbis:* Rao, *Rec. Indian Mus.*, **25**, pp. 199–219, figs. 1–14.

1933. *Indoplanorbis:* Baker, *J. Morphol.*, **55**, pp. 1–9, pls. i-ii.

This genus was created by Annandale *et al.* (1921) for the common Indian Planorbid, *Indoplanorbis exustus* (Deshayes). It differs from true *Planorbis* in the structure of the branchial process, the radula; and the genitalia and in the characteristic facies of the shell.

***Indoplanorbis exustus* (Deshayes, 1834)**

1834. *Planorbis exustus* Deshayes, *Voy. Belanger. Indes-Orient. Zool.*, p. 417, pl. 1, figs. 11–13 (Type-locality: India).

1921. *Planorbis (Planorbis) exustus:* Germain, *Rec. Indian Mus.*, **21** (1), pp. 26–39, pl. iv, figs. 11, 17 & 18.

1921. *Indoplanorbis exustus:* Annandale and Prashad, *Rec. Indian Mus.*, **22**, p. 580.

Material: No. of examples studied: 208.

Lot. A: Coll. B. Prashad: (1) 26 exs., Z.S.I., Reg. No. M 14868/2, Sta. 4—Ponds in the course of a shallow irrigation streamlet, Gandarbal, alt. 1,820 M., 14-6-1921; (2) 35 exs., Z.S.I., Reg. No. M 14873/2, Sta. 18—A rice field along the bank of the hill stream, from the water works reservoir leading to the front farm at Harawan.

Lot. B: Coll. S. L. Hora: (3) 1 ex., Sta. 13—Tel-bal nullah near lower Tel-bal village, 30-5-1954; (4) 1 ex., Sta. 30—Streams in front of Chowalgam Rest House (Tehsil branch of Vishoo river), 10-6-1954; (5) 2 exs., Sta. 35—A channel of Acchabal stream at Thajiwara about 3 km. from Acchabal, 13-6-1954; (7) 8 exs., Sta. 40—Water Channel at Pingwana about 2·5 km. from Acchabal, 16-6-1954.

Lot. C: Coll. A. S. Rajagopalaiengar: (7) 5 exs., Sta. 3—Rice fields at Bareen (Nishat Bag) near Srinagar, 19-6-1955; (8) 35 exs., Sta. 7—Paddy fields near Bareen at the edge of Dal Lake; 24-6-1955; (9) 19 exs., Sta. 38—Rice fields at Pingwana about 2·5 km. from Acchabal, 14-7-1955, (10) 14 exs., Sta. 29—Mahi stream by the side of Akhran village about 3 km. from Acchabal, 14-7-1955; (11) 8 exs., Sta. 33 *a*—Paddy fields near Kalhar village on the bank of Bhring river, 16-7-1955; (12) 50 exs., Sta. 42—Stagnant water from a nullah between paddy fields near Bareen village, 29-7-1955.

Lot. D: Coll. K. S. Pradhan: (13) 1 ex., Sta. 99 *a*—Pools near about Ladura, Baramula, 5-9-1955.

Lot. E: Coll. V. P. Rao: (14) 3 exs., Paddy fields, Srinagar.

Distribution: India: throughout; Persia: Gwadur; Pakistan; Burma; Ceylon; Siam; Malay Peninsula; Indo-China; Cochin-China; Indonesia: Sumatra.

Remarks: Although this species can be found in paddy fields, streams and ponds of the Valley, it is not as common and widespread as the species of *Lymnaea*. All the specimens examined are more or less of normal features, though it is known to be a highly variable species. Prashad (1937) recorded it from Sohawa, Rawalpindi District, Punjab (now in Pakistan), but not from Kashmir.

Genus *Gyraulus* Charpentier, 1837

Type-species: *Planorbis albus* Müller

1837. *Gyraulus* Agassiz MS. in De Charpentier *Denkschr Schweiz. Gessel. Nat. Neuchatel*, **1**, p. 21.

1922. *Gyraulus:* Germain, *Rec. Indian Mus.*, **21** (2), p. 98.

1922. *Gyraulus:* Annandale, *Rec. Indian Mus.*, **24** (3), p. 361.

Shell small with rapidly increasing whorls and the last broadening towards the aperture.

This is represented here by a single species.

Gyraulus pankongensis (von Martens, 1882)

(Pl. I, Fig. 1)

1882. *Planorbis pankongensis* von Martens, *Mem. Acad. Imp. Sci. St. Petersbourgh*, (7) **30**, No. 11, p. 45, pl. iv, figs. 14 *a-c* (Type-locality: Lake Pankong, Tibet).

1922. *Planorbis* (*Gyraulus*) *pankongensis*: Germain, *Rec. Indian Mus.*, **21** (2), p. 110.

1937. *Gyraulus pankongensis*: Prashad, *Rec. Indian Mus.*, **39** (3), p. 272.

Material: No. of examples studied: 323.

Lot. A: Coll. B. Prashad: (1) 3 exs., Sta. 2—A very shallow slow-running stream with a sandy and muddy bottom, Srinagar, 6-8-6-1921; (2) 28 exs., Sta. 3—A pond about 1 M. deep on roadside near Missionary Hospital, Srinagar, 10-6-1921; (3) 4 exs., Sta. 4—Ponds in the course of a shallow irrigation streamlet, Gandarbal, alt. 1,820 M., 14-6-1921.

Lot. B: Coll. S. L. Hora: (4) 1 ex., Sta. 8—First terrace tank, Shalimar Garden, 26-5-1954; (5) 50 exs., Sta. 57—Paddy fields above Ferozepur stream, 23-6-1954; (6) 22 exs., Sta. 60—Paddy fields at Silunda village about 3 km. from Yarikha Rest House, 24-6-1954.

Lot. C: Coll. K. K. Tiwari: (7) 10 exs., Batakoot paddy fields, 13-5-1955; (8) 32 exs., Paddy fields, Banihal, 16 & 22-7-1955; (9) 10 exs., Paddy fields, Batote, 2-8-1955.

Lot. D: Coll. A. S. Rajagopalaiengar: (10) 30 exs., Sta. 1—Paddy fields, Batakoot, 16-6-1955; (11) 12 exs., Sta. 8—Stagnant water in lowest tank, Shalimar Garden, 25-6-1955; (12) 6 exs., Sta. 11—

Lowest tank in Shalimar Garden, 27-6-1955; (13) 4 exs., Sta. 30–A swampy area by the roadside about ½ km. from Thajiwara near Acchabal, 15-7-1955; (14) 7 exs., Sta. 37—Stagnant water pools about 1·5 km. from Ningli Forest Rest House, on the road to Sopur, 23-7-1955; (15) 22 exs., Sta. 42—Stagnant water from a nullah between paddy fields near Bareen village and bordering Dal Lake, 29-7-1955; (16) 24 exs., Sta. 43—Stagnant pools by the roadside opposite Dal Lake near Gagribal, 30-7-1955; (17) 24 exs., Sta. 44—Stagnant water in the lowest terraced tank in Shalimar Garden, 31-7-1955; (18) 34 exs., Sta. 47—From paddy fields near Tangmarg, 2-8-1955.

Distribution: India: Kashmir; Central Asia: China: Tibet.

Remarks: Prashad (1937) has briefly discussed the views of von Martens, Weber, and Germain regarding the affinities of this species with other allied species.

We have critically examined the specimens and compared them with the holotype figured by von Martens. There is no doubt that they are identical with this species, but certain variations are also noticeable. Of the entire collection, Lot A above bears the most striking resemblance to the holotype save that the shells are thinner. The connection between the inner and outer lips is considerably straight. The specimens in the Lots B, C and D are very much thinner and so neither the aperture nor the columella appears with a thick deposit of shell. The number of whorls is generally 3 to 4. Some of the shells are nearly flat, while others show a varying degree of concavity ventrally with a corresponding convexity dorsally and the aperture consequently appearing rather oblique. In a few cases, the body whorl shows signs of carination.

Genus *Hippeutis* Charpentier, 1837

Type-species: *Hippeutis fontanus* Lightfoot

1837. *Hippeutis* Agassiz MS. in De Charpentier, *Denkschr. Schweiz. Gessel. Nat. Neuchatel*, **1**, p. 22.

1923. *Hippeutis:* Germain, *Rec. Indian Mus.*, **21** (3), pp. 159-160 (as a subgenus of *Planorbis*). Shell small and thin, with the spire partially exposed. The aperture is obliquely heart-shaped. This genus is represented by a single species in the collection.

Hippeutis fontanus (Lightfoot, 1786)

(Pl. I, Figs. 5, 6 & 7)

1786. *Helix fontana* Lightfoot, *Phil. Trans.*, **26** (1), p. 165, pl. ii, fig. 1 (Type-locality: Europe).

1878. *Planorbis (Hippeutis) complanatus:* Nevill, *Sci. Res. Sec. Yerkand Mission*, Mollusca, p. 11.

1923. *Planorbis (Hippeutis) fontanus:* Germain, *Rec. Indian Mus.*, **21** (3), pp. 160-163.

Material: No. of examples studied: 27.

Lot. Coll. A. S. Rajagopalaiengar: (1) 5 exs., Sta. 37—Stagnant water pools about 1·5 km. from Ningli Forest Rest House, on the road to Sopur, 23-7-1955; (2) 12 exs., Sta. 43—Stagnant pools by the roadside opposite Dal Gate (near Gagribal), 30-7-1955; (3) 10 exs., Sta. 44—Stagnant water in the lowest terraced tank in Shalimar Garden, 31-7-1955.

Distribution: Asia: Transcaucasia; West of Siberia; Yarkand; Europe: England; France; South Spain; Portugal; Norway; Sweden; Finland; Switzerland; Italy; Albania.

Remarks: The shells are flat, lenticular and almost transparent with prominent transverse striae, deeply open umbilicus and cordate-shaped aperture.

The present collection is identical with the shells collected by Dr. Stoliczka from Yarkand which are now found in Z.S.I. In the collection under study the shells are slightly larger and more transparent.

This species is known to inhabit still and undisturbed waters and in Kashmir too it is found in stagnant waters only.

This is the first record of the genus and species from Kashmir.

Order STYLOMMATOPHORA

Family SUCCINEIDAE

Genus *Succinea* Draparnaud, 1801

Type-species: *Helix putris* Linnaeus [= *Succinea oblonga* Draparnaud]

1801. *Succinea* Draparnaud, *Tabl. Terr. Fluv. France*, p. 55.

1914. *Succinea:* Gude, *Fauna Brit. India*, Mollusca-II. [Trochomorphidae-Janellidae], pp. 445-447.

1924. *Succinea:* Rao, *Rec. Indian Mus.*, **26** (5), pp. 377-378.

1937. *Succinea:* Prashad, *Rec. Indian Mus.*, 39 (3), pp. 273-274.

This genus is represented in the collection by two species, *viz.*, *Succinea indica* Pfeiffer and *Succinea* prox. *daucina* Pfeiffer.

***Succinea indica* Pfeiffer, 1849**

1849. *Succinea indica* Pfeiffer, *Proc. Zool Soc. London*, p. 133 (Type-locality: Bhim Tal, Uttar Pradesh, India).

1914. *Succinea indica:* Gude, *Fauna Brit. India*, Mollusca-II (Trochomorphidae-Janellidae), p. 447.

1924. *Succinea indica:* Rao, *Rec. Indian Mus.*, **26** (5), pp. 378-382, pl. xxviii, figs. 4-9.

1937. *Succinea indica:* Prashad, *Rec. Indian Mus.*, **39** (3), p. 274.

Material: No. of examples studied: 99.

Lot. A: Coll. B. Prashad: (1) 66 exs., Z.S.I., Reg. No. M 14845/2, Sta. 13—Shadipur, Half-way between Srinagar and Gandarbal, in a small lake at the banks in vegetation and rice field; (2) 4 exs., Z.S.I,. Reg. No. M 14847/2, Sta. 16—Dal Lake, eastern corner near Gagribal.

Lot. B: Coll. A. S. Rajagopalaiengar: (3) 10 exs., Sta. 7—Paddy fields near Bareen at the edge of Dal Lake, 24-6-1955; (4) 1 ex., Sta. 38—By boat in Dal Lake around Char Chinari (West), 26-7-1955; (5) 18 exs., Sta. 42—Stagnant water from a nullah between paddy fields near Bareen village bordering Dal Lake, 29-7-1955.

Distribution: India: Kashmir: Srinagar; Punjab: Gurdaspur; Uttar Pradesh: Kumaon Hills: Bhim Tal; Manipur Valley; Burma: South Shan States; Pakistan: Peshawar; U.A.R.: Alexandria.

Remarks: The shells are thin, horny and extremely fragile. When fresh, the colour of the shell is light brown or dirty amber. The live animal has fine dark dots all over the mantle which can be seen through the transparent body whorl. Ventral surface of foot is without any spots. In other respects it conforms to the description given by Annandale and Prashad (1921). They were collected mostly from among weeds lining irrigation channels feeding paddy fields.

Succinea sp. prox *daucina* Pfeiffer

Material: Coll. A. S. Rajagopalaiengar: 1 ex., Sta. 41—Stagnant pools by the roadside opposite Dal Lake (near Gagribal), 28–7–1955.

Remarks: A heavily encrustated example with a considerably thick and opaque shell represents this species. The columellar fold is thin and very slightly reflexed. The peristome is shining white inside. The outer lip descends straight downwards.

We are not inclined to refer this specimen to any known Indian succineids due to lack of sufficient material, but it appears to approximate *Succinea daucina* Pfeiffer in general appearance and in having a more tumid body whorl than in other species.

Class **BIVALVIA**

Order EULAMELLIBRANCHIATA

Family CORBICULIDAE

Genus *Corbicula* Megerle von Mühlfeldt, 1811

Type-species: *Tellina fluminalis* Müller

1811. *Corbicula* Megerle von Mühlfeldt, *Mag. Ges. naturf. Fr. Berlin*, **5** (1), p. 38.

1928. *Corbicula:* Prashad, *Mem. Indian Mus.*, **9**, p. 14.

Prashad (1928) while revising the Asiatic species of the genus *Corbicula* dealt in detail with its synonymy.

This genus is represented here by a single species, *Corbicula cashmiriensis* Deshayes.

Corbicula cashmiriensis Deshayes, 1854

1854. *Corbicula cashmiriensis* Deshayes, *Proc. Zool. Soc. London*, p. 344 (Type-locality: Kashmir).

1910. *Corbicula fluminalis* var. *oxiana* Weber., *Zool. Jb. Syst. Abth.*, **29**, pp. 308–310.

1928. *Corbicula cashmiriensis:* Prashad, *Mem. Indian Mus.*, **9**, p. 20, pl. iii, figs. 14–18.

1937. *Corbicula cashmiriensis:* Prashad, *Rec. Indian Mus.*, **39** (3), pp. 274–275.

Material: No. of examples studied: 505.

Lot. A: Coll. ? (1) 15 exs., Z.S.I., Reg. No. M 7413–7437/1, Kashmir; (2) 20 exs., Sta. 2—Kashmir.

Lot. B: Coll. B. Prashad: (3) 9 exs., Sta. 15—Manasbal Lake, 2–7–1921.

Lot. C: Coll. H. S. Pruthi: (4) 1 ex., Srinagar, 8–9–1932.

Lot. D: Coll. S. L. Hora: (5) 13 exs., Sta. 13—Tel-bal nullah near lower Tel-bal, 30–5–1954; (6) 33 exs., Sta. 25—Wular Lake collection with boats, 4–6–1954; (7) 1 ex., Sta. 67—Anchar Lake from off Anchar village, 29–6–1954.

Lot. E: Coll. A. S. Rajagopalaiengar: (8) 18 exs., Sta. 5 *a*—From sand on the pathway leading from Bareen village into Dal Lake, 22–6–1955; (9) 233 exs., Sta. 29—Mahi stream by the side of Akhran village about 4 km. from Acchabal, 14–7–1955; (10) 10 exs., Sta. 30—A swampy area by the roadside ¼ km. from Thajiwara near Acchabal, 15–7–1955; (11) 150 exs., Sta. 36—By boat along the border of Wular Lake near Ningli, 22-7-1955; (12) 2 exs., Sta. 39—By boat in the Tel-bal stream near Dal Lake, 26-7-1955.

Distribution: It is quite apparent from Prashad's (1928) account that the species is confined to Kashmir; it occurs in the river Jhelum and waters connected with it.

Remarks: A complete description of the species can be obtained from Deshayes (1854), Sowerby (1878), and Prashad (1928).

In the large collection we find that shells from Wular Lake are of various sizes and stages of development. Externally most of the shells are dark in colour while a few are brown. When fresh the interior of the shell is bluish-white. Absence of any sinus in pallial line is noteworthy.

The largest specimen from the Wular Lake measures about 55 mm. in breadth and 50 mm. in height.

Family SPHAERIIDAE

Genus *Sphaerium* Scopoli, 1777

Type species: *Sphaerium corneum* Linnaeus

1777. *Sphaerium* Scopoli, *Introd. Hist. Nat.*, p. 397.

1921. *Sphaerium:* Prashad, *Rec. Indian Mus.*, **22** (4), p. 614.

1937. *Sphaerium:* Prashad, *Rec. Indian Mus.*, **39** (3), p. 276.

This genus is represented by a single species, *viz.*, *Sphaerium kashmirensis* Prashad in the collection before us.

***Sphaerium kashmirensis* Prashad, 1937**

(Text-Fig. 1)

1937. *Sphaerium kashmirensis* Prashad, *Rec. Indian Mus.*, **39** (3), pp. 276-277, text-fig. 1 (Type-locality: Wular Lake, Kashmir).

Material: No. of examples studied: 101.

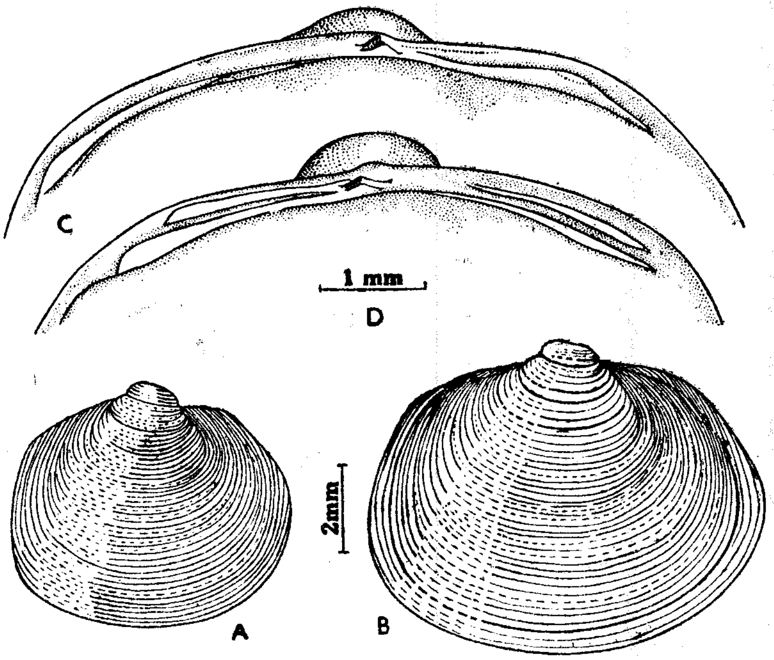
Lot. A: Coll. ? (1) 10 exs., Sta. 3—Kashmir; (2) 1 ex., Sta. 4—Kashmir.

Lot. B: Coll. S. L. Hora; (3) 5 exs., Sta. 68—The Sind river at Shalboog, 29-6-1954.

Lot. C: Coll. A. S. Rajagopalaiengar: (4) 50 exs., Sta. 1—Paddy fields at Batakoot, 16-6-1955; (5) 5 exs., Sta. 8—Stagnant water in the lowest terraced tank in Shalimar Garden, 25-6-1955; (6) 5 exs., Sta. 11—Stagnant water in the lowest terraced tank, Shalimar Garden, 27-6-1955; (7) 1 ex., Sta. 36—By boat along the border of Wular Lake near Ningli, 22-7-1955; (8) 2 exs., Sta. 37—Stagnant water pools about 1·5 km. from Ningli Forest Rest House on the road to Sopur, 23-7-1955; (9) 1 ex., Sta. 38—By boat in the Dal Lake around Char Chinari (West), 26-7-1955; (10) 5 exs., Sta. 39—By boat in the Tel-bal stream near Dal Lake, 26-7-1955; (11) 1 ex., Sta. 40—By boat from Nishat Bagh to Dal Gate (Gagribal) along the eastern border, 28-7-1955; (12) 5 exs., Sta. 42—Stagnant water from a nullah between paddy fields near Bareen village and bordering Dal Lake, 29-7-1955; (13) 10 exs., Sta. 44—Stagnant water in the lowest terraced tank, Shalimar Garden, 31-7-1955.

Distribution: This species is confined to Kashmir.

Remarks: Prashad (1937) described this species from a solitary specimen which does not appear to be full-grown. We have carefully compared the collection with his holotype and the text-figure and found that most of the examples of similar size conform to Prashad's description, especially in the character of calculation of umbones. But in some cases, the anterior side is more produced than in the holotype, while the anterior margin also somewhat pointed and not evenly curving as he states. Further, in older and larger specimens, particularly from Sind River at Shalboog [*vide* Lot. B (3) above], the shell is more elongate ovate than in the holotype (*see* Text-Fig. 1). In the very young stage, however, the shell appears more or less elliptical.



TEXT-FIG. 1. *Sphaerium kashmirensis* Prashad. (A) Holotype in the National Zoological Collection, Z.S.I.; (B) a full-grown specimen from the Sind River at Shalboog, Kashmir; (C) hinge-teeth in the left valve of a specimen of *S. kashmirensis* Prashad; (D) hinge-teeth in the right valve of a specimen of *S. kashmirensis* Prashad.

The figure given here illustrates the points of variations. A shell from Shalboog is compared with the holotype. The teeth characters are also illustrated.

Genus *Pisidium* Pfeiffer, 1821

Type-species: *Pisidium amnicum* Jenyns

1821. *Pisidium* Pfeiffer, *Naturg. Deutsch. Moll.*, **1**, pp. 17, 123.

1925. *Pisidium:* Prashad, *Rec. Indian Mus.*, **27** (5), p. 407.

1937. *Pisidium:* Prashad, *Rec. Indian Mus.*, **39** (3), p. 275.

Prashad (1925 *a*) has fully supported Woodward (1913) in accepting the validity of the genus *Pisidium* and also its sub-generic divisions. Further, he has also stressed the need for a change in the definition of the genus in the light of discoveries made independently by Odhner and Stelfox that the shell of *Pisidium* is porous and not hairy.

This is represented by a single species in the collection.

Pisidium hydaspicola Theobald, 1878

1878. *Pisidium hydaspicola* Theobald, *J. Asiat. Soc. Bengal*, **47**, p. 147 (Type-locality: Shupion in Kashmir).

1925. *Pisidium hydaspicola*: Prashad, *Rec. Indian Mus.*, **27** (5), p. 414, pl. vii, figs. 5–7 *a*; pl. viii, figs. 5–6.

1937. *Pisidium hydaspicola*: Prashad, *Rec. Indian Mus.*, **39** (3), p. 275.

Material: No. of examples studied: 371.

Lot. A: Coll. ? (1) 10 exs., Rampur, Kashmir, 11–4–1916; (2) 1 ex., Z.S.I., Reg. No. M 12535/2, Kashmir; (3) 2 exs., Z.S.I., Reg. No. M 12536/2, Kashmir; (4) 1 ex., Z.S.I., Reg. No. M 12537/2, Kashmir; (5) 1 valve, Z.S.I., Reg. No. M 12538/2; (6) 1 ex., Z.S.I., Reg. No. M 12539/2, Kashmir; (7) 1 ex., Z.S.I., Reg. No. M 12540/2, Kashmir; (8) 1 ex., Z.S.I., Reg. No. M 12541/2, Kashmir.

Lot. B: Coll. F. J. Mitchell: (9) 1 ex., Z.S.I., Reg. No. M 12545/2, Kashmir.

Lot. C: Coll. S. L. Hora: (10) 1 ex., Sta. 15—Channels of the Harawan Hatchery, 30–5–1954.

Lot. D: Coll. K. K. Tiwari: (11) 5 exs., Paddy fields, Banihal, 15–7–1955.

Lot. E: Coll. A. S. Rajagopalaiengar: (12) 20 exs., Sta. 10—A slow-moving stream between paddy fields at the edge of Dal Lake near Bareen, 27–6–1955; (13) 55 exs., Sta. 22—Stagnant pool by the side of the canal of Lidar River, Pahalgam, on way to Chandanwari, 8–7–1955; (14) 20 exs., Sta. 26—A pond full of floating vegetation by the side of Naghdandi Ashram about 1·5 km. from Acchabal, 13–7–1955; (15) 18 exs., Sta. 28—Channels between rice fields at Pingwana about 2·5 km. from Acchabal, 14–7–1955; (16) 16 exs., Sta. 29—Mahi stream by the side of Akhran village about 4 km. from Acchabal, 14–7–1955; (17) 50 exs., Sta. 30—A marshy area by the roadside about ¼ km. from Thajiwara near Acchabal, 15–7–1955; (18) 6 exs., Sta. 32—Round about Kokarnag springs and stream, 16–7–1955; (19) 18 exs., Sta. 34—Weeds of a channel of the Acchabal Hatchery, 17–7–1955; (20) 36 exs., Sta. 35—Terraced tanks of the Acchabal Garden, 17–7–1955; (21) 16 exs., Sta. 39—By boat in the Tel-bal stream near Dal Lake, 26–7–1955; (22) 1 ex., Sta. 40—By boat from Nishat Bagh to Dal Gate (near Gagribal) along the eastern border, 28–7–1955; (23) 74 exs., Sta. 42—Stagnant water from a nullah between paddy fields near Bareen village and bordering Dal Lake, 29–7–1955.

Lot. F: Coll. K. S. Pradhan: (24) 16 exs., Sta. 42—Slow-running stream about 3 km. north-west of P.W.D. Rest House, Sonamarg, 30–7–1955.

Distribution: This species is confined to Kashmir.

Remarks: Prashad (1925) has dealt in detail with the characters of the species including its shell, hinge teeth, anatomy of soft parts, and affinity. It belongs to the same group as the European *P. casertanum* (Poli).

The material comprising shells in different stages of growth is in general agreement with the description given by Prashad. Shells are mostly yellowish, but those from Sonamarg are quite large in size and dark brown in colour.

Apart from the scrapings of mud at the edges of ponds, etc., in which they have been generally known to occur, a large number of specimens was also collected from meshes of floating aquatic algae (probably *Spirogyra* sp.) and root bunches of plants partially submerged in streams,

V. NOTES ON ZOOGEOGRAPHICAL SIGNIFICANCE

A brief account of the environmental characters of Kashmir and the general features of its fauna is given by Hora *et al.* (1955). Apart from the ecological and geographical features of Kashmir which are highly interesting, it is equally so to study the zoogeography of its fauna. Probably Kashmir is the only part of the Indian Union where one can find a common meeting place of two

TABLE I

Distributional chart of aquatic and amphibious molluscs of Kashmir

Name of the species	Ethiopian	Nearctic	Palaearctic				Oriental		
			Europe	Northern and Central Asia	Asia Minor	Kashmir	Indian	Indo-Chinese	Malayan
1. *Viviparus variatus* Frauenfeld	—	—	—	—	—	×	×	—	—
2. *Valvata piscinalis* (Müller)	—	—	×	×	×	×	—	—	—
3. *Bulimus tentaculatus* (Linnaeus) var. *kashmirensis* Nevill	—	—	—	—	—	×	—	—	—
4. *Lymnaea stagnalis* (Linnaeus)	—	—	×	×	×	×	—	—	—
5. *Lymnaea luteola* f. *typica* (Lamarck)	—	—	—	—	—	×	×	—	×
6. *Lymnaea luteola* f. *succinea* Deshayes	—	—	—			×	×		
7. *Lymnaea auricularia* (Linnaeus)	—	—	×	×	—	×	—	—	—
8. *Lymnaea brevicauda* Sowerby	—	—	—	—	—	×	—	—	—
9. *Lymnaea lagotis* f. *striata* Andreae	—	—	—	×	—	×	—	—	—
10. *Lymnaea lagotis* f. *costulata* von Martens	—	—	—	×	—	×	—	—	—
11. *Lymnaea lagotis* f. *solidissima* Kobelt	—	—	—	×	—	×	—	—	—
12. *Lymnaea lagotis* f. *defilippii* Issel	—	—	—	×	—	×	—	—	—
13. *Lymnaea truncatula* (Müller)	×	×	×	×	—	×	—	—	—
14. *Planorbis planorbis* (Linnaeus) var. *tangitarensis* Germain	—	—	—	×	—	×	—	—	—
15. *Planorbis rotundatus* Poiret		—	×	×	—	×	—	—	—
16. *Indoplanorbis exustus* (Deshayes)	—	—	—	—	—	×	×	×	×
17. *Gyraulus pankongensis* (von Martens)	—	—	—	×	—	×	—	—	—
18. *Hippeutis fontanus* (Lightfoot)			×	×		×	—	—	—
19. *Succinea indica* Pfeiffer	×	—	—	—	—	×	×	×	×
20. *Corbicula cashmiriensis* Deshayes	—	—	—	—	—	×	—	—	—
21. *Sphaerium kashmirensis* Prashad	—	—	—	—	—	×	—	—	—
22. *Pisidium hydaspicola* Theobald	—	—	—	—	—	×	—	—	—

faunal elements, *viz.*, Palaearctic from the Central Asiatic region in the north and Oriental from the Indian region in the south.

An analysis (*see* Table I) of aquatic and amphibious species of molluscs occurring in the Valley indicates briefly the following points:—

1. There is a preponderance of Palaearctic element in the fauna. Out of 18 species including 8 varieties represented in the collection, as many as 12 species including 6 varieties are Palaearctic.
2. The number of species of Oriental origin is very much less, *i.e.*, only 4 species including 2 varieties are represented.
3. The number of species confined to Kashmir (endemic or autognathous) is 4 and a variety.
4. None of the Indian (Oriental) species which have penetrated into Kashmir have given rise to any endemic form. Thus, their extension to the Valley appears to be more recent geologically than the Palaearctic species which seem to have well established themselves there and given rise to endemic forms.
5. The endemicity of species in the valley is sufficiently high in proportion to the total number. The formidable physical barriers of Kashmir which have subjected it into a state of isolation may have contributed greatly to this.

Hora *et al.* (1955) observe: "the variety of the fauna is poor but it is compensated by each form being represented by large populations. The chief reason for this phenomenon appears to be the rigorous of climate which only a few species have been able to cope with; but once this hurdle had been crossed the species have flourished abundantly; the lack of competition and enemies accelerating the process." Our conclusions on molluscs seem to be in complete agreement with Hora *et al.*'s analysis.

VI. LITERATURE CITED

Annandale, N., B. Prashad and Amin-Ud-Din *1921*. The aquatic and amphibious Mollusca of Manipur. *Rec. Indian Mus.*, **22** (4): 529–631, pls. 5.

—— and H. S. Rao 1925. Materials for a revision of the recent Indian Limnaeidae (Mollusca Pulmonata). *Ibid.*, **27** (3): 137–189.

Baker, F. C. 1908. *Science* n.s., **27**: 943 (This reference has not been seen by us).

——— 1911. The Lymnaeidae of North and Middle America (Recent and Fossil). *Chicago Acad. Sci.*, spl. publ. No. 3: 1–539, pls. 58.

Deshayes, G. P. 1834. Descriptions of the Mollusca collected during Belanger's voyage to the East Indies, & C. *Voy. Belanger aux Indes—Orient. Zool.* (This reference has not been seen by us).

Deshayes, M. G. P. 1854. Descriptions of new shells from the collection of Hugh Cuming, Esq. *Proc. Zool. Soc. Lond.*, Pt. **22**: 317–371.

Germain, L. 1918. Mollusques terrestres et fluviatiles de l'Asie Anterieure: 8^{e} Note sur quelques Planorbes asiatiques. *Bull. Mus. Hist. Nat.*, Paris, **24** (4) : 271–283.

——— 1921. Catalogue of the Planorbidae in the Indian Museum (Natural History), Calcutta. *Rec. Indian Mus.*, **21**: 1–210 (1921–24).

Hora, S. L., G. M. Mulik and H. Khajuria 1955. Some interesting features of the aquatic fauna of the Kashmir Valley. *J. Bombay Nat. Hist. Soc.*, **53** (1): 140–143.

Hubendick, B. 1951. Recent Lymnaeidae. Their variation, morphology, taxonomy, nomenclature and distribution. *Kungl. Svenska Vetens. Akad. Handl.*, 3 (1): 6–225, text-figs. 369, pls. 5.

Mozley, A. 1935. The freshwater and terrestrial Mollusca of Northern Asia. *Trans. Roy. Soc. Edin.*, **58** (3): 605–695, pls. 5.

Nevill, G. 1878. Mollusca II—Mollusca from Kashmir and neighbourhood of Mari (Murree) in the Punjab. *Sci. Res. Sec. Yarkand Mission*: 14–21.

——— 1885. *Hand List of Mollusca in the Indian Museum, Calcutta. Pt. II. Gastropoda, Prosobranchia, Neurobranchia (Contd.)*, x + 306 pp., Calcutta.

Pilsbry, H. A. and J. Bequaert 1927. The aquatic mollusks of the Belgian Congo with a geographical and ecological account of Congo Malacology. *Bull. Amer. Mus. Nat. Hist.*, **53**: 69–602, pls. 68.

Prashad, B. 1925 *a*. Notes on Lamellibranchs in the Indian Museum. 6. Indian species of the genus *Pisidium*. *Rec. Indian Mus.*, **27** (5): 405–422, pls. 2.

——— 1925 *b*. On a collection of land and freshwater fossil molluscs from the Karewas of Kashmir. *Rec. Geol. Surv. India*, **56** (4): 356–361, pl. 29 (1926).

——— 1928. Revision of the Asiatic species of the genus *Corbicula*. 1. The Indian species of *Corbicula*. *Mem. Indian Mus.*, **9** (1): 13–27, pls. 2.

——— 1937. Scientific results of the Yale North India Expedition. Biol. Rep. No. 21. Aquatic and amphibious molluscs. *Rec. Indian Mus.*, 39 (3): 261–277.

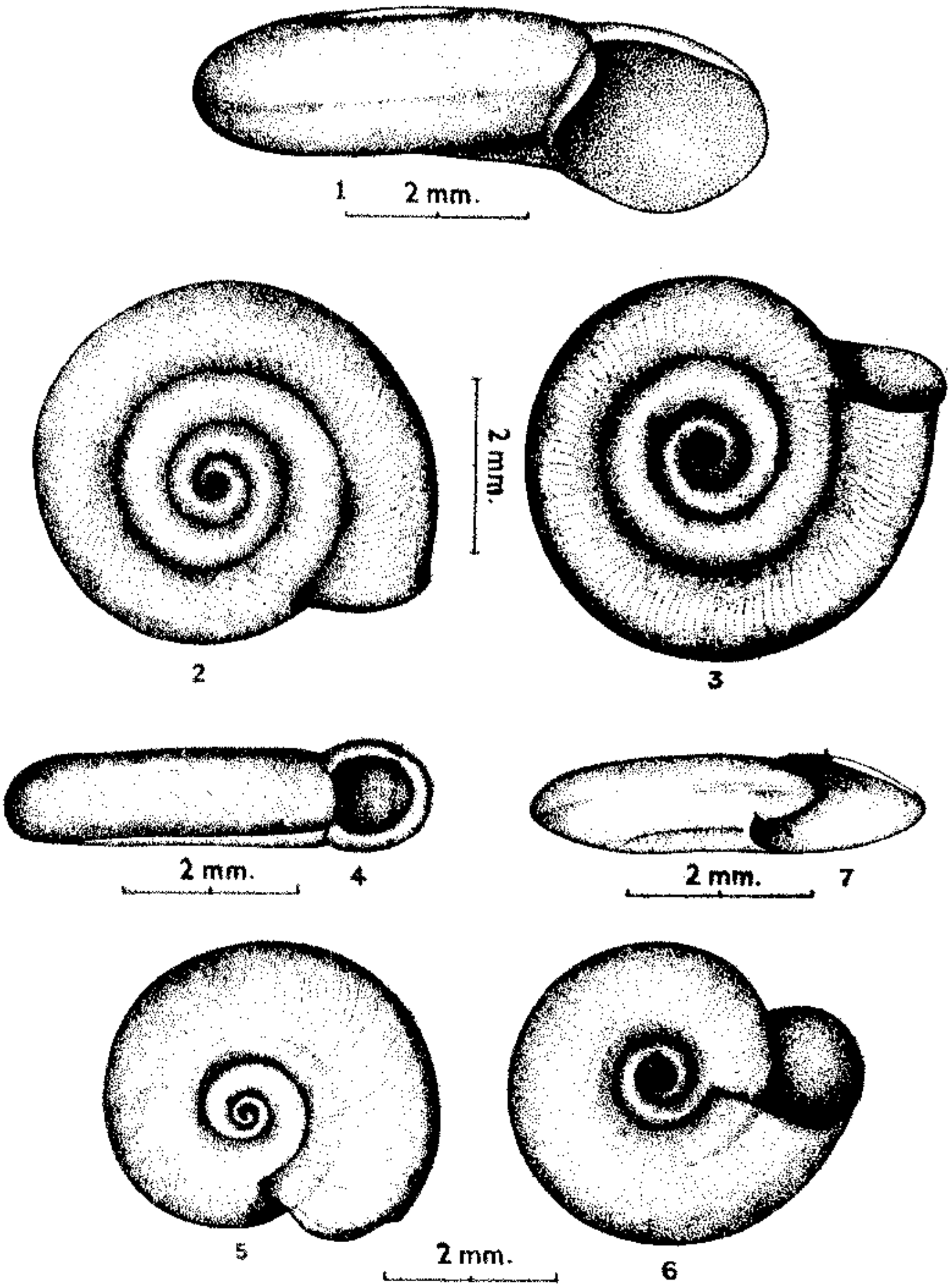
Sowerby, G. 1878. In Reeve's *Conch. Icon.*, 20, *Cyrena*.

Theobald, W. 1878. Notes on the land and freshwater shells of Kashmir, more particularly of the Jhilum Valley below Srinagar and the hills north of Jamu. *J. Asiat. Soc. Beng.*, **47** (2): 141–149.

Weber, A. 1910. Über Binnenmollusken aus Ost-Turkestan, Kashmir und West Tibet. *Zool Jb. Syst. Abth.* **29**: 299–312.

Woodward, S. P. 1856. On the land and freshwater shells of Kashmir and Tibet, collected by Dr. T. Thomson. *Proc. Zool. Soc. Lond.*, Pt. **24**: 185–187.

Woodward, B. B. 1913. *Catalogue of the British Species of Pisidium (Recent and Fossil)*, viii + 144 pp. + xxx pls. (British Museum, Natural History), London, S.W.



Figs. 1-7. Fig. 1. *Gyraulus pankongensis* von Martens. Front view of a specimen from Srinagar. Figs. 2, 3 & 4. *Planorbis rotundatus* Poiret. Dorsal, ventral and front views respectively of a specimen from Shalimar Garden near Srinagar. Figs. 5, 6 & 7. *Hippeutis fontanus* (Lightfoot). Dorsal, ventral and front views respectively of a specimen from Dal Gate, Gagribal near Srinagar.

A COLLECTION OF MOLLUSCS FROM THE COCHIN HARBOUR AREA

P. V. Cheriyan

Marine Organism Scheme (Forest Research Institute),
Oceanographic Laboratory, Ernakulam-6, India

Abstract

Fifty-one species of molluscs belonging to 25 families that occurred in the bottom fauna collections made during November, 1958 to November, 1959 from ten fixed stations in and around the Cochin harbour, on the south-west coast of India, have been identified. Out of the fifty-one species only 25 are represented by live specimens. Their place and period of occurrence and abundance have been discussed in relation to the substratum and salinity conditions. Probable reasons for the presence of marine and brackish water forms in the estuary have been pointed out.

The most important works on the molluscan fauna of the Indian region are by Smith (1901), Preston (1909, 1914, 1915 and 1916), Hornell (1910, 1916, 1917, 1948 and 1951), Gude (1914), Annandale and Kemp (1916), Prashad (1920, 1921, 1921 *a* and 1932), Winckworth (1927, 1940 and 1940 *a*), Gravely (1927, 1941 and 1942), Crichton (1941) and Satyamurti (1952, 1956 and 1960). But, except for the papers by Preston (*loc. cit.*) and Satyamurti (*loc. cit.*) very little is known about the molluscs of the Cochin backwater region. Here an attempt is made to study the molluscs of the Cochin Harbour area that are found in the bottom fauna collections made from ten fixed stations during November 1958 to November 1959. The details of the collections are given in Cheriyan, 1966.

A list of species collected is given below :—

Class GASTROPODA

Family Neritidae

Genus *Nerita* Linne.
Nerita albicilla Linne.

Family Littorinidae

Genus *Littorina* Ferussac
Littorina undulata Gray

Family Potamididae

Genus *Cerithidea* Swainson
Cerithidea fluviatilis (Potiez and Michaud)

Family Calyptraeidae

Genus *Calyptraea* Lamarck
Calyptraea (Crucibulum) extinctorium Lamarck

Family Naticidae

Genus *Natica* Scopoli
Natica marochiensis Gmelin
Natica tigrina (Roding)

Family CYPRAEIDAE

Genus *Cypraea* Linne.
Cypraea talpa Linne.

Family CYMATIIDAE

Genus *Cymatium* (Bolten) Roding
Cymatium pileare (Linne.)

Family MURICIDAE

Genus *Thais* (Bolten) Roding
Thais margaraticola (Broderip)
Thais tissoti (Petit)

Family NASSIDAE

Genus *Nassa* (Martini) Lamarck
Nassa ceylonica G. and H. Nevill

Class SCAPHOPODA

Family DENTALIDAE

Genus *Dentalium* Linne.
Dentalium octangulatum Donovan
Dentalium aparinum Linne.
Dentalium elpis Winckworth

Class PELECYPODA

Family NUCULANIDAE

Genus *Nuculana* Link
Nuculana mauritiana (Sowerby)

Family ARCIDAE

Genus *Arca* Linne.
Arca lateralis Reeve
Arca inaequivalvis Bruguiere
Arca tortuosa Linne.
Arca indica Gmelin

Family MYTILIDAE

Genus *Mytilus* Linne.
Mytilus viridis Linne.

Genus *Modiolus* Lamarck
Modiolus striatulus (Hanley)
Modiolus undulatus (Dunker)
Modiolus tulipa (Lamarck)

Family PECTINIDAE

Genus *Pecten* (Klein) Osbeck
Pecten tranquebaricus (Gmelin)

Family OSTREIDAE

Genus *Ostrea* Linne.
Ostrea forskalii Gmelin

Family LUCINIDAE

Genus *Lucina* Lamarck
Lucina ovum Reeve

Family VENERIDAE

Genus *Dosinia* Scopoli.
Dosinia modesta (Sowerby)
Dosinia cretacea (Reeve)
Dosinia trigona (Reeve)
Dosinia histrio (Gmelin)

Genus *Meretrix* Lamarck
Meretrix casta (Chemnitz)
Meretrix ovum Deshayes

Genus *Venus* Linne.
Venus imbricata Sowerby

Genus *Venerupis* Lamarck
Venerupis macrophylla Deshayes

Genus *Paphia* (Bolten) Roding
Paphia marmorata (Reeve)
Paphia malabarica (Chemnitz)

Genus *Catelysia* E. Romer
Catelysia opima (Gmelin)

Genus *Circe* Schumacher
Circe scripta (Linne.)

Genus *Chione* Megerle von Muhlfeld
Chione tiara (Dillwyn)

Family CORBICULIDAE

Genus *Villorita* Griffith and Pidgeon
Villorita cyprinoides (Gray)
Villorita cyprinoides var. *cochinensis* (Hanley)

Family MACTRIDAE

Genus *Standella Gray*
Standella pellucida (Gmelin)

Family DONACIDAE

Genus *Donax* Linne.
Donax spiculum Reeve

Family PSAMMOBIIDAE

Genus *Gari* Schumachner
Psammobia ameythystus (Wood)

Family SEMELIDAE

Genus *Theora* H. and A. Adams
Theora opalina (Hinds)

Family TELLINIDAE

Genus *Tellina* Linne.
Tellina rhodon Hanley
Tellina pinguis Hanley

Family SOLENIDAE

Genus *Solen* Linne.
Solen lamarckii Deshayes
Solen aquae-dulcioris (Ghosh)

Family PHOLADIDAE

Genus *Pholas* Linne.
Martesia striata (Linne.)
Pholas (*Monothyra*) *orientalis* Gmelin

Nerita albicilla **Linne.**

1942. *Nerita albicilla*. Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, p. 18.

1952. *Nerita albicilla*. Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 6, p. 58, pl. iii, Fig. 6.

Large number of live specimens are found during March to May attached to jetty piles and shore embankments. During the other months they are scarce. Largest specimen measured 15 mm. in height and 20·5 mm. in breadth. In the bottom collection only dead shells are obtained.

Locality : Stations III, VII, VIII, IX and X.

Littorina undulata **Gray**

1942. *Littorina undulata*. Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, p. 20.

1952. *Littorina undulata*. Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, p. 66, pl. IV, Figs. 5 *a* and 5 *b*.

Collections from the lake bed consist only of shells, but live specimens are found on jetty piles, stone embankments and pillars of bridges in the harbour area. Largest number is noted during March to July. In June and July when the salinity is low they creep upwards on the jetty piles and pillars of bridges and congregate above water line in groups. During August, dead shells are observed on the shores of the backwaters. Largest shell measured 18·2 mm. in height and 12·3 mm. in breadth.

Cerithidea fluviatilis **(Potiez and Michaud)**

1942. *Cerithidea fluviatilis*. Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, pp. 24 and 25.

1952. *Cerithidea fluviatilis*. Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, p. 80, pl. V, Figs. 7 *a* and 7 *b*.

Live specimens as well as dead shells are very common in the collections. At station IX very few live specimens are obtained during May, but a large bed of this species was found near the shore, about 30 yards from the station. During the monsoon months they are not found on the surface, but burrow 6" to 8" deep into the soil to tide over the unfavourable conditions. The largest specimen in the present collection measured 24·5 mm. in height and 9·8 mm. in breadth. At the stations around the Willingdon Island though shell fragments have been obtained, live specimens have not so far been observed.

Locality : Stations IV, VI, VII, VIII, IX and X.

Calyptraea (Crucibulum) extinctorium Lamarck

1942. *Calyptraea* (*Crucibulum*) *extinctorium.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, p. 35.

1952. *Calyptraea* (*Crucibulum*) *extinctorium.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, p. 96, pl. VI, Figs. 14 *a* and 14 *b*.

This species is represented in the present collection only by a few empty shells. The largest specimen measured 3·2 mm. in height and 8·0 mm. in breadth.

Locality : Stations II and X.

Natica marochiensis Gmelin

1942. *Natica marochiensis.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, p. 37.

1952. *Natica marochiensis.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, p. 107, pl. VIII, Figs. 1 *a* and 1 *b*.

A few live specimens were obtained from March to May, the largest of which measured 9·8 mm. in height and 8 mm. in breadth.

Locality : Stations I, III, IV, V and X.

Natica tigrina (Roding)

1942. *Natica tigrina.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, p. 108, pl. VIII, Fig. 2.

Three to five live specimens were obtained in each collection during January to April from stations I to V. From station X only dead shells were obtained. Maximum size 16·3 mm. in height and 13·5 mm. in breadth.

Cypraea talpa Linne.

1952. *Cypraea talpa.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, p. 129, pl. X, Fig. 1.

Represented in the present collection only by two shells, the larger of which measured 58·5 mm. in length. This is a marine species which usually occurs in corally regions such as Pamban, the Maldive and Laccadive Islands. Live specimens have not so far been observed on the Kerala coast. It is therefore possible, that the two shells obtained from station II might have drifted to the harbour entrance with tidal currents.

Cymatium pileare (Linne.)

1942. *Cymatium pileare.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, p. 44.

1952. *Cymatium pileare.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, p. 140, pl. XI, Figs. 7 *a* and 7 *b*.

A single shell measuring 60·8 mm. in height and 26·5 mm. in breadth was obtained from station II in June. As in the previous case it is possible that this must have also drifted in with the currents.

Thais margaraticola (Broderip)

1843–1878. *Recinula fiscellum.* Reeve, "*Conchologia Iconica*" III, iv, p. 28.

1942. *Thais margaraticola.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, p. 50.

Represented in the collection only by few shells from sandy and silty deposits. The largest one measured 7·1 mm. in height and 5·1 mm. in breadth.

Locality : Stations IX and X.

Thais tissoti (Petit)

1942. *Thais tissoti.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, p. 51.

1952. *Thais tissoti.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, p. 166, pl. XVI, Fig. 4.

All the specimens in the present collection are empty shells, most of which being occupied by hermit crabs. Maximum size 21·6 mm. in height and 13·7 mm. in breadth.

Locality : Station X.

Nassa ceylonica G. and H. Nevill

1942. *Nassa ceylonica.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 2, p. 59.

This species is fairly common at stations VIII and X during March and April. At other stations it is comparatively rare. Most of the shells obtained from station X were found occupied by hermit crabs. Largest specimen measured 11·3 mm. in height and 7·1 mm. in breadth.

Locality : Stations II, IV, V, VII, VIII and X.

Dentalium octangulatum Donovan

1956. *Dentalium octangulatum.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 3, pl. 1, Figs. 1 *a* and 1 *b*.

During the period of investigation twelve shells were obtained from station X. The largest measured 22·0 mm. in length and 3·5 mm. in diameter at the anterior end.

Dentalium aparinum Linne.

1956. *Dentalium aparinum.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 4 pl. 1, Figs. 2 *a* and 2 *b*.

Represented by three shells obtained from station X. Maximum length 16·3 mm. and diameter at the anterior end 2·6 mm.

Dentalium elpis Winckworth

1927. *Dentalium elpis.* Winckworth, *Proc. Malacol. Soc. London,* XVII, p. 168, pl. XIV, Figs. 6 and 7.

1956. *Dentalium elpis.* Satyamurti, *Bull. Mad. Govt. Mus. (Nat. Hist.)* I, No. 2, pt. 7, p. 5, pl. 1, Figs. 4 *a* and 4 *b*.

Three shells were obtained from station X, the largest of these measured 14·4 mm. in length and 2·7 mm. in diameter at the anterior end.

Nuculana mauritiana (Sowerby)

1941. *Nuculana mauritiana.* Gravely, *Bull. Mad. Govt. Mus. (Nat. Hist.)* V, No. 1, p. 32, Figs. 14 *a* and 14 *b*.

1956. *Nuculana mauritiana.* Satyamurti, *Bull. Mad. Govt. Mus. (Nat. Hist.)* I, No. 2, pt. 7, p. 16, pl. II, Figs. 1 *a* and 1 *b*.

This is a rare species represented in the collection by a few empty shells, the largest of which measured 5·5 mm. in length and 3·6 mm. in width.

Locality : Stations I, II, IV, IX and X.

Arca lateralis Reeve

1941. *Arca lateralis.* Gravely, *Bull. Mad. Govt. Mus. (Nat. Hist.)* V, No. 1, p. 33.

1956. *Arca lateralis.* Satyamurti, *Bull. Mad. Govt. Mus. (Nat. Hist.)* I, No. 2, pt. 7, p. 23, pl. II, Figs. 6 *a* and 6 *b*.

Live specimens have not been observed in the harbour area, but a few shells were obtained occasionally in dredge collections at stations IV and VI. The largest specimen in the present collection measured 14·5 mm. in length and 9·2 mm. in width.

Arca inaequivalvis Bruguiere

1956. *Arca inaequivalvis.* Satyamurti, *Bull. Mad. Govt. Mus. (Nat. Hist.)* I, No. 2, pt. 7, p. 24, pl. II, Figs. 7 *a* and 7 *b*.

A few live specimens and some shells were obtained in dredge collections. It usually occurs in silty regions during February to April. The largest specimen obtained measured 18·3 mm. in length and 11·3 mm. in width.

Locality : Stations II, V, VI and X.

Arca tortuosa Linne.

1941. *Arca tortuosa.* Gravely, *Bull. Mad. Govt. Mus. (Nat. Hist.)* V, No. 1, p. 33.

1956. *Arca tortuosa.* Satyamurti, *Bull. Mad. Govt. Mus. (Nat. Hist.)* I, No. 2, pt. 7, p. 26, pl. iii, Figs. 1 *a* and 1 *b*.

In the harbour area this species is represented by a few shells obtained from station X and a single shell from station II. The largest specimen measured 13·6 mm. in length and 6·9 mm. in width.

Arca indica Gmelin

1941. *Arca indica.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 34.

Shells of this species occur in fairly large numbers at stations II, V and X. Only a single live specimen was obtained from the harbour entrance in March. The largest of these measured 15·7 mm. in length and 9·1 mm. in width.

Mytilus viridis Linne.

1956. *Mytilus viridis.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 42, pl. V, Fig. 1.

Shells were occasionally found scattered in dredge collections. But live specimens occur in large clusters attached to submerged wooden and masonry structures in the vicinity of the harbour entrance during January to April. The largest specimen in the collection measured 60·5 mm. in length and 38·5 mm. in breadth.

Locality : Stations I to VI.

Modiolus striatulus (Hanley)

1909. *Modiola cochinensis.* Preston, *Rec. Ind. Mus.* III, p. 278, Fig. 2.

1941. *Modiolus striatulus.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, pp. 35-37.

Though this species occurs at all stations in the harbour area, it is abundant only at stations I–VI, where they form rich beds. Live ones are abundant during December to April.

Modiolus undulatus (Dunker)

1914. *Modiola undulatus* var. *crassicostata.* Preston, *Rec. Ind. Mus.* X, p. 304, Fig. 15.

1941. *Modiolus undulatus.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, pp. 35–37.

Occurs only close to the harbour entrance at station II. Live specimens are usually found attached to submerged parts of jetty piles, but shells of this species have been obtained in dredge collections from the same locality.

Modiolus tulipa (Lamarck)

1956. *Modiolus tulipa.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 33.

Represented in the present collection only by two partly worn-out shells collected from station I.

Pecten tranquebaricus (Gmelin)

1941. *Pecten tranquebaricus.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 39.

1956. *Pecten tranquebaricus.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 59, pl. VIII, Figs. 5 *a* and 5 *b*.

This is a marine species which is only rarely found in the harbour area. During the present investigation only two live specimens were obtained from station V in March. The larger of these measured 20·6 mm. in length and 18·7 mm. in breadth.

Ostrea forskalii Gmelin

1941. *Ostrea forskalii.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 41.

1956. *Ostrea forskalii.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2. pt. 7, p. 67, pl. X, Figs. 4 *a* to 4 *e*.

This species is usually found in large clusters on piles and other submerged masonry structures and iron pillars in the harbour area. During December to April when they attain a fairly large size they are collected by the local fishermen.

Lucina ovum Reeve

1941. *Lucina ovum.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 45.

1956. *Lucina ovum.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 6, pl. XII, Figs. 2 *a* and 2 *b*.

Represented in the collections only by a single shell measuring 14·3 mm. in length and 13 mm. in breadth, obtained from station X.

In the Cochin backwaters family Veneridae is represented by 13 species, including two economically important forms namely *Meretrix casta* and *Meretrix ovum*. *Paphia marmorata* and *Paphia malabarica* also possess thick shells suitable for building lime, but these are not so abundant as the former.

Dosinia modesta (Sowerby)

1941. *Dosinia prostrata* var. *modesta.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 50.

1956. *Dosinia modesta.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 117, pl. XVII, Figs. 4 *a* and 4 *b*.

This is a marine species which does not appear to thrive under estuarine conditions. In the present collection it is represented only by two shells, obtained in dredge collections from stations IV and X.

Dosinia cretacea (Reeve)

1941. *Dosinia prostrata* var. *cretacea.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 51.

1956. *Dosinia cretacea.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 118, pl. XVIII, Figs. 5 *a* and 5 *b*.

Live ones of this species appear to be rather rare in the harbour area. Only 12 specimens were altogether obtained from stations II, IV and V during December to May. But shells were fairly common in dredge collections at station X. Largest specimen measured 18·2 mm. in length as well as in breadth.

Dosinia trigona (Reeve)

1956. *Dosinia trigona.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 118, pl. XVII, Figs. 6 *a* and 6 *b*.

Though this is a marine species which has been recorded by Satyamurti (1956) from the Pamban area, a few worn-out shells were obtained in the present collections. The largest shell obtained measured 10·7 mm. in length and 10·5 mm. in width.

Locality : Stations II, VIII and X.

Dosinia histrio **(Gmelin)**

1932. *Dosinia* (*Austrodosinia*) *histrio*. Prashad, *Siboga Expeditie* CXVIII, p. 244.

1956. *Dosinia histrio*. Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 116, pl. XVII, Fig. 3.

Live specimens of this species have not so far been obtained from Cochin backwaters. Satyamurti recorded it from the Pamban region. Evidently it is a marine species which cannot withstand estuarine conditions. However, a few worn-out shells were obtained in dredge collections from stations in the vicinity of the harbour entrance. The largest one in the collection measured 24·8 mm. in length and 23·1 mm. in breadth.

Locality : Stations II, III, V and X.

Meretrix casta **(Chemnitz)**

1941. *Meretrix casta*. Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. I, p. 50.

1956. *Meretrix casta*. Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 111, pl. XVI, Figs. 2 *a* and 2 *b*.

This species usually occurs in shallow areas close to the barmouths of all the important backwaters of Kerala where they form rich beds. In the Cochin backwaters they are found near the harbour entrance especially in stations I and II. From other localities only shells were obtained in dredge collections. The largest specimen in the present collection measured 16·2 mm. in length and 11·8 mm. in breadth.

Locality : Stations I, II, VI, IX and X.

Meretrix ovum **Deshayes**

1916. *Meretrix ovum*. Annandale and Kemp, *Mem. Ind. mus.* V, (4), pp. 351-352.

1941. *Meretrix ovum*. Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, 1.

This is another economically important species which occurs along with *M. casta* in the vicinity of the harbour entrance. At other stations only shells are found. Largest specimen in the collection measured 37·7 mm. in length and 31·1 mm. in breadth.

Locality : Stations I, II, VI and X.

Venus imbricata **Sowerby**

1941. *Venus imbricata*. Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 51.

1956. *Venus imbricata*. Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 122, pl. XVIII, Figs. 4 *a* and 4 *b*.

Live specimens of this species have not so far been obtained from the harbour area or from any part of the Cochin backwaters. Satyamurti has recorded this from the Krusadai Islands.

Since the shells are small and light it is very likely that they have been drifted into the backwaters with tidal currents. They are also found among drift shells on seashore. The largest one in the present collection measured 12·2 mm. in length and 10·5 mm. in breadth.

Locality : Stations II, V, VI and X.

Venerupis macrophylla Deshayes

1941. *Venerupis macrophylla.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 52.

1956. *Venerupis macrophylla.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 127, pl. XIX, Figs. 5 *a* and 5 *b*.

This is also a marine species which has been recorded by Satyamurti from Pamban. The few dead shells obtained during the present investigations are evidently drift shells from the sea, the largest of which measured 10 mm. in length and 7 mm. in breadth.

Locality : Stations V and X.

Paphia marmorata (Reeve)

1843–1878. *Tapes marmorata,* Reeve, "*Conchologia Iconica*" XIV, No. VI, p. 26.

1941. *Paphia marmorata.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 52.

This species is represented by a few live specimens and a large number of empty shells. Live specimens were obtained during December to May. The largest specimen in the collection measured 19·7 mm. in length and 14·2 mm. in breadth.

Locality : Stations I, II, IV and X.

Paphia malabarica (Chemnitz)

1941. *Paphia malabarica.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 52.

1956. *Paphia malabarica.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 130, pl. XX, Figs. 3 *a* and 3 *b*.

Represented in the collection only by a few dead shells. This species was previously collected by Gravely from the Madras coast and by Satyamurti from Pamban. On the west coast it has been observed among drift shells on the seashore. Its presence in the Cochin harbour area may be due to the action of strong tidal currents.

Locality : Stations II, III, V, VII and X.

Catelysia opima (Gmelin)

1941. *Catelysia opima.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 52.

1956. *Catelysia opima.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 128, pl. XIX, Figs. 6 *a* and 6 *b*.

Gravely observes that *Catelysia opima* is a backwater species. But Satyamurti has recorded it from Pamban which is purely a marine environment. It is not found in Cochin backwaters. However, a single live specimen was obtained from the entrance to the harbour. This immature specimen measured 8·7 mm. in length and 6·4 mm. in width.

Circe scripta (Linne.)

1941. *Circe scripta.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 48.

1956. *Circe scripta.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 105, pl. XV, Figs. 2 *a* and 2 *b*.

Only two shells were obtained from the vicinity of the harbour entrance. This species is commonly found among drift shells along the coast. Satyamurti has recorded it from Kundugal Point, Krusadai Island, and Pamban. As in the few cases mentioned above, the presence of these shells in the harbour area can only be attributed to the action of drift currents. The larger of these measured 5·5 mm. in length and 4·5 mm. in breadth.

Locality : Station V.

Chione tiara (Dillwyn)

1941. *Venus tiara.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 51.

1956. *Chione tiara.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 125, pl. XIX, Figs. 2 *a* and 2 *b*.

This species has been previously recorded from the sea. In the present collection it is very rare and is represented only by 3 live specimens obtained from station IX in March 1959 when the salinity was 28·85‰. It has not been observed from any part of the harbour area or the rest of the backwaters. The largest specimen obtained measured 13·6 mm. in length and 12·2 mm. in breadth.

Villorita cyprinoides (Gray)

1921. *Villorita cyprinoides.* Prashad, *Rec. Ind. Mus.* XXII, p. 114.

1960. *Villorita cyprinoides.* Satyamurti, *Bull, Mad. Govt. Mus.* (*Nat. Hist.*) VI, No. 4, p. 150.

Villorita cyprinoides is a purely brackish water species which cannot withstand high salinity. It is usually found in extensive beds near the farthest ends of the backwaters where the salinity does not exceed 15‰. During the summer months when the salinity increases above this level, they burrow deep into the soil and thus escape the adverse conditions. Since they are very sensitive to increase in salinity their distribution does not extend to the harbour area. Only empty shells have been obtained from the harbour area and these have been evidently carried to this region by the strong flood currents.

Locality : Stations V, VI and X.

Villorita cyprinoides var. *cochinensis* (Hanley)

1921. *Villorita cyprinoides* var. *cochinensis.* Prashad, *Rec. Ind. Mus.* XXII, p. 116.

1960. *Villorita cyprinoides* var. *cochinensis.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) VI, No. 4, p. 151, pl. XXI, Figs. 2 *a* and 2 *b*.

Unlike the former species, *Villorita cyprinoides* var. *cochinensis* is capable of tolerating a wide range of salinity up to a maximum of 34‰. It is therefore found in parts of the backwaters nearer to the barmouth wherever the bottom deposit consists of sand and silt. It seems to avoid regions where the bed is formed of a high percentage of silt. At station VII where the bed is formed of a high percentage of sand it is very abundant and has been collected throughout the year. Large specimens were obtained during December to April and young ones during August and September when the salinity is comparatively low.

Locality : Stations VII–X.

Standella pellucida **(Gmelin)**

1843–1878. *Standella pellucida.* Reeve, "*Conchologia Iconica*" VIII, pt. xx, p. 118.

1941. *Standella pellucida.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, pp. 53–55.

This species occurs in fairly good numbers during the dry season in most of the stations with a silty bottom. But during the rainy months only empty shells are found in dredge collections and young ones are obtained during November and December when the salinity begins to increase after the monsoon rains. The size of the largest specimen in the collection is 18·5 mm. in length and 11·3 mm. in breadth.

Locality : Stations III, IV, V, VIII and X.

Donax spiculum **Reeve**

1843–1878. *Donax spiculum.* Reeve, "*Conchologia Iconica*" VIII, ix, p. 67 (*Incl. D. dussumieri* Bertin).

1941. *Donax spiculum.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 56.

This is a marine species which has been previously recorded from the Madras coast by Gravely. Live specimens have not so far been observed in the backwaters. But large number of shells are found at station X and a few at station I. The largest shell obtained measured 16·1 mm. in length and 9·2 mm. in breadth.

Psammobia ameythystus **(Wood)**

1932. *Gari ameythystus.* Prashad, "*Lamellibranchiata of the Siboga Expedition*" pp. 303–304.

1941. *Psammobia ameythystus,* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 58.

This is a marine species which is represented in the present collection only by three shells obtained from station X, and the largest one measured 28·5 mm. in length and 17·2mm. in breadth.

Theora opalina **(Hinds)**

1914. *Theora opalina.* Preston, *Rec. Ind. Mus.* X, p. 310.

This is also a marine species, six shells of which were obtained from station IV. The largest of these measured 16·9 mm. in length and 10·7 mm. in breadth.

Tellina rhodon **Hanley**

1932. *Tellina rhodon.* Prashad, "*Lamellibranchiata of the Siboga Expedition*" p. 194, pl. V, Figs. 37–38.

1941. *Tellina rhodon.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, pp. 59–61.

Only a single live specimen was obtained close to the harbour mouth in March. A few dead shells were also collected from the Ernakulam shore opposite the harbour entrance. This species has been previously recorded by Gravely from the Madras coast. The largest shell in the present collection measured 11·2 mm. in length and 7 mm. in breadth.

Locality : Stations II and V.

Tellina pinguis Hanley

1843-1878. *Tellina pinguis.* Reeve, "*Conchologia Iconica*" XVII, xxxi, 172.

1941. *Tellina pinguis.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, pp. 59–61.

A few live specimens and a number of shells were collected from the vicinity of the harbour entrance, the largest of these measured 8·5 mm. in length and 7·6 mm. in breadth.

Locality : Stations III, V and X.

Solen lamarckii Deshayes

1941. *Solen lamarckii.* Gravely, *Bull. Mad. Govt. Muss.* (*Nat. Hist.*) V, No. 1, p. 63, Fig. 23 *b*.

1956. *Solen lamarckii.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 159, pl. XXIV, Fig. 2.

Only a single shell measuring 33·3 mm. in length and 7·1 mm. in breadth was obtained from Station VII.

Solen aquae-dulcioris (Ghosh)

1920. *Neosolen aquae-dulcioris.* Ghosh, *Rec. Ind. Mus.* XIX, pp. 57–58, pl. ii.

1941. *Solen aquae-dulcioris.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. I, pp. 62–64.

According to Gravely this is a common backwater species. Here five to six live specimens were obtained in each dredge collection during the dry months from stations VIII and IX. The largest specimen measured 16·3 mm. in length (excluding foot and siphon) and 5 mm. in breadth.

Martesia striata (Linne.)

1941. *Martesia striata.* Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 22.

1956. *Martesia striata.* Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 168, pl. XXV, Figs. 2 *a*–2 *c*.

Martesia striata is a wood-boring mollusc which is found in large numbers on all submerged timber structures in the Cochin harbour area. They burrow into wood only to accommodate themselves, but do not feed on timber. So even though various processes of chemical treatments have been tried for the preservation of submerged timber structures it has not so far been possible to prevent the attack of this borer. Empty shells of *M. striata* are found in dredge collections. These have evidently been liberated when infected timber crumbled.

Locality : Stations I–X.

Pholas (*Monothyra*) *orientalis* (Gmelin)

1941. *Pholas* (*Monothyra*) *orientalis*. Gravely, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) V, No. 1, p. 66.

1956. *Pholas* (*Monothyra*) *orientalis*. Satyamurti, *Bull. Mad. Govt. Mus.* (*Nat. Hist.*) I, No. 2, pt. 7, p. 167, pl. XXV, Fig. 1.

This species is very rarely found in the dredge collections. Only 3 shells were obtained from station I, the largest of which measured 32 mm. in length and 8·5 mm. in breadth.

ACKNOWLEDGEMENTS

The author is grateful to Dr. C. V. Kurian, D.Sc., Professor of Marine Biology and Oceanography, University of Kerala, for his valuable help and guidance throughout this work. Thanks are also due to Dr. S. T. Satyamurti, Superintendent, Government Museum, Madras, for his help in confirming the identification of a few doubtful species. The investigation was carried out as a part of the work of the Cochin Centre of the Marine Organism Scheme of the Forest Research Institute, Dehra Dun.

LITERATURE CITED

ANNANDALE, N. AND S. W. KEMP 1916. Fauna of the Chilka Lake, Mollusca Gastropoda and Lamellibranchiata. *Mem. Ind. Mus.*, **5** (4): 327–374.

CHERIYAN, P. V. 1966. Polychaetes from the Cochin harbour area. *Bull. Dept. Mar. Biol. Oceanogr.*, **2**: pp. 41–50.

CRICHTON, M. D. 1941. Marine shells of Madras. *Journ. Bomb. Nat. Hist. Soc.*, **42**: 323–341.

GHOSH, E. 1920. Anatomy of the Solenidae. *Rec. Ind. Mus.*, **19**: 57 and 58, pl. 2.

GRAVELY, F. H. 1927. Littoral Fauna of Krusadai Island. Mollusca. *Bull. Mad. Govt. Mus.* (*Nat. Hist.*), **1** (1): 95–109.

——— 1941. Shells and other animal remains found on the Madras Beach. I. Groups other than Snails. *Ibid.*, New Sr. N.H. Sect., **5** (1): 1–112, Text-figs. 31.

——— 1942. Shells and other animal remains found on the Madras Beach. II. Snails, etc., (Mollusca-Gastropoda). *Ibid.*, **5** (2): 1–110, 17 figs.

GUDE, G. K. 1914. Fauna of British India, Mollusca, II, pp. 1–520.

HORNELL, J. 1910. The edible Molluscs of the Madras Presidency. *Bull. Mad. Fish. Dept.*, **2**: 1–51.

——— 1916. Indian varieties and races of *Turbinella*. *Mem. Ind. Mus.*, **6**: 109–122.

——— 1917. A Revision of the Indian species of *Meretrix*. *Rec. Ind. Mus.*, **13**: pt. 3, 153–174.

——— 1948. The Study of Indian Molluscs. *Journ. Bomb. Nat. Hist. Soc.*, **48** (1), 543–569 and 750–744, pls. II & III.

——— 1951. Indian Molluscs. *Bomb. Nat. Hist. Soc.*, pp. 1–94.

PRASHAD, B. 1920. Notes on lamellibranchs in the Indian Museum Nos. 1–2. *Rec. Ind. Mus.*, **19**: pt. 4, 165–174, figs. 1 and 2 pl. IX, Figs. 1–8.

——— 1921. Notes on lamellibranchs. *Ibid.*, **22**: 111–119, pl. XV.

——— *1921 *a*. Report on the freshwater gastropod molluscs of lower Mesopotamia. *Ibid.*, **18**: 215–227.

——— 1932. Siboga—Expeditie, Pelecypoda, *Monograph*, **118**: 1–353, pls. 1-9.

PRESTON, H. B. 1909. Description of two new shells from South India. *Rec. Ind. Mus.*, **3**: 277 & 278.

——— 1914. Mollusca from the Chilka Lake on the east coast of India. *Ibid.*, **10**: 297–310.

——— 1915. A further report on Mollusca from lake Chilka on the east coast of India. *Ibid.*, **11**: 289–310.

INVESTIGATIONS ABOUT THE MOLLUSC FAUNA IN SUBMARINE CAVES

FERDINAND STARMÜHLNER

1st Zoological Institute, University of Vienna (Austria)

ABSTRACT

1. The present study deals with the mollusc fauna of sublittoral maritime caves of the steep Mediterranean chalk/rock shore (Tyrrhenian Sea, Italy and North Adriatic Sea, Yugoslavia). The caves investigated into have their entrance below the water surface, there is open communication with the sea, and the water volume is higher than 1 cubic meter. They are living spaces without phytal growth, with a decrease in light of 0·5 to 1%, counted from the surface irradiation, and with a surface exposition of more than 2 to 10%. They are mainly colonized by rheophile, heliophobe and sessile animal associations and their concomitant fauna.

2. Until this date, a total of 72 mollusc species have been found in the Mediterranean submarine caves:

Polyplacophora	6 species	
Gastropoda:		
Prosobranchia	36 „	(Gastropoda total: 47 species)
Opisthobranchia	10 „	
Pulmonata	1 „	
Bivalvia	16 „	
Cephalopoda	3 „	
GRAND TOTAL	72 species	

Of the aforementioned groups of the Polyplacophora, and of the Gastropoda species the Rhipidoglossa, Docoglossa, and most of the Taenioglossa (exception: *Fossarus*-species, *Triphoris perversa*) colonize just the cave entrances which show still some algal growth. They fail to occur in the central parts of caves.

3. All molluscs, found in the submarine caves investigated into, may be stated to be speleophile and speleoxen, respectively, since they also colonize the free littoral, mostly in shadowy regions. Spelebiontous maritime molluscs have not yet been determined.

4. In the submarine caves there are no sediment inhabitants (*e.g.*, Scaphopoda, among the Gastropoda-Prosobranchia the Naticacea, among the Opisthobranchia the Cephalaspidea, among the Bivalvia the Protobranchia, Glycimeridae, Cardiacea, Veneracea, Tellinacea, Solenacea, etc.). Furthermore no pelagic forms (*e.g.*, Heteropoda, Pteropoda, Argonautacea) and no mere algivorous species, like most of the Taenioglossa, Anaspidea and algae-sucker such as many of the Sacoglossa occur.

5. In a profile, beginning with the shrub-like algae of the free, sunny littoral (*Halopitys incurvus*, *Digenea simplex*, *Cystoseira* sp.), passing on to cushion and crust-like algae in the shadow of the cave entrances (*Peyssonelia squamaria*, *Pseudlithophyllum* sp.) to the dark central parts of the caves with pure animal growth (Porifera, Bryozoa, Hydrozoa, Anthozoa, Ascidiacea, sessile Polychaeta, Balanidae, *Ostrea*, *Chama*, etc.) the various mollusc groups show the following frequency (counted in % of mollusc-species found in the specimens of the Tyrrhenia-Expedition 1952 near Sorrento, Italy).

Group		Shrub- and tuft-like algae in the sunny free littoral	Shrub-, tuft-, cushion- and crust-like algae in the shadowy free littoral and cave entrances	Pure animal growth in the dark central parts of the caves
Polyplacophora	..	3%	9·8%	0
Gastropoda:				
Prosobranchia	..	83%	49·4%	11%
Opisthobranchia	..	4%	3·4%	4%
		(total: 87%)	(total: 52·8%)	(total: 15%)
Bivalvia	..	10%	37·4%	85%
TOTAL	..	100%	100·0%	100%

The Polyplacophora are mainly found on the cushion- or crust-like algae in the shadow of the cave entrances (*Callochiton laevis-Ischnochiton rissoi* assoc.), and are absent in the phytal-less, dark cave centers.

The Prosobranchia—a primarily algivorous group—have the highest species—and individual numbers in the clogged shrub- and tuft-like algae of the free, sunny littoral (*Bittium reticulatum-Rissoa variabilis* assoc.). In the shadowy areas (*Clanculus jussieui-Columbella rustica* assoc.) they significantly decrease in number, whereas in the cave centers there are only rapacious and saprophagous species (*Cantharus d'orbigny-Muricidea blainvillei* assoc.) or sponge-specialists to be found like the *Fossarus costatus* and *F. ambiguus-Nassa incrassata* assoc.

The Opisthobranchia are represented in the free littoral (*Bullaria striata-Runcina calaritana* assoc.) as well as in the caves, here the number of species and individuals are rather few. In the caves on the Hydrozoas an *Idulia coronata-Berghia coerulescens* assoc. was found and on the sponges a *Peltodoris atromaculata-Discodoris cavernae* assoc.

The Bivalvia as active filtrators have their optimal living conditions on the dark and, therefore, phytal-less walls of the caves being greatly exposed to the breakers and waves. Here, they reach a maximum number of species and individuals and form an *Ostrea edulis* f. *tarentina-Beguinea calyculata* assoc., which sometimes changes over into a *Arca lactea-Lithophaga lithophaga* assoc. Towards the cave entrances and the free, shadowy and sunny littoral, they largely recede—due to the algae competition. In the undergrowth of the shrub-like algae there lives a scanty *Musculus costulatus-Chama gryphoides* assoc.

6. The distribution of the molluscs living in caves is directly or indirectly dependent upon the decrease in light and the exposure to breakers and waves:

A. The decrease in light causes a recession of the high-growing algae and there is thus less space-competition for sessile filtrators such as the Bivalvia which occur in huge numbers there.

B. In addition, a favourable exposure to the breakers and waves facilitates optimal provision for sessile filtrators such as the Bivalvia.

C. Heavy Hydrozoa-growth in the epilithion of the caves provides favourable conditions for many Aeolidiacea as to their supply of nutritive substances, heavy Porifera-growth likewise for the Doridacea and for *Fossarus*.

D. Carnivorous and saprophagous species among the Prosobranchia, like Muricidae, Nassidae, Buccinidae and Fusidae find favourable nutrition-conditions in the sessile and errant fauna of submarine caves.

I. INTRODUCTION

WITHIN a short period of time, new investigation methods may revolutionize a science, or sectors of it that had all but been overlooked up to that date. In the field of maritime biology, in order to conduct maritime biological investigations, skin diving has brought about a vast amount of new data. Diving by means of goggles, fins, a snorkel, or compressed-air apparatus, has enabled the maritime biologist to collect and measure at the place of his investigation, just like the land biologist has always done. Prior to that, the maritime biologist was completely dependent upon collections with nets and trawls, and frequently large areas had to be searched in order to bring enough material aboard.

When the grappling irons were developed, remarkable results were achieved, investigating the symbiotic associations on the sediment of the bottom (sand, mud, clay) on primary and secondary rocky bottoms. However, even this method failed.

It is only the diver who may collect, observe and measure in waters of rocky littorals. Formerly mainly professional divers in diving apparel collected, under the supervision of maritime biologists, but even some brave scientists dared to dive to the bottom of the sea and consequently reported that they had seen a vast variety of species. More than 100 years ago—as early as 1845—the famous French biologist Milne-Edwards dived in the Gulf of Naples, the biologist A. Dohrn followed in 1881, and the French man Boutan at Banuyls sur Mer in 1892.

The first large-scale diving expedition was conducted by Gislen and his associates in the Gullmarfjord, Sweden, in 1930. He was employing scaphanders. The numerous quantitative collections yielded enough material to describe rather differentiated animal associations with the frequent occurrence of molluscs as guide forms. Kitching, Macan, Gilson (1934) examined, equipped with Beebe-bells, the Wembury-Bay (Southern Devons) and set up a nomenclature for the animal associations they found there according to the prevailing algae and fungi. In these associations also numerous molluscs are listed as characteristic forms. In 1938 Bursa and Wojtusiak (according to Starmühlner (1955 *a*) conducted qualitative and quantitative collections on soft bottoms in the Bay of Danzig (Est-sea), employing Beebe-bells likewise, and were able to prove that the bivalve *Mya arenaria*, in former times represented very rarely in the collections yielded by the grappling irons, was present at a much higher rate at the site of investigation. These authors, too, set up a nomenclature after prevailing algae where molluscs are represented in abundance.

By the conservative methods of maritime biology, namely collecting by nets and trawls, it had not been possible to investigate submarine caves. The only exception were grottos whose entrances were wide enough to allow for collections conducted from the boat. Investigations of this kind were made by Funk (1927), Van Gaver and Simon-David (1934) and Pax (1937). In 1949, it was H. Hass who published for the first time an investigation of a cave by means of skin diving and he studied the Bryozoan fauna of the caves and grottos of Capri. This technique as well as the equipment needed for it has decisively been improved in the past few years and has resulted in definite progress regarding the investigations into the living space of submarine caves, hitherto all but unknown. In 1948, R. Riedl of the Zoological Institute, University of Vienna (Austria), set forth the first submaritime expedition "AUSTRIA" to be conducted in Southern Italy and thus furnished scientific proof that this method was suited for the investigation into littoral caves. In the course of this expedition, collections were also made in submarine caves and thus the plan was created to investigate a number of other submarine caves in the littoral regions of the Mediterranean. In 1952, the Austrian Tyrrhenia Expedition was started under the direction of R. Riedl, together with numerous specialists in the fields of zoology and botany. The rocky littoral near Sorrents, in the Gulf of Naples, was chosen, for there were numerous small and large caves to be found. With the exception of the Protozoa almost the entire plant and higher animal-groups were collected and worked (*see* Riedl, 1966).

In the years followed R. Riedl and E. Abel continued their studies of the Hydroidea, Anthozoa and Pisces in the Tyrrhenian caves; for comparative purposes, the caves of the Northern Adriatic Sea (Rocky littoral at Rovinj-Yugoslavia) were investigated where Kirsteuer (1963) and Rutzler (1965 *a* and 1965 *b*) worked the Nemertinia and the Porifera. In numerous training courses of the 1st Zoological Institute, University of Vienna, during the years of 1954 through 1967, the author conducted further collections of molluscs in the caves near Rovinj. The records of molluscs of the Tyrrhenian submarine caves were published by Starmühlner (1955 *a* and *b*). The results concerning the molluscs of the North Adriatic submarine habitats have not yet been published.

In the past decade, general studies of the fauna in maritime caves were conducted and published by Drach (1951 and 1958), Laborel (1956 and 1960), Laborel and Vacelet (1958), Peres and Picard (1949) and Sara (1961). More detailed data on molluscs in maritime caves are rather sparsely represented in the literature apart from the results of the aforementioned Tyrrhenia Expedition—thus by Arndt (1936), cited according to Van Gaver and Simon-David (1936), Corroy *et al.* (1958), Peres and Picard (1949), Portmann (1958), and Haefelfinger (1961).

The extensive description of the present status of maritime cave biology by Riedl (1966) contains a vast number of pictures, charts and literature references.

II. INVESTIGATION METHODS AND INVESTIGATION AREAS

On the Austrian Tyrrhenia Expedition, quantitative specimens were taken, usually from an area of 1/16 square meter (squares of 25 cm. length). By taking such samples, the mesofauna was well represented in its variety, the size ranging from 1 to 50 mm. In this range the major part of the littoral molluscs is also included. For molluscs with a size over 50 to 100 mm. such as the large muricids, the area covered at one time is too small and very mobile forms—such as the Cephalopoda—cannot be captured. At least two collectors were occupied with taking each sample (Fig. 1); the selected place was then worked with hammer and chisel. Of course, on the site of the collection all measurable ecological data were taken down (position and inclination of the bottom, plant growth, exposure to light and tide). One diver chiselled off the top layer *plus* the plants growing on it while his partner held a plastic bag with a wide opening in such manner that more than 90% of the loosened material could almost always be collected. After the top layer was chiselled off to a depth of 10 cm. in order to collect the endolithion as well, the collecting bag was sealed off hermetically to prevent a drifting-off of the material. The material collected was poured into a glass dish in the field laboratory. By the deterioration of climate method developed by Riedl (1953), first the O_2-sensitive Opisthobranchia were secured. These animals, if present, came up to the surface approximately within half an hour, together with Turbellaria, Nemertini, Annelida, Crustacea, etc., and could be simply removed with pipette.

During this time also the major part of the Prosobranchia represented in the sample could be collected when they crawled from the algae, sponges, etc. Approximately 6 to 8 hours later the sample was poisoned with Formol and shaken, in order to find the rest of the shell-bearing molluscs. Finally the sample, especially from the dredge, was searched carefully by means of a magnifying glass and binoculars. The Opistobranchia were then preserved like the smaller Prosobranchia and Bivalvia for histological purposes in Bouin's fluid, the larger Prosobranchia and Bivalvia in 70% alcohol. All Opisthobranchia found were recorded with colours according to life, or photographs were taken by flashgun and bellows apparatus.

As already mentioned in the introduction, the molluscs were collected from submarine caves and partly from the rocky littoral of the Tyrrhenian Sea in the Gulf of Naples, near Sorrento (Italy), and also from the North Adriatic littoral, off the province of Istria, Yugoslavia. In both areas tide-caves were investigated, whose entrance were either completely or at least partly immersed under water. Most of the caves studied had a water volume of more than 1 cubic meter, the largest of them like the cave "Ost 39" (the fishermen of Sorrento had named this grotto "tuffo-tuffo" Starmühlner, 1955 *a* and *b*; Riedl, 1966) or the grotto on the insular Banjole on the Adriatic west shore of the city of Rovinj, having a length of approximately 20 meters into the chalky rock, where they end as a crude sac.

According to the definition by Riedl (1966) a genuine maritime cave has a water volume of more than 1 cubic meter and its entrance (s) are more than half-immersed under water; the cave also has a sufficiently large communication with the open sea. The light decreases to 0·5% to 1% of the surface intensity whereas at least 2 to 10% of the surface exposure to tidal waves is present, According to Riedl (1966), these are following types of maritime caves to be distinguished as to their morphology:

A. entrance partly under water
  - (*a*) tide gorge
  - (*b*) grotto (Fig. 2)
  - (*c*) gulley
  - (*d*) archway
  - (*e*) tunnel
  - (*f*) channel

B. entrance completely immersed (Fig. 3)
  - (*a*) niche
  - (*b*) bulge cave—sometime with an air dome
  - (*c*) slit
  - (*d*) arcade
  - (*e*) passage
  - (*f*) corridor

Cave 0/39, Capo di Sorrento, is according to the tide either a grotto, or a bulge cave with an air dome, and inside it changes into a blind gulley. The Banjole cave is a grotto with a front and a rear part, connected by a passage.

III. Systematic Part

There has been determined a total of 72 mollusc species in Mediterranean maritime caves, more than one-third of this number were, however, present only near the entrances and receded toward the dark cave centres. The data available at present are based on the findings by Starmühlner (1955 *a* and *b*) as well as on the investigations of Corroy *et al.* (1958) and Peres and Picard (1949).

List of Species

	Free littoral	Cave entrance	Cave centre
POLYPLACOPHORA			
LEPIDOPLEURIDA			
(1) *Lepidopleurus cinereus* (L.)	+	+	—
CHITONIDA			
(2) *Callochiton laevis* (Montagu)	+	+	—
(3) *Chiton corallinus* Risso	+	+	—
(4) *Acanthochiton fascicularis* (L.)	+	+	—
(5) *Ischnochiton rissoi* (Payraudeau) ..	+	+	—
GASTROPODA			
PROSOBRANCHIA			
ZEUGOBRANCHIA			
(6) *Haliotis tuberculata* Lam.	+	+	—
(7) *Emarginula elongata* O. G. Costa ..	+	+	?
(8) *Diodora gibberula* (Lam.)	+	+	—

	Free littoral	Cave entrance	Cave centre
PATELLACEA			
(9) *Patella coerulea* L.	+	+	–
(10) *Patella lusitanica* Gmelin	+	+	–
TROCHACEA			
(11) *Clanculus jussieui* (Payraudeau)	+	+	–
(12) *Monodonta turbinata* (Born)	+	+	–
(13) *Calliostoma laugieri* (Payr.)	+	+	–
(14) *Cantharidus exasperatus* (Pennant)	+	+	–
TAENIOGLOSSA			
(15) *Littorina neritoides* (L.)	+	+	–
(16) *Fossarus ambiguus* (L.)	+	+	+
(17) *Fossarus costatus* (Brocchi)	+	+	+
(18) *Alvania cimex* (L.)	+	+	–
(19) *Cingula pulcherrima* (Jeffreys)	+	+	?
(20) *Triphora perversa* (L.)	+	+	+
(21) *Cerithiopsis tubercularis* (Montagu)	+	+	–
(22) *Bittium reticulatum* Da Costa	+	+	–
(23) *Vermetus arenarius* (L.)	+	+	+
(24) *Vermetus triqueter* Bivone	+	+	+
RACHIGLOSSA			
(25) *Murex trunculus* L.	+	+	+
(26) *Muricidea blainvillei* (Payr.)	+	+	+
(27) *Tritonalia edwardsi* (Payr.)	+	+	+
(28) *Tritonalia aciculata* (Lam.)	+	+	+
(29) *Lachesis granulata* (Risso)	+	+	–
(30) *Columbella rustica* (L.)	+	+	–
(31) *Nassa costulata* (Renieri)	+	+	–
(32) *Nassa incrassata* (Muller)	+	+	+
(33) *Pisania maculosa* (Lam.)	+	+	+
(34) *Cantharus d'orbigny* (Payr.)	+	+	+
(35) *Cantharus leucozonus* (Philippi)	+	+	+
(36) *Fusus pulchellus* Philippi	+	+	+
(37) *Fusus rostratus* (Olivi)	+	+	+
(38) *Fusus syracusanus* (L.)	+	+	+
(39) *Fasciolaria tarentina* (Lam.)	+	+	+
(40) *Mitra cornicula* (L.)	+	+	–
TOXOGLOSSA			
(41) *Conus mediterraneus* Bruguiere	+	+	–
(42) *Philbertia linearis* (Montagu)	+	+	?

	Free littoral	Cave entrance	Cave centre
OPISTHOBRANCHIA			
SACOGLOSSA			
(43) *Thuridilla hopei* (Verany)	+	+	–
(44) *Elysia viridis* (Montagu)	+	+	–
(45) *Bosellia mimetica* Trinchese	+	+	–
NOTASPIDEA			
(46) *Pleurobranchea* sp.	..	..	..
NUDIBRANCHIA			
DORIDACEA			
(47) *Discodoris cavernae* Starmühlner	?	?	–
(48) *Peltodoris atromaculata* Bergh	+	+	+
(49) *Duvaucelia villafranca* Vayssiere	+	+	–
AEOLIDIACEA			
(50) *Berghia coerulescens* (Laurillard)	+	+	+
(51) *Embletonia pulchra* (Alder and Han.)	+	+	–
(52) *Idulia coronata* (Gmelin)	+	+	+
PULMONATA			
(53) *Gadinia garnoti* (Payraudeau)	+	+	+
BIVALVIA			
TAXODONTA			
(54) *Arca noae* L.	+	+	+
(55) *Arca barbata* L.	+	+	+
(56) *Arca lactea* L.	+	+	+
(57) *Modiolus barbatus* (L.)	+	+	–
(58) *Musculus costulatus* (Risso)	+	+	–
(59) *Brachyodontes minimus* (Poli)	+	+	–
(60) *Mytilus galloprovincialis* Lam.	+	+	–
(61) *Lithophaga lithophaga* (L.)	+	+	+
(62) *Avicula tarentina* Lam.	+	+	+
(63) *Ostrea edulis* L.	+	+	+
(64) *Lima lima* L.	+	+	?
EULAMELLIBRANCHIATA			
(65) *Beguinea calyculata* (L.)	+	+	+
(66) *Chama gryphoides* L.	+	+	+
(67) *Saxicava arctica* (L).	+	+	?
(68) *Gastrochaena dubia* (Pennant)	+	+	+
(69) *Pholas dactylus* L.	+	+	+

	Free littoral	Cave entrance	Cave centre
CEPHALOPODA			
(70) *Loligo vulgaris* Lam.	+	+	+ (eggs!)
(71) *Octopus vulgaris* Lam.	+	+	+
(72) *Ozaena moschata*	+	+	?

Annot.: + = found; — = not found; ? = occurrence possible.

Now that species found to date have been listed, a few statements may be added regarding their abundance in maritime caves.

Lepidopleurus cajetanus.—For the first time reported by Corroy *et al.* (1958) who found them at cave entrances in the region of Cassis (France).

Callochiton laevis.—Found abundantly on cushion-like (*Halimeda, Peyssonelia, Pterocladia*) and crust-like (*Pseudolithophyllum*) algae at cave entrances and dowy overhangings. This red-colored species accounted for up to 25% of all molluscs and 90% of all Polyplacophora found there. With the algae gradually receding towards the dark cave centres, this species also quickly disappeared.

Acanthochiton fascicularis.—Found sporadically besides the aforementioned species on *Pseudolithophyllum* sp. crusts of the cave entrances.

Ischnochiton rissoi.—Sporadic occurrence besides *Callochiton laevis* on cushion-like algae such as *Peyssonelia squamaria* and *Pterocladia capillacea.*

Haliotis tuberculata.—Was not found in tide gorges, but rather frequently in small-sized caves, sticking to the rear side of the stones in areas where the boulders lay dispersed (*e.g.*, off Rovinj, Istria).

Emarginula elongata.—An otherwise algal-feeding Rhipidoglossa; has been found only once on a *Euspongia-Tuberella* sponge bed in cave 0/39.

Diodora gibberula.—Found sporadically on cushion-like algae (*Peyssonelia*) at cave entrances, shadowy overhangings, and under stone-boulders.

Patella coerulea.—In the Banjole cave (Rovinj) this species was determined in middle waters in the free littoral as well as in the cave entrances. When the algae recede towards the cave centers, the Patellacea also disappear.

Patella lusitancia.—Some abundance as the aforementioned species, but in somewhat higher waters—rising above median water-level.

Clanculus jussieui.—Not infrequent in *Peyssonelia*-growth, sparsely on crust-like algae near cave entrances.

Monodonta turbinata.—This characteristic littoral mollusc was found in the Banjole cave, similarly to both *Patella*-species, near the entrance, as long as there were algae.

Calliostoma laugieri.—Starting from the shadow-algae, this species is sporadically represented to the *Balanus*-Porifera growth in the front part of the cave, as long as there is still some growth of (*Peyssonelia, Udotea, Pseudolithophyllum*) algae.

Cantharidus exasperatus.—Found sometimes in the shadow-algae-growth like *Halimeda tuna, Dictyopteris membranacea* at cave entrances and shadowy overhangings.

Littorina neritoides.—This supralittoral shore snail is widely distributed in the splashing zone of the Banjole cave (grotto) like both *Patella* species and *Monodonta turbinata.*

Fossarus ambiguus.—With *F. costatus* the only one of the Taenioglossa which could always be found in the dark parts of the cave, namely, on sponges in the Tyrrhenian caves. Investigations of the stomach showed that both *Fossarus* species feed upon Porifera. Therefore, their occurrence seems to be dependent on the abundance of the latter.

Fossarus costatus.—The second *Fossarus* species of the Tyrrhenia caves investigated are of the same dependency, but much more common (14–15% of all Prosobranchia found in the caves!).

Alvania cimex.—Sparsely at cave entrances, but always in the subgrowth of the shadow algae (*Dictyopteris, Peyssonelia*) where the snail is found up to the front parts of the caves.

Cingula pulcherrima.—Astonishingly a large number of juvenile forms of this tiny Rissoidae was found in a very dark part of the small cave 0/3 (Tyrrhenian Sea) on the ceiling in an algae-free *Astroides calycularis-Lithophaga lithophaga* growth; they were collected, however, from a place only 1 m. distance from the entrance. Possibly tiny snails were drifted in from the subgrowth of the shadow-algae at the entrance, when the waves went higher.

Triphora perversa (Fig. 4).—Found in the subgrowth of shrub-like algae, but also in the completely dark *Balanus*-Porifera growth in central parts of the caves. But *T. perversa* was determined also in larger depths in the Mediterranean as well as in the North Sea. Possibly this Cerithiidae is also saprophytous and also feeds upon decaying sponge particles.

Cerithiopsis tubercularis.—Found sporadically in the shadowy subgrowth of shrub-like and tuft-like algae; likewise on *Dictyopteris membranacea* and cave entrances and overhangings covered by *Pseudolithophyllum.*

Bittium reticulatum.—This snail found in abundance on the shrub-like algae of the free littoral feeds upon the intermediate and subgrowth of shadow-algae where it is found, such as *Cladophora, Halimeda* and *Dictyopteris* and may be collected also at the outer parts of the cave entrances.

Vermetus arenarius (Fig. 5) and *V. triqueter.*—Both species are not infrequently found on crust-like algae (*Pseudolithophyllum* of the cave) entrances and in the front part of the caves, on the side-walls, between *Balanus* colonies.

Murex trunculus (Fig. 6).—This muricid is the largest species found in the rocky littoral and in the innermost cave centres where the sediments in particular (decaying plant and animal particles are found there) offer favourable nutritional conditions for the saprophytic snails.

Muricidea blainvillei.—This small-size muricid found especially in the slits of the caves, in empty *Lithophaga* ducts, and between the *Balanus*-Porifera growth. Here a lot of organic matter and other decaying animal particles is deposited which the snail feeds on.

Tritonalia edwardsi.—This small-size muricid lives in caves, in the same slits like *M. blainvillei.* In cave 0/39 this species was found also in the dark gulleys in the background of the caves where the rock was just slightly covered by the crust-forming sponges *Leptopsammia* and *Petrobionta.* The snails found there had no pigmentation, were white, and with a worn and corroded shell.

Tritonalia aciculata.—The smallest muricid in the Mediterranean littoral was not infrequently found in the shadowy subgrowth of the shrub-, tuft- and cushion-like algae, but very sporadically in the cave centers.

Lachesis granulata.—Ascertained only at cave entrances and shadowy overhangings on *Halimeda tuna* growth.

Columbella rustica.—One of the most abundant species of the free littoral found in all types of algal growth, but much less frequently towards very shadowy rocks and cave entrances. In cave centers this snail was missing.

Nassa costulata.—Found very sporadically at cave entrances and front part of caves.

Nassa incrassata (Fig. 7).—This species also found frequently in the free littoral in the subgrowth (on epizoic sponges, Bryozoa, etc.) is also found abundantly in caves on sponges (upto 40% of the Prosobranchia species found there !). Its prime food seems to be decaying sponge particles.

Pisania maculosa.—A characteristic "saprophage" of the free littoral which may be found also in caves at locations where the tide drifts in organic matter.

Cantharus d'orbigny (Fig. 8).—The most abundant buccinid in the region of the shadow-algae (in *Halimeda tuna* growth, up to 25% of all Prosobranchia !) and in animal growth of the cave centers (15-20% of all Prosobranchia!). Investigations of the stomach show that this snail feeds on decayed small animals like crabs, worms, but also on decaying sponge particles.

Cantharus leucozonus.—Found somewhat less abundantly as the aforementioned species, but occurring on the same places.

Fusus pulchellus.—Sporadically on sponge mats (*Spongia-Aoptos* growth) in cave 0/39 *b* (Tyrrhenian Sea).

Fusus rostratus.—Found sporadically in the Banjole cave of Rovinj (Istria).

Fusus syracusanus.—Like *F. rostratus.*

Fasciolaria tarentina.—Not infrequently found on side-walls of cave centers, where the snail lives partly as a carnivore, partly on decaying animal particles.

Mitra cornicula.—Frequently in the subgrowth of shrub-, tuft- and cushion-like algae at cave entrances, in the shadow on *Halimeda, Peyssonelia* and *Dictyopteris* (sometimes more than 13% of all Prosobranchia found there). This species has not been observed in center of caves up to date.

Conus mediterraneus.—Sporadically this species was found in the Banjole cave (Rovinj) at the entrance, where it is represented abundantly in the rocky littoral.

Philbertia linearis.—Just one sample of this species was found in cave 0/39 near Sorrento on a Porifera-*Balanus* growth.

Thuridilla hopei (Fig. 9).—This conspicuous, multicolored Saccoglossa (Fig. 3) is sometimes collected from the algae in the littoral up to the crust-like algae (*Pseudolithophyllum*) of the cave entrances.

Elysia viridis.—Sparsely at cave entrances and shadowy overhangings where algae are found, but mostly only juvenile forms are collected. Riedl (1966) gives a photograph of a cluster, taken from a rocky overhanging (Marmaras, Chalkidike).

Bosellia mimetica (Fig. 12).—This sacoglossan species cleverly imitates in color and shape a "leaf" of *Halimeda tuna.* This species, described by Trinchese, was rediscovered only these past few years in the Mediterranean, by Portmann (1958) in the western part, and by Starmühlner when conducting diving excursions on shadowy sites with *Halimeda tuna* growth (small-size caves and sides of caves) near Rovinj (Istria). This species is strictly dependent upon *Halimeda tuna* and is an algae sucker, like most of the Sacoglossa.

Pleurobranchea sp.—A juvenile *Pleurobranchae,* which could not be determined more closely, was found on *Balanus*-Porifera growth in the cave center of 0/39 near Sorrento. Most of the Pleurobranchidae live on secondary hard soils, in greater depths, they feed upon ascidians, sponges, etc.

Discodoris cavernae.—Discovered by Starmühlner (1955 *a* and *b*) in the caves near Sorrento, where the light brown Doridacea, 11 to 15 mm. long, lives exclusively on Porifera. This species was found in almost all of the catches from the cave centers with animal growth (*Astroides calycularis*-Porifera, as well as *Balanus perforatus*-Porifera growth) where they reached 66% to 80% of all Opisthobranchia in these regions ! When investigating the Banjole cave in the Northern Adriatic Sea, this species was also represented.

Peltodoris atromaculata (Fig. 10 and 11).—This rather large dorid, white, with dark brown spots, lives exclusively on the sponge *Petrosia ficiformis*, which means that it is entirely dependent upon this sponge. Haefelfinger (1961) studied the biology of *P. atromaculata* and found out that these Doridacea only feed upon *Petrosia* tissue where distinct areas of feeding were to be found. The sponge *Petrosia* often is the dominant group in caves and shadowy places and almost always is accompanied by *P. atromaculata*.

Duvaucelia villafranca.—One individual only was found among *Peyssonelia squamaria* growth, on the ceiling of a submarine slit near Sorrento where also crust-like chalk-algae and Porifera were forming the intermediary growth.

Berghia coerulescens.—A midget form of Aeolidiacea which possibly represents a new species (?) was observed several times, interspersed with Hydrozoa of the cave centers near Sorrento.

Embletonia pulchra.—One individual was found on crust-like chalk-algae and meagre sponge- and *Balanus* growth on the ceiling of submarine tunnel near Sorrento.

Idulia coronata.—Sporadically on little hydrozoan stems between *Pseudolithophyllum*-growth at the cave entrances, as well as among animals caught in cave centers.

Gadinia garnoti.—This was the only pulmonate of the investigated region of the Tyrrhenian Sea which we found to penetrate from the tidal zone of the free littoral into grottos and caves with air domes, where it settles in the so-called "air-seas"—hollow spaces, filled with air, in the cave ceiling. It feeds from the endolithic chalk-algae, possibly also upon sponges.

Arca noae.—Found only sporadically, but continuously from the cave entrances into the central parts of the caves between Porifera and *Balanus*-colonies.

Arca barbata.—This species is found in the same places as *A. noae*, but mostly in larger numbers.

Arca lactea (Fig. 13*e*).—The smallest of the *Arca* species was the mussel found in greatest abundance, not only in the Tyrrhenian caves, but also in the subgrowth of the algae-growth in the free littoral. In the cave centers *A. lactea* reaches 20-35% of all molluscs found in the samples. The animals in most cases settle in small groups in little holes, slits, empty, *Lithophaga* ducts, *Balanus* shells, etc. Besides *Tritonalia edwardsi*, the *Arca lactea* was the only mollusc species in the innermost cave galleys of the 0/39 cave near Sorrento.

Modiolus barbatus.—Sporadically among shadowy cushion-like algae at cave entrances and overhangings.

Musculus costulatus.—This species is represented beginning with subgrowth of shrub-like algae in the sunny, free littoral, to the shadow-algae at the cave entrances and sporadically to the animal growths in the front part of the caves. However, compared to other mussel species, *M. costulatus* largely recedes in the shadowy regions.

Brachyodontes minimus.—The little mussel is found at median water-level of the low-tide. In rather shadowy regions the mollusc is represented only sparesely, only a few individuals were found in grottos and caves, almost under the water surface level.

Mytilus galloprovincialis.—Sporadically at cave entrances of the Banjole cave (Rovinj), almost directly under the water surface.

Lithophaga lithophaga (Figs. 14 and 15).—From the cave entrances to the cave centres, at places which are grossly exposed, the number of this boring mussel vastly increases. In cave 0/39 (Sorrento) it amounts to as much as 66% of all molluscs and 80% of all mussels found there and thus forms the dominant group there. The average individual number was 20 per 1/16 square meter ! The maximum was 53 per 1/16 square meter ! In the cave profile it appears that *Lithophaga lithophaga* has its highest density of individuals on the walls, whereas it decreases towards the ceiling, and is all but non-existent towards the cave bottom.

Avicula tarentina.—Peres and Picard (1949) found this species in submarine grottos near Marseille. It could not however be ascertained in the caves near Sorrento, nor in the Northern Adriatic Sea.

Ostrea edulis.—In the areas investigated, only the forma tarentina could be found. In the subgrowth of the algae the oyster appears only sporadically. With the receding of algae towards shadowy biotops and cave centers they increase very much in number, in order to reach a maximum at largely exposed places in central parts of the caves. The places it prefers are jutting or overhanging rocks which are hard-hit by the waves. Here, the species reaches more than 16% of all molluscs found there and approximately 20% of all mussels found there; the average density varies between 80 and 140 individuals per 1/16 square meter. The oyster, however, disappears in genuine Porifera-growth, since there it is gradually overgrown by sponges and suffocated. Likewise, it recedes towards the cave bottom and niches where there is no direct exposure to tidal fluctuation.

Lima lima.—Sporadically in slits between *Balanus* and Porifera in the central part of cave 0/39 (Sorrento), where the mollusc surrounds itself with a "byssus-nest". Empty shells were frequently found in the slack on the bottom.

Beguinea calyculata.—Very frequently found in the free littoral in the subgrowth of tuft-like and crust-like algae grossly exposed to the tides as well as in the cave centers, especially at rather exposed places. In the free littoral near Sorrento the species reaches more than 63% of all mussels found there, in the caves approximately 10% of all mussels, and 7-9% of all molluscs found. The mussel settles, like the *Arca lactea*, in groups in slits, holes, etc. Due to the fact that theyare oft impeded in growing, there are misformations of the shells since they adapt themselves to the environment.

Chama gryphoides.—This species is found in greater abundance in the free littoral, gradually increasing in number from the subgrowth of the high shrub-like algae towards the shadowy, lower cushion-like, tuft- and crust-like algae. Particularly frequent is this species on exposed cave walls between *Balanus perforatus*-Porifera growth, where it reaches almost 8% of all molluscs found or more than 9% of all mussels.

Saxicava artica.—Only one individual, from a grossly exposed *Balanus perforatus-Ostrea edulis* growth was found in cave 0/39 (Sorrento).

Gastrochaena dubia.—This species is characteristic of the eulittoral on rocky shores very much exposed to the tide, where the boring mussel lives in the endolithion, and just reaches out of the bottom by means of a chalk tube containing the siphons. It is found off Sorrento, just as in the North Adriatic Sea off Rovinj, at cave entrances and in cave centres, but never reaches the same abundance there as it does in the free littoral. Possibly overgrowing sponge-masses thwart a larger occurrence of this species.

Pholas dactylus.—This is a boring mussel which can be found deep inside the cave, but have not been found often in the caves of the chalk regions that have been investigated to date (Riedl, 1966).

Loligo vulgaris.—Photographs have been taken under water by Svoboda (according to Riedl, 1966) in a 30 m. deep cave off Prvic (Yugoslavia). This animal seems to spawn sometimes in caves; otherwise it swims in the free sea.

Octopus vulgaris.—The octopuses, active in the night, hide themselves in slits and holes of caves during the day, and in most cases keep a shield of stones, empty shells, etc., for protection in front of their hiding place, by means of the suction cups of their tentacles. In the twilight the octopus leaves its hiding place and looks for its prey outside the cave.

Ozaena moschata.—According to snapshots taken under water by Moosleitner (Riedl, 1966) from a 7 m. deep cave off Marmaras (Chalkidike), the moschus-octopuses also seem to hide in caves during the day.

When studying the graph listing the mollusc species found up to date at the cave entrances and inside the caves of the Mediterranean, it becomes apparent that whole groups of molluscs are missing. Thus, all inhabitants of sediments (sand, silt, etc.) such as the class Scaphopoda, predatory Naticacea, the Pleurocoela (above all the Cephalaspidia) are missing. On the other hand the Anaspidea, which are partly free-floating, as well the Aplysiidae, may sometimes by mistake come into a cave, or else they are drifted in. Among the sediment-inhabiting mussels the Protobranchia, Isocardiacea, Mactracea, Tellinacea, Myacea, Anomalodesmata, Lucinacea, Cardiacea, Veneracea, and Solenacea are missing.

Naturally pelagic animals swimming in the sea, such as *Janthina*, Heteropoda, Pteropoda, and Argonautacea are not represented. In the plantless central parts of the caves there are no phytophagous, algae-feeding or sucking species. Of the 72 species mentioned there were only 31 species represented from the free littoral to the regions of the cave entrances or overhangings:

Lepidopleurus cinereus
Callochiton laevis
Chiton corallinus
Acanthochiton fascicularis
Ischnochiton rissoi
Haliotis tuberculata
Diodora gibberula
Patella coerulea
P. lusitanica
Clanculus jussieui
Monodonta turbinata
Calliostoma laugieri
Cantharidus exasperatus
Littorina neritoides
Alvania cimex
Cerithiopsis tubercularis
Bittium reticulatum
Lachesis granulata
Columbella rustica
Nassa costulata
Mitra cornicula
Conus mediterraneus
Thuridilla hopei
Elysia viridis
Bosellia mimetica
Duvaucelia villafranca
Embletonia pulchra
Modiolus barbatus
Mytilus galloprovincialis
Musculus costulatus
Brachyodontes minimus

Forty-one species could be determined up to date reaching from the free littoral over the cave entrances up to the dark central parts of submarine caves. Of these molluscs 10 species were found only sporadically and probably are not regular inhabitants of submarine caves of the Mediterranean:

Emarginula elongata
Cingula pulcherrima (only juv.)
Lima lima
Saxicava artica

Philbertia linearis
Pleurobranchea sp. (only juv.)
Avicula tarentina (in W. Mediterranean)
Pholas dactylus
Loligo vulgaris (only eggs)
Ozaena moschata

If we deduct those mollusc species which we should like to call speloxenous, since they are found only at cave entrances or very sporadically in the central parts of caves, there remains 31 speleophile species which have always been found and mostly in a substantial number, in sub marine caves of the Mediterranean:

Fossarus ambiguus
F. costatus
Triphora perversa
Vermetus arenarius
V. triqueter
Murex trunculus
Muricidea blainvillei
Tritonalia edwardsi
Tr. aciculata
Nassa incrassata
Pisania maculosa
Cantharus d'orbigny
C. leucozonus
Fusus pulchellus
F. rostratus
F. syracusanus
Fasciolaria tarentina
Discodoris cavernae
Peltodoris atromaculata
Berghia coerulescens
Idulia coronata
Gadinia garnoti
Arca noae
A. barbata
A. lactea
Lithophaga lithophaga
Ostrea edulis
Beguinea calyculata
Chama gryphoides
Gastrochaena dubia
Octopus vulgaris

No mollusc species just mentioned—with the exception of the *Discodoris cavernae*—was found up to now exclusively in caves, *i.e.*, there are no spelebiontous forms. *Discodoris cavernae*, a small inconspicuous species of Discodoridae, was observed only in caves (Starmühlner, 1955 *a* and *b*; Riedl, 1966), but similar to the large size *Peltodoris atromaculata* it lives only on Porifera. Obviously it appears in suitable shadowy locations (overhangings in the littoral, larger, darker depths) and also outside of caves, as far as these places have a growth of Porifera. Also, related species *Discodoris indecora* and *D. edwardsi* were dredged from places of the free bottom, even if from greater depths. The former species were found near Trieste (Northern Adriatic), the second in the Western Mediterranean, during the Traveilleur Expedition (According to Graeffe, Vayssiere, quoted by Starmühlner, 1955 *a* and *b*).

Among the cave species mentioned above 42% of them are predatory or saprophagous animals:

Murex trunculus
Muricidea blainvillei
Tritonalia edwardsi
Tr. aciculata
Cantharus d'orbigny
C. leucozonus
Fusus pulchellus
F. rostatus

Nassa incrassata
Pisania maculosa
F. syracusanus
Fasciolaria tarentina
Octopus vulgaris

In addition to these carnivorous species the sponge-feeding species should be listed here, representing 12·5%.

Fossarus ambiguus
F. costatus
Discodoris cavernae
Peltodoris atromaculata

also the Hydrozoa-feeding species with 6·5%:

Berghia coerulescens
Idulia coronata

Sixty-one per cent of the cave species feed exclusively upon animal matter. Also there are two more species which were found in central parts of the caves which may feed on animal matter—namely *Triphora perversa* and *Gadinia garnoti*, thus increasing the number to 67·5%.

The remaining 32·5% are plankton-feeding species, of which 25% are more suspension feeders, namely the mussels:

Arca noae
A. barbata
A. lactea
Lithophaga lithophaga
Ostrea edulis
Beguinea calyculata
Chama gryphoides
Gastrochaena dubia

The remaining 6·5% is accounted for by the detritus feeding species *Vermetus arenarius* and *Vermetus triqueter*.

In concluding we may state that the mollusc fauna of submarine caves which had been investigated is made up on the one hand by free-floating, carnivorous, and on the other hand by sessile, filtrating species. Among the carnivorous species the sponge and hydroid feeding lists are characteristic.

IV. THE DISTRIBUTION OF THE MOLLUSC GROUPS AND SPECIES OF THE SUBMARINE CAVES

When investigating the algae growth—starting from the sunny and proceeding to the shadowy littoral, to the cave entrances and their gradual changing into the animal growth in central parts of the submarine hollow spaces, there is a strict sequence to be observed as far as the mollusc fauna is concerned. Even the large molluscs show varying abundance in such a profile; from the ecological point of view, it is influenced mainly by the decreasing light and of secondary importance by exposure to the tide. The following algae and animal growths could be ascertained in the course of the Tyrrhenian expeditions:

(1) Sunny littoral,

(A) slight breakers, shrub-like algae;

Halopitys incurvus
Digenea simplex
Cystoseira sp.

(B) strong breakers, tuft-like algae:
Laurencia pillosa
Corallina mediterranea

(2) Shadowy littoral,
(A) slight breakers, shrub-like algae:
Dictyopteris membranacea

(B) strong breakers, tuft-like algae (overhangings, outer parts of cave entrances):
Cladophora prolifera
Pterocladia capillacea
Halimeda tuna

(C) strong breakers, cushion-like algae (inner parts of the cave entrance):
Peyssonelia squamaria

(D) strong breakers, crust-like algae (Changing from the cave entrances to the front parts of the caves):

Pseudolithophyllum sp. (Fig. 16)

(3) Caves,

(A) Pure Porifera
Spongia-Aaptos
Leptopsammia-Pterobionta sp.

(B) mixed Porifera
Astroides calycularis-Petrosia ficiformis
Balanus perforatus-Petrosia ficiformis
Balanus perforatus-Spongia sp.
Balanus perforatus-Penares sp.

(C) pure *Balanus perforatus* (Fig. 17)

(D) mixed *Balanus perforatus* (refer to B)
Balanus perforatus-Lithophaga lithophaga

(E) mixed *Astroides calycularis*
Astroides calycularis-Lithophaga lithophaga

The biotope correlation of the larger mollusc groups show the transitions (in % of all mollusc individuals found in these biotopes) as given in Table I.

In Table I the Polyplacophora show a distinct maximum abundance in the shadowy littoral, above all on cushion- and crust-like algae on overhangings and cave entrances. In the sunny littoral the Polyplacophora are found only in the subgrowth, which is formed by the aforementioned cushion- and crust-like algae, whereas they gradually recede towards the dark cave centres, together with the receding of these algae. In the subgrowth of the sunny as well as the shadowy shrub- and tuft-like algae growths there is a *Chiton olivaceus-Acanthochiton fascicularis* association, on the cushion-crust-like algae of the cave entrances a *Callochiton laevis-Ischnochiton rissoi* association dominating.

TABLE I

Correlation of the larger Mollusc-groups between sunny littoral, shadowy littoral, and cave entrances and cave centres

Group	Shrub- and tuft-like algae in the sunny free littoral	Shrub-, tuft-, cushion- and crust-like algae in the shadowy, free littoral and cave entrances	Pure animal-growth in the dark central parts of the caves
Polyplacophora	3%	9·8%	0
Gastropoda:			
Prosobranchia	83%	49·4%	11%
Opisthobranchia	4% (total: 87%)	3'4% (total: 52·'8%)	4% (total: 15%)
Bivalvia	10%	37·'4%	85%
TOTAL	100%	100%	100%

Among the gastropods, the Prosobranchia show their maximum abundance as to the number of species and individuals, in the sunny and shadowy shrub-like algae, a fact that may be deduced to the numerous phytophagous forms, above all the animals feeding upon the existing growth. In the sunny plant zones, a *Bittium reticulatum-Rissoa variabilis* association dominates; in the shadowy plant zones a *Clanculus jussieui-Columbella rustica* association. With the receding algal growth towards the cave centers the algae-feeding Gastropoda recede as well and the carnivorous or slime-filtering species become dominating. Whereas on genuine sponge growth of the caves near Sorrento a *Fossarus costatus-Nassa incrassata* association was found, a *Cantharus d'orbigny-Muricidea blainvillei* association was characteristic of the animal colonies in the many cave slits.

The Gastropoda-Opisthobranchia are represented to an equal degree in the free littoral and in the caves, as far as number of species and individuals is concerned. Also with the Prosobranchia in the free littoral, phytophagous forms dominate, for shrub-like algae in sandy soil (*e.g.*, near Sorrento) a *Bullaria striata-Runcina calaritana* association was characteristic, in shadowy tuft-like algae, *e.g.*, *Halimeda tuna*, a *Bosellia mimetica* association may be found. On the plant growth in the cave centers the *Discodoris cavernae* association was typical of genuine Porifera growth, for *Petrosia ficiformis-Peltodoris atromaculata* association. On the Hydroidea growth, however, a *Idulia coronata-Berghia coerulescens* association was characteristic.

The Bivalvia are found very sporadically in the subgrowth of the shrub-like algae where they have no favourable conditions for filtering and are superseded by a *Musculus costulatus-Chama gryphoides* association which is poor in number. With the recession of the taller algal competition on shadowy places which are largely exposed to the breakers, the number of species and individuals (sessile or boring Bivalvia) greatly increase. Among the cushion-and crust-like algae a *Lithophaga lithophaga-Ostrea edulis* association develops at favourably exposed places which gradually changes in the cave centers into a *Ostrea edulis-Beguinea calyculata-Arca lactea* association, where the boring *Lithophaga lithophaga* recedes somewhat, especially where the Porifera growth is strong.

In Tables II and III and Fig. 18 the average individual, and species-numbers (taken from the collections of the Tyrrhenia-Expedition 1952, after Starmühlner (1955 *a* and *b*) of the significant mollusc groups of the various specimens (algae or animal growth) are compared. Figures are individuals per square meter and in % of individuals of species found.

TABLE

Correlation of the larger mollusc-groups: Halopitys incurvus, Digenea simplex, Cystoseira *sp.*, Corallina Peyssonelia squamaria, Pseudolithophyllum *sp. growth in the free littoral and on the cave*

Sun irradiation:		Sunny free littoral Surface-light: 100–10%				
Exposition:		Feeble			Strong	Feeble
Types of growth:		Shrub-like algae			Tuft-like algae	Shrub-like algae
Growth		*Halopitys incurvus*	*Digenea simplex*	*Cystoseira* Sp.	*Corallina mediterranea*	*Dictyopteris membranacea*
Polyplacophora	Sp.	0	4	2	4	2
	Sp.%	0	15	5	10	5
	I.	0	21	2	35	14
	I.%	0	2·5	0·5	5	3
Prosobranchia	Sp.	33	19	28	28	23
	Sp.%	89	70	76	75	64
	I.	420	860	380	497	300
	I.%	33	95	92·5	74	70
Opisthobranchia	Sp.	1	1	0	2	4
	Sp.%	3	4	0	5	11
	I.	25	1	0	39	15
	I.%	6	0·1	0	6	3
Bivalvia	Sp.	3	3	7	6	7
	Sp.%	8	11	19	15	20
	I.	5	20	28	104	105
	I.%	1	2·4	7	15	26
Mollusca total	Sp.	37	27	37	40	36
	Sp.%	100	100	100	100	100
	I.	450	902	410	675	434
	I.%	100	100	100	100	100

Explanation:

Sp.: number of species found; Sp. % : % of all mollusc species found ; I.: number of individuals/

II

mediterranea, Dictyopteris membranacea, Pterocladia capillacea, Halimeda tuna, Cladophora prolifera, *entrances with the animal growth* Balanus-*Porifera,* Astroides calycularis *in the cave centres*

Shadowy, free littoral Reflected light: 100–1% Strong								→ →				Cave entrance Diffusion light: 1–0·1%								Cave center 0·01–0% Strong			
Pterocladia capillacea				Tuft-like algae *Halimeda tuna*				*Cladophora prolifera*				Cushion-like algae *Peyssonelia squamaria*				Crust-like algae *Pseudolithophyllum* sp.				Animal growth *Balanus*—Porifera			
Sp.	Sp.%	I.	I.%	Sp.	Sp.%	I.	I.%	Sp.	Sp.%	I.	I.%	Sp.	Sp.%	I.	I.%	Sp.	Sp.%	I.	I.%	Sp.	Sp.%	I.	I.%
4				2				2				2				3				0			
	50				7				7				10				12				0		
		160				56				37				60				37				0	
			50				24				4				22				5				0
1				18				20				10				10				10			
	12·5				64				74				50				40				50		
		32				117				805				80				153				100	
			10				50				82				30				18				11
0				0				0				1				3				2			
	0				0				0				5				12				10		
		0				0				0				4				65				38	
			0				0				0				1				8				4
3				8				5				7				3				8			
	37·5				23				13				35				16				40		
		128				61				138				124				570				750	
			40				26				14				47				63				80
8				28				27				20				25				20			
	100				100				100				100				100				100		
		320				234				980				268				825				888	
			100				100				100				100				100				100

square meter ; I. % ; % of all mollusc-individuals found,

TABLE III

Correlation of the larger mollusc-groups between the algal communities from the sunny free littoral, the shadowy free littoral, and the cave entrances with the animal communities in the cave centers

		Sunny, free littoral			Shadowy, free littoral		Cave entrance →		Cave center
		All sunny							
		shrub-like algae	tuft-like algae	All sunny shrub- and tuft-like algae	Shadowy shrub-like algae	All shadowy tuft-like algae	All shadowy cushion- and crust-like algae	All shadowy shrub-tuft- cushion- and crus.-like algae	Animal growth *Balanus* Porifera *Astroides calycularis*
Polyplacophora	Sp.	2–4	4	2–4	2	2–4	2–3	2–4	0
	Sp.%	6	10	18	5	14	10	10	0
	I.	8	35	21·5	14	84	48	49	0
	I.%	1·5	5	3	3	16	3	9·8	0
Prosobranchia	Sp.	13–33	28	13–33	23	1–20	10	1–23	5–16
	Sp.%	80	70	75	64	62	45	57	46·5
	I.	533	497	515	300	325	116	247	100
	I.%	94	74	83	70	63	22	43·4	11
Opisthobranchia	Sp.	1–2	2	1–2	4	0	1– 3	1– 4	3– 4
	Sp.%	2	5	3·5	11	0	3	6	16
	I.	9	38	24	15	0	34	17	38
	I.%	1·5	6	4	3	0	6	3·4	4
Bivalvia	Sp.	3–7	6	5	7	3·5	7–9	3–9	5–12
	Sp.%	12	15	13·5	20	24	36	27	37·5
	I.	18	101	59·5	105	103	347	187	750
	I.%	3	15	10	24	21	63	37·4	85
Mollusca total	Sp.	27–37	40	27–40	36	8–28	22–25	8–36	10–32
	Sp.%	100	100	100	100	100	100	100	100
	I.	568	672	620	434	518	545	500	888
	I.%	100	100	100	100	100	100	100	100
				620 ind./sq. m.				500 ind./sq. m.	888 ind./sq m.
				27–40 species				8–36 species	10–32 species

Explanation : ber of species found; Sp. %: % of all mollusc-species found;

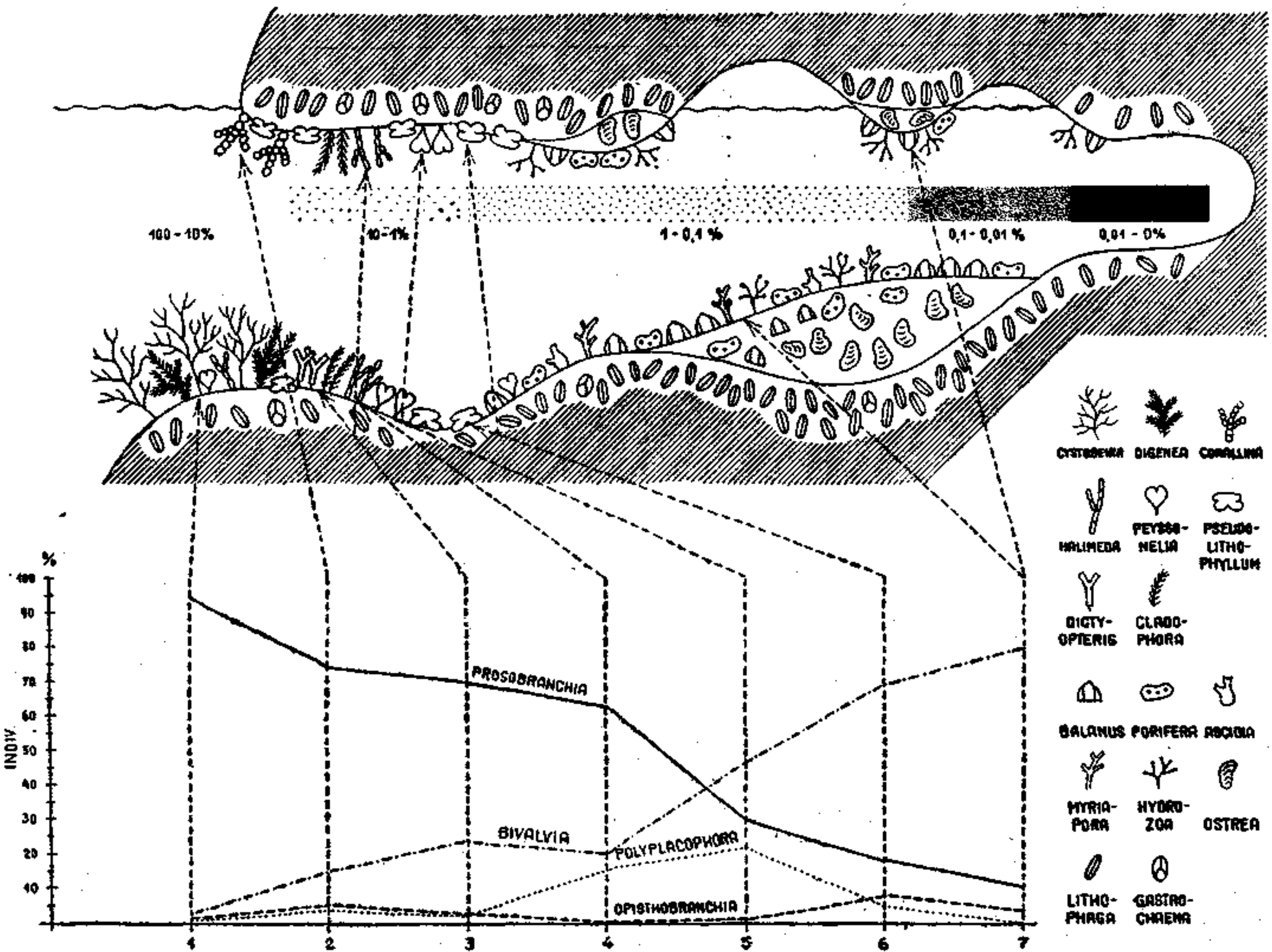


FIG. 18. Schematic profile of a submarine cave with decrease of light (100–10%, 10–1%, 1–0·1%, 0·1—0·01%, 0·01–0% of surface light) and change from algal growth in the free, sunny littoral, the shadowy littoral and the cave entrance to the pure animal growth in the cave center in correlation with the abundance of the mollusc-groups: (1) Shrub-like algae (sun irradiation); (2) Bush-like algae (sun irradiation); (3) Shadowy shrub-like algae; (4) Shadowy bush-like algae; (5) shadowy cushion-like algae; (6) Shadowy crust-like algae; (7) Animal growth in dark central parts of the cave

Both tables and Fig. 18 show for the Polyplacophora a distinct peak in the regions of the shadowy littoral. The large areas of the cushion and crust-like algae (above all *Peyssonelia squamaria, Pseudolithophyllum* sp. but also the *Halimeda tuna* among the tuft-like algae), offer the best opportunity for the Polyplacophora with their broad foot to stick on, and at the same time is the best feeding place for them. In the cave centers the phytophagous Polyplacophora are completely lacking.

The Prosobranchia have their maximum abundance (approx. 550 ind./square meter) in the region of the shrub and tuft-like algae with their dense subgrowth, on the sunny littoral, where the phytophagous species have their optimal living conditions. The absolute peak was taken from a shrub-like algae growth of *Digenea simplex*, growing in quiet waters, where 2,300 individuals per square meter were counted. More than 900 individuals were accounted for by *Bittium reticulatum* and more than 830 individuals by *Barleeia rubra*. Both species are characteristic growth-feeders and live especially on Diatomaea.

But also in regions of the sunny eulittoral where tuft-like algae are largely exposed to the breakers, Prosobranchia, feeding upon the subgrowth, may occur in masses (in summer—juvenile forms). Thus for *Laurencia papillosa* 1,700 individuals per square meter were counted; 1,200 *Cingula glabrata* var. *turrita* and more than 450 *Barleeia rubra*, both tiny Rissoidae. In a *Corallina rubra* growth 1,120 individuals per square meter were found, among them almost 500 *Barleeia rubra* and almost 300 *Bittium reticulatum*.

In the shadowy littoral the density in the shrub- and tuft-like algae still reach high levels (average of 300 ind./sq.m.) even though they remain far behind the figures of the specimens in the sunny littoral. This is explained by the reduced food supply, since the subgrowth with Diatomaea recedes to a great degree at shadowy places. However, sometimes there are mass-occurrences to be observed, too, above all if juvenile forms prevail; thus in shrub-like algae *Dictyopteris membranacea*, 625 Prosobranchia/sq. m., among them 224 *Bittium reticulatum*, were found; in tuft-like algae *Cladophora prolifera*, 1,800 Prosobranchia/sq. m. with 656 *Gibbula clandestina*, 432 *Alvania lineata*, 208 *Alvania montagui*, etc.

In the rather shadowy cushion-like algae (*Peyssonelia squamaria*) and crust-like algae (*Pseudolithophyllum* sp.) at cave entrances or overhangings, the individual number of the Prosobranchia drops from 80 to 150 ind./sq. m. The highest number was reached in a *Pseudolithophyllum*-growth of the inner part of the cave entrance, where 320 individuals per square meter were determined; among them was *Fossarus ambiguus*, a spongefeeder, found in abundance since the Porifera had a thick subgrowth, particularly of *Petrosia ficiformis*.

Among the specimens taken from the dark walls of the cave centers, containing Porifera—*Balanus perforatus*—and *Astroides calycularis* growth, the density is the same as at the cave entrances, namely, about 100 ind./sq. m. The highest density among Porifera was 350 Prosobranchia/sq. m., of them 96 *Nassa incrassata*, 96 *Pollia leucozona* and 80 *Cantharus d'orbigny*, which live either as saprophagous or as predatory animals. There are no phytophagous forms at all.

With the Bivalvia, the density increases in accordance with the recession of the competing algae, beginning from the free littoral towards the cave entrances and the cave centres. In the higher shrub-tuft- and cushion-like algae there are sessile Bivalvia only in the subgrowth of the stems between chalk-algae and sponge-crusts. Their living conditions are rather unfavourable due to the strong subgrowth of entangled algae, and they have not many possibilities to attach themselves. Only on the genuine crust-like algae at rather shadowy places (overhangings, cave entrances) they increase in density provided the places are very much exposed to the breakers; they reach their maximum numbers in the plant-free cave centers where the breakers are strong. The average density at cave entrances is approx. 570 ind./sq. m. The absolute maximum taken on the Tyrrhenia expedition in the caves near Sorrento was 3,570 mussels/sq. m. in a *Balanus perforatus-Petrosia ficiformis* growth, which was partly intergrown with *Astroides calycularis*. Among them were 1,490 *Ostrea* *edulis*, 850 *Lithophaga lithophaga*, 415 *Arca lactea*, and *Beguinea calyculata*, and 260 *Chama gryphoides*. When comparing the density in the algal growth of the free, sunny littoral, it appears that it increases significantly in number at places where the tuft-like algae (*Corallina mediterranea*) are largely exposed to the waves. In the shrub-like algae of the shadowy regions (*Dictyopteris membranacea*) the density reaches 105/sq. m. and is likewise much higher than in the sunny shrub-like algae (*Halopitys incurvus*, *Digenea simplex*, *Cystoseira* sp., etc.) where there are approx. 16 mussels/sq. m. The receding subgrowth of the algae growing in the shade is the decisive factor for better living conditions of the suspension-feeding molluscs.

When summarizing the results to date on the distribution of the molluscs in submarine hollow spaces, it appears that it largely depends—directly or indirectly—on two exogenous factors:

(1) The decreasing light.

(2) The exposure to the breakers.

(1) *Decreasing light.*—The decrease in the surface light in submarine caves allows a distinctionl into various light zones, counted from the cave entrance (Fig. 18):

(1) Surface light zone of the sunny, free littoral: 100–10% of the surface light

(2) Reflected light zone of the shadowy littoral: 10–1% of the surface light

(3) Diffused-light of the inner parts of the cave entrances: 1–0·1% of the surface light

(4) Reflected diffusion-light of the central parts of the caves: 0·1–0·01% of the surface light

(5) Low-light, and lightless dark zone of the rear regions of the caves: 0·01–0% of the surface light

The distribution of these zones is dependent upon the location and depth of the cave, as well as from the angle at which the light is coming in (Riedl, 1966). The effect of the decreasing light stands in direct relation to the distribution of the algae as has been confirmed by Ernst (1959) at the Tyrrhenia-Expedition. Thus the shrub-like algae (*Halopitys incurvus*, *Digenea simplex*) and the tuft-like algae (*Cladophora prolifera*, *Pterocladia capillacea* and *Halimeda tuna*) are determined in the diffused light zone (at Northern walls, overhangings, front parts of the cave entrances), whereas they are followed by *Peyssonelia squamaria* and *Pseudoliphophyllum* sp. growths in the regions of the diffused light zone. In the reflected diffused light zone, and in the low-light and dark zone (*i.e.* at 0·1 % of the surface light) there are only such groups as Porifera, Balanidae, Ascidia, Hydrozoa, and Anthozoa, like *Astroides calycularis* and, likewise the sessile Bivalvia.

Linked with the occurrence and the recession of the algae are the phytophagous Polyplacophora and Gastropoda. When the algae disappear, and with them the phytophagous species, in the reflected-diffusion as well as low light zone, the saprophagous and predatory Gastropoda prevail. The latter ones may be found in the algae of the free littoral, too, but there they are surpassed by far in number by the masses of phytophagous species.

On the other hand, the occurrence of the sessile Bivalvia is a symptom. This group shows in the surface light zone of the free littoral their minimum occurrence—due to the competition the fast-growing algae present there which offers very unfavourable living conditions for the filtrating forms. Only at places largely and favourably exposed to the breakers and waves, such as in *Corallina mediterranea* growths, the density of the Bivalvia increases. In meagre subgrowth of the algae of the shadowy littoral, where the lack of light thwarts a better development of the algae subgrowth, the Bivalvia are represented in greater abundance. In the diffused, reflected diffusion, and low light zone (*i.e.* at 1% of the entire surface light), together with the gradual receding of the competing algae, the density increases to reach 4 to 6 times the number of the shadowy, free littoral.

The Polyplacophora are dependent for their existence upon the low-growing, flat or crust-like algae (*Peyssonelia, Halimeda, Pseudolithophyllum* and other scaly chalk-algae) which offer them food and the possibility to attach in a zone of breaker and waves. Therefore, their maximum abundance is in the regions of the reflected and diffused light zones between 10–0·1% of the surface light.

(2) *Exposure* :—Besides the decreasing light the inclination of the bottom in submarine caves towards the water flow is important for the distribution of the species. The exposure to fluctuation (according to Riedl, 1966) is dependent on the littoral exposure, the depth of the water, the contents of substrates, and the type of substrate. No measurements have yet been taken from the investigated area of the Tyrrhenia-Expedition near Sorrento and the collection area of the Northern Adriatic regions. According to Riedl (1966) they have been undertaken in rocky regions only by water-construction engineers. The distribution of organisms dependent upon this fluctuation throws a light, however, on the importance of exposure. Among them are sessile filtrators, which are dependent on continuous fresh supply of water. Among the molluscs of submarine caves there are certain Gastropoda-Prosobranchia, the *Vermetus* species (slime-filtrators), just as all sessile Bivalvia that have been found. In the shrub-like algae of the sunny, free littoral which grow best at quiet places with slight waves, sessile Bivalvia are most sporadic in their occurrence. Not only do the algae compete for space, the water fluctuation is too slight, and the food supply low. Only at the basal thallus, covered by crust-like algae, Bryozoa, Porifera, etc., small sessile Bivalvia such as the *Arca lactea, Beguinea calyculata, Musculus costulatus* still find suitable living conditions. Much better living conditions are offered to the Bivalvia in the tuft-like algae, like *Corallina mediterranea*, which develop, as already mentioned, in the sunny littoral, at locations largely exposed to the breakers and waves. In the shadowy region of the free littoral the Bivalvia show a distinct maximum abundance on crust-like chalk algae which occur not only in the diffused light zone, but also at rather exposed places (overhanging rocks, cave entrances, etc.). Likewise, the mass occurrence of the sessile Bivalvia in the central parts of tide-caves is dependent not only on the lack of light and therefore, the lack of the competing algae, but is also related to the strong fluctuation of the water which offers most favourable living conditions for filtrators. The water transport of the cave mussels taking an average size of 15–50 mm. (like *Beguinea calyculata, Arca lactea, Lithophaga lithophaga, Ostrea edulis, Arca barbata, Chama gryphoides*) is, according to Riedl (1966), 0·75 to 1·1 litre/per hour/per individual. This would mean that in the investigated caves near Sorrento, at an average density of 750 mussels per sq.m. the water transport would be between 550 and 825 litres/hour, at locations with mass occurrence, as in cave 0/39 (Sorrento), where the density was 3,570 mussels/sq.m., even 2,500 to 4,000 litre/hour.

Towards the blind gulleys of bag-like caves, where the fluctuation lessens, the abundance of the sessile bivalves is greatly reduced. This decrease takes place in submarine caves more quickly the deeper the cave is situated and with lesser influence of the breakers and waves. In 20–30 m. depth only the cave entrances are inhabitated, the center being without animals.

Also, the occurrence of certain Opistobranchia is indirectly dependent upon the light and exposure conditions. Many species live exclusively on one type of food, thus most of the Aeolidiacea feed on Hydrozoa, many Doridacea feed on Porifera; therefore, they are bound to the existence of such food. Hydrozoa belong to the characteristic sub- and intermediary growth on exposed cave walls, therefore will be found some of the Aeolidacea, like the *Idulia coronata, Berghia coerulescens,* etc. Porifera—especially the compact forms—prefer locations with less exposure, at walls away from the strong breakers and waves, and at the cave bottom. On them Doridacea, like *Peltodoris atromaculata* (on *Petrosia ficiformis*) or *Discodoris cavernae* are found.

Finally, in the layers of the animal growths of the caves a definite distribution of the molluscs may be distinguished. Riedl (1966) differentiates 3 layers (Fig. 19):

(1) *Endolithion*

(*a*) *Primary layer.*—10–15 cm. deep is the layer of chalk-boring sessile animals separate from the group of the active filtrators. Besides, the sponge *Cliona*, the polychaete *Polydora*, and

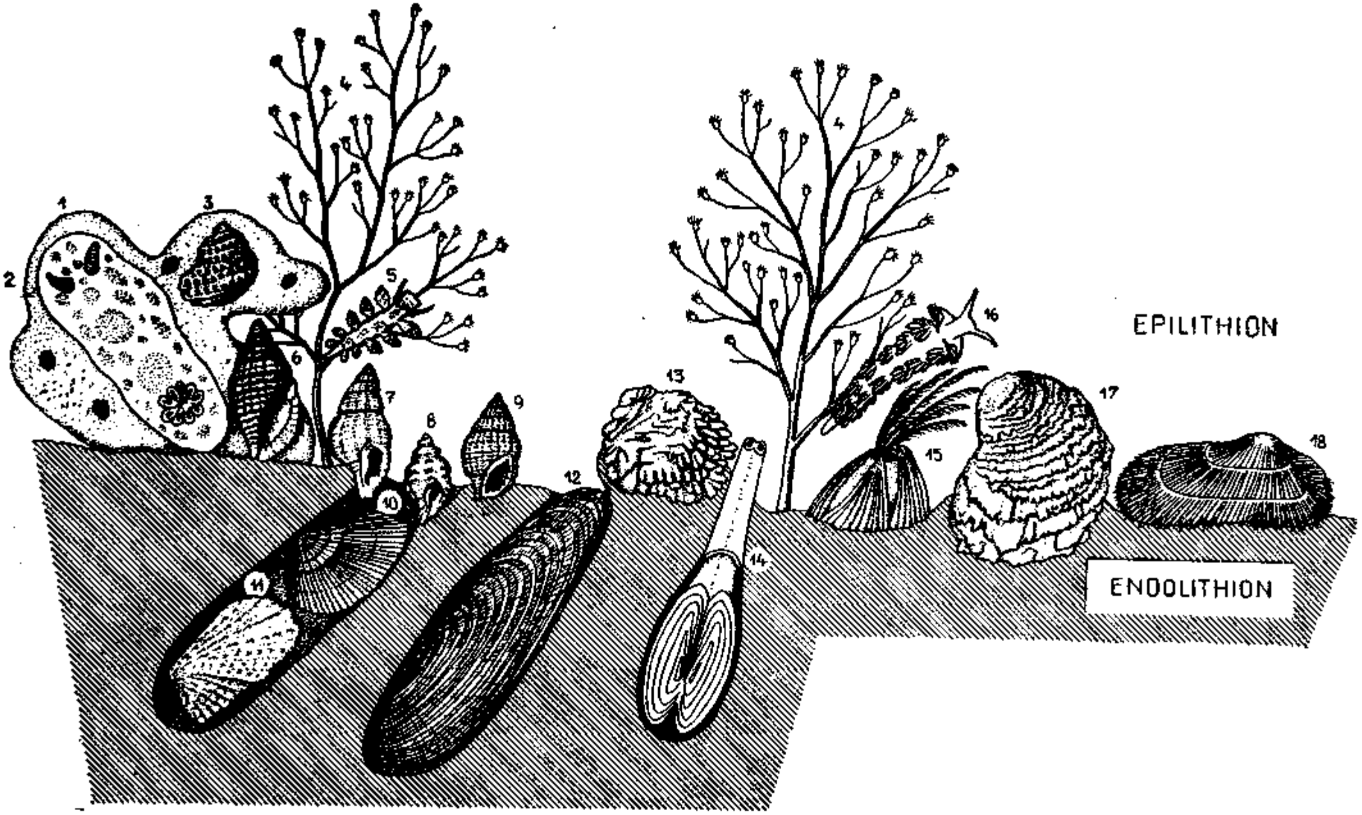


FIG. 19. Schematic section of a wall in cave center with the molluscs in the Endo-epilithion and super growth: (1) *Petrosia ficiformis* (sponge); (2) *Peltodoris atromaculata*; (3) *Fossarus costatus*; (4) *Eudendrium racemosum* (Hydrozoa); (5) *Idulia coronata*; (6) *Cantharus d'orbigny*; (7) *Tritonalia edwardsi*; (8) *Muricidea blainvillei*; (9) *Nassa incrassata*; (10) *Arca lactea*; (11) *Beguinea calyculata*; (12) *Lithophaga lithophaga*; (13) *Chama gryphoides*; (14) *Gastrochaena dubia*; (15) *Balanus perforatus*; (16) *Berghia coerulescens*; (17) *Ostrea edulis*; (18) *Arca barbata*

particularly the Bivalvia, such as *Lithophaga lithophaga*, *Gastrochaena dubia* and *Pholas dactylus* should be mentioned. These boring organisms may hollow out up to 3/4 of the rock without losing its compactness.

(*b*) *Secondary layer*.—here are the settlers of old empty boring ducts of the above-mentioned boring animals. To this group belong among the sessile animals, the Bryozoa, Porifera, Serpulidae, etc.; also the mussels *Arca lactea*, *Beguinea calyculata*. Furthermore, there occur also small errant forms, among the Gastropoda, the small muricid species, then the nassid and buccinid species.

(2) *Epilithion*

(*a*) *Crust-growth*.—these reach a depth of 20-30 cm. and are formed of active and passive filtrators. The basic elements of the mass are Porifera and Ascidia, where numerous errantia (Polychaeta, Turbellaria, Echinodermata, Crustacea, etc.), occur. On Porifera, gastropods such as *Fossarus*, Muricidae, Nassidae, Buccinidae, Fusidae as well as Doridacea occur. On Ascidia, *Pleurobranchus* occurs.

(*b*) *Chalk-shell-bearing animals*.—the basic element is formed in the first place by Bivalvia with *Ostrea edulis* and *Chama gryphoides*: furthermore, sessile Polychaeta (*Serpula*, *Protula*), Bryozoa, and especially *Balanus perforatus* must be mentioned. Among the errant forms, between the mussels, there are also species of Muricidae, Nassidae, Buccinidae, and Fusidae.

(3) *Super-growth*

Hydrozoa and Anthozoa sometimes form whole "underwater meadows" over the epilithion. On these "meadows," there are food specialists to be found such as some of the Aeolidiacea, *Idulia coronata*, *Berghia coerulescens*. Sometimes also the sucking Sacoglossa may be found.

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Prof. Dr. Rupert Riedl (Wien) for general submarine cave information, Mr. Camillo Nossian for making the figures, Mrs. M. Wimmer-Mizzaro, Dr. H. Splechtna, Mr. Moosleitner, Dr. K. Rützler, Mr. Krienke and Prof. Dr. R. Riedl for the photographs. I thank also Mrs. Th. Klooss for the translation from German into English.

LITERATURE CITED

ALBOREL, J. 1956. Premidres notes de plongée sur les peuplements marins en eaux grecques. *C.R. Acad. Sci., Paris*, **242**: 565–567.

ARNDT, W. 1936. Fortschritte der Kenntnis der tierischen Bewohnerschaft von Meereshöhlen. *Mitt. Hohlen-u. Kartsforsch. Berlin* (*Jahrgang*, 1936): 137–141.

CORROY, G., C. GOUVERNET, J. CHOUTEAU, A. SIVIRINE, R. GILET AND J. PICARD 1958. Les Résurgences sous-marines de la région de Cassis. *Bull. Inst. Océanogr. Monaco*, **1131**: 1–36.

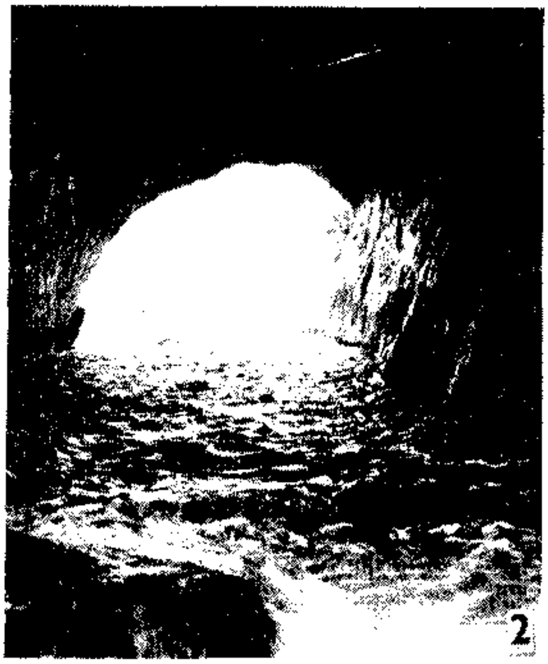
DRACH, P. 1951. Les peuplements de fond rocheu en zone littoral profonde. *Ann. Biol.*, **27**: 271–279.

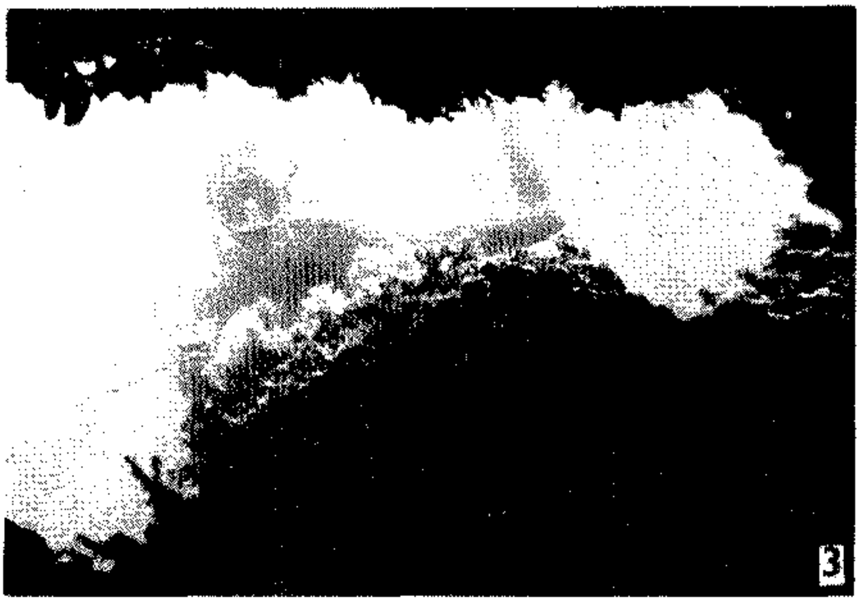
——— 1958. Essai methodique sur les Recherches Biologiques en Scaphandre autonome. Journees des 24 et 25 fevrier 1958: 29–47.

ERNST, J. 1959. Studien über die Seichtwasser-Vegetation der Sorrentiner Kuste. Ergebnisse der Osterreichischen Tyrrhenia-Expedition 1952. Teil XIII. *Pubbl. Sta. Zool. Napoli*, **30** (Suppl.): 470–518.

FUNK, G. 1927. Die Algenvegetation des Golfs von Neapel nach neueren ökologischen Untersuchungen. *Ibid.*, **7** (Suppl.): 1–503.

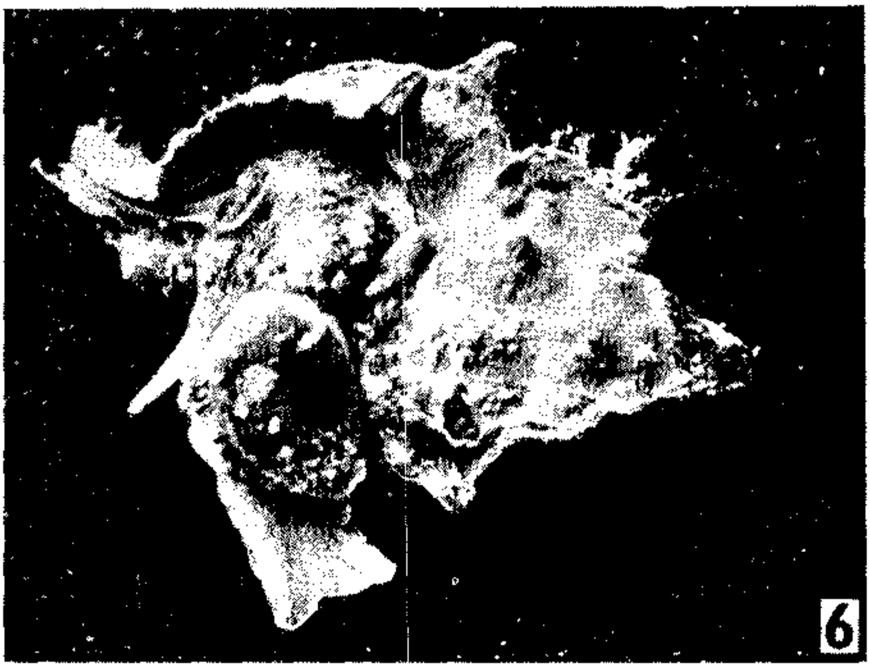
GISLÉN, T. 1930. Epibiosis of the Gullmar Fjord I and II. A study in Marine Sociology. Kristinebergs Zoo. Stat. 1877–1927. *Skrif. Utg. av K. svens. Vetensk. Akad. Uppsala* (3) : 1–123 and (4): 1–380.

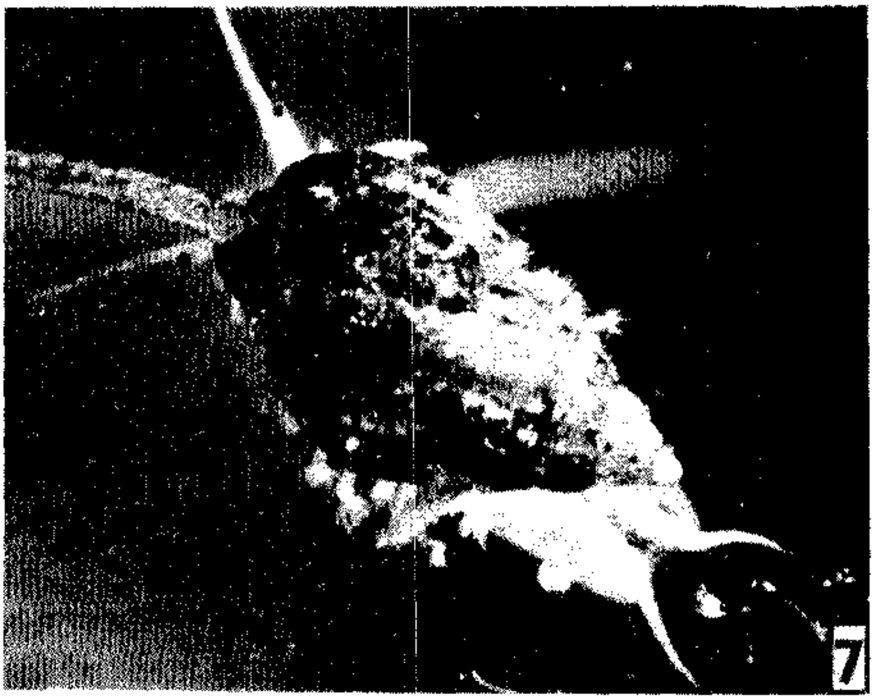




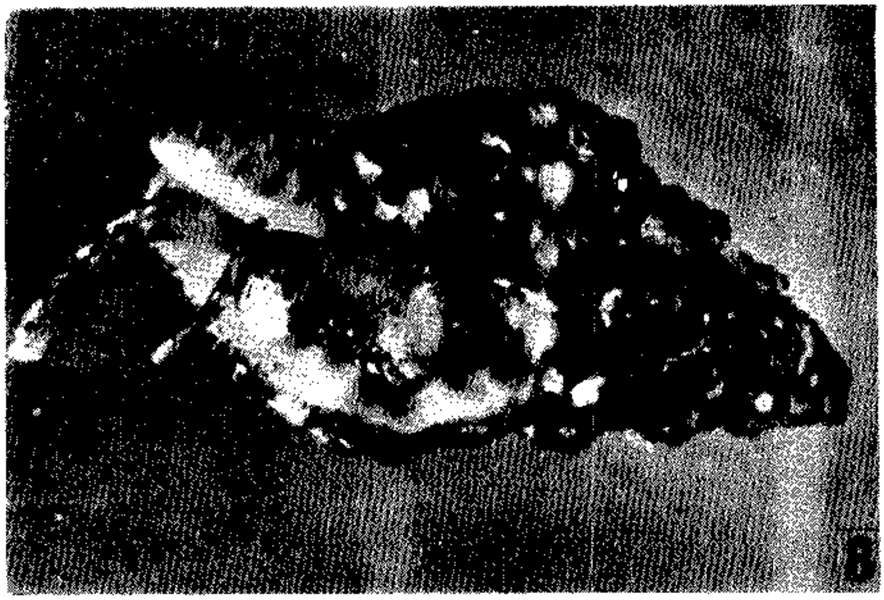
Figs. 1–3. (1) Two divers taking one specimen with hammer and chisel (Photo, Riedl); (2) Entrance of a grotto (Photo, Kaleske); (3) A diver before the entrance of a submarine cave (Photo, Riedl).

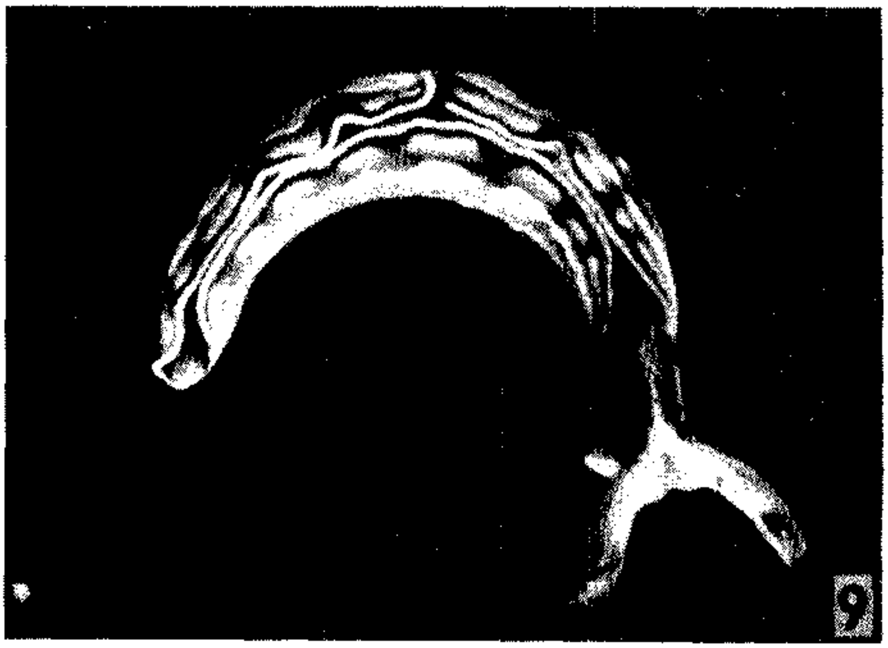
FIGS. 4–5. (4) *Triphora perversa* (L.) (Photo, Splechtna); (5) *Vermetus arenarius* (L.), on the shell an epifauna of sponges, Bryozoa, Serpulidae, Algae, etc. (Photo, Wimmer-Mizzaro).



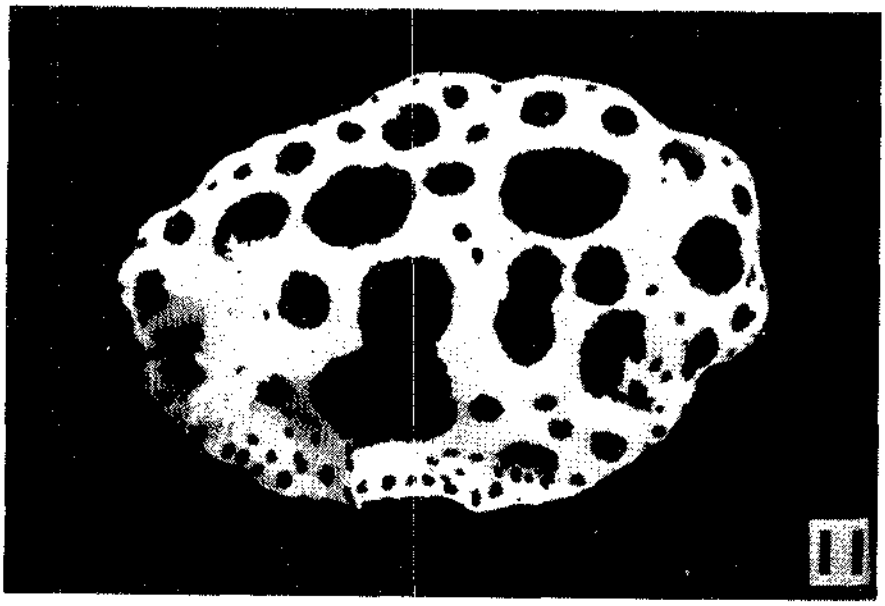


Figs. 6-7. (6) *Murex trunculus* L. (Photo, Wimmer-Mizzaro); (7) *Nassa incrassata* (Müller) (Photo, Spiechtna).

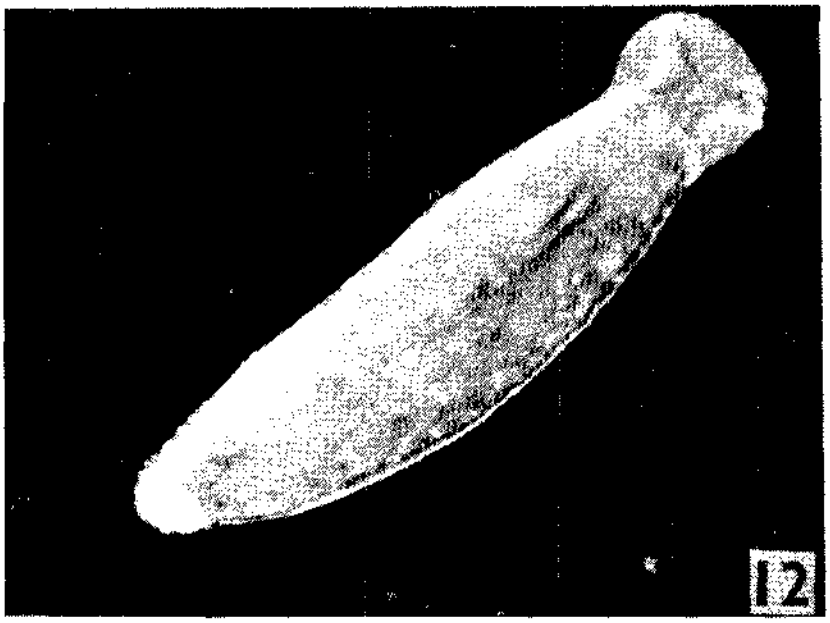




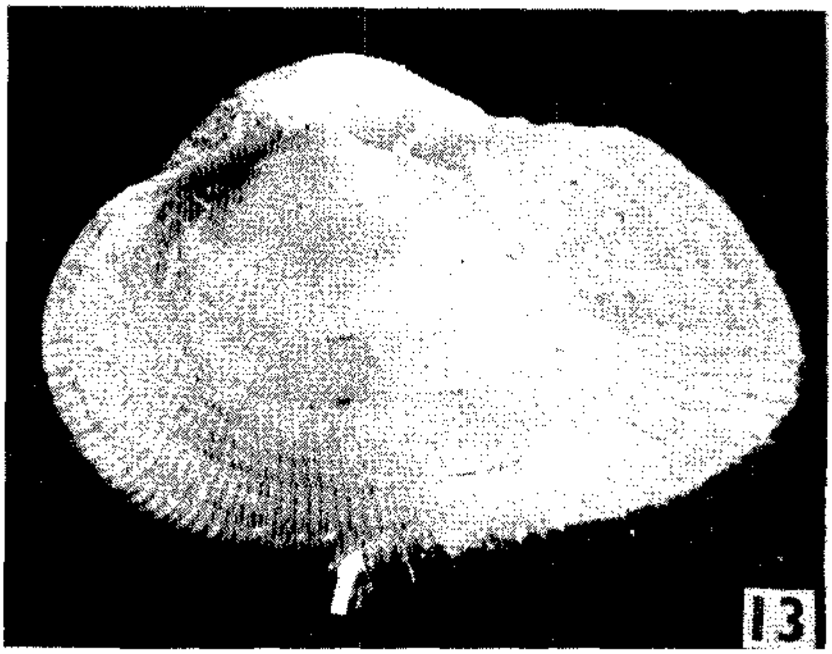
FIGS. 8-9. (8) *Cantharus d'orbignyi* (Payr.) (Photo. Splechtna); (9) *Thuridilla hopei* (Verany) (Photo. Wimmer-Mizzaro).



FIGS. 10–11. (10) A group of *Peltodoris atromaculata* Bergh on the sponge *Petrosia ficiformis* Poiret in a cave center (Photo, Moosleitner). (11) *Peltodoris atromaculata* Bergh (Photo, Wimmer-Mizzaro).

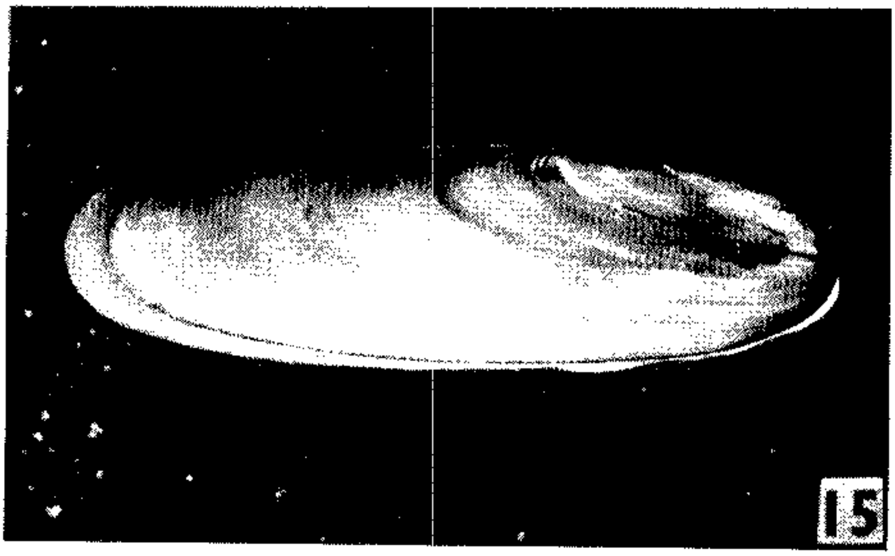


12

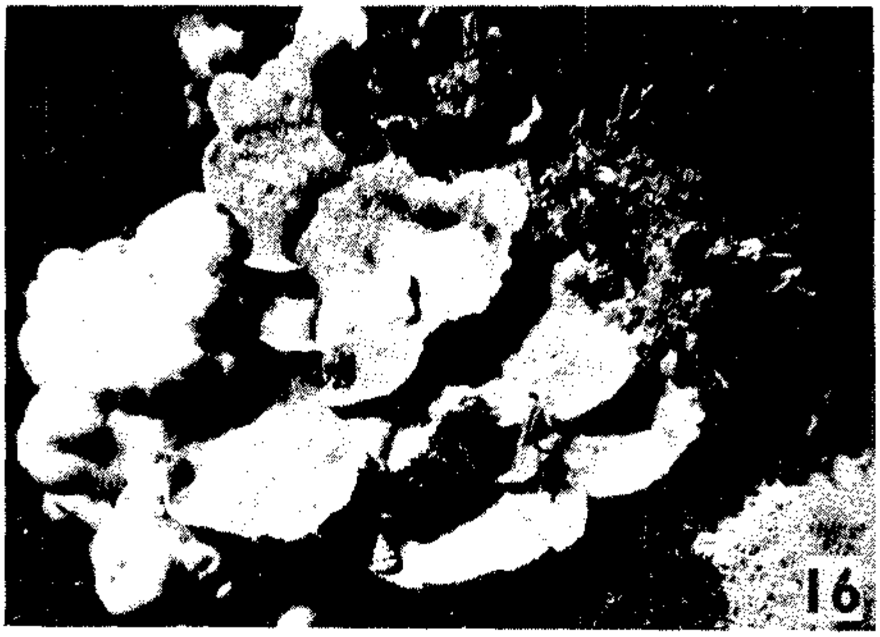


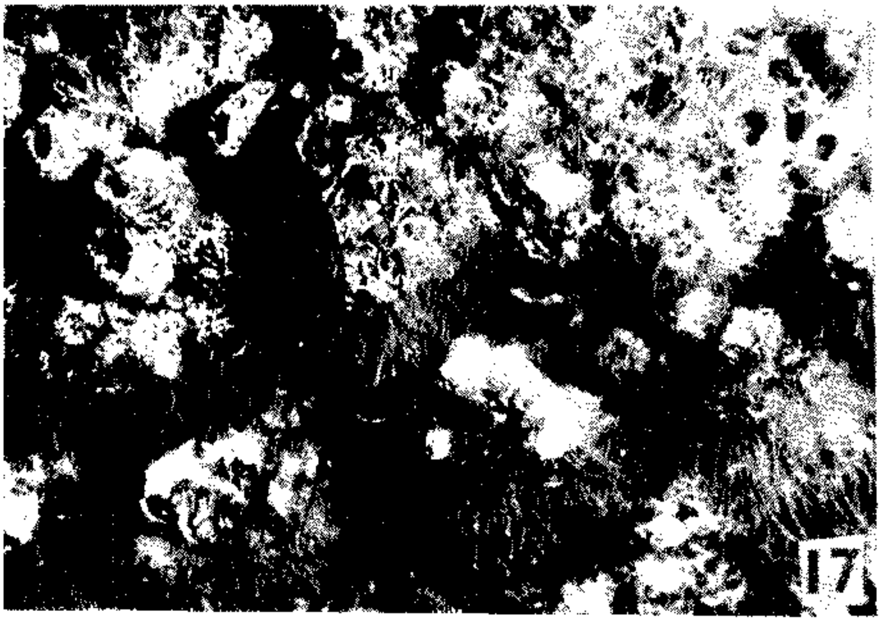
13

FIGS. 12–13. (12) *Bosellia mimetica*, Trinchese (Photo, Wimmer, Zoologisches Institut); (13) *Arca lactea* L. (Photo, Splechtna).



FIGS. 14–15. (14) *Lithophaga lithophaga* (L.), a boring mussel in submarine caves (Photo, Splechtna); (15) *Lithophaga lithophaga* (L.) (Photo, Splechtna).





Figs. 16-17. (16) Crust-like algae, *Pseudolithophyllum* sp. with *Agelas oroides* (Schmidt) and *Clathrella* sp. (Photo. Kürzler); (17) *Balanus perforatus* Brug. with Hydrozoa (Photo. Riedl).

Haefelfinger, H. 1961. Beitrage zur Kenntnis von *Peltodoris atromaculata* Bergh 1880 (Mollusca, Opisthobranchia). *Rev. Suisse Zool.*, **69**: 331–343.

Hass, H. 1949. Beitrag zur Kenntnis der Reteporiden. *Zoologica*, **37**: 1–138.

Kirsteuer, E. 1963. Beitrag zur Kenntnis adriatischer Nemertinen (Gen. *Tetrastemma, Oerstedia, Oerstediella*). *Zool. Jahrb. Anat.*, **80**: 555–616.

Kitching, J. T. Macan and H. Gilson 1934. Studies in sublittoral ecology. I. A submarine gully in Wembury Bay, South Devon. *J. Mar. Biol. Ass. U.K.*, **19**: 677–705.

——— 1960. Contributions d l'étude directe des peuplements bentiques sciaphiles sur substract rocheux en Mediterrané. *Rec. Trav. Stat. Mar. Endoume*, **33**: 117–173.

—— and J. Vacelet 1958. Etude des peuplements d'un grotte sous-marine du Golfe de Marseille. *Bull. Inst., Océanogr. Monaco*, **1120**: 1–20.

Pax, F. 1937. *Parazoanthus axinellae* als Höhlenbewohner. *Nat. Ist. Ital. German. Biol. mar. Rovigno d'Istria* (2 vol.), **2**: 3–16.

Pérès, J. and J. Picard 1949. Notes sommaires sur le peuplement des grottes sous-marines de la region de Marseille, *C. R. Som. Séances Soc. Biogéogr.*, **26**: 42–45.

Portmann, A. 1958. *Bosellia mimetica* Trinchese, Opisthobranche retrovué en mediterrané. *Vie et Milieu.* 9 (1): 74–80.

Riedl, R. 1953. Quantitativ ökologische Methoden mariner Turbellarienforschung. *Osterr. Zool. Zeitschr.*, **4**: 108–145.

——— 1966. Biologie der Meereshöhlen. Topographie, Faunistik und Okologie eines unterseeischen Lebensraumes. *Eine Monographie. P. Paray, Hamburg*, 636 pp.

Rutzler, K. 1965 *a*. Substratsstabilität im marinen Benthos als ökologischer Faktor dargestellt am Beispiel adriatischer Poriferen. *Int. Revue. ges. Hydrobiol.*, **50**: 281–292.

——— 1965 *b*. Systematik und ökologie der Poriferen aus Litoralschattengebieten der Nordadria. *Zeitschr. Morphol. Okol. Tiere*, **55**: 1–82.

Sarà, M. 1961. La fauna di Poriferi delle grotte delle isole Tremiti. Studio ecologico e sistematicol. *Arch. Zool Ital.*, **46**: 1–59.

Starmühlner, F. 1955 *a*. Zur Mollukenfauna des Felslitorals und submariner Höhlen am Capo di Sorrento (I). Ergebnisse der Österreichischen Tyrrhenia-Expedition 1952, Teil IV. *Österr. Zool. Zeitschr.*, **6**: 147–249.

——— 1955 *b*. Zur Molluskenfauna des Felslitorals und submariner Höhlen, am Capo di Sorrento (II) Ergebnisse der Österreichischen Tyrrhenia-Expedition 1952, Teil. IV. *Ibid.*, **6**: 631–713.

Van Gaver, J. and G. Simon-David 1934. Recherches sur le peuplement du canal souterrain du Rove. *Bull. Inst. Océanogr. Monaco*, **641**: 1–11.

Discussion

Dr. A. A. Karande: Is it possible to correlate the photoreceptive organs of the animals with the molluscan distribution or is it a chance distribution?

Dr. Ferdinand Starmühlner: The distribution depends on the type of feeding of the animal.

A COMPARATIVE STUDY OF TWO AUSTRALIAN PARYPHANTID SNAILS, WITH NOTES ON THEIR TAXONOMIC RELATIONSHIPS

BRIAN J. SMITH

Curator of Invertebrates, National Museum of Victoria, Australia

ABSTRACT

The gross morphology of *Victaphanta atramentaria* (Shuttleworth, 1852) and *Victaphanta compacta* (Cox and Hedley, 1912) is compared. These are two species of carnivorous snails of the family Paryphantidae which occur in two small separate areas of Victoria, Australia. A more detailed comparison is made of their reproductive systems, their radulae and their shells. From this a detailed list is drawn up of the various structural differences between these very closely related species. These include the geographic ranges, the mean shell size and shape, the skin and mucus colour, the shape of the various radulae teeth, the number of teeth per row and the mean number of rows. Other differences include the relative sizes of the penis, and the relationship between the vas deferens and the penis. From these anatomical details an attempt is made to compare these two species with the rest of the Paryphantidae and to justify their separation off into a separate genus of their own from the genus *Paryphanta* (after Iredale). It is concluded that this separation seems justified on the evidence so far known but a closer investigation of the genus *Paryphanta* is required.

INTRODUCTION

VICTORIA has two species of large native snails of the family Paryphantidae whose taxonomic status is under a cloud. The first to be described was *Nanina atramentaria* (Shuttleworth, 1852) which was transferred to the genus *Paryphanta* by Albers (1861). The other species was described as *Paryphanta compacta* (Cox and Hedley, 1912). These species, however, show a number of differences from the other members of the genus, all of which occur in New Zealand. This was recognised by Iredale in 1933 and he proposed a new genus, *Victaphanta*, for the two Victorian species with *Victaphanta atramentaria* as the genotype. Unfortunately, although the genus description is valid it has been considered inadequate by a number of workers for practical purposes and has therefore been deliberately ignored. This paper is intended as reinforcement of Iredale's description of the genus and a comparative study of the two species at a level sufficient to point out the various differences between them.

Genus *Victaphanta* Iredale, 1933

Type species *Nanina atramentaria* Shuttleworth, 1852

Agnathous, carnivorous snail with genital opening on the right side of the head just below the right optic tentacle. Pharynx is strongly muscular, cylindrical, as long as the head-foot cavity with two, distally fused, retractor muscles. Radula spatulate, without rachidian; teeth aculeate, unicuspid with distinct oblong base plate bearing anterior and posterior protuberances. Reproductive system simple; hermaphrodite gland lobate embedded in the digestive gland; common duct glands obvious; spermatheca small in the region of the junction of the albumen gland and common duct; spermathecal duct free from the common duct, entering the uterus close to the junction with the common duct. Receptaculum seminalis complex. Uterus long and narrow opening into the small genital atrium; vas deferens free from common duct, attached to the outer wall of the uterus, running in a loop past the genital atrium and entering the penis towards its distal end; penis long with a terminal retractor.

Shell depressedly globose, thin, composed mainly of conchin with very little calcarious material. Umbilicus small to nearly closed. Glossy, inner whorls white to yellow to light brown, outer whorls dark brown to black; spire nearly flat, suture deeply impressed. Aperture oblique, ovate-lunate. Sculpture consists of fine concentric line on the upper surface, lower surface smooth.

There are only two species known belonging to this genus, *Victaphanta atramentaria* (Shuttleworth, 1852) and *Victaphanta compacta* (Cox and Hedley, 1912). These two species are compared below.

GEOGRAPHIC RANGES

These two species are confined to two small areas of temperate rain-forest in southern and central Victoria, Australia. The distribution is shown in Fig. 1. *V. atramentaria* is confined to the Dandenong Ranges and the east-central part of the Great Dividing Range. *V. compacta* is confined to the Otway Ranges in the south-west part of the State. They are only found in the wet litter in fern gullies of climax rain-forest. A very high moisture level in the environment seems essential for their survival.

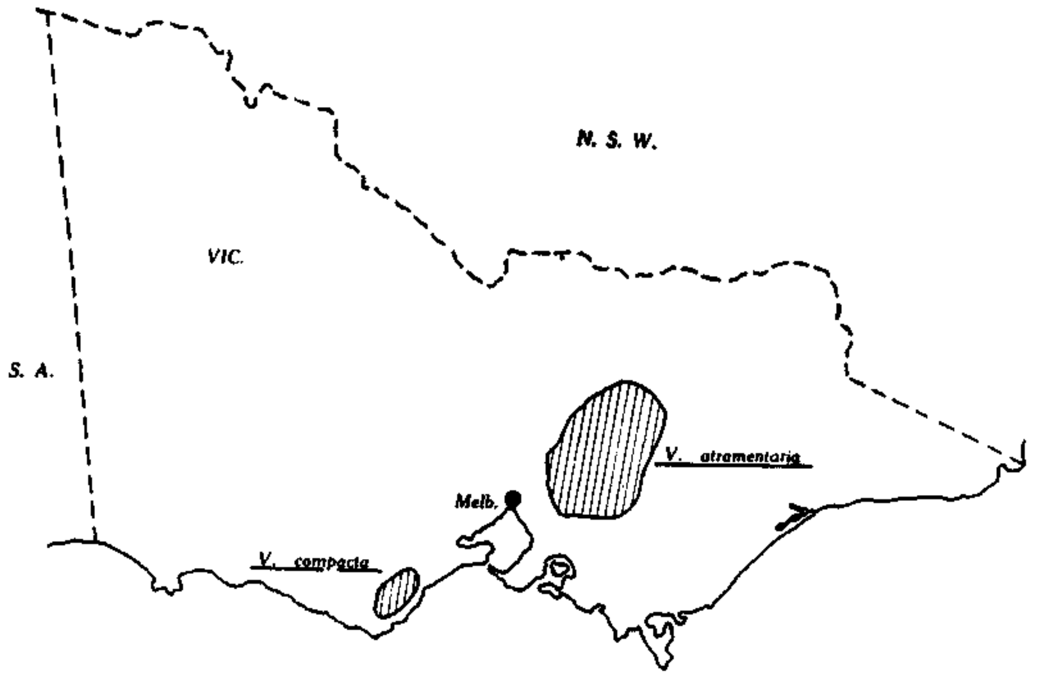


FIG. 1. A map of Victoria, Australia, showing the areas of distribution of *V. atramentaria* and *V. compacta*.

EXTERNAL FEATURES

The shell of both species is dark brown to black with *V. atramentaria* tending to be black and dull while *V. compacta* is relatively browner and glossier. The shell of *V. atramentaria* is larger and less globular in shape.

In order to compare the shape of the shell 44 shells of each species were measured. As a measure of "globularness" the maximum width (at the aperture) was divided by the depth from the top of the shell to the umbilicus in each case. The mean of this ratio was taken for each species group and the two means were compared by "*t* test," the distributions being normal.

Mean of width/columella depth for *V. atramentaria* = 2·37
Mean of width/columella depth for *V. compacta* = 1·93
No. of shells of each species measured = 44
= 14·36

Thus the greater globularness shown by *V. compacta* is significant.

Another constant difference between the shells of the two species is the extent of the closure of the umbilicus. The umbilicus in *V. atramentaria* is narrowly open and the internal spire is clearly visible. The umbilicus of *V. compacta,* on the other hand, is practically closed by the reflection of the inner insertion of the aperture margin. This difference is shown in Fig. 2.

Other external differences seen between the two species include the colour of the animal. In *V. atramentaria* the body colour is black with some orange, a bright orange frill round the foot and a white foot. The mucus, too, is bright orange and extremely sticky and viscous. In *V. compacta* there is a complete absence of orange pigment both in the skin and the mucus. The body colour and the frill around the foot are black and there is some black pigment in the sole of the foot. The mucus is colourless and less viscous than in *V. atramentaria.*

Davies (1913) mentioned small glandular papillae associated with the inferior tentacles in *V. compacta.* I could not find these structures in either of the species.

INTERNAL FEATURES

For this work three specimens of each species were dissected and five radulae from each species were mounted. A general description of the anatomy of *V. atramentaria* and *V. compacta* has been given by Murdoch (1905) and Davies (1913). A more detailed description of the anatomy of these two species will be published elsewhere in the near future.

The anatomy of these two species is very closely similar. The only differences readily apparent are in the radula and the reproductive system. The nervous system also shows some differences but these will be described elsewhere.

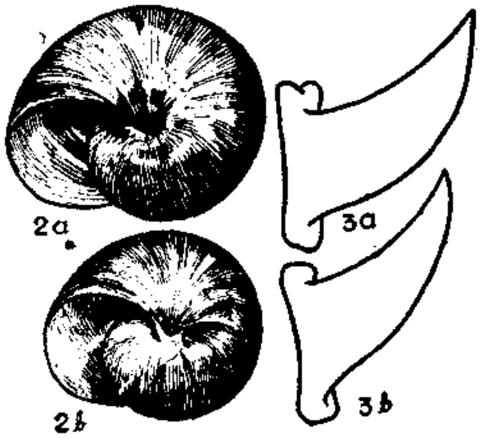
The radulae in both species consist of aculeate, unicuspid teeth with no clear division into tooth type, except according to size. The teeth increase in size from the margins to a maximum about four teeth from the centre and then decrease sharply. There is a distinct space in the midline showing the absence of the rachidian. Teeth formulae for the two species are as follows:

V. atramentaria 64–0–64 × 102–105 rows to 67–0–67 × 102–105 rows.
V. compacta 60–0–60 × 99–103 rows to 63–0–63 × 99–103 rows.

The shape of the teeth, too, shows very slight differences between the species. The teeth of *V. atramentaria* are more solid in appearance and the posterior extremity of the base plate bears a slight notch not present in *V. compacta.* This gives the appearance of two knobs on the end. This is shown in Fig. 3.

The reproductive systems of the two species are also very similar, but do show one or two differences between the species. The gross structure of the entire reproductive system of *V. atramentaria* is shown in Fig. 4 (*a*). Special features are the long penis with the vas deferens entering it just before the posterior end. The penis is equal in size, or longer than the uterus. These are the two features which differ in *V. compacta,* the penis and uterus structure of which is shown in Fig. 4 (*b*).

Here the vas deferens enters at the posterior extremity of the penis and the penis is shorter in length than the uterus.



FIGS. 2-3. (2) Camera lucida drawings of the ventral views of the shells of (*a*) *V. atramentaria* and (*b*) *V. compacta* showing the differences in umbilicus structure; (3) Drawings of radular teeth of (*a*) *V. atramentaria* and (*b*) *V. compacta*.

DISCUSSION

The family Paryphantidae is a large, diverse family confined to Australasia except for two genera in South Africa. Much work has been done on reporting distribution and describing shells, particularly by Powell (1930, 1946, 1949) for the genus *Paryphanta* in New Zealand and by Iredale (1933, 1938) on several Australian genera. Far less work has been carried out on the anatomy of members of this family, the most notable work being by Kondo (1943) on the genus *Ouagapia*. It is, however, only by reference to the anatomy that any real headway in the taxonomy of this group can be made. Iredale (1933, 1938) created five new genera for the Australian paryphantids and although his descriptions are technically valid they have been ignored by most reviewers as being insufficiently described for practical purposes (Solem, 1959 and Zilch, 1960). In the case of the Iredale genus *Victaphanta* it is my contention that it is a valid genus. When considering its differences from related genera it is necessary to consider the anatomy of the groups as well as the shell characters. There are two generic groups which should be considered as being closely related to *Victaphanta*. Firstly the genus *Paryphanta* (Albers, 1850) with *Paryphanta busbyi* (Gray, 1840) as genotype, the anatomy of which was described by (Murdoch, 1902). The other is *Powelliphanta* (O'Connor, 1945) described as a subgenus of *Paryphanta*, the genotype being *Paryphanta* (*Powelliphanta*) *hochstetteri* (Pfeiffer, 1862) the anatomy of which was described by Goodwin-Austin (1893).

Victaphanta differs from *Paryphanta* is possessing sculpture lines on the upper surface of the shell; in having a smaller shell and a nearly closed umbilicus instead of being large. The penis and vas deferens structure differs in that the vas deferens runs inside the penis sheath in *Paryphanta* whereas it is external in *Victaphanta*. *Victaphanta* differs from *Powelliphanta* in possessing sculpture on the shell and also in the presence of a rachidian in the later group.

The two species of the genus *Victaphanta* are very closely similar in many ways but can be separated by shell, radula, and reproductive differences as well as with reference to their geographical ranges.

During this work I came across a number of major difficulties. The chief one occurred when attempting to trace the original type of *Victaphanta atramentaria* with accurate locality data. So far my enquiries point strongly towards the probability that the type is lost. If this proves to be the case then because of ambiguities in the original type locality data and description I will designate a neotype and describe the species properly again.

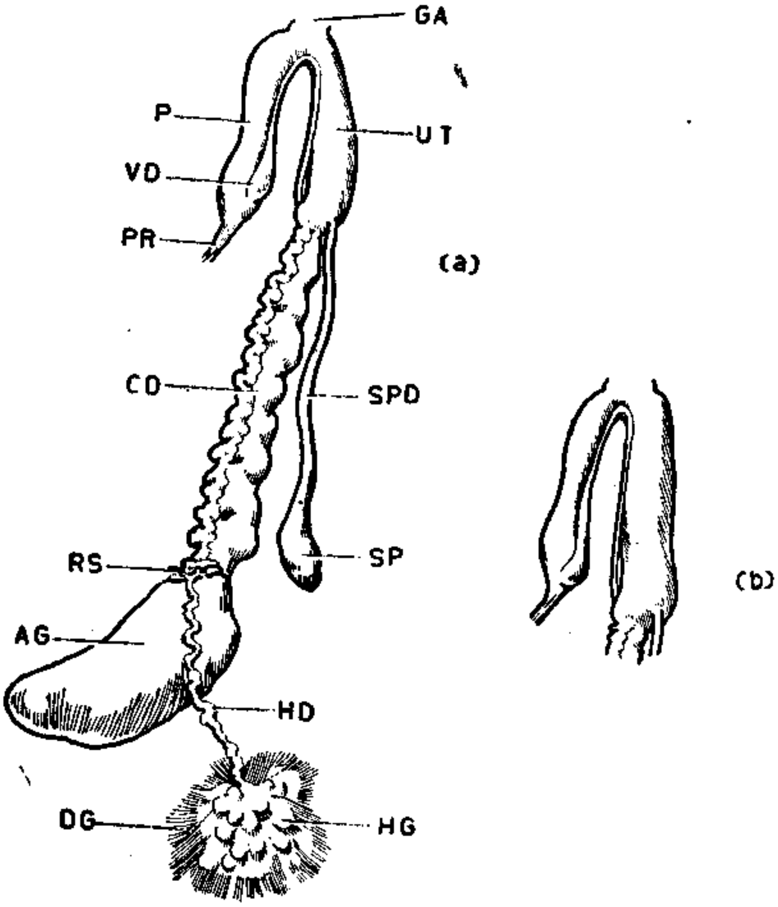


FIG. 4. (*a*) A diagram of the reproductive system of *V. atramentaria*; (*b*) A diagram of the penis-uterus complex of *V. compacta* showing the differences in structure to *V. atramentaria*. (AG) Albumen gland; (CD) Common duct; (DG) Digestive gland; (GA) Genital atrium; (HD) Hermaphrodite duct; (HG) Hermaphrodite gland; (P) Penis; (PR) Penis retractor muscle; (RS) Receptaculum seminalis; (SP) Spermatheca; (SPD) Spermathecal duct; (UT) Uterus; (VD) Vas deferens.

ACKNOWLEDGEMENTS

I wish to thank Dr. G. Ettershank for his assistance with the statistics, and Mr. R. Miller for his assistance with the reproduction of the figures.

LITERATURE CITED

ALBERS, J. C. 1850. *Die Heliceen*, 1: *Aus., Leipzig.*

——— 1861. *Ibid.*, 2: *Aus., Leipzig.*, p. 48.

Cox, J. C. and Hedley, C. 1912. An index to the land shells of Victoria. *Mem. Nat. Mus. Vic.*, **4**: 1–11.

Davies, O. B. 1913. The anatomy of two Australian land snails, *Paryphanta atramentaria*, Shuttleworth and *P. compacta*, Cox and Hedley. *Proc. R. Soc. Vic.*, **25** (N.S.), pt. II: 221–228.

Goodwin-Austin, H. H. 1893. On the molluscan genus *Paryphanta* and on the anatomy of *P. hochstetteri*, Pfr. *Proc. Malac. Soc. Lond.*, **1**: 5–7.

Gray, J. E. 1840. New land shells from New Zealand. *Ann. Mag. Nat. Hist.*, **6** (1): 317.

Iredale, T. 1933. Systematic notes on Australian land shells. *Rec. Aust. Mus.*, **19** (1): 37–59.

——— 1938. A basic list of the land Mollusca of Australia (Part III). *Aust. Zool.*, **9** (2): 83–124.

Kondo, Y. 1943. Anatomical studies of three species of *Ouagapia* (Pulmonata: Agnatha: Paryphantidae). *Occ. Pap. B.P. Bishop Mus.*, **17** (19): 229–248.

Murdoch, R. 1902. Anatomy of *Paryphanta busbyi*. *Trans. N.Z. Inst.*, **35** : 258–262.

——— 1905. On the anatomy of *Paryphanta atramentaria* Shuttleworth. *Ibid.*, **38**: 313–316.

O'Connor, A. C. 1945. Notes on the eggs of New Zealand Paryphantidae, with description of a new subgenus. *Trans. R. Soc. N.Z.*, **75**: 54–56.

Pfeiffer, L. 1862. *Mal. Bl.*, **8**: 146.

Powell, A. W. B. 1930. The Paryphantidae of New Zealand: their hypothetical ancestry, with descriptions of new species and a new genus. *Rec. Auck. Inst. Mus.*, **1** (1): 17–56.

——— 1946. The Paryphantidae of New Zealand. No. V. Further new species of *Paryphanta*, *Wainuia* and *Rhytida*. *Ibid.*, **3** (2): 99–136.

——— 1949. The Paryphantidae of New Zealand. No. VI. Distribution, hybrids and new species of *Paryphanta*, *Rhytida* and *Schizoglossa*. *Ibid.*, **3** (6): 347–367.

Shuttleworth, R. J. 1852. *Mitth. Natf. Ges. Bern*, p. 194.

Solem, A. 1959. Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. *Fieldiana*, **43**: 1–359.

Zilch, A. 1960. Gastropoda—Euthyneura. *Handbuch der Palaozoologie*, **6**: 1–834.

AN ALTERNATE VIEW ON THE PHYLOGENY OF THE MOLLUSCA[1]

HAROLD W. HARRY

Texas A and M Marine Laboratory, Galveston, and Rice University, Houston, Texas, U.S.A.

ABSTRACT

The phylogeny of the Mollusca to class level is traced by noting the advent, modification and loss of particular characters, relative to similar courses of events of numerous other characters. Incipient segmentation in ancestral stages is assumed, but it did not reach the harmonious regularity of the annelids. The Mollusca and Annelida are traced from a vermiform ancestor which was considerably more complex than the Platyhelminthes. A Prochiton stock gave rise to the Polyplacophora, which in turn were ancestors to the Aplacophora. All other molluscs arose through a separate line, the Proconchifera, of which Monoplacophora were an early derivative. Proconchifera further gave rise to a group called Mesoconchifera, which gave rise to Probivalvia and Metaconchifera. Probivalvia were ancestors separately to Bivalvia and Scaphopoda; from the Metaconchifera arose separately the Gastropoda and Cephalopoda. The median dorsal mantle cavity, attributed by other writers to the remote promollusc, is thought to have arisen only at the metaconchiferan stage, since it is present only in the Gastropoda and Cephalopoda.

INTRODUCTION

THE enormous diversity of the Mollusca, which ranks about third in the number of living species of animals, makes it difficult to formulate a definition which will apply to all members of the group but none outside it, and at the same time be reasonably brief. Perhaps this is why the phylogeny of this group has received so much attention in elucidating what the molluscs are. E. Ray Lankester (1883, reprinted 1891) was among the first to approach the problem in this way. His proposal of a primitive first mollusc, from which all later ones were derived, has been followed with slight modifications of detail by most authors, excepting only a few who advocated a polyphyletic origin of the group. The latter alternative only introduces a logical regression, for surely the molluscs of today must have had a common metazoan ancestral species, however remote. A special case of the polyphyletic theory of molluscan origins is one proposed by Verrill (1896), that the molluscan classes were already differentiated in some pelagic form similar to a rotifer, and the molluscan larva of today recapitulate that stage in phylogeny. This would require the independent origin of many adult characters, such as coelom, gills, radula, etc. But since all molluscan classes do have a number of fundamental characters in common, it seems likely that they had a common immediate ancestry, shortly before those features arose which differentiate classes.

What is a biological character? For present purposes a character may be defined as any attribute which varies among the things considered, and which is inherited. Characters of organisms are only recognizable because they vary. There are thus two or more alternate conditions of every character among organisms which are quite similar in several other characters, but the latter characters have again their alternates in still other organisms.

An organism is defined by the assemblage of its characters. It has no being apart from this assemblage, considered collectively. Other than weight and size, and simple enumeration of meristic ones, biological characters cannot be expressed mathematically. That is, they cannot be quantitated in such a way that they may be subjected to mathematical manipulation. Indeed, the analysis of characters is one of the major problems in a study of this kind. Is the radula a

---

[1] Study supported by National Science Foundation Grant GB-2753.

character? It may vary by being present or absent. Yet it in turn has multiple attributes: the number of teeth in a transverse row, the number of rows (both meristic characters), the size and form of the individual teeth, the shape of a transverse row (chevron-shaped or rectilinear, etc.).

Characters may be particular structures, such as a radula in the molluscs, or the cartilage, bone, and notocord of vertebrates; or a character may be merely topographical; an arrangement of parts, such as the pattern of peripheral protein molecules on the surface of a virus, or the dorsal position of the central nervous system in vertebrates, or the tripartite arrangement of the molluscan body plan into head, foot, and visceral mass. Even non-physical attributes may be included, such as behavior (time of reproduction, reaction to gravity, light, or other stimuli).

The analysis of characters will long continue to be subject to revision, and that is why exploration of the method of studying phylogeny is more important than dogmatically asserting that characters are precisely as stated in the outline below. Assuming that complex organisms arose from simpler ones, and excepting degeneracy resulting from parasitism, it is the task of phylogenetic study to determine what the simpler ancestors were, and what particular events occurred in the evolutionary history of the more complex ones. The problem is to determine which characters appeared first, relative to the appearance of each additional character or character alternate of the more complex organism.

Since we cannot go back in time and observe the events as they actually happened, and the paleontological data are regrettably meagre, the internal congruity of any phylogenetic scheme must serve as its validation. There are several minor criteria which are helpful. One is that the more widely distributed a character alternate is among organisms otherwise very dissimilar, the earlier it appeared relative to the character alternates which differentiate the groups under consideration. The converse of this rule is not always true. Empirically, it seems likely that a character may have been lost several times independently, but characters appear independently very infrequently.

That some characters have arisen independently several times can scarcely be doubted. Examples are hemoglobin in molluscs otherwise dissimilar, the slug-like and patellate shape in snails (essentially the reduction or loss of character: the visceral mass as a dorsal projection), and complex eyes. Any scheme proposed is subject to modification as characters are more aptly defined, as new ones are discovered and introduced into such a system. It is very difficult to include all known characters of the molluscs, without rendering the results too bulky. But key characters may be sought and others related to them on the basis proposed.

Phylogenetic studies of this kind should act as a stimulus to learning more about a group of animals—their general biology. It presents a framework to which all biological data can be related, and consequently gives such data a significance which they may otherwise lack. This sort of system rejects the shackles of orthodox classification, which so often diverts attention to its own ends, of determining whether a group should be of one taxon or another. Yet if not hampered by classification during its pursuit, it will ultimately lead to a more satisfactory one. Classification at the level of orders in the prosobranchs and bivalves is notoriously controversial at present, and this may be resolved by the approach here advocated.

We may modify some, and reject other subjective terms which are frequently used in phylogenetic studies. Primitive, when applied to a character or character alternate, means one which arose first, relative to another. When speaking of a whole organism as primitive, we mean that it has more character alternates which arose first than does some other organism with which it is compared. Advanced is the opposite of primitive. Specialized and adaptive are terms which may be superfluous. Every organism is adapted to the environment where it lives, being suited structurally and functionally to that situation. That its characters may not be suited for envrironmental changes imposed on it at some future time, might mean that it is specialized, unadaptable to new surroundings. Yet such an evaluation would necessarily depend on what environmental changes occurred. Many animals do survive new, different environments imposed on them, or even invade them themselves. When this happens, it is obvious that the characters necessary for survival in the new environment must have been present before the animal entered it.

Once a physical character is lost, to the extent that the controlling genes would be lost as well, the character seems never to reappear. But characters of a topographical nature, which are based on the relative position of structures and possibly not under direct control of genes, may be rearranged to simulate an original position. Thus the heart, originally dorsal, sinks to surround the rectum in molluscan phylogeny, and may further fall below it (Ostreidae) or again rise above it, as in Anomiidae of the bivalves and in all the cephalopods, or move to one side of the rectum, as in the advanced gastropods.

It is possible that there may be an unexpressed potential in some ancestral forms, only manifest in populations of their descendants, which have diverged in other ways. In modern biological theory, this might be explained as the appearance of genes for producing a particular character, which were somehow at first unable to produce it (because of inhibitory genes, or similar reasons). Such phenotypic characters would be classed as originating independently, whereas fundamentally they did not, since the genes required for their manifestation were present but unexpressed in some common ancestor. Examples usually seem to occur in animals which are fairly closely related. The peculiar deciduous larval ectoderm of solenogastres and protobranch bivalves is one example. Another is the slight tendency for the visceral mass to coil about the tertiary body axis in *Neopilina*, a character not prominently manifest outside of the gastropods and cephalopods (unless the prosogyrous umbones of some bivalves be the same thing?). That genes must be present before the

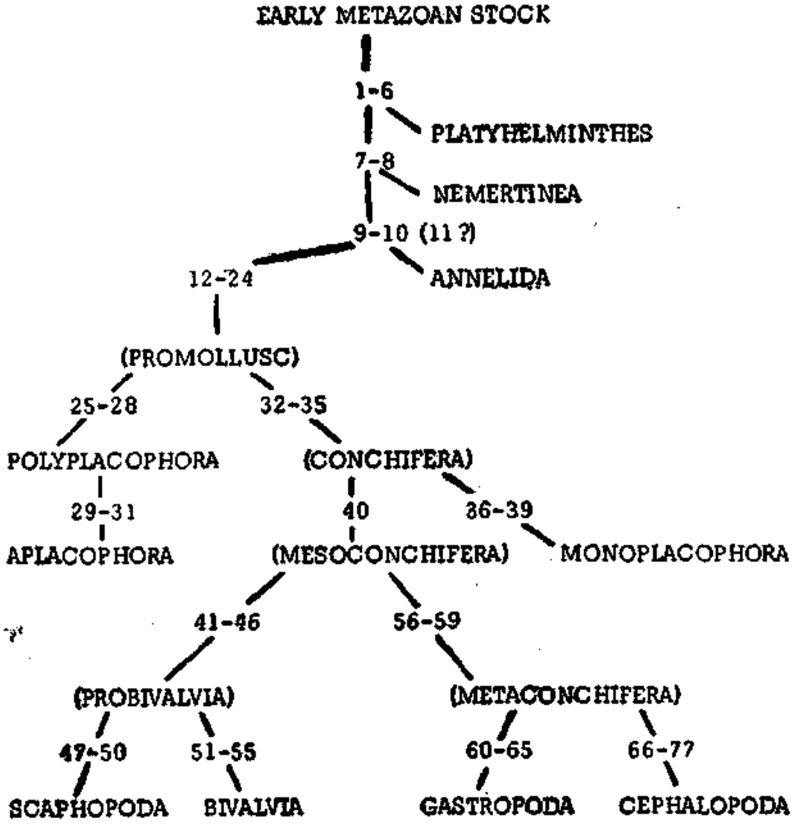


FIG. 1. Diagram of the phylogeny of the molluscan classes. Numbers correspond to numbered items in the text. Hypothetical groups are enclosed in parentheses.

character which they control appeared, seems as reasonable to postulate as to assume that characters fitting an organism for a new, adjacent environment must be present before it can viably enter that environment.

Elsewhere I used this method for a scheme of evolution of the higher limnic Basommatophora (Harry, 1964). In the present study the origin of the molluscs and differentiation of the major groups, to approximately class level, will be considered. The method is cumulative, meaning that at any given level, all characters cited up to that time are present in the organism, unless specifically noted as modified or lost. It is convenient to number the characters, thus approximating the sequence in which they arose, but allowing for divergence of stocks (Fig. 1). Some characters may be difficult to separate in the time sequence, because species with the necessary combination of characters are not known. These are sometimes grouped under one number, mend such expediency. Other characters are so intimately related that one depends upon another, rarely for pairs may have appeared almost simultaneously; examples are tissue differentiation depending on multicellularity, and cephalization depending on bilateral symmetry.

The net result of such an approach gives a pattern of phylogeny in general similar to those which have been proposed before, but differing in important details. The scheme proposed by Naef (1926) remains fundamental to all future studies of this kind. Since then, important new data have appeared, and there has been refinement of the theoretical concepts of genetics and evolution. I have omitted the extensive characterization of major groups usually added to phylogenetic accounts (Naef, 1926; Morton and Yonge, 1964). To add them would make the paper too long, and require determining the scheme of phylogeny within the classes, whereas the present account is restricted merely to determining the ancestral type of each. Most of the relevant material is in Pelseneer's (1906) volume on Mollusca, which is still unsurpassed after sixty years the single most useful source book in the group. Grassé's (1960) *Traité de Zoologie* has important articles on Polyplacophora, Aplacophora, Monoplacophora, and Bivalvia. I have not seen Hyman's (1967) partial treatment of the Mollusca, which appeared as this was being typed. The numerous shorter papers on molluscan phylogeny are listed in Naef (1926), with important later contributions cited in the bibliographies of Grassé's Traité (1960), Morton and Yonge (1964), and Hunter and Brown (1965).

THE PROMOLLUSC

The immediate molluscan ancestor, or Promollusc, probably had the characters 1-24, which arose approximately in the order listed.

1. It was multicellular, with much diversity of tissue type.

2. It was triploblastic.

3. It was bilaterally symmetrical, with a medial body axis, parallel to the substrate (the primary body axis).

4. Cephalization had occurred, so that the individual was divided into head and body proper. There was a concentration of sense-organs at the anterior end, where the mouth was also located. From a circumoral ring of nervous tissue pairs of nerve cords extended dorsally and ventrally. These were joined to each other by cords in the transverse plane, which could already be distinguished as connectives (joining cords of two different pairs, and not crossing the midline) or commissures (joining cords of the same pair, and crossing the midline). But the whole nervous system might have been little more than a nerve net, with somewhat more orderly arrangement of parts than is usual in nervous systems of that grade of development. Nerve cells were randomly distributed about the cords, and concentration into ganglia was scarcely evident.

The visceral organs were still contained in the body proper, not pushed dorsally to form a visceral mass. The animal was elongate, cylindrical or slightly flattened dorso-ventrally, thus essentially vermiform. It was probably without gills or locomotor appendages, and sufficiently small in size that ciliary action of a surface epithelium provided the chief mechanism of movement, supplemented by muscular activity of the body wall.

5. It was marine, free living, and crawled on the bottom.
6. The gametes were shed into the sea. The embryo developed with holoblastic spiral cleavage, and the blastomeres had determinant (mosaic) differentiation at a very early stage of cleavage. The mesoderm arose by strands budding from the lip of the blastopore.
7. The cilia of the embryo were not uniformly distributed over the surface, but grouped into several regions, which characterize a distinctive larval type, called the trochophore. This has an apical and abapical tuft, and an equatorial band of cilia.
8. It had a complete digestive tract, poorly differentiated into special organs. The anus was terminal. There may have been salivary glands, but there probably was no liver, in the sense of a distinct gland with ducts leading into the digestive tract. Possibly the liver had independent origins in the molluscs, arthropods, vertebrates and echinoderms. A stomach was probably differentiated at this stage.
9. It was coelomate, and the coelom developed by the schizocoelous method. Additional structures which depend on the presence of a coelom for their existence were also present: a pulsating heart, located dorsal to the digestive tract, with a median ventricle and one or (more likely) several pairs of auricles, placed laterally. The heart was situated in a pericardium. There was a nephrostomate excretory system. The gonads, from which the coelom itself may have developed, utilized the nephrostomal mechanism of the excretory system for the passage of gametes to the exterior. The circulatory system was of the open type. The coelom did not impinge greatly upon the haemocoel (blastocoel).
10. There was metamerism, but poorly developed. Some segmental repetition of the mesodermal structures, such as coelomic sacs, gonad, kidneys, auricles of the heart, was probably present, but the secondary impression of this segmentation on such structures as nervous system and external epithelium (or any skeletal structures produced by the latter) was vague. The number of incipient segments was small, about 6 or 8.
11. The atrium of the digestive tract became cuticularized, and small denticles of cuticle were present behind the atrium, in the pharyngeal region. The pharynx was also invested with muscles which projected it to the mouth, and manipulated the denticles in grasping food.

The molluscs have sometimes been derived from the Platyhelminthes (Graham, 1957; Morton and Yonge, 1963), but that group could scarcely have been the immediate ancestor. Of the characters cited above, only one through 6 are shared with the Platyhelminthes of today. We may add characters 7 through 10 (or 11), which are shared by both annelids and molluscs, and still not arrive at an organism which belongs to either of those groups. There is little reason to believe that these several characters, of such fundamental nature, arose independently in molluscs and annelids. Therefore these two phyla probably had a more proximate common ancestor than the Platyhelminthes, with which they are indeed remotely related.

The major difficulty in relating the molluscs to the annelids is the poor segmentation of the former. This may only indicate that the molluscs diverged from the common ancestral stock when metamerism itself was poorly developed. Hyman (1951) is probably right in thinking that mesodermal segmentation arose several times in the animal kingdom. But the remnants of incipient segmentation of the molluscs may well be a common heritage with the annelids, in view of the other characters these two groups share.

Metamerism as shown by the annelids, arthropods, and chordates has close correlation of repeated units among several organ systems, so that somites are recognizable. This complex character probably appeared only gradually. These groups are harmoniously metameric, whereas the molluscs are only inharmoniously so. Molluscs seem never to produce somites in the embryos, but this may be a result of the inharmonious nature of their metamerism, and because what little tendency there was to it has been largely obscured in modern forms. Considerable obliteration of metamerism (essentially loss of a character) can be found in all of the harmoniously segmented phyla cited above. Several characters by which Graham (1955) relates the molluscs to the flatworms, may be those of a metazoan ancestor of the flatworms, which were retained by that group and molluscs, but lost by annelids: extra-cellular digestion, abundant epidermal glands, and locomotion by pedal cilia supplemented by muscular movement.

At this stage the molluscs and annelids diverged. The annelids increased the harmony of segmentation, and enlarged in size by extending the primary body axis, at the same time adding more segments. A cuticle developed over the entire surface of the body, providing a firmness which allowed the development of parapodia, and a substance from which the annelidan setae are formed. The coelom further expanded to obliterate the hemocoel, and the circulatory system became closed (perhaps not in all species).

The Nemertinea may have arisen along this path also, diverging approximately after number 8 of the above sequence. The metameric arrangement of their gonads suggest that numbers 9 and 10 in the sequence might need to be reversed, that incipient segmentation appeared before the coelom proper (excluding gonads) and its derivatives. Meristic arrangement of intestinal pouches of the nemertians is excluded from the evidence of incipient segmentation, since no animal with harmonious mesodermal metamerism shows evidence of segmentation of the endodermal derivatives. Meristic digestive pouches have undoubtedly originated several times independently, being present in some Turbellaria, Nemertinea, Hirudinea and even some solenogastres.

The distinctive larval type of the Nemertinea may be a special modification of a trochophore. At least, it is not a uniformly ciliated larva such as the Platyhelminthes have. Although details differ, the deciduous larval ectoderm of nemerteans may have its counterpart in solenogastres and protobranch bivalves (*see* below).

The ancestral stock of the molluscs underwent the following modifications after the separation of an annelid stock:

12. The dorsal surface of the body, behind the head, secreted a cuticle which was augmented by calcareous inclusions. These were various initially, and may have taken the form of spicules in some, plates in others. Whether this cuticle is identical with that in annelids is not very clear. In the latter group it covers the whole body, whereas in molluscs it seems to have been restricted to the dorsal surface.
13. The body increased in size, but became more equidimensional, approaching a sphere rather than a cylinder.
14. The viscera tended to bulge dorsally, protruding as a visceral mass. At first this bulge was slight, about as much as that present in chitons.
15. A lamella of epithelium and underlying mesodermal tissues extended downward from the edge of the visceral mass, forming a groove around the latter. This hypopeplar or subnotal cavity was initially of equal depth throughout; it persists in some members of all classes of recent molluscs. Currents produced by ciliary action of the epithelium lining this groove entered it at the anterior end, and exited behind. Such is still the condition in chitons and primitive bivalves, and postulated to be the direction of current flow in *Neopilina*. The epithelium covering the visceral mass and projecting lamella is called the mantle. In the literature, this cavity is often not distinguished from

a further development of it, in the median line posteriorly and both are called the mantle cavity.

With the appearance of the visceral mass, the tripartite division of the molluscan body into head, foot, and visceral mass was completed. These three divisions are strongly imprinted on the form of nearly all molluscs, and collectively they are not recognizable in any other group of animals. Within the phylum, each body region has shown major structural changes independent of the others. Besides the antero-posterior, or primary body axis which appeared with bilateral symmetry and cephalization, a secondary body axis was produced by the dorsal bulging of the visceral mass. This axis was initially very short, but became much longer in some groups of later origin.

In conjunction with the appearance of the increased size and visceral mass, other structural changes occurred.

16. The anus moved from a terminal position to a more dorsal one, opening in the midline behind, in the hyponotal groove.

17. Gills appeared. They were of a distinctive form, each gill consisting of a central axis, attached to the body for a varying part of its length, or only at its base. From this axis were suspended pairs of flat plates, or lamellae. This form of gill may have developed independently in such unrelated groups as the decapod Crustacea. But in Mollusca, although they have undergone a number of transformations and frequently been lost, the true gill seems to have developed only once. Other respiratory structures, which may be termed neobranchs, seem to have developed a number of times, at varying parts of the body.

Initially the gills were arranged in pairs in the hypopeplar cavity, toward the hind end of the body, and they constituted one manifestation of the incomplete segmentation. The five or six pairs present in *Neopilina* probably represent the maximum number of incipient segments which the primitive promollusc achieved; although some chitons have about 80 pairs, only one or two pairs at the posterior end of the series seem to show correlation with segmental structures of the mesoderm. In tetrabranch cephalopods two pairs also exist, but in all other recent molluscs the number has been reduced to one pair (most bivalves, most diotocardian prosobranch gastropods) or to one member of one pair (more advanced prosobranchs), or the true gills have been lost entirely (many snails, scaphopods, and some Aplacophora).

18. The radula was improved (postulated incipiently in 11, above). It became a ribbon of cuticle, the posterior end of which is situated in a sac, where the ribbon is continually renewed. Intrinsic muscles surrounding the pharynx attached along its side, and a radular support appeared beneath it, serving as a fulcrum over which it could be drawn back and forth. That the cuticularized atrium is important in the functioning of the radula has often been under-emphasized in the literature. Portions of this atrial cuticle were to become thickened, forming jaws, in several molluscan groups independently. The thickened musculature of the pharynx constituted a buccal mass. Nothing quite like this is known in other phyla, but there may be a few annelids which approximate it. Lemche and Wingstrand (1960) consider such a mechanism in the eunicid polychaetae, *Ophryotrocha*, to be a typical radula. The figure of this structure as published by Wesenberg-Lund (1938) does indeed resemble a molluscan radula, especially if we compare it with the several types of the Aplacophora (*see* Fischer-Piette and Franc, 1960: 1670 ff). But detailed studies on accessory mechanisms, such as musculature and the presence of a radular support, seem to be lacking for the annelidan structure.

19. A pair of salivary glands was added at the pharyngeal region (or earlier ?).

20. A distinct liver was formed, with two major lobes, each having a duct leading into the stomach.

21. A pair of buccal pouches appeared, caused by lateral expansions of the esophagus immediately behind the odontophore. These persist in Polyplacophora, *Neopilina*, and many prosobranch gastropods today.

22. A subradular sense-organ appeared. This is a small pouch in the midline of the floor of the buccal cavity, in front of the radular mechanism. It has sensory epithelium lining its interior, and special ganglia associated with it. It persists only in *Neopilina*, the chitons, cephalopods, and scaphopods of today.

23. The osphradia appeared as paired structures, one near each gill. This is an organ peculiar to the whole phylum, but it was lost in many major groups.

24. The trochophore larva added some adult characters, including a pair of eyes, a pair of otocysts, a shell gland, and the body was divided into three parts in early development. It retained the equatorial band of cilia of the more simple trochophore, but the elaborate velum characteristic of several groups which arose later had not yet appeared. A pair of embryonic head kidneys (protonephridia) were also present, but these may have arisen much earlier. They disappear before the larva metamorphoses into the adult.

The nervous system of the molluscs presents special difficulties in establishing homologies. After the appearance of the visceral mass the basic pattern was considerably modified (No. 4 above). It is not presently possible to trace each step in the modification, but we may point out that the visceral commissure probably represents dorsal nerve cords, and the pedal ones ventral nerve cords of other groups. Something of the nerve net is retained in connectives between the Pleurovisceral connectives (in chitons, *Neopilina*) and multiple pedal commissures (in chitons, some primitive prosobranchs). Concentration of nerve cells into ganglia seems to have occurred independently several times within the phylum. The ganglia appeared at the junction of two nerve cords, and sometimes on a nerve near the organ which it innervates. The appearance of the parietal ganglia near the gills and osphradia is an example of the latter case. A tendency for the ganglia to become concentrated in the cephalic region also occurred independently several times.

Figure 2 suggests the generalized basic pattern from which the nervous system of the several classes may be derived through loss of parts and topographical changes.

ORIGIN OF CLASSES

The characterization of the promollusc as envisioned here differs from the usual one given in the literature in several important respects. A particular shell type was not specified; there was as yet no median dorsal mantle cavity; inharmonious segmentation was manifest, and a generalized coelom was present. Two major stocks diverged from the Promollusc, the Polyplacophora and Conchifera.

POLYPLACOPHORA (25–28)

25. This stock developed an exoskeleton of two types: There were eight shell plates developed in linear sequence in the midline of the back. These expanded and articulated with each other, but they did not extend to the mantle margin. Each shell piece consists of an upper and lower part, of which the upper one, exposed to the environment, has cellular extensions reaching to its outer surface, forming peculiar sense-organs called esthetes. The smaller of these may only respond to tactile or chemical stimuli, but

some of them are large, multicellular, and have developed into distinct eyes, complete with lens, retina and chorion. Peripheral to the shell plates the mantle became covered by an acellular cuticle, into which cells from the underlying mantle epithelium often extend, producing the second skeletal element, calcareous spicules. Although the shell of chitons has sometimes been thought to contain elements not homologous with the shell of other molluscs, Beedham and Trueman (1967) have persuasively argued that they are identical with the outer and inner layers found in the Conchifera.

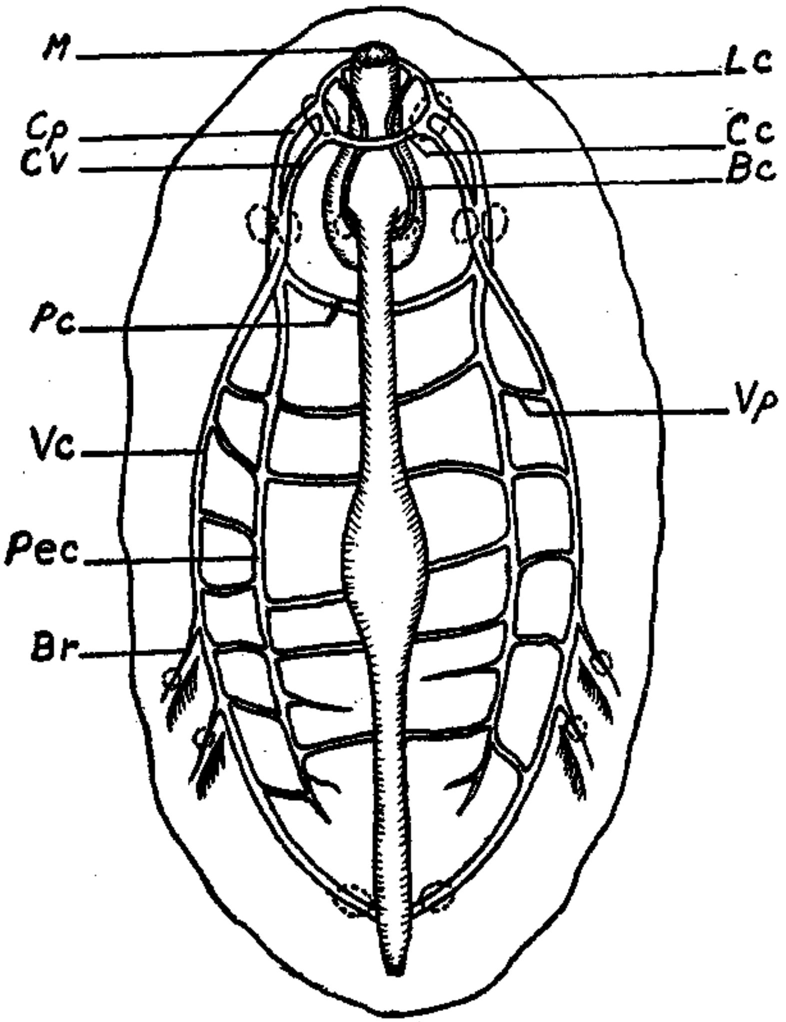


FIG. 2. Diagram of the dorsal view of the nervous system of the Promollusc. Position of future ganglia are indicated by dashed circles. (BC) Buccal commissure; (Br) branchial nerve; (Cc) cerebral commissure; (Cp) cerebro-pedal connective; (Cv) cerebro-pleural connective; (Lc) labial commissure; (M) mouth; (Pc) pedal commissure; (Pec) pedal cord; (Vc) visceral cord; (Vp) viscero-pedal connective.

26. The otocyst and cephalic eyes were lost. Cephalic eyes are present in larval chitons, thus suggesting that they were present in some ancestral population.

27. The incipient metamerism became more inharmonious. Although eight plates are present in all chitons, the number of gills may vary from a few pairs at the posterior part of the body to eighty pairs, extending almost to the head, and with no obvious correlation of the pairs. The heart may have one, two or even four pairs of openings into the median ventricle. A single pair of gonads open at the base of a pair of gills just before the renopores from the single pair of kidneys. This suggests a tendency for two segments at the posterior end of the body to be more harmoniously developed than segments elsewhere.

28. The generalized coelom (*i.e.*, not actually pericardium, kidney or gonad) was lost.

The nervous system of chitons is similar to that of the Promollusc imagined in Fig. 2. The labial commissure is present, pedo-visceral connectives are present, there are numerous pedal commissures (showing no correlation with the shell plates), and ganglia are poorly developed.

It is of interest that the radular characters are remarkably constant in all chitons. There are only 17 teeth in a transverse row. The teeth of one row are not all alike. They recall the general pattern of *Neopilina*, and the middle part of the primitive snail radula, of the rhipidoglossan type. The stomach is varied in different species, and in at least some of them has a muscular wall, for grinding the food. No crystalline style is present. Chitons feed chiefly on microscopic algae and detritus on rocks. The intestine is long often with several coils before it ends behind in the median anus. The intestine is imbedded in the liver, of which there are two well-developed lobes, opening by separate ducts into the stomach.

APLACOPHORA (SOLENOGASTRES: 29–31)

The Aplacophora are a group of marine, worm-like molluscs which seem to have developed directly from the chitons by means of further loss of parts.

29. They have lost the shell plates, but retain an external mantle with cuticular covering. In some species the cuticle has spicules imbedded, similar to those of chitons.

30. The foot degenerated, and is represented by a narrow lamella, in a median ventral groove which is formed by the edges of the mantle brought together in the midline below.

31. The digestive tract has been simplified. The presence of a radula is one major feature linking them with the molluscs rather than the worms. In contrast to chitons, radular types are highly diversified.

The nervous system is very similar to that of the Polyplacophora. There is a single pair of typically molluscan gills in a posterior mantle cavity in some species. In other species they are replaced by neobranchs. That the mantle cavity is slightly larger behind seems to be a natural consequence of crowding of the gills, the anus and coelomic pores as a result of the extreme reduction of the visceral mass and the hyponotal cavity. It is probably not indicative of an immediate common ancestry with the group termed below the Metaconchifera, since there is no elongation of the secondary body axis. A few species are hermaphroditic. This has probably developed quite independently from that of several other major molluscan groups.

Like the chitons, they have no cephalic eyes nor otocysts. The larval ectoderm which is later shed (or resorbed) and does not become the adult ectoderm in solenogastres (*see* Thompson, 1960) and protobranch bivalves has no obvious adaptive value (usefulness), and therefore it is not surprising that it was lost in subsequent phylogeny. The seven dorsal plates noted by Pruvot (1890) in a single specimen of developing *Nematomenia* (and widely copied in several major works cited by Thompson) may not represent the shell plates of chitons. As Thompson (1960) has noted, they have not been found in embryos of the four other species of solenogastres studied.

Even if the plates were not present, the absence of a pronounced secondary body axis, the type of skeleton, the form of the foot (obviously degenerated), form of true gills (when present), and the presence of a radula would relate the solenogastres more closely to the chitons than to the bivalves (*see* Thompson, 1960).

The Conchifera (32–35)

The Conchifera includes the Monoplacophora, Bivalvia, Scaphopoda, Gastropoda, and Cephalopoda.

32. The shell became a single cap-shaped piece, with the apex probably initially near the middle. The margin of the shell coincided with the outer margin of the mantle, and there was neither girdle nor spicules. The inner of two calcareous layers was nacreous (contrast chitons).
33. The visceral mass became more pronounced, as the secondary axis began to elongate.
34. A crystalline style was developed in the digestive tract, doubtlessly in gradual stages.
35. The heart and pericardium sank from their initial dorsal position, to envelope the rectum.

Monoplacophora (36–39)

The modern Monoplacophora differ chiefly from the conchiferan stock in a few minor characters.

36. The gills lost one member of each pair of their lamellae along the gill axis.
37. The pedal nerve cords lost all commissures except the extreme anterior and extreme posterior.
38. The osphradium was lost.
39. Eyes were lost, but the otocysts were retained.

Perhaps the forward position of the shell apex and its very slight curve about the tertiary axis (at right angles to the secondary axis, and above the primary one) represents an incipient tendency which became exaggerated in Gastropoda and Cephalopoda. A coiled protoconch described and figured for *N. galatheae* may be a fanciful interpretation of poorly preserved material. The protoconch of *N. ewingi* is simple, cap-shaped (Clarke and Menzies, 1959). If the protoconch were coiled, it would imply that *Neopilina* had descended from an ancestor with coiled visceral mass, and this is improbable. The patelliform shell in this species is more likely to be primary, whereas the cap-shaped shell of all other recent molluscs is secondary, that is, derived from ancestors that has a multicoiled shell and visceral mass.

Another character by which *N. ewingi* was differentiated from *N. galatheae*, an additional pai of gills at the front of the series, seems of little value as a species difference. For not only is ther some doubt as to the actual number of pairs of gills in *N. galatheae*, but the number may var slightly, as it does in some chitons with multiple gill pairs (Hunter and Brown, 1965).

Neopilina is remarkable in retaining a more harmonious segmentation than any other livin mollusc. There is a pair of large, unspecialized coelomic sacs, extending dorsally over th viscera. These are situated in front of a pair of pericardial sacs, containing a heart with two pair of auricles, and two ventricles which join to form a single cavity further forward. There are als two pairs of gonads in front of the pericardium, but below the viscera. The kidneys open in th hyponotal cavity, at the base of the gills. There are eight pairs of retractor muscles, running between the shell and the foot. Ten pairs of connectives between the pedal and pallial nerve cords complete the segmental structures. But none of the segments are complete, in the sense that they contain all of every character that is metamerically represented. Thus the auricles are in different segments from the gonads, and the segmentation of the nerves may alternate with that of the muscles and other structures. The several pairs of gills are evenly distributed along the body, not crowded to the hind end as they are in chitons which have only a few pairs of gills.

Perhaps this metamerism, which includes most of the body except the head, is significant in another respect: there is no median dorsal mantle cavity, such as appeared later in the gastropods and cephalopods. Those two features may be incompatible. To refer *Neopilina* to an earlier position in phylogeny would require assuming even more loss of characters (32–34) in the Polyplacophora than necessary to construct such a scheme with minimal changes.

A sub-radular sense-organ is present; the mouth is surrounded by extended lips dorsally and dendritically branched tentacles are prominent behind the lip. The radula has only 11 teeth in a transverse row, and about 40 rows are present. The rows are chevron-shaped (a primitive character), and the teeth in one row are of several types. The stomach has a bilobed liver opening into it and a caecal pouch near the origin of the intestine which is supposedly a crystalline pouch similar to that of some bivalves and gastropods but not present in the Polyplacophora. The intestine is coiled in several loops, and the anus opens in the midline behind.

THE CONCHIFERA ALSO GAVE RISE TO THE MESOCONCHIFERA (40)

40. Segmentation was further reduced until only two segments remained at the posterior end of the body. These segments were manifest by two pairs of auricles in the heart, two pairs of ctenidia, and two pairs of osphradia. Whether the single pair of kidneys and single pair of gonads which now remained were of the same segments is a moot question. An early derivative of the mesoconchiferan stock were the Probivalvia.

PROBIVALVIA (41-46)

41. The undifferentiated coelom was lost, as well as all evidence of metamerism, or there remained only one segment (Naef, 1926, refers to them as monomera), which is essentially the same thing.

42. The shell was modified from a simple cone shape to one of two lateral pieces, joined dorsally by a thickening of the periostracum to form a ligament. Muscles passed from one valve to the other, opposing the ligament functionally. There were originally two such adductor muscles, located anteriorly and posteriorly.

Articulating right and left skeletal elements seem to have evolved several times in molluscs. Besides the bivalves s.s., there is the chiton *Schizoplax* and the recent discovery of bivalved gastropods, which ranks high in its importance to phylogenetic studies. Boettger (1962) has cited two other unrelated gastropods which seem to have developed this phenomenon independently.

Probably at first the conic shell of the probivalve ancestor developed a median marginal notch in front and behind. At the same time it developed strong ciliary currents on the gills which caused the water to flow in at the front and out at the back. It could still hold on to the substrate, keeping most of the shell margin tight against it for protection. The enhanced ciliary currents brought with them a new and rich source of food, the plankton. At first the Probivalvia did not rely on this source of food. They lived near the bottom of rocks and in pockets where silt could accumulate, and algal growth was inhibited,

43. The lips of the mouth developed as appendages (perhaps appendages were already present in the conchiferan stock: there are similar ones in *Neopilina*). These appendages extended across the surface of the silt and into it, bringing back to the mouth organic detritus.

44. Cephalic eyes were lost, but the otocysts were retained.

45. The nervous system became modified into a definite pattern. The major ganglia of the major nerve rings became pronounced. A pair of cerebral ganglia were connected by a short cerebral commissure above the esophagus, in front of the buccal mass. The pleural ganglia migrated from the pedal ganglia up to the cerebrals and fused with them. There were long cerebro-pedal connectives and the palliopedal connectives fused with these for the lower half or more of their length. Pleuro-visceral cords led to a pair of visceral ganglia under the rectum, and the visceral ganglia were close together. There was also a labial commissure attached to the cerebral ganglia, and passing under the buccal atrium. It had a pair of labial ganglia, which gave rise to labio-buccal connectives, which passed to a pair of buccal ganglia under the origin of the esophagus from the buccal mass (*see* Pelseneer, 1906: 234–235, and 199).

46. The foot became modified from a plantar, creeping sole to one which was as at first still plantar, but folded in the midline. It was inserted closed into the sandy substrate and then opened, providing a hold which could pull the animal down head first into the soft material. Such a foot remains in the protobranch bivalves. A fimbriated collar around a keel-shaped foot of the scaphopods, similar to that of the heterodont bivalves, acts in the same way. It is possible that the keeled part of the scaphopod foot represents a later outgrowth of the fimbriated, expansive part, and this may be another example of a disjunct character which seems to arise independently in two fairly closely related groups (scaphopods and advanced bivalves).

SCAPHOPODA (SOLENOCONCHA: 47–59)

The scaphopods or tusk shells developed from the Probivalvia at this state, by undergoing the following modifications:

47. The two valves of the shell and mantle lobes, still indicated in the larva, fused in the midline ventrally. This formed a closed tube, which elongated in the antero-posterior direction. There is not universal agreement on the position of the body axes in scaphopods. Some authors (Naef, 1926; Morton and Yonge, 1964) consider the long axis of the shell to be dorso-ventral or secondary and thus compare the mantle cavity with the median dorsal extension of same which I here assume to have arisen in a different stock (Metaconchifera, below). Perhaps embryological studies will settle the question.

48 The ability to produce nacre was lost.

49. The crystalline style sac was lost [or much reduced: Morton (1959) cites a possible remnant in *Dentalium entalis*].

50. The (true molluscan) gills, osphradia, and heart were lost.

The cephalic tentacles, emerging from two lobe-like masses at the base of a short proboscis, are said to carry particulate food to the mouth, but I have not been able to find cilia on them in live material of *Dentalium texasianum*. They squirm by muscular action, however. There is a well-developed radula, and the labial commissure persists in the nervous system. Two kidneys are present, but apparently only a single gonad.

A second stock arose from the Probivalvia to become the true bivalves;

BIVALVIA (PELECYPODA, LAMELLIBRANCHIA: 51–55)

51. The radula was lost. Some protobranchs still retain lateral oral pockets which may be homologous to similar ones in *Neopilina*, chitons, and Archaeogastropoda.

52. The labial and buccal commissures were lost. The ganglia were reduced to cerebrals, pedals, and viscerals.

53. The axis of the single pair of gills which remained with the obliteration of segmentation became suspended by a muscular septum, which on contraction caused a pumping action to occur. The septum persists well up in the bivalve branch of phylogeny, but has received scarce attention outside of studies on the protobranchs.

54. The lips of the mouth were further pulled out to form labial palps, which at first had an appendage which gathered food from the substrate (*see* No. 43, above).

55. A byssal gland appeared in the foot (or perhaps only beyond the protobranchs).

METACONCHIFERA (56–59)

To the characters of the Mesoconchifera were added the following:

56. There was an elongation of the secondary axis (apical-pedal axis).

57. A dorsal median mantle cavity appeared, pushing into the hind end of the visceral mass. This was merely an invagination of the hypopeplar cavity. Into this new cavity migrated the two pairs of gills and osphradia, the anus, the renopores, and gonopores (if these were separate from the renopores), so that these structures were further protected from the environment.

58. In the growth of the animal, the elongated secondary axis became coiled about the tertiary body axis. This is at right angles to both previous axes, but passes through only the visceral mass, and is thus well above the foot and primary body axis. The coiling was perhaps not extensive at first, consisting of only a few whorls (complete coils, of 360°), which expanded in size very rapidly. It was moreover symmetrically planispiral (all coils in the same plane). The mass of the coils was thrown forward, over the head of the animal (exogastric coiling). Seen from the left side, the coils would be turned counterclockwise. It remains exogastric and symmetrical in some cephalopods (*Nautilus*, but not *Spirula*).

59. Epipodial lobes developed. These may have been present earlier, although there is no evidence of any such in the chitons or *Neopilina* nor the bivalves. These are extensions from the side of the foot, on both sides. They may have tentacles on them, which are very motile and highly sensory. On each side of the head are small cephalic lobes, which may be thought of as separate parts of the main epipodial flange.

The dorsal median mantle cavity is here assumed to be a very late development of molluscan phylogeny, contrary to most previous accounts, which would have it present as early as the promollusc. But no such cavity is present in any class except cephalopods and gastropods. The presence of this cavity, with the associated factors of extending the secondary axis and increasing the role of the tertiary axis are probably related to the reduction of segmentation and to the major phylogenetic trends within these two classes. When this cavity appeared ciliary currents entered it laterally, passed to the apex of the cavity, and down the midline behind. This was a natural consequence of the late appearance of this cavity. The ciliary currents already entered at the anterior end of the animal, and thus approached the median dorsal mantle cavity laterally. Actually, the tertiary axis was incipiently present as far back as the Conchifera and that is why the apex is over the anterior margin of the shell in *Neopilina*, rather than in the middle.

The Metaconchifera still retained evidence of two body segments near the posterior end of the body, and an undifferentiated coelom in addition to the coelomic derivatives (heart, kidneys, and gonads). Their nervous system showed multiple pedal commissures, and a labial commissure, but ganglia were only poorly differentiated. They were still without any indication of the asymmetry of the gastropods s.s.

For many of the hypothetical stages postulated in the present outline there is no fossil evidence, a fact rationalized away by the remoteness in time (Precambrian) at which these many mutations occurred. However, there is abundant fossil evidence of a group which could well represent the stage we have called the Metaconchifera. These are the Bellerophontidae, a group of planispiral snail-like species which lived at least from late Cambrian through early Mesozoic time. They were symmetrical, with shells of a few rapidly expanding coils. There were no septa in the whorls (hence they are not considered to be cephalopods), but a pair of retractor muscle scars have been found in some of them. Moreover, a median notch, like that in *Pleurotomaria*, or a series of median holes, like those in *Haliotis* and young *Fissurella*, may be homologous to those structures in the latter groups. The water must have entered the median dorsal mantle cavity, which was probably still posterior, on both sides, and exited medially, through the notch or the holes. Knight *et al.* (1960) have reviewed these fossils extensively.

GASTROPODA (60–65)

The Metaconchifera gave rise to two major groups, the Gastropoda and the Cephalopoda. The Gastropoda arose through the following mutations:

60. Segmentation was obliterated (or reduced to one segment, *see* No. 41 above), but there initially remained one pair of kidneys, two auricles to the heart, and two gonads.

61. Torsion appeared. This is a complete twisting of the secondary body axis through 180°, along the right side of the body, so that the median dorsal mantle cavity comes to lie over the head; the coil of the shell is swung about, so that its major mass lies over the hind part of the foot. Such a shell is endogastric. The organs of the median dorsal mantle cavity which were originally on the left before torsion are on the right after torsion, and *vice versa*. A twisting of the esophagus in many gastropods clearly shows torsion in the adult, but the most remarkable feature of it is that the visceral nerve ring was twisted into a figure eight. The absence of torsion in the two pedal retractors, which remain distinctly separated in some primitive snails, is difficult to explain.

62. The generalized coelom was also retained initially. However, this persists, as a much reduced vestige, in only one group of recent snails, the Neritidae. It was presumably lost independently in all others.

63. The subradular sense-organ was lost.

64. An operculum was added to the dorsal, posterior part of the foot.

65. The visceral mass and shell no longer coiled planispirally about the tertiary body axis, but in a helicoid fashion during growth, so that the apex of the mass of coils projected to the right of the primary axis of the snail. This was the first evidence of asymmetry, which becomes progressively pronounced in snails through loss of the organs on one side of the body. All recent snails have at least this much asymmetry. Several times during the phylogeny of snails, groups have reverted to planispiral coiling, and even projected the spire on the left side (hyperstrophy).

The veliger larva has not been cited as a characteristic of either the bivalves or snails. In the most primitive members of both groups, Protobranchia and Archaeogastropoda, the larva is scarcely more than a trochophore. Veligers developed by a pulling-out of the equatorial ciliated band of the trochophore, and this probably happened independently in the advanced members of both groups.

Except for streptoneury, the nervous system was still very primitive, in having multiple pedal commissures, a labial commissure, and with the ganglia poorly differentiated. A crystalline style was retained in the stomach (but lost in many advanced snails). The radula had numerous teeth in transverse, chevron-shaped rows. Besides the central tooth, nearly every one of the first few adjacent teeth (laterals) had a distinctive shape, similar to *Neopilina* and the chitons. The marginals (ones fartherest from the central) were very numerous, and alike in shape. This is essentially the rhipidoglossan radula. The rectum continued to penetrate the heart.

CEPHALOPODA (66–77)

The chief mutations which occurred in the metaconchiferan stock leading to the cephalopods are as follows:

66. The plantar foot was modified to form a circlet of flaps or tentacles around the mouth, and also a funnel which fitted into the aperture of the median dorsal mantle cavity. This funnel could direct the outward flow of water, backward, forward, or to either side. The exact homologues of these parts in other molluscs is still somewhat debated but most students are agreed that they have their counterparts in the foot of the gastropods.

67. The musculature of the wall of the median dorsal mantle cavity became more abundant and was used to contract the cavity, forcing the water out through the funnel. This served the several functions of aerating the gills (which now depended very little on ciliary activity), for removing renal and digestive wastes, and even for moving the animal about by means of jet propulsion.

The swift motion of which these animals were now capable afforded them not only an enhanced escape mechanism, but allowed them to become predaceous carnivores.

68. The atrial cuticle in front of the buccal mass became much thicker (as it did in many gastropods independently) forming jaws. These were of two large pieces, dorsal and ventral, with sharp edges and a sharp median point. The ventral overlaps the dorsal one. They closely resemble the beak of a parrot, and are used to bite off chunks of food. The radula, now rather useless, is none-the-less still present (except in Cirrhoteuthidae, which has lost it). It is remarkably uniform throughout the group, having 7 (rarely 8 or 6) teeth in a transverse row. There are a central, two laterals, and one marginal tooth, and the centrals and laterals are fang-like, a character which arose independently in many carnivorous gastropods, and Aplacophora.

69. A rectal caecum was developed. This stored melanin pigment which could be ejected as a cloud, useful in defence.

70. The heart again moved dorsal to the rectum.

71. The central nervous system became very concentrated in the head. The labial commissure persists.

72. A cartilage-like endoskeletal structure appeared in the head, partly surrounding and protecting the brain.

73. The eyes became more complex, developing a size and structure similar to the vertebrate eye,

74. Chromatophores of a peculiar kind appeared in the integument (or perhaps only beyond the tetrabranchiate stock ?). These were small sacs with pigment, which could contract by themselves, but which were expanded by means of radial muscle fibers attached around their periphery. The expansion and contraction is very rapid, and under nervous control.

75. The circulatory system became a partly closed, *i.e.*, true capillaries formed, with an endothelial lining. At first this was only partial, and blood sinuses of the haemocoel remained around the viscera, with capillaries limited to the muscular body wall. The cephalopods may have increased the efficiency of their circulatory system by doing this, a phenomenon which has progressed almost to completion in the Dibranchia, but they have only hemocyanin in their blood as an oxygen carrying pigment. This seems to be rather inefficient, and these animals, unlike many marine gastropods and bivalves, die quickly in the presence of low oxygen.

76. The shell developed transverse partitions, with a thin tube leading through each chamber. The chambers were filled with a gas, which counteracted the weight of the shell and provided buoyancy, in keeping with their pelagic tendencies. The ability to form a nacreous lining was retained.

77. The eggs were provided with an enormous amount of yolk. As a result, fewer eggs were produced than in most molluscs, the free swimming, ciliated larva was lost, and development became direct. This so modified the larval development as to make it difficult to study homologies with other molluscs. The eggs were encased in gelatinous capsules.

Initially, the primitive cephalopod retained a large, undifferentiated coelom, and prominent evidence of two pairs of body segments. There are two pairs of ctenidia and osphradia, two pairs of auricles to the heart, and two pairs of kidneys in *Nautilus*, the only living representative of the tetrabranchiate cephalopods. One pair of each of those structures was further lost in the major group of recent cephalopods, the Dibranchia (squids and octopi). A subradular sense-organ was retained. This is not a pouch, as it is in other molluscs, but a papillate tubercle on the floor of the buccal mass, in front of the radula. A pair of otocysts was also retained. Since the eggs were encased in a tertiary covering, it was essential that they be fertilized before this covering was put on. Instead of a penis, one (rarely two or several) of the arms developed differently from the rest, and served chiefly to transfer sperm, in spermatophores.

Literature Cited

Beedham, G. E. and E. R. Trueman 1967. The relationship of the mantle and shell of the Polyplacophora in comparison with that of other mollusca. *Jour. Zool., London*, **151**: 215–231.

Boettger, C. R. 1962. Gastropoden mit zwei Schalenklappen. *Verhand. Deutsch. Zool. Gesellsch. Wien.*, Pp. 403–439.

Clarke, A. H. and R. J. Menzies 1959. *Neopilina (Vema) ewingi*, a second living species of the Paleozoic class Monoplacophora. *Science*, **129**: 1026–1027.

Fischer-Piette, E. and A. Franc 1960. Classe des Aplacophores. In *Traité de Zoologie*, P. Grassé, Editor, et Cie, Paris, **5** (2): 1625–1654.

——— 1960. Classe des Polyplacophores. *Ibid.*, **5** (2): 1701–1785.

Franc, A. 1960. Classe des Bivalves. *Ibid.*, **5** (2): 1845–2133.

Graham, A. 1955. Molluscan diets. *Proc. Malacol. Soc. London*, **31**: 144–159.

Harry, H. W. 1964. The anatomy of *Chilina fluctuosa* Gray reexamined, with prolegomena on the phylogeny of the higher limnic Basommatophora. *Malacologia*, **1** (3): 355–385.

Hunter, W. R. and S. C. Brown 1965. Ctenidial number in relation to size in certain chitons, with a discussion of its phyletic significance. *Biol. Bull.*, **128**: 508–521.

Hyman, L. H. 1940–1967. *The Invertebrates.* McGraw-Hill, New York, 6 Vols.; 1940, Vol. 1, Protozoa through Ctenophora, 726 pages; 1951, Vol. 2, Platyhelminthe and Rhynchocoela, the acoelomate Bilateria, 550 pages. 1967, Vol. 6, Pt. 1, Mollusca: Aplacophora, Polyplacophora, Monoplacophora, Gastropoda, 800 pages (Not seen).

Knight, J. B., L. R. Cox, A. M. Keen, R. L. Batten, E. L. Yochelson and R. Robertson 1960. *Archaeogastropoda.* In *A Treatise on Invertebrate Palaeontology*, R. C. Moore, Editor, Geol. Soc. Amer., Tulsa, Okla, Pt. I, Mollusca i, 351 pages.

Lankester, E. R. 1891. Mollusca. *In* Zoological Articles contributed to the *Encyclopaedia Britanica*, pp. 95–158. Adams and Charles Black, London. (Originally appeared 1883, in Vol. 16 of the Ed. 9 of the *Encyclopaedia*, which I have not seen).

Lemche, H. and K. G. Wingstrand 1959. The anatomy of *Neopilina galatheae* Lemche. *Galathea Reports*, 3: 9–17.

——— 1960. Classe des Monoplacophores. In *Triaté de Zoologie*, P. Grassé, Editor, 5 (2): 1787–1821.

Morton, J. E. 1959. The habits and feeding organs of *Dentalium entalis.* *Jour. Mar. Biol. Assn. U.K.*, **38**: 225–238.

—— and C. M. Yonge 1964. Classification and structure of the Mollusca. In *Physiology of the Mollusca*, K. M. Wilbur and C. M. Yonge, Editors, Academic Press, New York, **1**: 1–58.

Naef, A., 1926. Studien zur generellen Morphologie der Mollusken. 3 Teil. Die typischen Beziehung der Weichtierklassen untereinander und das Verhaltnis ihrer Urformen zu anderen Coelomaten. *Ergeb. u. Fortschr. d. Zool.*, **6**: 27–124.

Pelseneer, P., 1906. Mollusca. In *A Treatise on Zoology.* E. R. Lankester, Editor. Adams and Black, London, **5**: 355 pages.

Pruvot, G., 1890. Sur le development d'un solenogastre. *C.R. Acad. Sci. Paris*, **114**: 1211–1214.

Thompson, T. E., 1960. The development of *Neomenia carinata* Tullberg (Mollusca Aplacophora). *Proc. Royal Soc. Ser.* **B**, **153**: 262–278.

Verrill, A. E., 1896. The molluscan archetype considered as a veliger-like form, with discussions of certain points in molluscan morphology. *Amer. Jour. Sci. Ser.*, 4 (8): 91–99.

Wesenberg-Lund, E. 1938. *Ophryotrocha geryonicola* refound and redescribed. *Meddeland Göteborgs Musei Zool. Avd.*, **81**: 1–13.

ON THE OPISTHOBRANCHIATE FAUNA OF THE GULF OF KUTCH[1]

K. R. NARAYANAN

Fisheries Research Station, Jamnagar, India

ABSTRACT

The studies on the marine fauna of the Gulf of Kutch, though initiated by Hornell (1909-10), have been revived only very recently by Gideon, Menon, Rao and Jose (1957), Menon, Dasgupta and Dattagupta (1961) and Kundu (1965). The rich opisthobranchiate molluscan fauna of this part of the Arabian Sea has not received much attention, even though the other groups of the Phylum Mollusca of this Gulf and the North-Western Coast of India have been dealt with at length. Eliot's works on the nudibranchs collected by Townsend from Karachi and Maskat (1905) and those collected by Hornell (1909) and the account given by Menon *et al.* (1961) appear to be the only information on them.

On the whole there has not been much work done on this group of animals from the Indian Coast excepting those initiated by Kelaart (1859), Alder and Hancock (1864), Farran (1905), Smith (1906), Eliot (1906, 1909, 1910 and 1916), and O'Donoghue (1932). Most of these works are based on the collections made along the South-Eastern Coast of India, Gulf of Mannar and Ceylon.

The present work which deals with 25 species of tectibranchs and nudibranchs, belonging to nine families, collected from the Gulf of Kutch, adds, in the first instance, to the information on the marine fauna of the Gulf of Kutch and secondly gives an account of the extent, to which different groups of opisthobranchs are distributed along the Indian Coast.

THE monumental work of Alder and Hancock (1866), who described the nudibranchs collected by Walter Eliot from the East and South Indian and Ceylonese coasts, is perhaps the first detailed account on the Indian opisthobranchs. The above work was followed by Eliot's (1906) review of the species described by Alder and Hancock (1866), in the light of the studies made by Kelaart (1858 and 1859), Farran (1905), and Bergh (1905). The other information on the Indian Opisthobranchs is made available from the works of Eliot (1905, 1909, 1910, and 1916), Hornell (1924 and 1951), O'Donoghue (1932), Gravely (1927 and 1942), Satyamurthi (1952), Rao (1935, 1937, 1952, 1961, and 1963), Patil (1952), Gideon, Menon, Rao and Jose (1957), Rao and Alagarswami (1960), and Menon, Dasgupta, and Dattagupta (1961). Most of the information available on the Indian Opisthobranchiata is based on the specimens collected from the South, South-East, and East Coast of the subcontinent. The only information available on this group of gastropods from the Western Coast, as far as the author knows, is from the works of Eliot (1905 and 1909), Gideon *et al.* (1957), and Menon *et al.* (1961), who have so far recorded twenty-two species from Karachi-Maskat, Okhamandal, and the Gulf of Kutch. The present paper, therefore, proposes to give an account of the opisthobranchiate fauna of the Gulf of Kutch, in the Arabian Sea, based on a collection of twenty-two species, belonging to nine families.

A few of the species, dealt with in the present paper, have been recorded from Karachi-Maskat, Okhamandal, and other parts of the Gulf of Kutch by previous authors. *Elysia grandifolia* Kelaart, *Placomopherus ceylonicus* Alder and Hancock, *Dendrodoris nigra* Stimpson, and *Bornella digitata* Adams and Reeve, which are found in the author's collection also have been recorded previously by Eliot (1905 and 1909) and Menon *et al.* (1961). All the remaining species, dealt with here, are being recorded for the first time from the Gulf of Kutch. Also, the author is not aware of any previous records of such species from the West Coast of India and hence presumes them to be new records from that coast.

---

[1] Presented at the Symposium on Mollusca with the kind permission of the Director of Fisheries, Gujarat State, Ahmedabad.

The materials for the present work were collected from the inter-tidal zone of the different coral reefs of the Gulf of Kutch, between 1963 and 1967. Most of the specimens were collected by the author himself. A few were collected and sent to him by Messrs. R. Ramanandan, P. Gopalakrishnan and M. S. Michael of the Marine Biological Research Station, Government of Gujarat, Port Okha. The materials were studied at the Fisheries Research Station, Jamnagar. Some of them, however, were identified at the Madras Government Museum, Madras, with the help of the specimens preserved there.

The species dealt with in this paper are listed below. The classification followed is that of Thiele (1931), as adopted by Satyamurthi (1952).

Phylum MOLLUSCA

Class GASTROPODA

Subclass *OPISTHOBRANCHIA*

Order PLEUROCOELA (TECTIBRANCHIA)

Series *APLYSIACEA*

Family APLYSIIDAE

1. ***Aplysia benedicti*** **Eliot**

Order SACOGLOSSA

Family ELYSIIDAE

2. ***Elysia grandifolia*** **Kelaart**

Order ACOELA

Suborder PLEUROBRANCHOMORPHA

Family PLEUROBRANCHIDAE

Subfamily PLEUROBRANCHINAE

3. ***Berthellina minor*** **Bergh**

Subfamily PLEUROBRANCHAEINAE

4. ***Pleurobranchaea morula*** **Bergh**

Suborder NUDIBRANCHIA

Series *DORIDACEA*

Family POLYCERIDAE

5. ***Placomopherus ocellatus*** **Ruppell & Leuckart**
6. ***Placomopherus ceylonicus*** **Alder & Hancock**
7. ***Placomopherus*** **sp.**

Family DORIDIDAE

Subfamily GLOSSODORIDINAE

8. ***Hypselodoris infucata*** **(Ruppel & Leuckart)**

9. ***Hypselodoris* sp.**

Subfamily DORIDINAE

10. ***Archidoris minor* Eliot**

Subfamily DISCODORIDINAE

11. ***Discodoris boholiensis* Bergh**

Subfamily KENTRODORIDINAE

12. ***Kentrodoris funebris* Kelaart**

Subfamily PLATYDORIDINAE

13. ***Hoplodoris desmoparypha* Bergh**

Family DENTRODORIDIDAE

14. ***Dendrodoris nigra* Stimpson**

15. ***Doriopsilla miniata* Alder & Hancock**

***Doriopsilla miniata* var.**

Family PHYLLIDIDAE

16. ***Phyllidia zeylanica* Kelaart**

Family ARMINIDAE

Subfamily DERMATOBRANCHINAE

17. ***Dermatobranchus semistriatus* Baba**

Subfamily ARMININAE

18. ***Armina* sp.**

19. ***Armina (Linguella) cinerea* Farran**

Family BORNELLIDAE

20. **Bornella *digitata* Adams & Reeve**

Family TERGIPEDIDAE

21. ***Hervia ceylonica* Farran**

22. ***Hervia militaris* Alder & Hancock**

It has not been possible for the author to study some of the specimens dealt with here in an exhaustive manner, as they were sent to him in preserved condition. Such specimens were very much shrunken and had lost their natural colour. However, a few of such specimens had notes indicating their natural colouration. Even in such specimens there was no information about the external parts such as the gills, rhinophores, etc., and so much so, studies with regard to their specific status was practically impossible.

The present paper, it is hoped, would, in the first instance, add to the information on the marine fauna of the Gulf of Kutch, the studies on which were initiated by Hornell (1909 and 1919) and later revived by Gideon *et al.* (1957), Menon *et al.* 1961, and Kundu (1965), and secondly would contribute to the knowledge on the distribution of the Opisthobranchiate Gastropoda along the West coast of India.

SYSTEMATIC ACCOUNT

Order PLEUROCOELA (TECTIBRANCHIA)

Series *APLYSIACEA*

Family APLYSIIDAE

***Aplysia benedicti* Eliot (1899)**

(Figs. 1 *a*, *b*, and *c*)

A good many specimens of this species have been collected from Hanuman Dandi Reef (Port Okha), Pirotan Island (Off Jamnagar), and Sikka. Length varies from 8 to 10 cm. and breadth between 5 and 7 cm. Body soft and elongately ovoid with a smooth skin. The posterior end of the body is drawn out to form a tail. Tentacles large and leaf-like. Rhinophores cylindrical and cleft at their tips. Parapodia large. Mantle thin and encloses the shell, which is large, ovate in outline, thin and transparent. Ctenidium single situated on the right side between the mantle and the foot. Radula has many closely set teeth with a median tricuspid tooth. Natural colouration greenish-black with irregular ocellate spots.

Order SACOGLOSSA

Family ELYSIIDAE

***Elysia grandifolia* Kelaart (1858)**

(Figs. 2 *a* and *b*)

Two specimens collected from Poshitra Reef in June, 1965, and ten specimens from Hanuman Dandi Reef (Port Okha) collected on December 27, 1966, constitute the material. They varied from 3 to 6·5 cm. in length.

When alive, they had beautiful olive green colouration on the wings and rather pale greenish tinge in the centre of the dorsal side. There are many black spots scattered irregularly on the dorsal surface. The margin of the body is characterised by an exterior black and interior golden-yellow lining, which are continued to the rhinophores.

The shape of the body more or less resembles a leaf. The tail is pointed. Pericardial thickening is rather longish in four of the specimens, while in others it is somewhat triangular and swollen. Reticulations, arising from this thickening, which are characteristic of this species, are very prominent in the present forms and they are found scattered all over the body.

The head is anteriorly placed, engulfed between the anterior projections of the wings. Head carries rhinophores, which are shrunken in most of the specimens, and the mouth ventrally. Radula typical in having only a single row of teeth.

Order ACOELA

Suborder PLEUROBRANCHOMORPHA

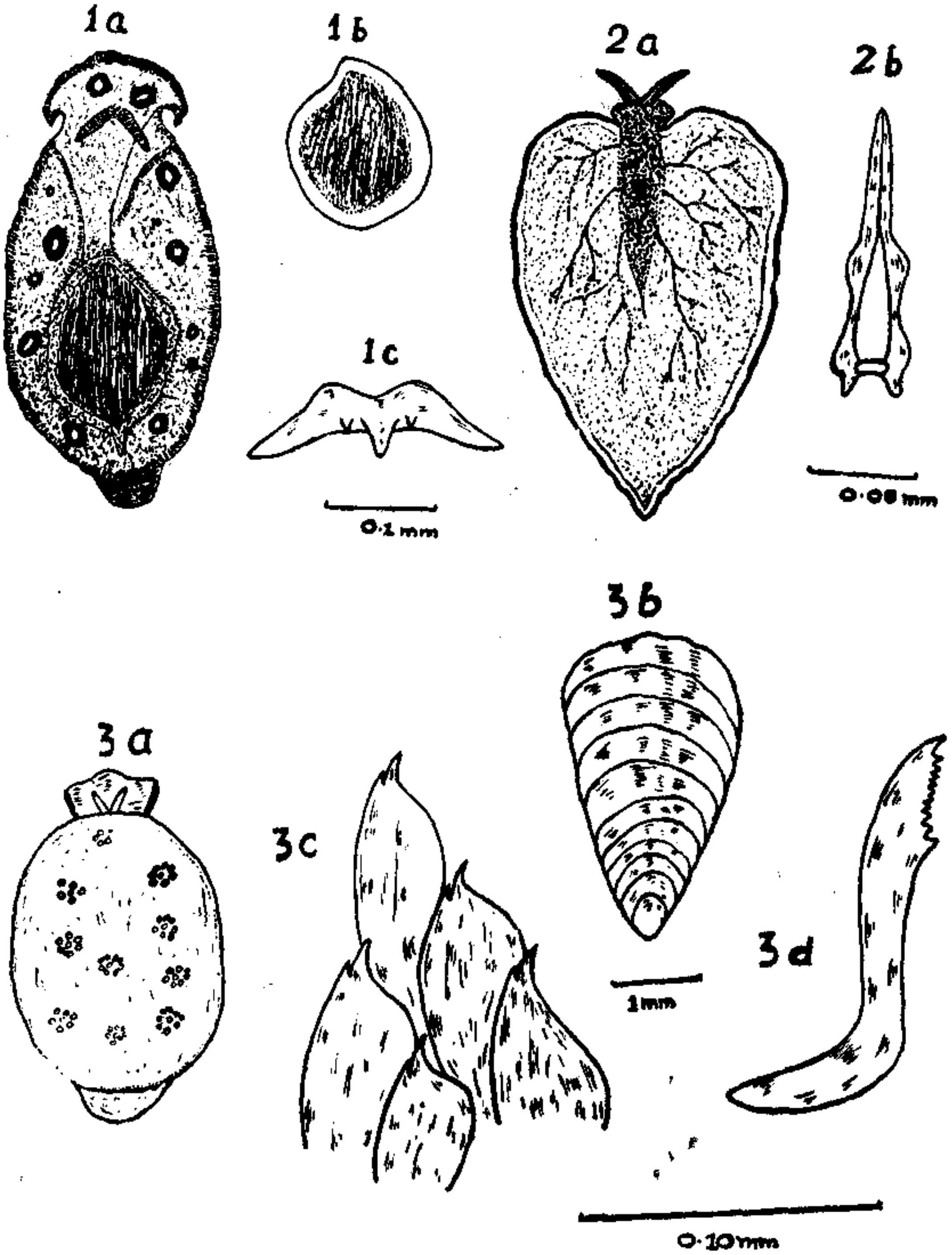
Family PLEUROBRANCHIDAE

Subfamily PLEUROBRANCHINAE

***Berthellina minor* Bergh (1905)**

(Figs. 3 *a* to 3 *d*)

Eighteen specimens, varying between 15 and 30 mm. in length, collected from Okha and nearby areas and preserved in the Fisheries Museum at Port Okha, two fresh specimens, measuring 10



FIGS. 1–3. Figs. 1 *a–c*. *Aplysia benedicti* Eliot. (*a*) Dorsal view. (*b*) Shell. (*c*) Median tooth. Figs. 2 *a–b*. *Elysia grandifolia* Kelaart. (*a*) Dorsal view. (*b*) Tooth from radula. Figs. 3 *a–d*. *Berthellina minor* Bergh. (*a*) Dorsal view. (*b*) Shell. (c) Jaw elements. (*d*) Single tooth from radula.

and 17 mm. in length and 6 and 12 mm. in breadth respectively, collected from Dona Reef in December, 1966, and a single fresh specimen, measuring 12 mm. in length, 10 mm. in breadth and 6 mm. in height, collected from Pirotan Island in June, 1967, constitute the material.

The fresh specimens were bright orange in colouration with groups of minute white specks scattered irregularly on the dorsal surface. The preserved specimens, however, had become quite brownish in the preservative.

Body ovate, inflated, and high. The dorsum is highly convex. Mantle ample and smooth. Oral tentacles modified as velar flap and had an orange-coloured body. Rhinophores situated dorsal to the velar flap, are tubular, and very close to each other, especially at their bases. On either side of the rhinophores is an ocellate black spot, which is not clear in some of the specimens. Foot ovate, broad, and bright orange in colour with a smooth sole.

Between the mantle and the foot, on the right side, is the ctenidium which is plume-shaped and has 17 to 20 pectinate lamellae on either side of the rhachis, which is tuberculated, corresponding to the lateral lamellae.

The genital organs are fleshy and flap-like situated anterior to the ctenidial base. Anus is situated at the dorso-posterior side of the ctenidial base at about two-third of its length.

The labial armature consists of two horny plates, which are broad anteriorly and tapering posteriorly. On these plates are arranged many smooth hook-like elements. Radula is rather large and has about 108 rows of teeth. Teeth are typical with ten denticles on the inner side.

The shell is about 4·5 mm. long and 2·5 mm. broad at the widest end. It is rather triangular, thin and flat and anteriorly placed. On the dorsal side of the shell are seen many ring-like markings.

I doubtfully place the present specimens under the species *Berthellina minor* Bergh, since they differ in a few respects from *Berthella minor* described by Bergh (1905), such as the external colour pattern, variation in the number of gill lamellae, more rows of teeth in the radula and less number of denticles in the teeth. Also, the present forms show some similarity towards the Ceylonese form, *Pleurobranchus* (*Berthella*) *citrinus* (Ruppell and Leuckart) described by Farran (1905), especially in the external colour pattern. However, the presence of only ten denticles in the teeth and varied radular count differentiate the present forms from *Pleurobranchus* (*Berthella*) *citrinus* (Ruppel and Leuckart) Farran (1905). It is possible that the present forms are a local variation of *B. minor* Bergh (1905).

Subfamily PLEUROBRANCHAEINAE

Pleurobranchaea morula Bergh (1905)

(Figs. 4 *a* to 4 *c*)

A single specimen was collected from the trawl net catches of the Survey Vessel, Gulfshrimp, of the Department of Fisheries, Gujarat State, during her operations in April, 1965, at 25 to 30 meters depth off Pirotan Island.

Body is elongate and ovoid in shape. The anterior buccal parts have been protruded and hence have the form of a proboscis, similar to that of *Pleurobranchaea meckeli* illustrated by Pelseneer (1906).

Mantle broadly ovate and covers the major portion of the body. Its dorsal surface is thick and characterised by reticulate groove-like depressions, which makes the dorsal surface look uneven. Rhinophores project from the sides, anterior to the mantle, and are cylindrical with conical distal ends. Their surface is smooth and has a longitudinal slit at the posterior side. Anterior to the rhinophores are the oral tentacles, which are fused to form a veil. The veil is rather triangular and they bear on the posterior surface many creamy tubercles, which are more numerous and larger towards the sides. Foot is broad anteriorly and tapering posteriorly, which extends beyond the margin. Foot margin is wavy and the sole is characterised by the presence of several globular swellings.

Between the mantle and the foot on the right side is the pectinate ctenidium 19 mm. long, with 25 lamellae on the upper row and 24 on the lower row. The genital orifice is situated anterior to the attachment of the gill rhachis as an anterior, thin, rolled-up fleshy flap and a posterior lobe, bearing the opening to the exterior. The anal opening is situated hidden by the upper row of the ctenidium at a level, just in front of its centre. A shell is absent altogether.

Jaw plates pale yellow and measure 35 mm. in length and 10 mm. in breadth and bear many rows of four, five, or six-sided elements with 3 to 5 denticles. Radula quite large and measures 15 mm. in length and 11 mm. in breadth and is brown in colour. Teeth are uniform, large, sharp, and possess a denticle. There are about 38 rows of teeth, each row bearing about 75 teeth on either side of the naked rhachis.

The animal had a flesh colouration, when caught, which has turned brownish in the preservative, and measures 85 mm. in length (including the protruded buccal parts), 34 mm. in breadth, and 22 mm. in depth.

The present form differs from *Pleurobranchaea brocki* Bergh, which has been reported from Madras coast by Gravely (1942), in the smaller number of lamellae on the ctenidium and different dental formula. Rachidian tooth, which is always found in *P. brocki* Bergh, is absent in the present specimen. Some of these differences were also observed in the same species by Vayssiere (1901) and Farran (1905). Farran's specimen also had a furrowed and rough mantle surface, pointed and upwardly bent tail, a frontal margin with two rows of minutely tuberculate papillae, and a dental formula of 29 × 56.0.56. Similarly, the present form bears resemblance to *P. maculata* Quoy and Gaimard, described by Vayssiere (1901), which possesses 23 to 25 pinnules in the gill and a radular formula, 80.0.80. The absence of any papillae, however, differentiate it from the present form. Further, *P. maculata* is said to be white to yellowish in colour. The resemblance of the present form to *P. meckeli* Leue, described by Vayssiere (1901) and Pelseneer (1906), also can be ruled out due to the differences in the external colouration and radula. The characters of *P. tarda* (Verrill) Vayssiere (1901), *viz.*, the reddish-brown colour, general structure of the body and rhinophores, reticulations on the mantle surface, posteriorly narrowed foot, and the dental formula, 70.0.70 do tally with those of the present form; but the absence of any papillae in *P. tarda* differentiates it from the present one. The present specimen bears more resemblance to *Pleurobranchaea morula* Bergh (1905), which has two regular rows of twelve small cones or papillae on the velum and a radular formula 40 × 50.0.50. Therefore, though not with confidence, it has been listed under that species.

Suborder NUDIBRANCHIA

Series *DORIDACEA*

Family POLYCERIDAE

Subfamily POLYCERINAE

***Placomopherus ocellatus* Ruppell & Leuckart (1828)**

(Fig. 6)

A single specimen was collected from Okha on March 3, 1967. The preserved specimen measured 20 mm. in length and was gelatinous and colourless. The natural colouration is said to be dull brown in ground colour with many violet-black spots and orange-red round or oval blotches.

The oral veil is large with numerous minute pinnate and bipinnate processes. The rhinophores are 2 mm. long, laminated, and yellowish-orange in colour. The branchiae are also of the same colour, five in number and situated in the centre of the dorsum.

The body carries three pairs of lateral processes on either side. The anterior two pairs are ramified and the third pair bears knobs coloured in orange-red. There are many other small processes also scattered irregularly on the mantle. Foot is narrow and tapers behind to form a tail.

Yellow jaw plates are triangular in shape and measure 1·4 mm. in length, 5 mm. in width at the broadest part. Radula bears 15 rows of teeth. The rhachis is broad and traversed by cross-lines. Rachidian tooth is absent in all rows. Each row bears on either side 3 innermost hamate teeth and 9 plate-like outer teeth. Radula is yellow in colour.

The characters of the present specimen approximate those of *P. ocellatus* Rupp. and Leuck. However, it varies from the same species described by Eliot (1908) from the Red Sea, in the colour pattern on the body and in the third pair of the lateral processes. But, Eliot (1908) himself has remarked that 'The colour of this species varies and appears to depend on its food'.

Placomopherus ceylonicus Alder & Hancock (1866)

(Figs. 5 *a* and 5 *b*)

Three specimens collected from Okha in 1963 have been preserved at the Fisheries Station at Port Okha. The biggest specimen measured 35 mm. in length, 15 mm. in breadth, and 20 mm. in height.

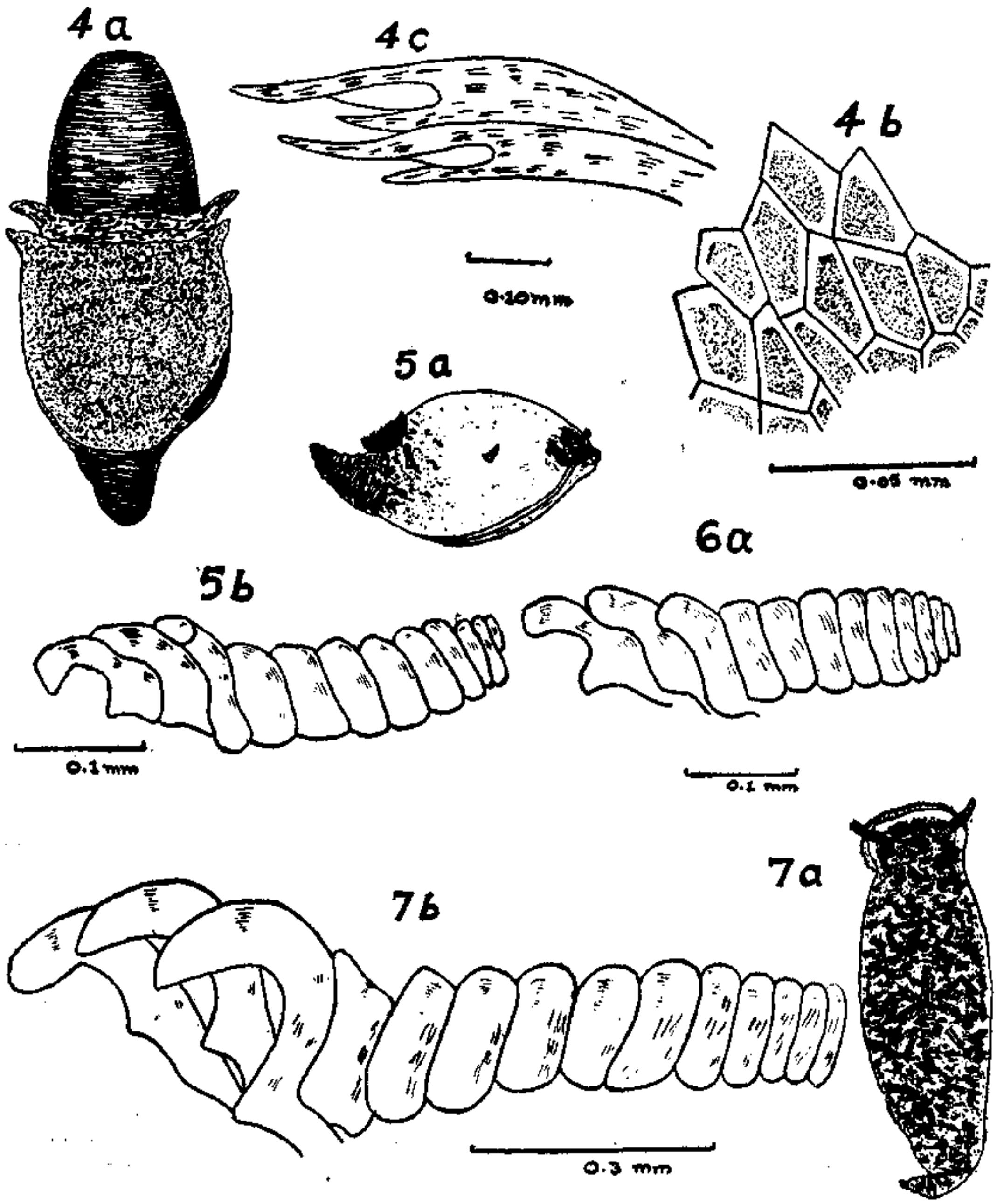
In preservative, the animals are plump, high, and laterally compressed. Foot is narrow, long and produced posteriorly to form a tail, which extends beyond the mantle margin, 14 mm. long, in the biggest specimen, and bent upwards. Its lateral sides are highly folded.

Body is on the whole dull whitish transparent and jelly-like. But the spaces in between the rhinophores and the branchiae and posterior margin of the mantle have a greenish ground colour and are characterised by the presence of many small projections and wart-like protuberances. These areas are mottled in blackish-brown. The rhinophores are about 5 mm. long in the biggest specimen, colourless and laminated. Oral veil is continued as a ridge towards the posterior part of the rhinophores.

The branchiae consist of mainly three major plumes—an anterior median one, and two lateral ones, which are again branched into two. So much so, the gills appear to be five in number, foliaceous and tuft-like. The circle is incomplete and open behind, where the anus is situated on a small round papilla. The spaces on either side and behind the branchiae are mottled and greenish in colour, with many small papillae and protuberances.

Three pairs of lateral processes are present. The anteriormost pair is situated between the rhinophores and the gills and are conical in shape and colourless. The second pair is situated at a level of the anterior margin of the gills. They are greenish basally and bear pinkish knobs at their ends. The third pair is at the posterior margin of the gills at a level higher than that of the second pair. They also, like the second pair, bear pink knobs.

The anterior veil and other oral parts are highly shrunken. However, the mouth could be seen as a round opening on a rather round labial thickening. Labial plates are yellowish-brown and triangular. Radula is yellowish-brown with 18 complete and 2 incomplete rows of teeth. The first and second rows, which are incomplete, have 5 and 8 plate-like teeth respectively on either



FIGS. 4–7. Figs. 4 *a–c*. *Pleurobranchaea morula* Bergh. (*a*) Dorsal view. (*b*) Jaw elements. (*c*) Tooth. Figs. 5 *a–b*. *Placomopherus ceylonicus* Alder & Hancock. (*a*) Lateral view. (*b*) A half row of radula *in situ*. Fig. 6. *Placomopherus ocellatus* Rupp. & Leuck., one half row of radula *in situ*. Figs. 7 *a–b*. *Placomopherus* sp. (*a*) Dorsal view. (*b*) A half row of radula *in situ*.

side. The remaining rows have 3 inner hamate teeth and 9 outer plate-like teeth on either side. Rhachis is plain with cross-lines.

The present forms agree with Alder and Hancock's (1866) description of the species *Placomopherus ceylonicus*, in most of the points. They differ from the description in that they do not have any spots or blotches of brown, yellow or orange, the posterior pairs of lateral processes bear pinkish knobs, and the absence of any ridges on the body. The difference in the external colour pattern can be ruled out since the present materials have been in the preservative from 1963. Eliot's (1909) description of the same species collected from Kiu Point (Okhamandal) shows that they too had coloured knobs on the posterior pair of the lateral processes. *P. imperialis* Angas also is said to have purpled-coloured knobs, but only on the last pair. Further, *P. imperialis* is reported to possess five inner hamate teeth in the radula, which differentiates *P. imperialis* from the present forms. It is, therefore, felt that the present specimens are more allied to *Placomopherus ceylonicus* Alder and Hancock (1866) and hence recorded under that species.

Placomopherus sp.

(Figs. 7 *a* and 7 *b*)

A single specimen collected from Balapur area in December, 1966, constitute the material.

The animal is fairly large and measures 56 mm. in length, 16 mm. in breadth, and 20 mm. in height. In external appearance, it is gelatinous, dirty white with brownish-black mottlings all over the body. The mottlings are, however, more on the dorsal surface. There are dirty white spaces in between the mottlings. The large oral veil bears numerous minute branched processes. Rhinophores are white in colour and laminated. They are placed at a distance of about 35 mm. from the anterior margin. Their bases are mottled like the body, while the distal parts are white. There are three pairs of lateral processes. The first pair is rather pointed while the second and third pairs bear knob-like structures at their distal ends. The knobs also are mottled and blackish-brown in colour. Anterior to the first pair of the lateral processes, on the right side, is another single process with a pointed tip.

Foot very long, narrow, and produced posteriorly to form a tail, which extends beyond the mantle margin.

Jaw plates are yellowish-brown, 2 mm. long and triangular in shape. The maximum breadth is 1 mm. Radula brownish and measures 5 mm. in length and 3 mm. in width at the broadest portion, with three anterior incomplete and 20 complete rows of teeth. The anterior three rows have no hamate teeth and have a formula, $7 + 0.0.0 + 7$, $9 + 0.0.0 + 9$ and $10 + 0.0.0 + 10$ respectively. As regards the complete rows, all have three inner hamate teeth and varied numbers of marginal plates. The first six rows have 11 marginals, the next four have 12, and the remaining six have 13 marginals on either side of the rhachis. The dental formula, therefore, varies from $11 + 3.0.3 + 11$ to $13 + 3.0.3 + 13$.

The present specimen approximates in some respects *Placomopherus ceylonicus* Alder and Hancock (1866); but *Placomopherus ceylonicus* is described by Alder and Hancock (1866) as yellow, orange, or deep orange in colour with a dental formula, $18 \times 9\text{–}10 + 3.0.3 + 10\text{–}9$. Eliot (1909) has observed a dental formula, $11\text{–}15 + 3.0.3 + 15\text{–}11$, in some of his specimens of the same species from Okhamandal. The increased number of marginals in Eliot's (1909) specimens were confined to the posterior portion of the radula. The present form differs from *P. ocellatus* Ruppell and Leuckart (1828) also, in the external colour pattern. Further, *P. ocellatus* Ruppell and Leuckart (1828) is said to possess a dental formula, $13\text{–}21 \times 9\text{–}10 + 3.0.3 + 10\text{-}9$.

It is, therefore, felt that the present form is a varied species which should be placed between *Placomopherus ceylonicus* Alder and Hancock (1866) and *Placomopherus ocellatus* Ruppell and

Leuckart (1828). Though the external colour pattern can be ruled out as a local variation, the radula indicates that the present form is different from the other species of this genus.

Family DORIDIDAE

Subfamily GLOSSODORIDINAE

Hypselodoris infucata (Ruppell & Leuckart)

(Figs. 8 *a* to 8 *c*)

Three specimens measuring 30, 20, and 15 mm. collected from Pirotan Island on March 15, 1967, constitute the material. They were found to swim freely in knee-deep waters in the rocky pools among coral reefs.

When alive, their ground colour was bluish (paler in the smaller specimens) with many yellowish-orange round or oval patches and numerous blue spots scattered all over the dorsum. The mantle margin had a border consisting of a compact row of blue spots. The mantle surface appeared to be smooth; but when examined under a lens it was found to possess many minute granulations. Rhinophores orange-red coloured and have about 15 lamellae. Branchiae, which are highly retractile, consist of ten orange-red pinnate gills, arranged around the anus in a complete circle. The anal portion also was beautiful blue in colour, when alive.

The ventral colouration is pale blue. Oral tentacles very small and appear only as small projections on either side of the mouth. Foot oval, narrow, and elongate, bluish in colour and produced posteriorly to form a tail, which extends beyond the mantle margin. Jaw plates made of minute hooks. Radula with 69 rows of teeth, which are colourless, bent, and bicuspid.

The present forms appear to be a variety of *Chromodoris infucata* (Ruppell and Leuckart) [= *C. crossei* (Angas) Bergh; *C. semperi* Bergh; *C. uncinata* Bergh and *C. diardii* Kelaart]. The author has followed Odhner's (1957) suggestion and adopted the generic name *Hypselodoris* Stimpson instead of *Glossodoris* Ehrenberg, as adopted by Burn (1961).

A similar glossodorid has been collected from Pirotan Island and described as *Chromodoris universata* Prat by Gideon *et al.* (1957). Unfortunately not much information is available on that specimen.

Hypselodoris sp.

(Figs. 9 *a* to 9 *c*)

Three specimens were collected from Okha in 1963 and preserved at the Fisheries Museum at Port Okha. In the preservative, they measured 45, 26 and 23 mm. in length and had become completely white. There is no information as regards the natural colour of these animals.

The white mantle is smooth without any papillae or granulations and not very wide. Its margin is very thick. Foot fairly long, narrow, and drawn out posteriorly to form a tail. Foot is comparatively transparent in one of the specimens. In the larger two specimens, however, the tail is not very prominent. Head, oral tentacles, and rhinophores are completely withdrawn in all the specimens. The lamellae on the rhinophores of the smallest specimen could be made out. Gills also have been withdrawn in the two larger specimens; but in the smallest, however, there are well-expanded nine pinnate gills arranged in a circle in a round branchial pouch. Anus is very prominent on a projection in the centre of the branchial ring. Jaw plates with minute hooks. Radula bears 66 rows of hamate and bicuspid teeth. There are about 100 teeth on either side of the naked rhachis.

It has not been possible to identify this species since it has been in preservative and hence colourless and contracted.

Subfamily DORIDINAE

Archidoris minor Eliot (1903)

A single preserved specimen, which is reported to have been collected from Okha in 1963, forms the material.

The preserved specimen measures 36 mm. in length and 21 mm. in breadth and is chestnut-coloured on both sides. Mantle surface provided with many large, whitish translucent tubercles, which are scattered irregularly. Tubercles in the centre of the dorsum are larger than those on the margins.

Rhinophores blackish-brown and laminated. The branchiae, though withdrawn to some extent, appear to be six in number and tripinnately branched. They are coloured as the dorsum. Foot broad, long, and oval. Its anterior margin is differentiated into dorsal and ventral laminae and notched along the median line. Mouth is a vertical slit placed on a small projection in between the foot and the mantle. Oral tentacles are cylindrical and translucent. Labial armature consists simply of plate-like structures without any rods or hooks. Radula thin and simple bearing 40 rows of simple hamate teeth. Rhachis is naked.

The specimen approximates in many respects *Archidoris minor* Eliot (1903).

Subfamily DORIDINAE

Subfamily DISCODORIDINAE

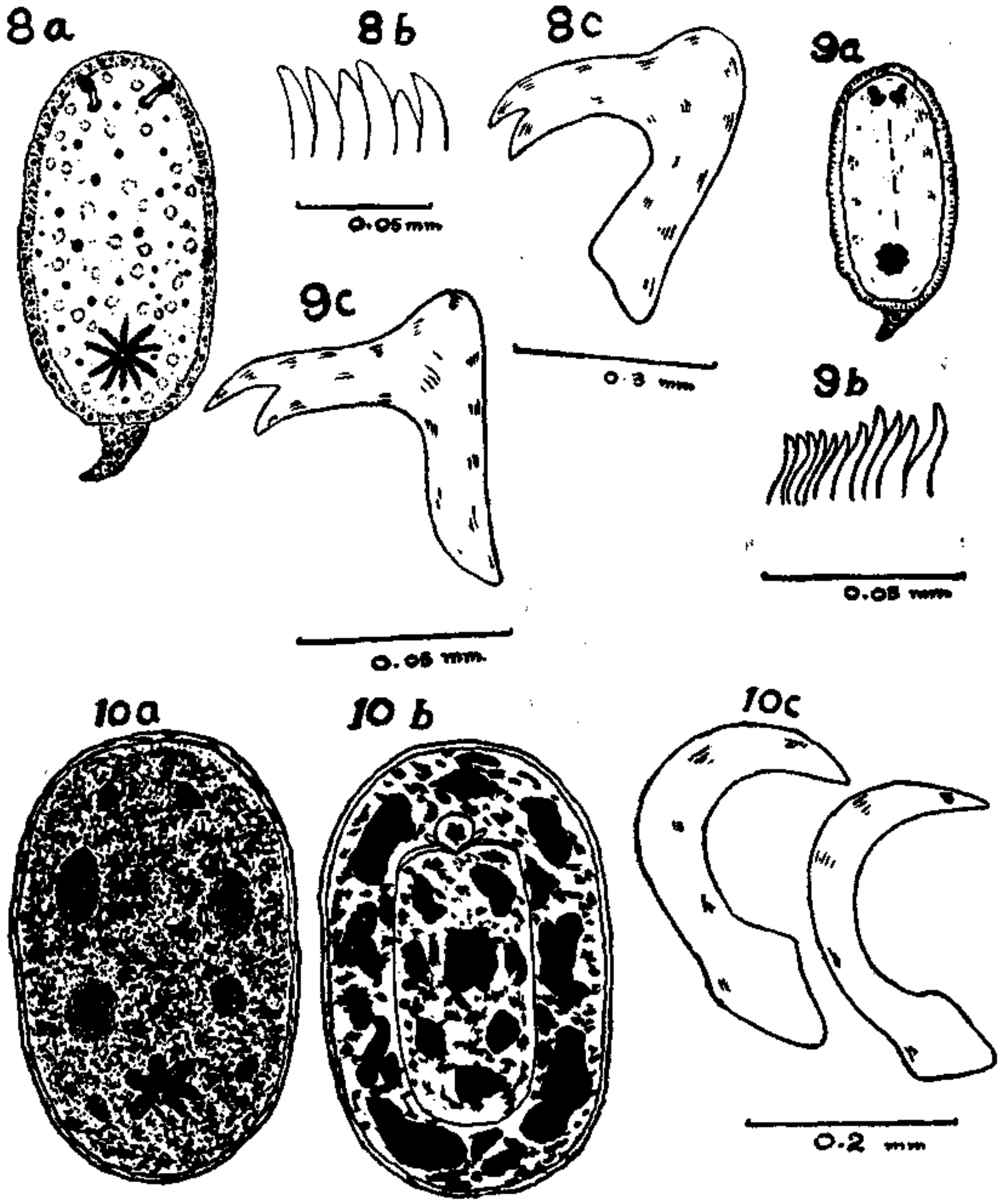
Discodoris boholiensis Bergh (1877)

A single specimen was collected from Pirotan Island on October 14, 1966. The animal is oval in outline and flat in form. When alive, it measured 30 mm. in length and 22 mm. in breadth and had a yellowish-pink colour dorsally and was pale ventrally. Mantle is wide with free margin. Mantle surface appears to be smooth, but on closer examination is found to be thickly papillated. There are many small brownish-black flecks irregularly scattered all over the mantle surface. Rhinophores and branchiae appear to be of the same colour as the mantle. The branchiae though withdrawn to some extent appear to be tripinnately branched. Their exact number could not be determined.

Foot oval, broad anteriorly and rather narrow posteriorly. Anterior margin of foot differentiated into dorsal and ventral flaps, both of which are notched along the antero-median line. Oral tentacles are digitiform and whitish. Labial armature consists of two roughly triangular plates, about 2 mm. long. Radula has simple hamate teeth arranged in 20 complete and 2 imcomplete rows. The formula varies from 35.0.35 to 40.0.40. Rhachis is naked.

The colour of the animal, dorsal papillation, and the radula very strongly suggest that the present form is *Discodoris boholiensis* Bergh (1877).

This species has been recorded by Rao (1961) from the Gulf of Mannar; however, it appears to be a new record from the West Coast,



FIGS. 8–10. Figs. 8 *a–c*. *Hypselodoris infucata* (Rupp. & Leuck.). (*a*) Dorsal view. (*b*) Jaw element. (*c*) Tooth from radula. Figs. 9 *a-c*. *Hypselodoris* sp. (*a*) Dorsal view. (*b*) Jaw elements. (*c*) Tooth from radula. Figs. 10 *a-c*. *Hoplodoris desmoparypha* Bergh. (*a*) Dorsal view. (*b*) Ventral view. (*c*) Tooth from radula.

Subfamily KENTRODORIDINAE

***Kentrodoris funebris* Kelaart (1859)**

(Figs. 11 *a* to 11 *d*)

The present collection consists of many specimens collected from Okha, Movada Reef, Pirotan Island, Chusna and Ajad Islands, and the Rozy Creek. They were found creeping on the mud flats, swimming in knee-deep waters among seaweeds or resting in the crevices of rocks and corals. The size varied from 15 to 60 mm. in length, 5 to 36 mm. in breadth and 2 to 20 mm. in height. Body is rather flat, oval in outline, and brilliant greenish-yellow in colour, with many pinkish-brown to blackish blotches all over the body. Smaller specimens, however, had rather transparent, waxy white colour with paler blotches.

Body smooth and provided with many minute thick-set papillae all over dorsally. Mantle very wide and covers the complete body. It is ornated dorsally with many beautiful pinkish-brown to blackish blotches scattered all over. The blotches in the mid-dorsum are larger and those on the margin are smaller. Generally, they are round or ovate in shape. In some specimens, there are only a few blotches on the dorsal side of the foot, while in others there are many of them arranged in a linear fashion along the foot margin. The blotches, when closely examined, were found to consist of very minute papillae, which bear the pigments at their tips. The papillae, excepting those on the blotches, have the same colour as the body. Skin is velvety smooth and supported by transparent, rod-like spicules.

Rhinophores are highly contractile into a pouch. Their length varies from 2 to 12 mm. and have a white to greenish-yellow stalk and a conical, black and laminated distal club. The number of lamellae in the rhinophoral club is around 19. The colour of the rhinophoral club is also variable from pinkish-brown to jet black.

The branchial circle is incomplete posteriorly. There are six foliaceous and tripinnately branched branchiae, the rhachis of which are coloured as the blotches. Anus is situated in the centre of the branchial ring and its margin also is coloured as the blotches. Branchiae can be withdrawn into a pouch, which when the animal is disturbed, can be seen as a crescent-shaped transverse slit, closed with an anterior and posterior lips, the former being longer than the latter and overhangs the latter.

Foot is oval in shape with a flat sole. Its anterior margin is divided into a dorsal and ventral flap, both of which are notched anteriorly. The demarcation of the dorsal and ventral laminae extends as far back as the lateral margin of the foot. The notch in the antero-median line of the dorsal lamina is deep and hence there is an ample flap on either side.

Mouth situated between the foot and the mantle at the anterior end as a vertical slit. Oral tentacles are digitiform and in most of the specimens, tipped with pinkish-brown to pinkish-black or even dark black colour.

Labial armature is typical. However, the radula showed certain amount of variation. Teeth are arranged in 20 to 25 rows. Rhachis is naked and the formula varies from 18.0.18 to 29.0.29. Teeth are simple and hamate.

The penis is situated on the right side between the mantle and the foot and carries a median transparent spine. This character differentiates the Kentrodorids from Discodorids and based on the presence or absence of the penial stylet, Odhner (1939) has separated the subfamily Kentrodoridinae from Discodoridinae. Odhner's (1939) classification is followed by the author for describing the present specimen.

Even though the present species is the commonest nudibranch in the Gulf of Kutch, it appears not to have been recorded previously. The only records of *Kentrodoris funebris* Kelaart (1859) from the Indian coasts are that of Alder and Hancock (1866) and Eliot (1906) from South India and of Kelaart (1859) from Ceylon. *Platydoris townsendi* described by Eliot (1905) from Karachi-Maskat has only external similarity towards the present form. It is likely that a 'Dorid'' from the Karwar coast described by Patil (1952) is the present species. However, Patil (1952) has not given any detailed account of that species and so nothing can be said about his specimens.

It is, therefore, felt that the present account is the first definite record of this species from the West Coast of India.

Subfamily PLATYDORIDINAE

Hoplodoris desmoparypha Bergh (1880 & 1905)

(Figs. 10 *a* to 10 *c*)

The present collection consists of three specimens, all of them collected from Pirotan Island on October 15, 1965. The animals were attached to coral rocks and due to their external colouration, it was difficult to locate them in their environments. All three specimens are quite large, flat and oval. They measured, when collected, 75 × 52 × 20 mm., 71 × 52 × 15 mm. and 72 × 45 × 15 mm. One of the specimens underwent self-mutilation, when narcotised.

Mantle hard and leathery, dark brownish to blackish-brown in colour, with many irregular, oval or round black patches. Dorsum provided with many thick-set hard granulations, which are dark at the centre and rather yellowish at the sides. The hard skin is supported by rod-like transparent spicules.

Foot sole and the ventral side of the mantle dull white, but the ground colour is often concealed with pinkish-brown patches. These patches are not so close on the foot sole, where they appear mostly as big round or oval patches irregularly arranged.

The rhinophoral opening is rather oval, slightly raised, and margined with granulations. Rhinophores are shrunken, in which condition they measure 5 mm. Their stalk is whitish with pinkish-brown spots and their distal ends are lamellate and of the same colour as the dorsum.

There are six foliaceous, tripinnately branched gills, which have been withdrawn to a great extent. They were dirty white, when the animals were alive. The branchial ring is incomplete and open behind, where the anal papilla (about 2 mm. long) is situated.

Foot flat and oval with its anterior margin split into dorsal and ventral flaps and notched anteriorly. The differentiation of the two laminae extends as far back as the lateral margin of foot.

Mouth situated on a round labial thickening, not as a vertical slit. Oral tentacles are white, 3 mm. long and flat, are not round or digitate. Sex-organs could not be studied since they are completely shrunken.

Lips provided with many minute rods borne on two triangular plates. Radula has 40 rows of teeth and the formula appears to be 80–85.0.85–80. Teeth are simple and hamate.

The buccal cavity is blackish-brown in colour.

The present specimens correspond, in many respects, to *Hoplodoris desmoparypha* Bergh (1880 and 1905) (= *Platydoris papillata* Eliot, 1906 *a*, pp. 648).

Family DENDRODORIDIDAE (= DORIDOPSIDAE)

Dendrodoris nigra **Stimpson**

Two specimens collected on May 13, 1967, from Kiu Point constitute the material. The specimens are fairly big, squarely ovate, and measure 44 × 27 × 13 mm. and 36 × 21 × 11 mm. Natural colour greyish-blue. Dorsum very smooth, gelatinous and bluish in preservation. Rhinophores have been withdrawn, but their tips could be seen as small bluish projections. Branchiae black and tripinnately branched. Their divisions are not very clear, but there appear to be eight gills altogether, which are very closely placed to the posterior margin of the mantle. Mantle margin is paler than the mid-dorsum and highly wringled. Foot is ovately square, with thick wringled margins and dark grey in colour. Anterior margin of the foot is grooved and in this groove is situated the mouth as a small opening. The head is not at all distinct in both specimens. Oral tentacles, labial armature, and radula are absent.

Menon *et al.* (1961) have recorded this species previously from Pirotan Island.

Doriopsilla miniata **Alder & Hancock (1866)**

(Fig. 12)

Two specimens measuring 30 and 25 mm. in length and 21 and 17 mm. in breadth respectively, collected from Dona Reef on December 10, 1966, form the material. They are dull yellow dorsally. The mid-dorsum is rather darker in colouration than the margins. Colouration on the ventral surface and on the foot sole is pale yellow. There are no coloured blotches or spots anywhere on the body.

Dorsally the mantle bears on the dorsal surface many nodule-like round tubercles. They appear to be closely set; however, there are spaces left in between them. Tubercles on the mid-dorsum are larger than those on the margins, the latter being smaller and widely set. There are many yellowish-white reticulations around the tubercles on the dorsal surface. Skin is supported by colourless, transparent, rod-like spicules. The mantle is wide and overhangs the foot on all sides. The mantle margin is wavy and on their ventral side are many reticulations, as on the dorsum, which run across the body.

The rhinophores have been completely withdrawn. Their sheaths are tube-like, with smooth margins, and projecting slightly above the mantle surface. Nothing can be said about the branchiae since they have been withdrawn completely. The branchial pouch is round. Foot is a flat oval sole, measuring 21 × 14 mm. in the bigger specimen and 20 × 11 mm. in the smaller specimen, with a notched anterior margin.

Mouth is a small opening in between the mantle and foot anteriorly. There are no indications of oral tentacles, labial armature, or radula.

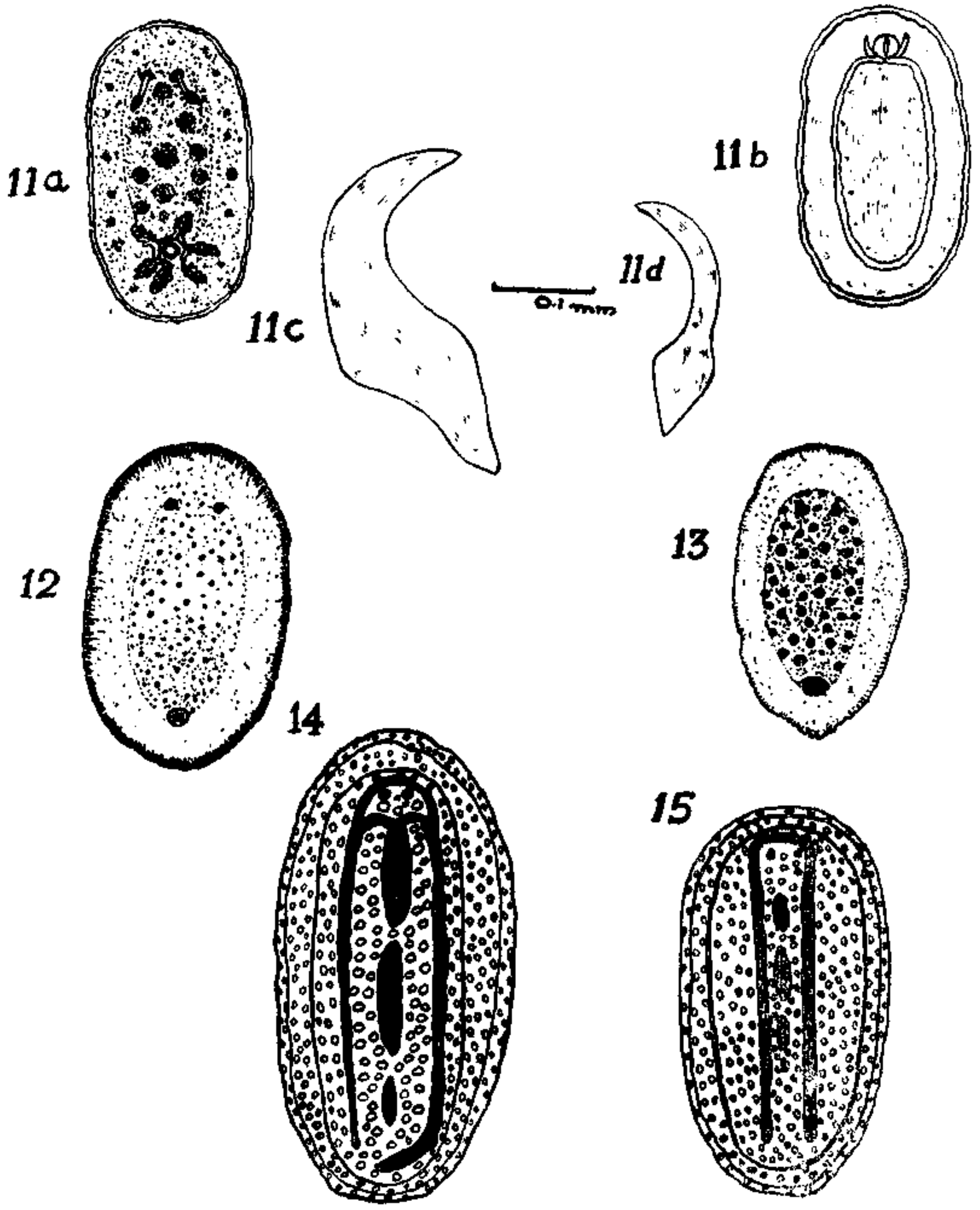
The characters of the present specimens approximate that of *Doriopsilla miniata* Alder and Hancock (1866) and it appears that the present forms are a pale variety of *D. miniata* Alder and Hancock (1866).

Doriopsilla miniata **var.**

(Fig. 13)

Two specimens measuring 25 and 28 mm. in length collected from Okha form the material. One of them has lost its natural colour and became grey, while the other one retains its reddish colour, especially on the tubercles.

Dorsal surface of the mantle is studded with round reddish tubercles. The tubercles on the mid-dorsum are bigger than those on the mantle margins. Rhinophores, which appear to have been reddish, have been withdrawn in both specimens. However, their laminated distal ends could be



FIGS. 11–15. Figs. 11 *a–d*. *Kentrodoris funebris* Kelaart. (*a*) Dorsal view. (*b*) Ventral view. (*c*) Outermost tooth from radula. (*d*) Innermost tooth from radula. Fig. 12. *Doriopsilla miniata* Alder & Hancock, dorsal view. Fig. 13. *Doriopsilla miniata* var., dorsal view. Figs. 14–15. *Phyllidia zeylanica* Kelaart, dorsal views.

seen slightly. Secondary branchiae, which also are reddish in one specimen and paler in the other, are pinnate and twelve in number. They form a complete ring around the anus. Foot elongate and its margins are highly wringled. Just in front of the foot is the round suctorial mouth, placed on a round proboscis-like structure. Labial armature, radula, and oral tentacles are absent.

The present forms appear to be a variety of *D. miniata* Alder and Hancock (1866) differing from it in the presence of more branchiae and in the normal position of the anus. Similar variations have been observed in this species by Alder and Hancock (1866) and Satyamurthi (1952).

Family PHYLLIDIDAE

Phyllidia zeylanica Kelaart (1859)

(Figs. 14 and 15)

The present collection consists of two specimens, measuring 22 and 20 mm. in length, collected from Pirotan Island. They are oval in outline. Dorsal surface of the mantle, in the smaller specimen, is adorned by five longitudinal rows of beautiful pink tubercles. These rows, excepting the median one, are joined in a semicircular fashion along the anterior and posterior margins, so as to form outer and inner oval ridges rather parallel to the mantle margin. Each ridge is composed of many tubercles arranged irregularly in groups of two or three. The median ridge is slightly split in the centre and the interspace is filled in by a black line. Similarly, the spaces between the other ridges are also characterised by thick black lines. These lines, excepting the median one, are joined along the anterior and posterior margins in a semicircular fashion. The black lines and the ridges, therefore, are arranged alternately. The animal is very bright and beautiful, with its pink tuberculate ridges and the intermediate black lines.

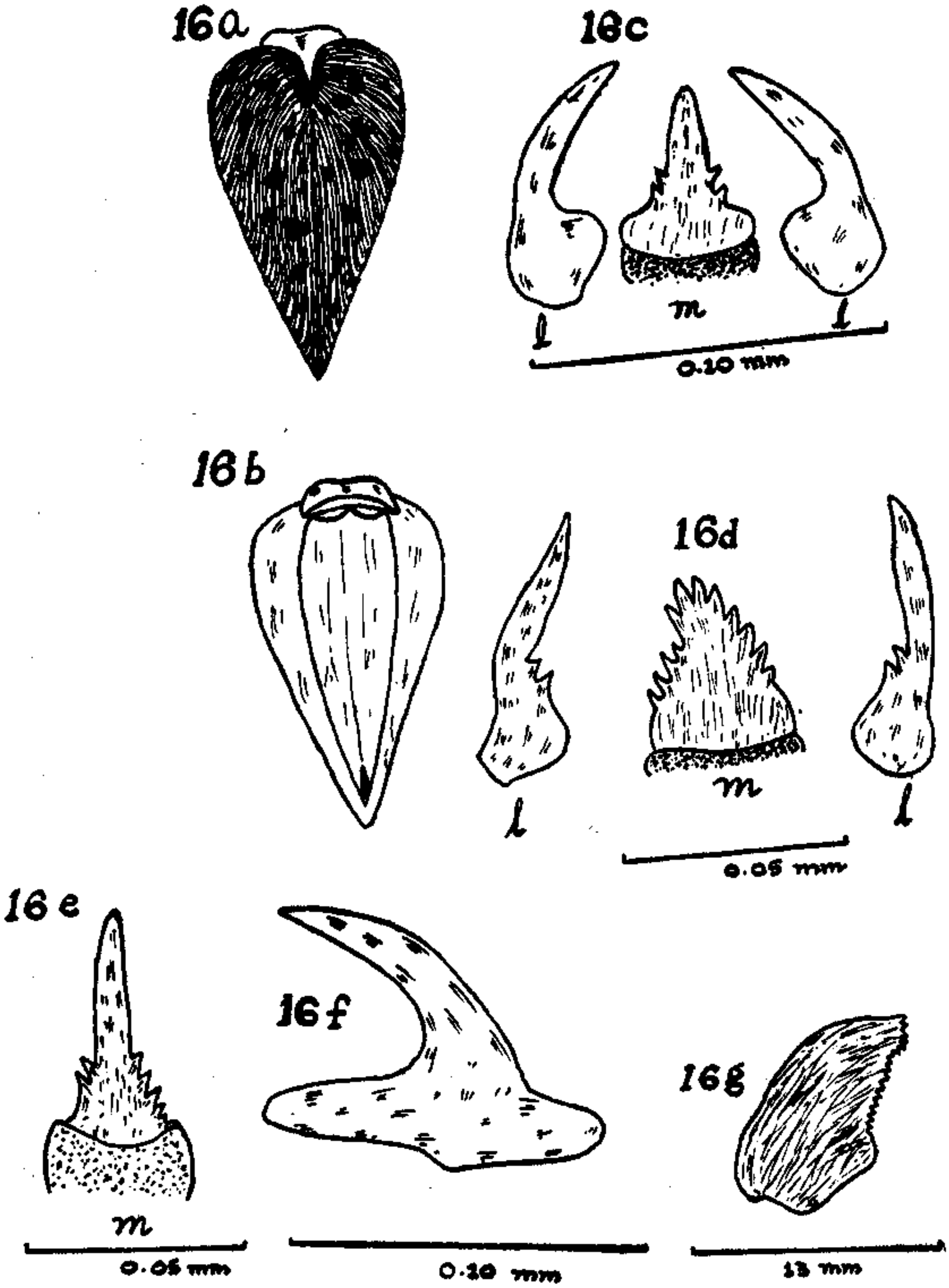
The bigger specimen is similar to the small one in all respects except (1) the median row of tubercles is more widely split and the black line in between is longer and broader, (2) the black lines on either side of the median ridge are broader and not continuous.

Rhinophores in both the specimens are also black with colourless stalks. It is difficult to differentiate the rhinophores from the black lines, if they are not fully extended.

Ventral side of the mantle and the foot have uniform bluish-grey colour. Foot margins are, however, paler. In between the foot and the mantle are 45 to 50 gill lamellae of the same colour as the foot. Anus is situated dorsally.

The black rhinophores and oral tentacles and the general pattern of the dorsum suggest that the present specimens are closely allied to *Phyllidia zeylanica* Kelaart (1859) [Eliot (1906 *a*), pp. 674]. Eventhough the foot sole is coloured as in *Phyllidia varicosa* Lamarck, there are no indications of a median line in the present forms. Bergh (1869) regards *P. zeylanica* Kelaart to be equivalent to *P. varicosa* Lamarck. However, as remarked by Eliot (1906 *a*) they appear to be two distinct species.

The characters of the present specimens tally precisely with the descriptions of Kelaart [1859, *Ann. Mag. Nat. Hist.*, 3 (3): 494] even to the size and colouration. They are, therefore, recorded under the species, *P. zeylanica* Kelaart (1859).



FIGS. 16 *a–g*. *Dermatobranchus semistriata* Baba. (*a*) Dorsal view. (*b*) Ventral view. (*c*) to (*e*) Different types of median and lateral teeth, *m*: Median tooth, *l*: Lateral tooth. (*f*) Outermost marginal tooth. (*g*) Jaw plate.

Family ARMINIDAE

Subfamily DERMATOBRANCHINAE

Dermatobranchus semistriatus Baba (1949)

(Figs. 16 *a* to 16 *g*)

About 20 specimens collected long ago from Okha and a single fresh specimen collected on May 13, 1967, from Kiu Point were examined. The colour of the preserved specimens varied from pale flesh to pinkish, with many irregular black spots. In a few of the specimens the colour has faded out completely and they have become white and transparent. The fresh specimen had a yellowish-pink colour dorsally and paler ventrally, with many black spots all over dorsally and along the mantle margin.

Length varies between 25 and 45 mm. Body is more or less soft and sluggish, broad at the anterior end and tapering posteriorly. Posterior end of the body is rather pointed. Oral shield is broad and squarely rounded, pale pinkish in the fresh specimen and more or less transparent in the preserved ones. Mantle broader than the foot and grooved anteriorly along the mid-dorsal line, just behind the rhinophores. Rhinophores are withdrawn in most of the specimens and their clubs are of a darker shade than the dorsum. Pattern of the mantle surface is distinct in having 23 to 27 ridges of the same colour pattern as the dorsum originating from the ridge-like thickening on either side of the anterior groove of the mantle. These ridges are arranged on either side of a median straight ridge, not parallel to it, but going towards the mantle edges. There are about 9 to 11 primary ridges on either side of the median one. The interspaces between the primary ridges are filled in by the secondary ones. The mantle edges are not even, brown to blackish-brown in colour, and bear conidiophores.

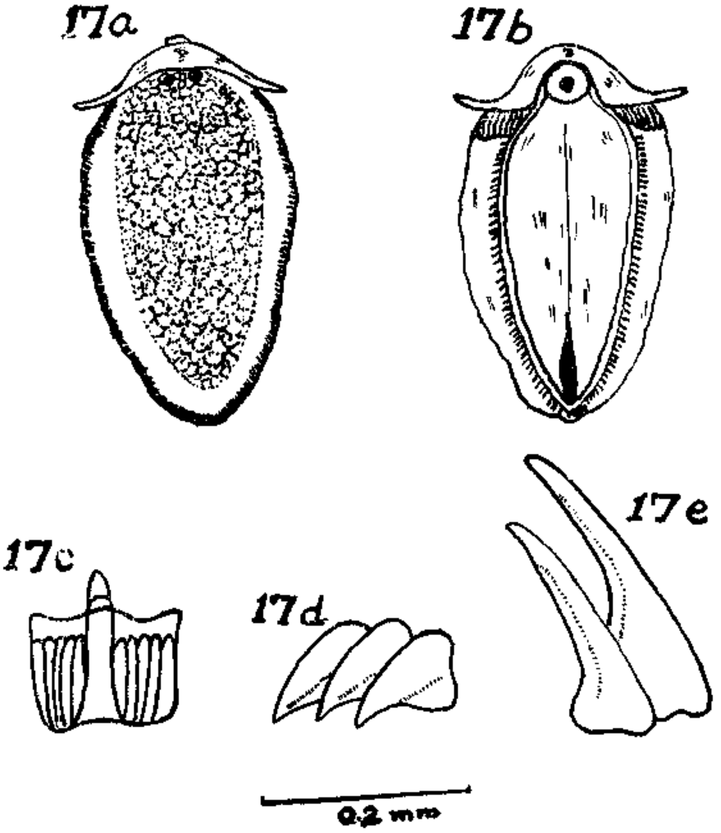
Foot is broad anteriorly and pointed posteriorly, and is narrower than the mantle. On the right side in between the foot and the mantle could be seen, with great difficulty, the genital and renal orifices. Gills and lateral lamellae are completely absent.

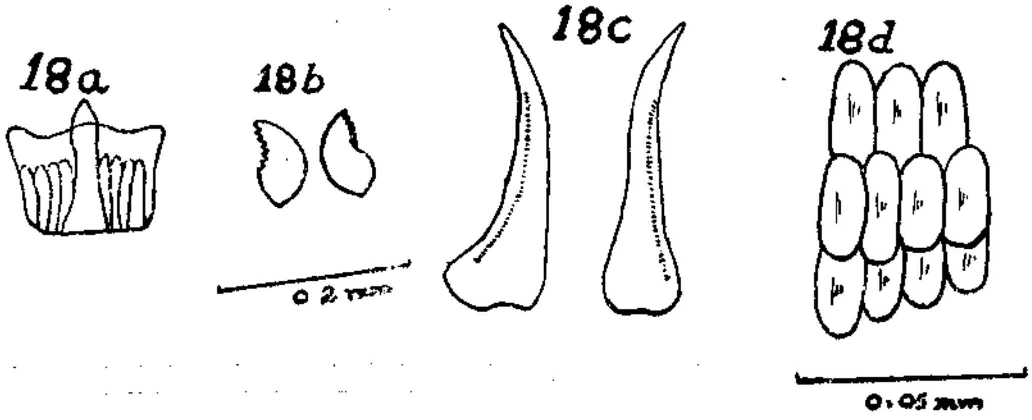
Labial armature consists of brownish to blackish-brown jaw plates with as many as 16 to 20 dentitions on the inner side. Radula, which is colourless and transparent, showed great variation in the number of teeth rows and the nature of teeth. In one specimen which had 27 rows of teeth, the median tooth was rather simple with two denticles on either side of the median cusp. All the remaining teeth were simple hamate without any denticulations.

Another specimen, which had about 42 rows of teeth, had median teeth, in the first nine anterior rows, with 8 to 10 denticles on either side. The distal end of the cusp itself was split so as to form two denticles. The next four rows had their median teeth with three to four denticles on either side of the cusp. All the remaining rows had only two denticles on either side of the cusp of the median tooth. Further, in this specimen, the first lateral teeth of the anterior few rows had two to three denticles, which gradually disappeared towards the posterior end. The laterals were not half the median tooth in this specimen. Marginals were simple and hamate. The number of teeth in each row of teeth also varied, in the same animal, from 38 to 50. There was a gradual decrease in the number of teeth towards the posterior end of the radula.

A third specimen had 38 rows of teeth in the radula. The cusps of the median teeth were simple, like those in the first specimen described above, with two to six dentitions on either side. The number of denticles were not uniform on either side. There were about 48 simple hamate teeth on either side of the median tooth.

Teeth in all the specimens were white and transparent. The dental formula of the present specimens does not tally with those given by Bergh (1905), Eliot (1906), Baba (1937), and Eales (1938)





FIGS. 17–18. Figs. 17 *a–e*. *Armina* (*Linguella*) *cinerea* Farran. (*a*) Dorsal view. (*b*) Ventral view. (*c*) Median tooth. (*d*) Lateral teeth. (*e*) Outermost marginals. Figs. 18 *a–d*. *Armina* sp. (*a*) Median tooth. (*b*) Lateral teeth. (*c*) Outermost marginals. (*d*) Jaw elements.

in respect to *D. striatus* v. Hasselt. The dental formula does not tally well with that of *D. semistriatus* Baba (1949) also. However, the presence of 20-25 ridges on the back suggests that they are more allied to *D. semistriatus* Baba (1949) and hence recorded under that species. It is also possible that the present collection contains more than a single species of the genus *Dermatobranchus* and hence it is proposed to treat them separately later.

Subfamily ARMININAE

Armina (Linguella) cinerea Farran (1905)

(Figs. 17 *a* to 17 *e*)

Two specimens were collected from the trawl net catches of the Survey Vessel, "Gulfshrimp", of the Department of Fisheries, Gujarat State, at a depth of about 16 fms. off Pirotan Island in May, 1966.

The bigger specimen measured 30 mm. in length and 18 mm. in breadth. It is colourless in the preserved condition and the tubercles on the dorsum have been mostly scraped off. However, the tubercles on the anterior portion of the dorsum have been retained. The smaller specimen measured 24 mm. in length and 15 mm. in breadth. It is rather twisted due to preservation but retains the dorsal tubercles, which are thickly packed on the dorsal surface of the mantle and grey in colour. The mantle border is yellowish. There are neither ridges nor lines on the dorsum.

Rhinophores are not clearly seen in both specimens. The anterior shield is well developed, transparent, and its lateral ends are long and pointed.

Foot is broad, ovate anteriorly and rather pointed posteriorly. On either margin of the foot, anteriorly, are 15 gills followed by about 32 side lamellae.

Mouth is situated on a round thickening in front of the foot. Labial armature consists of two oval jaw plates attached to each other. They are 5 mm. long and 1 mm. broad. Radula has 37 rows of teeth. The median tooth has five denticles on either side of the median cusp. There are about 65 serrated teeth on either side of the rhachidian tooth.

Radular formula and tubercles on the back suggest that the present specimens might be *Armina (Lingulella) cinerea* Farran (1905) (Eliot, 1906 *a*; pp. 680). Hence, they are recorded under that species.

Armina sp.

(Figs. 18 *a* to 18 *d*)

A single preserved specimen collected from Balapur Bay in 1963, measuring 36 mm. in length and 17 mm. in breadth, form the material. The animal has a pinkish colouration in the preservative and has shrunk to a great extent.

Dorsum has neither ridges nor lines and is plain, but on examining under a lens very minute tubercles could be seen. It appears that the mantle margins might have been of a paler colour than the rest of the mantle, when the animal was alive. Anterior shield is wide, rather transparent and extends laterally as a thin and pointed projection. Rhinophores have been withdrawn completely. Foot 25 mm. long, 10 mm. broad anteriorly and pointed towards the posterior end.

In between the foot and mantle are 14–15 gills continued by 36 side lamellae.

Mouth situated on a round thickening. Labial armature consists of two jaw plates measuring about 4 mm. in length and 1·5 mm. in breadth. These plates are provided with 2 to 3 rows of plates along the inner margin. Radula has 32 rows of teeth. Median tooth has four denticles on either side of the cusp. There are about 50 to 55 serrated teeth on either side of the median tooth.

It has not been possible to assess the specific status of the present specimen.

Family BORNELLIDAE

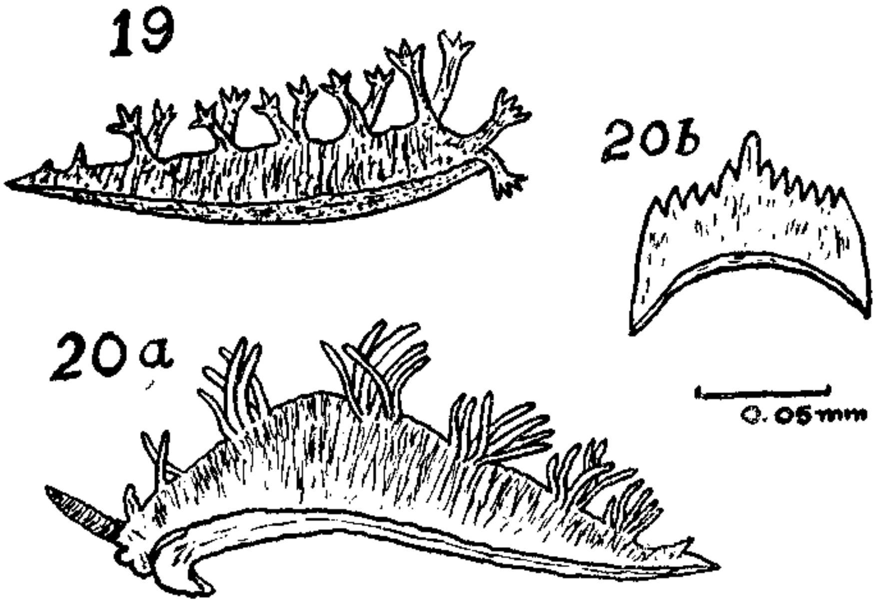
Bornella digitata **Adams & Reeve (1850)**

(Fig. 19)

This species is represented in the collection by a single specimen from Okha. The preserved specimen measures 52 mm. in length, 5 mm. in width and 5 mm. in depth. Body slender, narrow, greatly elongate and strongly compressed laterally. It has a flesh colouration in the preservative. The sides of the head are produced in front into two rounded star-like lobes with about 6 short radiating finger-shaped processes on the margin. The dorsal tentacles are large, club-shaped and obliquely laminated. The dorsal margin of the dorsal tentacles bear four small and elongated processes. There is a longitudinal row of five branchial processes on either side of the dorsum with a single small median sixth one. The paired branchial processes are borne on short peduncles and are branched at the free margin into three to four short processes. Body narrows considerably towards the posterior end, where it terminates in a pointed tail. Foot narrow and elongate and reduced very much in the present specimen. The surface of the integument is covered with many irregular tubercles.

The present species has been recorded previously by Eliot (1905 and 1909) from Karachi and Chindi Reef (Okhamandal) and by Menon *et al.* (1961) from Pirotan Island.

Family TERGIPEDIDAE



FIGS. 19–20. Fig. 19. *Bornella digitata* Adams & Reeve, lateral view. Figs. 20 *a–b*. *Hervia ceylonica* Farran. (*a*) Lateral view. (*b*) Tooth.

Hervia ceylonica **Farran (1905)**

(Figs. 20 *a* and 20 *b*)

A single specimen measuring 20 mm. in length was collected from Kiu Point on May 13, 1967. The preserved specimen is rather transparent and yellowish. Body narrow and tapering posteriorly. Cerata are arranged in five complete rows with a poorly developed sixth row. They also are coloured as the body, but the ramification of the liver can be seen clearly in grey shade. Oral tentacles are pointed, 5 mm. long, and have a rather swollen base. Rhinophores 4 mm. long and shorter than the oral tentacles. Antero-lateral portion of the foot produced into tentacles, measuring about 1 mm. in length. Foot narrow, broad anteriorly and produced behind as a pointed tail. Jaw plates yellowish, thin, and bear denticulated cutting edges. Radula uniseriate with 20 teeth, which bear 5 to 7 lateral denticulations.

The present species is a new record from the West Coast of India. It has also been recorded previously from Ceylon by Farran (1905) and from South-East Coast by O'Donoghue (1932) and Satyamurthi (1952).

Hervia militaris Alder & Hancock (1866)

Many specimens varying between 12 to 23 mm. in length were collected from Dona Reef in December, 1966.

They are thin and long with a broader anterior end and a tapering, pointed posterior end. Body whitish and the cerata dark grey to light black in colour with white tips. However, they are reported to be brilliant violet in colour when alive. Rhinophores stout and half the length of the anterior tentacles, which are long and tapering towards their ends. Cerata are somewhat pointed and arranged in 6 to 8 rows on either side of the dorsal portion. Even though they are confined to the margins in most of the specimens they meet in the centre in some of them. Foot narrow, broad anteriorly, and pointed posteriorly. The antero-lateral margins of the foot produced into small tentacles. Radula with 17 uniseriate teeth each with denticles on either side of the median denticle.

The present specimens approximate in many respects *Hervia militaris* Alder and Hancock (1866); however, they differ from the descriptions of this species given by Alder and Hancock (1866) in the external colour pattern and in the number of teeth in the radula. They are, therefore, doubtfully listed under that species.

ACKNOWLEDGEMENTS

The author wishes to place on record his indebtedness towards Mr. Robert Burn, Hon. Associate in Conchology, National Museum of Victoria, Australia, for the help and guidance given by him in the identification of most of the species dealt with in this paper and for making available some of the literature on Opisthobranchiata, referred to in this paper. He is thankful to Dr. S. T. Satyamurthi, Director of Museums, Madras, and Mr. G. N. Kesavaram, Curator (Zoology) in the Madras Government Museum, for extending all facilities for comparing some of his specimens with those in the Madras Government Museum and to Miss A. Vimala, Asst. Curator (Zoology) in the Madras Government Museum, for translating the outstanding French and German literature into English. He is also thankful to Messrs. R. Ramanandan, M. S. Michael and P. Gopalakrishnan of the Marine Biological Research Station, Government of Gujarat, Port Okha, for helping him with field collections.

Special thanks are due to Mr. K. V. Nawathe, Director of Fisheries, Government of Gujarat, Ahmedabad, who has very kindly accorded permission to undertake the present work and to present the same in the Symposium on Mollusca. But for the guidance and suggestions of Mr. C. R. Easwaran, Research Officer, Fisheries Research Station, Jamnagar, it would not have been possible for the author to undertake the present studies and to prepare the present paper; hence, to him the author is very grateful.

LITERATURE CITED

Adams, A. and L. Reeve 1850. Zoology of the Voyage of H.M.S. Samarang, 1850, Mollusca.

Alder, J. and A. Hancock 1884–85. *A Monograph of the British Nudibranchiate Mollusca, with Figures of all Species.* The Ray Society, London, Pts. 1–7.

——— 1866. Notice on a collection of Nudibranchiate Mollusca made in India by Walter Eliot Esq. with descriptions of several new genera and species. *Trans. Zool. Soc., Lond.*, **5**: 113–147.

Baba, Kikutaro 1949. *Opisthobranchia of Sagami Bay.* Tokyo, Iwanami, 159 pp.

——— 1937. Opisthobranchia of Japan. *J. Dept. Agric., Kyushu Univ.*, **5** (7): 316–317.

Bergh, R. 1870–1875. *C. Semper's Reisen im Archipel der Philippinen: Th. 2, Wissenschaftliche Resultate.* Malacologische Untersuchungen. Wiesbaden., Bd. 1, Nudibranchs.

——— 1876–1878. *Ibid.*, Bd. 2, Nudibranchs.

——— 1880–1892. *Ibid.*, Bd. 3, Nudibranchs of Mauritius, the Sunda Sea and System der Nudibranchia.

——— 1880–1887. *Ibid.*, Bd. 4, Supplements including Marseniadae.

——— 1904–1908. *Ibid.*, Th. 6, Bd. 9, Nudibranchs, Pleurobranchidae, Aplysiidae, etc.

——— 1884. Report on the Nudibranchia dredged by H.M.S. "*Challenger*" during the years 1873–76, **10**: 1–151.

——— 1905. Die Opisthobranchiata der "Siboga" Expeditie. *Siboga Exped. Monograph.*, **50**: 1–248.

Burn, Robert 1961. A New Doridid Nudibranch from Torquay, Victoria. *The Veliger*, **4** (2): 55–56. North California Malacozoological Club, Berkeley, California.

Eales, N. B. 1938. *John Murray Expedition* 1933–34, *Scientific Reports*, **5** (4): 77–112. *A Systematic and Anatomical Account of the Opisthobranchia.* British Museum (Natural History), London.

Eliot, Charles 1899. Notes on Tectibranchs and naked Molluscs from Samosa. *Proc. Acad. Nat. Sciences of Philadelphia*, **51**.

——— 1903 *a*. On some nudibranchs from East Africa and Zanzibar. *Proc. Zool. Soc., Lond.*, **1**, Pt. 2: 250–257.

——— 1903 *b*. *Ibid.*, **2**, Pt. 3: 354–385.

——— 1905. Nudibranchs of the Indo-Pacific Islands. Notes on a collection dredged near Karachi and Maskat. *J. Conch.*, **11** (8): 237–256.

——— 1906 *a*. On the nudibranchs of Southern India and Ceylon, with special reference to the drawings by Kelaart and the collection belonging to Alder and Hancock preserved in the Hancock Museum at Newcastle-on-Tyne. *Proc. Zool. Soc., Lond.*, **2**: 636–691.

——— 1906 *b*. *Ibid.*, **2**: 999–1008.

——— 1906 *c*. Nudibranchiata with some remarks on the families and genera and a description of a new genus, *Doridomorpha*. In: *Fauna and Geography of the Laccadive and Maldive Archipelago*, **2**: 540–573, Cambridge.

——— 1908. Report on the marine biology of the Sudanese Red Sea, 11,. Notes on a collection of nudibranchs from the Red Sea. *Journ. Linn. Soc. (Zool), Lond.*, **31** (1907–15): 86–122.

——— 1909. Report on the Nudibranchs Collected by Mr. James Hornell at Okhamandal in Kattiawar in 1905–06. *James Hornell's Report to the Government of Baroda on the Marine Zoology of Okhamandal in Kattiawar*, Pt. 1: 137–145, Williams and Norgate, London.

——— 1910. Notes on nudibranchs from the Indian Museum. *Rec. Ind. Mus.*, **5**: 247–252.

——— 1916. Mollusca Nudibranchiata. *Mem. Ind. Mus.*, **5**: 377–379.

Farran, G. P. 1905. Report on the Opisthobranchiate Mollusca collected by Prof. Herdman. In: *W. A. Herdman's Report on the Pearl Oyster Fisheries of the Gulf of Mannar*, 3. *Suppl. Report*, **21**: 329–364. The Ray Society, London.

Gideon, P. W., P. K. B. Menon, S. R. V. Rao and K. V. Jose 1957. On the marine fauna of the Gulf of Kutch: A preliminary survey. *J. Bombay Nat. Hist. Soc.*, **54** (3): 690–706.

GRAVELY, F. H. 1942. Shells and other animal remains found on the Madras beach. *Bull. Mad. Govt. Mus. (Nat. Hist.)*, **5** (2): 1–104.

——— 1927. Littoral fauna of Krusadai Island, Mollusca. *Ibid.*, **1** (1): 1–196.

HORNELL, JAMES 1909. *Report to the Government of Baroda on the Marine Zoology of Okhamandal in Kattiawar*, Pt. 1, Williams and Norgate, London.

——— 1919. *Ibid.*, Part II.

——— 1924. The common Molluscs of South India. Rep. 6 of 1921. *Madras Fisheries Bulletin*, **14**: 97–215.

——— 1951. *Indian Molluscs.* Bombay Nat. Hist. Soc., Bombay.

KELAART, E. F. 1858. Description of little known species of Ceylon nudibranchiate molluscs and zoophytes. *J. Cey. Br. of Roy. Soc., Colombo*, **3**: 488–496.

——— 1859. On new species of Ceylonese nudibranchiate molluscs. *Ann. Mag. Nat. Hist.*, Sr. 3, **3**: 291–304 and 358–496.

——— 1859. *Ibid.*, **4**: 267–270.

KUNDU, H. L. 1965. On the marine fauna of the Gulf of Kutch, Part 3—Pelecypods. *J. Bombay. Nat. Hist. Soc.*, **62** (2): 84–103.

——— 1965. *Ibid.*, **62** (3): 211–244.

MENON, P. K. B., A. K. DATTAGUPTA AND D. DASGUPTA 1961. On the marine fauna of the Gulf of Kutch, Part 2 —Gastropoda. *Ibid.*, **58** (2): 475–494.

O'DONOGHUE, C. H. 1931. Notes on Nudibranchiata from South India. *Proc. Malac. Soc. London*, **20**: 141–166.

ODHNER, N. H. 1939. Opisthobranchiate molluscs from the Western and Northern Coasts of Norway. *Ke. Norske, Vidensk. Selsk. Skr.*, **1**: 1–93.

——— 1957. *Chromodoris* contra *Glossodoris*, a systematic nomenclatural controversy. *Proc. Malac. Soc., London*, **32** (6): 250–253.

PATIL, A. M. 1952. Study of the marine fauna of the Karwar Coast and neighbouring islands. *J. Bombay Nat. Hist. Soc.*, **50** (3): 557.

PELSENEER, P. 1906. Mollusca. In: *Ray Lankester—A Treatise on Zoology*, Part 5, 173 pp., 157 Fig., Adams and Charles Black, London.

RAO, K. V. 1936. Morphology of *Kalinga ornata* (Alder and Hancock). *Rec. Ind. Mus.*, **38**: 41–79.

——— 1937. Structure and habits and early development of a new species of *Styliger* Ehrenbergh. *Ibid.*, **39**: 435–464.

——— 1952. *Cuthona adayarensis*, A new nudibranch (Mollusca: Gastropoda) from Madras. *J. Zool. Soc., India, Calcutta*, **3**: 229–238.

——— 1961. On two opisthobranchiate molluscs, *Placobranchus ocellatus* Hasselt and *Discodoris boholiensis* Bergh, from Indian waters not hitherto been recorded. *J. Mar. biol. Ass. India*, **3** (1 & 2): 253–259.

——— AND K. ALAGARSWAMI 1960. An account of the structure and early development of a new species of nudibranchiate gastropod, *Eolidina (Eolidina) mannarensis*. *Ibid.*, **2** (1): 6–16.

——— AND K. PRABHAKARA RAO 1963. *Styliger nigrovittatus*, Sp. Nov., A sacoglossan mollusca from the Gulf of Mannar. *Ibid.*, **5** (2): 232–238.

*RUPPELL, E. AND F. S. LEUCKART 1828. *Atlas zu der Riese im nordlichen Africa.* Neue Wirbellose Thiere des Rothen Meerus.

SATYAMURTHI, S. T. 1952. The Mollusca of Krusadai Island. 1. Amphineura and Gastropoda. *Bull. Mad. Govt. Mus. (Nat. Hist.)*, **1** (2), Pt. 6: 216–251.

THIELE, JOHANNES 1931. *Handbuch der systematischen Weichtierkunde*, 1. Jena Verlong. Von Gustav. Fischer, 1–778.

VAYSSIERE, P. A. 1901. *Monographe de famille des Pleurobranchides.* Ann. Sc. Nat., **32**.

---

* Not referred to in original.

DISTRIBUTION OF THE MARINE MOLLUSCS AT CAPE ANN, MASSACHUSETTS

RALPH W. DEXTER

Department of Biological Sciences, Kent State University, Kent, Ohio, U.S.A.

ABSTRACT

Surveys of marine life at Cape Ann were made particularly in 1933–37 and 1956–61. Incidental collecting was done at certain other years through 1967. Molluscs totalled 81 species (34 gastropods, 3 amphineurans, 1 scaphopod, 39 pelecypods, 4 cephalopods). Species distribution in the five natural areas was as follows: Ipswich Bay (64); North branch—Annisquam River (45); Little River (28); South branch—Annisquam River (26); Gloucester Harbor (41). Fourteen species were found in all five areas; 9 in all but one area; 13 in all but two areas; 14 were found in two areas; 31 were found in only one area. The latter were largely uncommon species or those with restricted habitat preference. Twenty species were predominantly intertidal and 61 predominantly subtidal. They occurred primarily in the following habitats: pelagic (4); ubiquitous bottom (3); solid surfaces (14); seaweeds (6); in wood (3); sediments (22); sand (22); mud (2); hard clay (1); marsh (4). Sand dwellers were more common in Ipswich Bay; mud dwellers were more common in Gloucester Harbor. Nudibranchs were more common in the harbor because of wharf pilings. Differences in the mollusc fauna are attributed largely to uncommon species of limited distribution and those with restricted habitat preferences.

I. INTRODUCTION

STUDIES on the marine molluscs at Cape Ann, Massachusetts, have been made since 1933. Annual surveys were conducted during the summers of 1933–1937 and of 1956–1961.[1] Incidental collecting and sampling have taken place during many other intervening years through the summer of 1967. The over-all objective was to determine the nature of the intertidal and shallow subtidal marine communities in that area, but special attention has been given to the ecology of the molluscs. Some reports have already been issued both on the marine communities in general and on the molluscs in particular (Dexter, 1942–45, 1947, 1951, 1956, 1962). Another study, employing different methods, was published by Clarke (1954).

The present paper is specifically concerned with the distribution of marine molluscs collected at Cape Ann over the past 35 years. Five areas are recognized for this purpose—1. Ipswich Bay, 2. North Branch of the Annisquam River, 3. Little River, 4. South Branch of the Annisquam River, and 5. Gloucester Harbor (*see* Fig. 1). It should be pointed out that the Annisquam water-way (including Little River) is a marine inlet with sea-water throughout the system. It is neither a river, as the official name indicates, nor is it an estuary. While a trickle of freshwater enters at four places the volume is not large and the greater bulk of water in the inlet is changed with every tide. Salt-water prevails throughout.

During the incoming tide, water flows in from Ipswich Bay and from Gloucester Harbor simultaneously. The currents proceed down the north branch and up the south branch of the Annisquam inlet respectively. The two currents meet at the junction of Little River into which both currents then flow. During the outgoing tide, the return flow begins in Little River and divides at its junction with the Annisquam channel, part of the water flowing southward into Gloucester Harbor and part flowing northward into Ipswich Bay. It has a mean tidal amplitude of 8·6 feet, but during periods of spring tides, it may be as much as 10·1 feet.

---

[1] Acknowledgment is made to the U.S. Atomic Energy Commission for aid given to this study 1956–61 [Contract AT (11–1)–411].

The bottom of Ipswich Bay is composed of hard sand with a margin of boulders and a granite ledge at the shore line. There are also several sandy beaches along the shore line. The bottom of the north branch of the Annisquam River is sandy, for the most part, with occasional outcrops of glacial boulders, but the sediments grade into soft mud in the side channels such as Lobster Cove, Goose Cove, Mill River, and Jones Creek. Most of these side channels and part of the main waterway are bordered by salt marshes. Little River and the south branch of the Annisquam River both have a soft, muddy bottom and are bordered by salt marshes. Gloucester Harbor has predominantly a mud bottom which grades into sand at the southern edge. Part of the harbor shore line is composed of glacial boulders or granite ledge with some gravel and sandy beaches and a few remnants of marsh, but much of the shore has been modified by man. Wharf pilings are numerous in the Inner Harbor, and the water is badly polluted in that area.

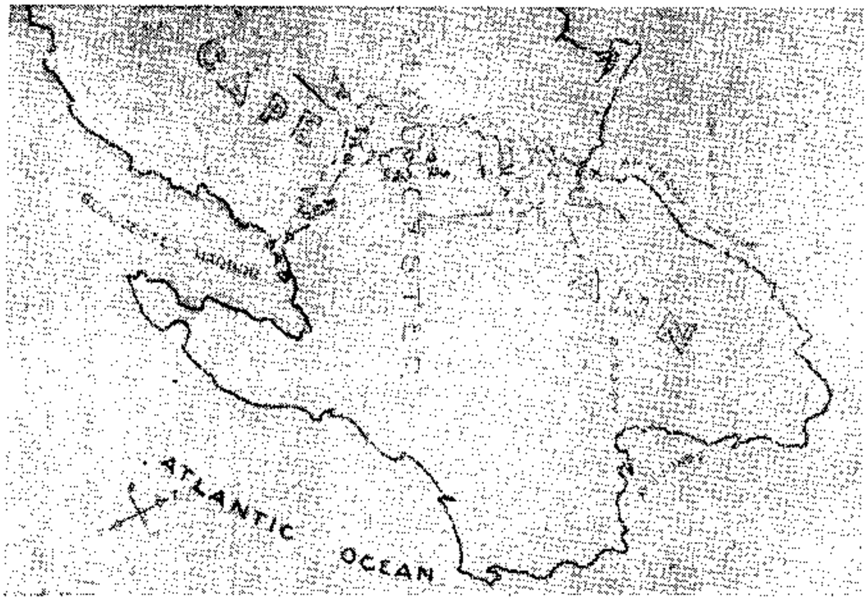


FIG. 1. Sketch Map of Cape Ann, Mass. Southern branch of the Annisquam River extends from Stations A to G; northern branch from Stations K to X. Little River extends from Stations H to J.

The accompanying table lists the species of molluscs collected at Cape Ann during the term of this study. There are 34 gastropods, 3 chitons, 1 scaphopod, 39 bivalves, and 4 cephalopods. Altogether 81 species have been recorded. In addition, two species have been introduced, although without much success (*Crassostrea virginica* and *Mercenaria mercenaria*). There is one record of an adventitious species (*Aequipecten irradians*). Also, shells for the following 12 species have been collected in the area. Some of these undoubtedly have been brought to the area by commercial fishing boats (especially *Busycon carica*, *B. canaliculatum*, and *Anomia simplex*). The others may be shells washed in from some considerable distance or they may represent uncommon species which have not yet been collected alive. Shell records only have been made for the following:

Busycon carica Gmelin
B. canaliculatum L.
Aphorrhais occidentalis Beck
Colus ventricosus Gray

Anomia simplex Orbigny
Musculus niger Gray
Venericardia borealis Conrad
Mesodesma arctatum Conrad

Puncturella noachina L.
Solemya borealis Totten
Macoma calcarea Gmelin
Cardita borealis Conrad

II. Geographical Distribution

Fourteen species have been found in all five areas, and as would be expected, they are among the most abundant species at Cape Ann. They are as follows:

Lacuna vincta
Littorina littorea
L. obtusata
L. saxatilis
Crepidula fornicata
C. plana
Lunatia heroes
Thais lapillus
Nassarius trivittatus
Mytilus edulis
Petricola pholadiformis
Macoma balthica
Hiatella arctica
Mya arenaria

Four species were collected in all areas except Little River where the water is very shallow, the bottom is soft mud, and there are few solid surfaces available for attachment. The four were : *Acmaea testudinalis, Aeolidia papillosa, Anomia aculeata,* and *Cerastoderma pinnulatum.*

Three species were found in all areas except the south branch of the Annisquam River. This, too, is an area of muddy bottom and did not contain *Urosalpinx cinerea, Pitar morrhuana,* and *Spisula solidissima.*

Two species of bivalves *Gemma gemma* and *Ensis directus* were found generally distributed except in Gloucester Harbor where few mud flats are available in which these species are generally found.

Five species characteristic of protected habitats were abundant and widely distributed throughout the Annisquam inlet, but were not found in the open-water habitats of Ipswich Bay and Gloucester Harbor. These were: *Melampus lineatus, Nassarius obsoletus, Solemya velum, Modiolus demissus* and *Tellina agilis.*

Six species, half of which are nudibranchs, were found in Ipswich Bay and its extension into the northern arm of the Annisquam, and again in Gloucester Harbor, but not in the mud bottom habitats of Little River and southern section of the Annisquam. These were:

Acanthodoris pilosa
Onchidoris bilamellata
Dendronotus frondosus
Modiolus modiolus
Teredo navalis
Lyonsia hyalina

One uncommon bivalve *Cyrtodaria siliqua* was found in the Annisquam inlet and Ipswich Bay, but not in Little River or Gloucester Harbor.

One snail *Mitrella lunata* was found only in the northern half of Cape Ann, but because of its small size, it could have been overlooked elsewhere. Four other species, *Facelina bostoniensis, Siliqua costata, Xylophaga atlantica,* and *Loligo pealei* were found only north of Little River.

Confined to the northern branch of the Annisquam and the Little River extension were two small snails, *Cingula aculeus* and *Ovatella myosotis,* found only in protected muddy habitats.

Found only in the deeper waters and more oceanic habitat of Ipswich Bay and Gloucester Harbor were the following eight species:

Ischnochiton ruber
Yoldia thraciaeformis
Placopecten magellanicus
Astarte undata
A. castanea
A. islandica
Crenella glandula
Illex illecebrosus

From Ipswich Bay 21 species were found that were not collected elsewhere. The hard sand habitat of the shallow portion was probably responsible for the presence of some of these species. Also, ten of them were taken only by commercial fishing boats trawling in Ipswich Bay to a depth of about 40 fathoms.

Crucibulum striatum
Velutina laevigata
Lunatia triseriata
Buccinum undatum
Colus stimpsoni
C. pygmaeus
Neptunea decemcostata
Scaphander punctostiatus
Haminoea solitaria
Chaetopleura apiculata
Symmetrogephyrus vestitus
Dentalium entale
Musculus discors
Chlamys islandicus
Clinocardium ciliatum
Barnea costata
Modiolaria substriata
Thracia conradi
Periploma leanum
Rossia tenera
Bathypolypus arcticus

Six species were restricted to Gloucester Harbor. One of these is the pelagic *Clione limacina*, one a nudibranch *Coryphella rufibranchialis* found along the hydroids of wharf pilings, and three of them were bivalves of the muddy bottom section of the Harbor. *Zirphaea crispata* was found in hard clay during an excavation in Gloucester Harbor.

Three rare species *Polinices duplicatus*, *Phacoides filosus*, and *Mulinia lateralis* were found only on the sandy bottom of the north branch of the Annisquam River, and one uncommon species *Hydrobia minuta* was found only on the marsh of Little River.

III. DISTRIBUTION BY HABITAT

Twenty species were predominantly intertidal, while 61 were predominantly subtidal (*see* Table I). Four species were pelagic: *Clione limacina*, *Rossia tenera*, *Loligo pealei*, and *Illex illecebrosus*. The following three species were ubiquitous bottom dwellers (on rocks, sand, and mud): *Littorina littorea*, *Modiolus modiolus*, and *Mytilus edulis*.

Fourteen species were found primarily on rocks and other solid surfaces (shells, wharf pilings, etc.) as follows:

Acmaea testudinalis
Crucibulum striatum
Acanthodoris pilosa
Dendronotus frondosus

Littorina saxatilis
Crepidula fornicata
C. plana
Urosalpinx cinerea
Thais lapillus
Coryphella rufibranchialis
Chaetopleura apiculata
Ischnochiton ruber
Symmetrogephyrus vestitus
Anomia aculeata

TABLE I

Distribution of the Marine Molluscs at Cape Ann, Mass.

Species	General abundance	Predominant habitat	Ipswich Bay	Annisquam River—N	Little River	Annisquam River—S	Gloucester Harbor
GASTROPODA (34)							
Acmaea testudinalis Müller ..	N	Su	X	X		X	X
Crucibulum striatum Say	R	Su	*X				
Lacuna vincta Turton ..	A	Su	X	X	X	X	X
Littorina littorea L. ..	A	I	X	X	X	X	X
L. obtusata L. ..	A	I	X	X	X	X	X
L. saxatilis Olivi ..	A	I	X	X	X	X	X
Cingula aculeus Gould ..	S	I		X	X		
Crepidula fornicata L. ..	C	Su	X	X	X	X	X
C. plana Say ..	C	Su	X	X	X	X	X
Velutina laevigata L. ..	R	Su	*X				
Polinices duplicatus Say	R	Su		X			
Lunatia heros Say ..	A	Su	X	X	X	X	X
L. triseriata Say ..	N	Su	X				
Urosalpinx cinerea Say ..	S	Su	X	X	X		X
Thais lapillus L. ..	A	I	X	X	X	X	X
Mitrella lunata Say ..	S	Su	X	X	X		
Buccinum undatum L. ..	C	Su	X				
Colus stimpsoni Mürch ..	C	Su	X				
C. pygmaeus (Gould) ..	R	Su	X				
Neptunea decemcostata Say ..	N	Su	X				
Nassarius trivittatus Say	C	Su	X	X	X	X	X
N. obsoletus Say ..	A	I		X	X	X	
Scaphander punctostriatus Mighels ..	R	Su	*X				
Haminoea solitaria Say ..	R	Su	*X				
Clione limacina (Phipps)	S	Su					X

TABLE I (*Contd.*)

Species	General abundance	Predominant habitat	Ipswich Bay	Annisquam River—N	Little River	Annisquam River—S	Gloucester Harbor
Acanthodoris pilosa Abildgard	N	Su	X	X			X
Onchidoris bilamellata L.	S	Su	X	X			X
Dendronotus frondosus Ascanius	N	Su	X	X			X
Aeolidia papillosa L.	C	Su	X	X		X	X
Coryphella rufibranchialis Johnston	S	Su					X
Facelina bostoniensis (Couthou.)	N	Su	X	X			
Hydrobia minuta Totten	S	I			X		
Melampus lineatus Say	A	I		X	X	X	
Ovatella myosotis (Draparnaud)	S	I		X	X		
AMPHINEURA (3):							
Chaetopleura apiculata Say	R	Su	X				
Ischnochiton ruber L.	S	Su	X				X
Symmetrogephyrus vestitus Brod. and Sow.	R	Su	X				
SCAPHOPODA (1):							
Dentalium entale L.	R	Su	X				
PELECYPODA (39):							
Solemya velum Say	A	I		X	X	X	
Yoldia limatula Say	N	Su					X
Y. thraciaeformis Storer	S	Su	*X				X
Crenella glandula Totten	S	Su	X				X
Modiolus modiolus L.	C	Su	X	X			X
M. demissus Dillwyn	A	I		X	X	X	
Modiolaria substriata Gray	R	Su	X				
Mytilus edulis L.	A	I	X	X	X	X	X
Musculus discors L.	R	Su	*X				
Placopecten magellanicus Gmelin	S	Su	X				X
Chlamys islandicus Müller	R	Su	*X				
Anomia aculeata Gmelin	C	Su	X	X		X	X
Astarte undata Gould	S	Su	X				X
A. castanea Say	S	Su	X				X
A. elliptica (Hanley)	R	Su					X

TABLE I (*Contd.*)

Species	General abundance	Predominant habitat	Ipswich Bay	Annisquam River—N	Little River	Annisquam River—S	Gloucester Harbor
Arctica islandica L.	A	Su	X				X
Phacoides filosus Stimpson	R	Su		X			
Cerastoderma pinnulatum Conrad	C	Su	X	X		X	X
Clinocardium ciliatum Fabricius	R	Su	*X				
Pitar morrhuana Linsley	S	Su	X	X	X		X
Gemma gemma Totten	C	I	X	X	X	X	
Petricola pholadiformis Lamarck	N	I	X	X	X	X	X
Tellina agilis Stimpson	C	I		X	X	X	
Macoma balthica L.	A	I	X	X	X	X	X
Siliqua costata Say	S	I	X	X			
Ensis directus Conrad	A	I	X	X	X	X	
Spisula solidissima Dillwyn	C	Su	X	X	X		X
Mulinia lateralis Say	R	I		X			
Hiatella arctica L.	C	Su	X	X	X	X	X
Cyrtodaria siliqua (Spengler)	S	Su	X	X		X	
Mya arenaria L.	A	I	X	X	X	X	X
Barnea costata L.	R	Su	*X				
Zirfaea crispata L.	R	Su					X
Xylophaga atlantica Richards	N	Su	*X	X			
Teredo navalis L.	N	Su	*X	X			X
Lyonsia hyalina Conrad	S	Su	X	X			X
Pandora gouldiana Dall	S	Su					X
Thracia conradi Couthouy	R	Su	X				
Periploma leanum Conrad	R	Su	X				
CEPHALOPODA (4):							
Rossia tenera Verrill	R	Su	*X				
Loligo pealei Lesueur	N	Su	*X	X			
Illex illecebrosus Lesueur	A	Su	*X				*X
Bathypolypus arcticus Prosch	N	Su	*X				
Total spp. (81)			64 spp.	45 spp.	28 spp.	26 spp.	41 spp.

A = abundant S = scarce I = Intertidal N = numerous

C = common R = rare Su = subtidal * = From commercial fishing boats

Six species were found living primarily on seaweeds—*Lacuna vincta, Littorina obtusata, Onchidoris bilamellata, Aeolidia papillosa, Facelina bostoniensis,* and *Hiatella arctica.* Two species were found only in wood—*Xylophaga atlantica,* and *Teredo navalis.*

The following twenty-two species were found associated primarily with sediments of various types (sand and mud):

Mitrella lunata
Solemya velum
Yoldia limatula
Y. thraciaeformis
Modiolaria substriata
Placopecten magellanicus
Chlamys islandicus
Astarte undata
A. castanea
A. elliptica
Cerastoderma pinnulatum
Clinocardium ciliatum
Pitar morrhuana
Gemma gemma
Petricola pholadiformis
Tellina agilis
Macoma balthica
Ensis directus
Cyrtodaria siliqua
Mya arenaria
Lyonsia hyalina
Pandora gouldiana

Another twenty-two species were partial to sandy habitats as follows:

Velutina laevigata
Polinices duplicatus
Lunatia heros
L. triseriata
Buccinum undatum
Colus stimpsoni
C. pygmeus
Neptunea decemcostata
Nassarius trivittatus
Scaphander punctostriatus
Haminoea solitaria
Dentalium entale
Musculus discors
Arctica islandica
Phacoides filosus
Siliqua costata
Spisula solidissima
Mulinia lateralis
Crenella glandula
Thracia conradi
Periploma leanum
Bathypolypus arcticus

Only three species were restricted to mud, *Cingula aculeus, Nassarius obsoletus,* and *Barnea costata*; one (*Zirphaea crispata*) was found only in hard clay, while four were characteristic of marshland. These were: *Melampus lineatus, Ovatella myosotis, Hydrobia minuta,* and *Modiolus demissus.*

Ipswich Bay, with a bottom of hard sand grading into mud, contained 33 subtidal species of molluscs. On the other hand, Gloucester Harbor with a soft, muddy bottom, for the most part, contained 19 subtidal species from that habitat. Both areas have rocky margins and rock outcrops, and in those habitats the molluscs were much the same. Molluscs of the sediments, however, were quite different. Sand dwellers were more common in the Bay, while mud dwellers were more common in the Harbor. More nudibranchs were found in the Harbor where wharf pilings provide suitable habitat for hydroids on which the nudibranchs largely feed.

Differences in the molluscan fauna at Cape Ann are for the most part uncommon species of limited distribution or those with a narrow habitat preference.

LITERATURE CITED

CLARKE, ARTHUR, H. JR. 1954. Shell-bearing marine mollusks of Cape Ann, Massachusetts. *Nautilus*, **67**: 112–120.

DEXTER, RALPH W. 1942. Notes on the marine mollusks of Cape Ann, Massachusetts. *Ibid.*, **56**: 57–61.

——— 1943. A suggested counting frame for intertidal population studies. *Jour. Marine Res.*, **5**: 116–117.

——— 1944 *a*. The bottom community of Ipswich Bay, Massachusetts. *Ecology*, **25**: 352–359.

——— 1944 *b*. Annual fluctuation of abundance of some marine mollusks. *Nautilus*, **58**: 18–24.

——— 1945 *a*. Zonation of the intertidal marine mollusks at Cape Ann, Massachusetts. *Ibid.*, **58**: 135–142.

——— 1945 *b*. The genus *Pecten* at Cape Ann, Massachusetts. *Ibid.*, **59**: 69–70.

——— 1947. The marine communities of a tidal inlet at Cape Ann, Massachusetts: a study in bio-ecology. *Ecol. Monog.*, **17**: 261–294.

——— 1951. Dredging in shallow sea-water. *Turtox News*, **29**: 66–69.

——— 1956. Additional marine mollusks at Cape Ann, Massachusetts. *Nautilus*, **69**: 140–141.

——— 1962. Further studies on the marine mollusks of Cape Ann, Massachusetts. *Ibid.*, **76**: 63–70.

DISCUSSION

Dr. H. G. Kewalramani: You said that *Crassostrea virginica* and *Mercenaria mercenaria* had to be transplanted but not established in your area. What is the reason?

Dr. R. W. Dexter: Yes. Our winters are usually too cold for survival and the water temperature too low for reproduction. Hence, transplanted specimens do not reproduce, and they survive for only a few years.

STUDIES ON THE DISTRIBUTION OF SPECIES OF PROSOBRANCH AND PULMONATE SNAILS ON THE LIMESTONE HILLS OF MALAYA

R. D. PURCHON

Department of Zoology

AND

M. E. SOLARI

Department of Mathematics

Chelsea College of Science and Technology, University of London, U.K.

ABSTRACT

Tweedie (*Bull. Raffles Mus.*, Vol. 26, 1961) reviewed the literature regarding the distribution of air-breathing prosobranch and pulmonate snails, and tabulated the occurrence of over 100 species of these snails on 28 precipitous limestone hills in Malaya. He showed that of these snails, 70 species were each known from one hill only, 33 other species were known to occur on two or more of the limestone hills from which collections of shells had been made.

These species of snails have not yet been subjected to exhaustive study under controlled conditions, and we cannot exclude the possibility that at least some of them are not good species but are phenotypic varaints the form of which may depend on climatic variables such as temperature and humidity.

The present paper demonstrates that the distribution of all these "species" of snails is random, and conforms closely to the Poisson distribution. It is concluded that there is no faunal discontinuity in the area as a whole, and that there is no significant inter-specific competition between those species of snails which co-exist on the same limestone hill. In a number of cases a limestone hill has been shown to bear two or more species of snails which belong to the same genus. It is concluded that such sympatric species cannot have evolved *in situ* on that hill, for there would have been no effective agent to isolate their respective populations; it is suggested alternatively that these species evolved at an earlier date during a period of ecological isolation over a considerably larger area of land, and that subsequent to their emergence these species became concentrated upon these limestone hills, probably during a protracted period of subsidence and marine incursion.

THIS paper is an elementary study of the distribution of terrestrial prosobranch and pulmonate snails on 28 precipitous limestone hills in Malaya, based on the data supplied by Tweedie (1961). We have to confess that we have not made first-hand studies on the living snails which are the subject of this exercise. Tweedie reviewed the literature on these air-breathing snails and tabulated the recorded occurrences of over 100 species of snails on all of those Malayan limestone hills which have been studied with regard to their snail faunas; he showed that as many as 70 species are individually known from only one hill, while a further 33 species are each known from two or more hills. Many interesting questions arise with regard to these little-known terrestrial snails—how, when, and where did these species evolve, and how did they come to be confined to their present very restricted distributions? It is thought that the snails are calcicolous and that in consequence they are confined to the limestone hills. They are thought not to occur in the surrounding, non-calcareous country. It has been suggested that populations of snails occurring on individual limestone hills were as effectively isolated from each other as though they were isolated on oceanic islands, and that speciation was effected as the result of geographic isolation on these individual hills. This very interesting suggestion may be true in the main, but it fails to cover the recorded data in two

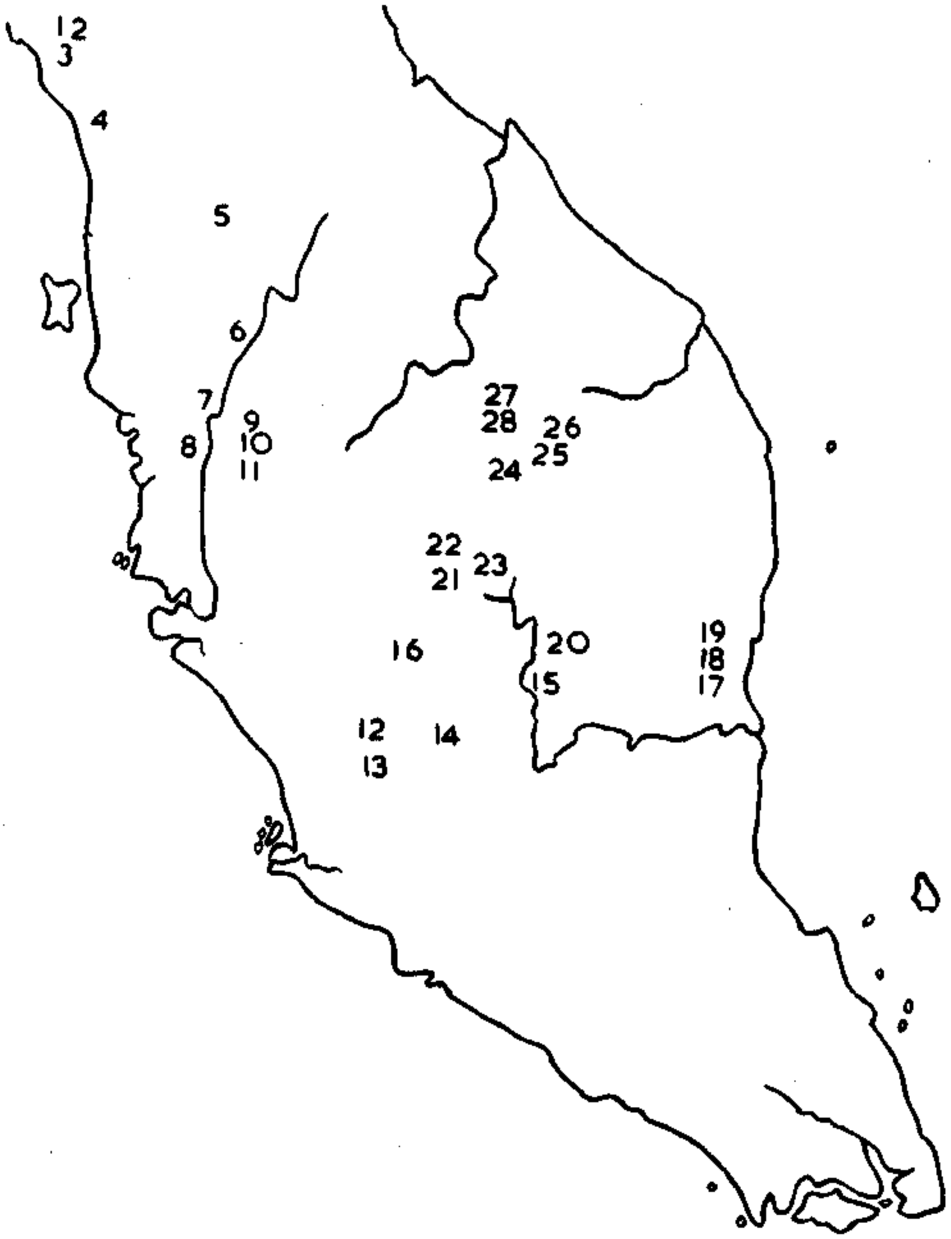


FIG. 1. Outline map of Malaya, showing the locations of the 28 limestone hills and the courses of the principal rivers.

respects:—*Firstly*, how can some species have succeeded in colonising two, three, or more hills when 70 other species are each confined to one single hill? Two species of *Gyliotrachela* are known from 6 and from 19 hills respectively; three species of *Diplommatina* are known from 8, from 12, and from 13 hills respectively; one species of *Paraboysidia* occurs on 10 hills. These six species collectively occupy all but 2 of the 28 hills, while 21 hills bear two or more of these six species. This is strong evidence that at least these species were originally not calcicolous, and were generally distributed throughout the country. Other species may have been much more recent in their origin, and may have been confined to a smaller area of country at the time of speciation. *Secondly*, how can any one hill bear two or more species in the same genus unless speciation had been completed prior to confinement of these species on that particular hill? Speciation can only proceed in isolation, and it is commonly held that sympatric species must have come together after an earlier, formative period of effective isolation.

Paton (1961) has shown that the 28 limestone hills which are the concern of this paper cannot be regarded as the remnants of a single extensive limestone plateau, for they belong to a number of different geological formations, this sometimes being true for neighbouring hills. It therefore seems probable that originally all these terrestrial snails were not calcicolous, but were generally distributed. Speciation may have been as a result partly of geographic isolation and partly of ecological isolation. Subsidence of the land, accompanied by marine incursion, may then have reduced the area of the land and concentrated the fully evolved species on neighbouring high land which by continued subsidence became reduced to individual islands or clusters of islands. Having already achieved specific status, any sympatric species trapped on these islands could co-exist there without cross-breeding. The presumed calcicolous habit was perhaps generally adopted during this period of isolation on these limestone islands. Elevation subsequently produced the present configuration of the land, the islands being converted to hills, but the snail faunas of the individual limestone hills were thereafter almost as effectively isolated from each other by the intervening alluvial soil as they were previously by sea-water.

Before proceeding further with this study it must be emphasised that none of these species of snails has been subjected to exhaustive study under controlled conditions in the laboratory. The "species" may be distinguished one from another by various features of the shell which may be partly dependent on such climatic factors as temperature and humidity. Some of the records may therefore concern phenotypic variants, and not "good species". Due to lack of information on phenotypic variation, and possible occurrence of clines based on climatic variables, we are obliged to pursue the investigation as though all the named species are "good". The statistical analysis which follows is in two parts.

1. *The distribution of* 70 *species, each of which is known to occur only on one single limestone hill.*—With reference only to the 70 species of snail each of which occurs on only one hill, any one particular hill may carry any number from 0 to 7 such species. By plotting the data in this way the abundance of species on the various limestone hills is found to conform to the Poisson distribution. The observed and the expected frequency distributions are set out in Table I, and the closeness of fit is recognisable at a glance. The χ^2 is very small (0·6902, with d. f. $= 3$, $P > 0 \cdot 5$) and the Poisson distribution with a mean of 2·50 fits very well indeed. This implies that these 70 species are distributed at random among the 28 limestone hills. The probability of the occurrence of a species on a hill does not vary from hill to hill in any significant manner. It seems that the occurrence of one species on a hill does not interfere in any way with the possible occurrence of a second, a third, or a fourth species on the same hill; *i.e.*, interspecific competition on these hills is negligible.

2. *The distribution of* 33 *species, each of which is known to occur on two or more limestone hills.*—Apart from the 70 species discussed above, Tweedie's tabulation shows 4 further species which were found only on one hill, but which were not specifically stated to be unique to the hill in question (perhaps these species had been recorded also from one or more sites outside Malaya ?). Setting these 74 species on one side, there remain 33 species of snails each of which occurs on two or more Malayan limestone hills. Study of the distribution of these 33 species permits an assessment of the degree of faunistic similarity between any two hills. Each hill can be compared with 27 other hills, recording for each comparison the number of species of snail which occur on both hills. The total number of comparisons of pairs of hills was $27 \times 14 = 378$, and the number of species common to a pair of hills was found to vary between 0 and 7. The data are set out in Table II where, however, hills 8, 9 and 10 are grouped together and treated as a single locality, for reasons which will be explained below.

TABLE I

No. of species per hill	Frequency observed (O) .	Frequency expected (E)	O − E	$\frac{(O-E)^2}{E}$
0	2	2·30	−0·30	·0391
1	5	5·75	−0·75	·0978
2	9	7·18	1·82	·4613
3	6	5·98	0·02	·0001
4 5 6 7	3 2 0 1 } = 6	6·79	−0·79	·0919
TOTALS ..	28	28·00		·6902

The mean = 2·50, variance = 2·39, χ^2 = ·6902, P > 0·5 ; the values in the expected frequency distribution are derived from the Poisson probabilities which are proportional to the sequence of terms in the formula:

$$\epsilon^m = 1 + m + \frac{m^2}{2!} + \frac{m^3}{3!} + \frac{m^4}{4!} + \ldots \frac{m^n}{n!} + \ldots \text{etc.}$$

where m is the mean, and where 4 ! = 4 × 3 × 2 × 1.

TABLE II

The number of species of snail which are common to any pair of limestone hills, hills 8, 9 *and* 10 *having been grouped into one unit*

Hill No.	1	2	3	4	5	6	7	8–10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
2	2																								
3	3	2																							
4	1	1	1																						
5	3	2	2	1																					
6	3	2	2	1	3																				
7	3	2	2	1	3	3																			
8–10	3	2	2	1	4	4	5																		
11	2	2	2	1	2	3	2	2																	
12	2	1	1	1	2	2	2	2	1																
13	2	1	1	1	2	2	2	2	1	6															
14	2	1	1	1	2	2	2	2	1	2	2														
15	1	1	1	0	1	1	1	1	1	1	1	0													
16	2	1	1	0	2	2	2	2	1	1	1	1	2												
17	2	1	1	1	2	2	2	2	1	3	3	2	2	1											
18	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1										
19	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	2									
20	1	1	1	1	1	1	1	2	2	3	3	1	2	1	3	1	1								
21	2	2	2	1	2	2	2	2	2	3	3	1	2	1	3	1	1	4							
22	1	1	1	1	1	1	1	1	2	3	3	1	1	1	3	1	1	5	5						
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0					
24	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	2	1	1				
25	1	1	1	1	1	1	1	1	1	1	1	1	2	1	3	0	0	2	3	2	1	2			
26	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	2	1	1	0	2	1		
27	0	0	0	0	0	0	0	0	1	2	2	0	1	0	1	1	1	3	3	4	0	1	0	2	
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Any pair of hills may share from 0 to 7 species of snail, and the frequency distribution of this variable seemed at first sight to approximate to the Poisson distribution. The data are set out in Table III, where it is shown that there is a serious excess of high values; there were 8 occasions where pairs of hills shared 5 or more species, whereas the Poisson distribution predicts only 2 or 3.

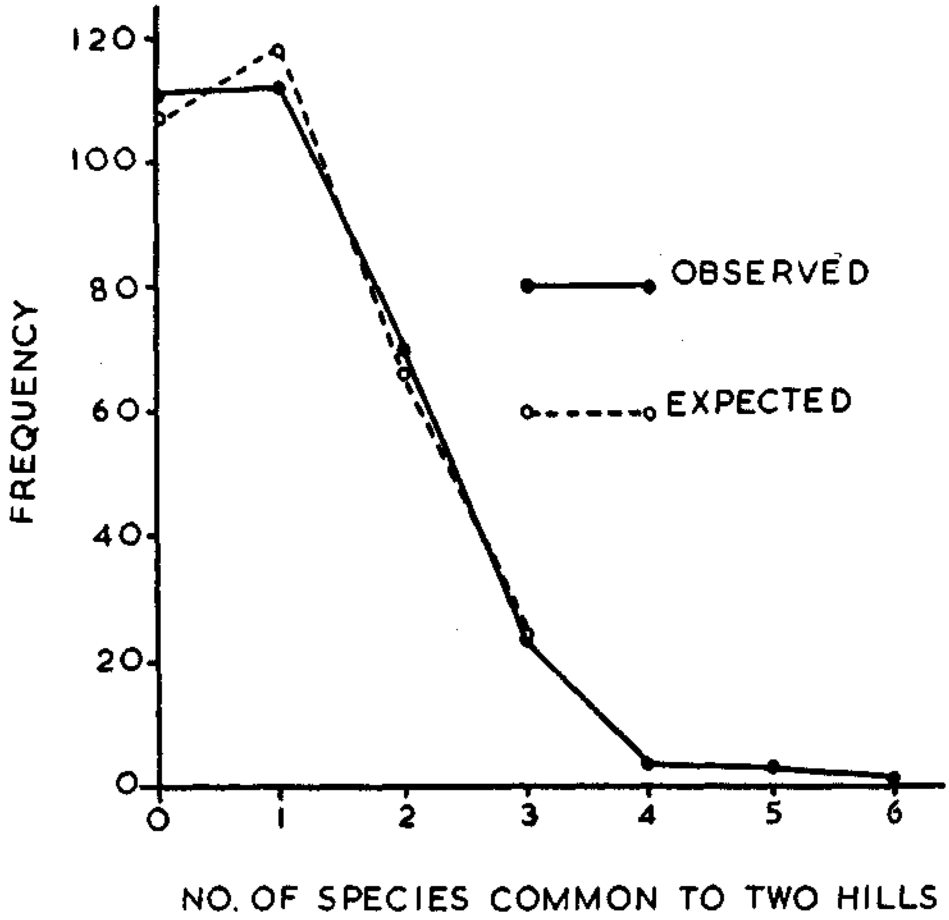


FIG. 2. Comparison of the observed and the expected numbers of species of snails common to pairs of limestone hills, showing the goodness of fit of the Poisson distribution. The data are set out in Table IV; *see* also Table II.

Examination of the tabulation of comparisons of all the hills showed that unusually high values were recorded for comparisons between hills 8 and 9, 8 and 10, 9 and 10. Since these three hills are situated fairly close together it seems possible that these high values are attributable to special circumstances operating in these particular cases. The tabulation of comparisons of the various hills was therefore amended to exclude comparisons between pairs of these three hills, *i. e.*, treating hills 8, 9, and 10 as a single locality.

The data as amended are set out in full in Table II. The amended frequency distribution was now found to conform closely to expectation according to the Poisson distribution, as shown in Table IV.

TABLE III

No. of species common to two hills	Frequency observed (O)	Frequency expected (E)	O − E	$\frac{(O - E)^2}{E}$
0	125	113·85	11·15	1·092
1	123	136·62	−13·62	1·358
2	87	81·97	5·03	0·309
3	30	32·79	− 2·79	0·237
4	5	9·84	− 4·84	2·381
5 6 7	4 2 } = 8 2	2·93	5·07	8·773
TOTALS ..	378	378·00		14·15

The mean = 1·20, variance = 1·446, $\chi^2 = 14{\cdot}15$; the Poisson distribution does not fit, due to excessive frequencies of 5 or more.

TABLE IV

No. of species common to two hills	Frequency observed (O)	Frequency expected (E)	O − E	$\frac{(O - E)^2}{E}$
0	111	107·11	3·89	·141
1	112	118·89	−6·89	·399
2	70	65·98	4·02	·245
3	24	24·41	− ·41	·007
4 5 6 7	4 3 1 } = 8 0	8·61	− ·61	·043
TOTALS ..	325	325·00		·835

The mean = 1·1108, $\chi^2 = 0{\cdot}835$, $P > 0{\cdot}5$, variance = 1·1754.

This indicates that as judged by the numbers of species common to any pair of hills there is no significant zoo-geographic discontinuity in the area studied. The distribution of species is random, except on hills 8, 9, and 10 which exhibit unusually high levels of faunistic affinity, and where the distribution of species of snails may have been influenced by unusual circumstances.

The unusual circumstances which may have been operative with special respect to hills 8, 9, and 10 may include the following:—

(*a*) Any two, or all three, hills may have arisen by the breakdown of a single larger hill by erosion, the great similarity of the snail faunas of the hills being primarily due to their common origin. If the snails were not originally calcicolous this theory could be true even for hills which do not belong to the same geological formation and which can never have comprised one extensive limestone plateau.

(*b*) At times of serious flooding, living snails may be transported by flotation on flood waters from one hill to another, thereby increasing the number of species of snail common to the two hills. (Tweedie suggested this possible mechanism for re-distribution of species of snails, but did not suggest that it was attributable to any particular hills.)

The three hills in question are: Gunong Pondok, Perak (No. 8); Sungei Siput hills and Gunong Techehel, Perak (No. 9); Gunong Kantang, Perak (No. 10). In future field work on the distribution of the snails of Malayan limestone hills, it would be desirable to try to test the proposition brought forward here that the snail faunas of hills 8, 9, and 10 have been subjected to different influences from those experienced by the snail faunas of the other Malayan limestone hills.

There is one remaining consideration of some importance. Reference to Table II shows that the hills differ greatly in the general extent to which they share species of snails with other hills. It is easy to summate, for each hill, the number of species it shares with all other hills. This having been done, the 28 hills have been placed in ranking order in Table V.

TABLE V

Hill No.	Total recorded affinities with all other hills	Hill No.	Total recorded affinities with all other hills
21	51	14, 15	25
12, 13, 20, 22	43	16	23
17	41	27	22
8, 9, 10	40	4	16
6, 7	37	26	13
1, 5	36	24	12
25	29	18, 19	10
11	28	23	3
3	27	28	1
2	26		

The random nature of the distribution of species of snail demonstrated in this paper is dependent on interaction of a number of random variables including the size and the antiquity of the hill, its proximity to other hills, the availability of suitable micro-habitats on its limestone surfaces, chance colonisation of the hill by species of snail, etc.; the *records* of distribution of species are also influenced by the number of visits by collectors and by the efficiency of collecting. Thus the low-ranking position of the hills on the right hand of Table V may be at least partly due to inadequate collecting. It would be particularly desirable to focus attention on hills 23 and 28 for future collecting trips.! It should be appreciated that the production of further collecting data from these hills is not likely to break the goodness of fit of field data with the Poisson distribution; additional data will simply alter the value of the mean, and the shape of the frequency distribution curve to the shape appropriate to a Poisson distribution with the new mean value.

ACKNOWLEDGEMENTS

We wish to thank Dr. A. D. Ansel, Marine Station, Millport, Isle of Cumbrae, Scotland, who kindly presented this paper on our behalf at the Symposium on Mollusca, Ernakulam, India, in January 1968.

LITERATURE CITED

PATON, J. R. 1961. A brief account of the geology of the limestone hills of Malaya. *Bull. Raffles Mus.*, **26**: 66–75.

TWEEDIE, M. W. F. 1961. On certain Mollusca of the Malayan limestone hills. *Ibid.*, **26**: 49–65.

BASIC DISTRIBUTION OF NON-MARINE MOLLUSKS

ALAN SOLEM

Field Museum of Natural History, Chicago, U.S.A.

ABSTRACT

The conventional zoogeographical realms, regions, and provinces are based upon the distribution patterns shown by birds and mammals, organisms whose major evolutionary radiation occurred during comparatively recent geological periods. An admirable summary of the world distribution into Ethiopian, Oriental, Australian, Nearctic, Palearctic, and Neotropical is given by Darlington (1957). Only in the tapirs and the families of lower vertebrates such as reptiles and amphibians, are disjunctive distributions common.

Mollusks, arthropods, and higher plant families agree in having disjunctive distributional patterns the rule rather than the exception. Although data on family and generic distributions for land and freshwater molluscs are incomplete for most zoogeographical areas, the broad patterns of distribution are clear.

The southern hemisphere areas are characterized by disjunctively distributed and relatively primitive land snail taxa, such as the Endodontidae, Acavacea, and Bulimuloidea. The Holarctic and Oriental land masses, including much of the tropical Asian and tropical African areas, have a fauna of more advanced taxa, such as the Polygyracea, Helicacea, and "zonitoid" taxa.

Faunistic boundaries of land snail distribution do not agree with those of the vertebrates. While New Guinea has an Australian vertebrate fauna, the land snails are oriental in affinities. Similarly, although the islands of Polynesia and Micronesia lack an endemic vertebrate fauna, they have a highly distinctive fauna of land snails that are endemic at the family or subfamily level.

Designation of land snail "realms, regions, and provinces" is premature, but indications of the general patterns are given.

INTRODUCTION

THE tidal wave of experimental studies on the cellular and subcellular levels, progressing from experimental physiology to biochemistry and molecular biology, which some now equate with " biology," has produced a generation of young biologists who are profoundly ignorant of such " classical" disciplines as systematics and zoogeography. I beg indulgence from my older and more classically oriented colleagues, but through sad experience realize that background information must be presented for the education of our experimental colleagues.

Zoogeography, the study of animal distribution, can be and has been approached from four different ways: (1) geographical zoology, or the distribution of particular groups of animals; (2) zoological geography, or the distribution of many animal groups in a particular area; (3) ecological animal geography, or the analysis of ecologic factors affecting animal distribution; and (4) historical animal geography, which attempts to determine the migration patterns of faunas through time and to study the origin and spread of particular animal groups. Each approach is useful and necessary, and often combinations of approaches will yield quite valuable insights. All levels of zoogeography are dependent upon systematic and faunistic data. Unless the distribution of the animals considered is well and accurately determined, the zoogeographic conclusions will be faulty at best, or erroneous. If the systematic relationships of the organisms are incompletely known, or the phylogenetic affinities incorrectly determined, then once more the zoogeographic results will be of little value.

It is no accident that the classical zoogeographic realms, regions and provinces have been determined through study of birds and mammals. These organisms are conspicuous and comparatively few in number, with only about 3,500 mammalian and 8,600 avian species. Quite understandably anthropomorphism has focused an inordinant amount of attention on their distribution and systematics. There probably have been at least 60 systematic mammalogists and ornithologists active in the last 100 years for every systematic malacologist. Thus, the mollusks, with about 100,000 species, are much more poorly known in terms of basic distribution and systematic affinities than are the over-studied birds and mammals. While students of vertebrate distribution now are able to focus on the dynamics of current distributions and have accumulated considerable data on distributions in past geological eras, the basic tasks of compiling ranges and determining systematic affinities remain to be done for mollusks and all other " invertebrate " taxa.

The classic exposition of major zoogeographic regions was by P. L. Sclater (1858), who divided the world into six major realms—Ethiopian, Nearctic, Palearctic, Neotropical, Australian, Oriental—based upon the distribution of land birds. Sclater's paper appeared before Darwin's work on evolution, and he viewed these areas as separate centers of creation. This in no way diminishes their overall utility in recognizing the basic pattern of higher vertebrate distribution. A. R. Wallace (1876) in his two-volume work, *The Geographical Distribution of Animals*, synthesized tremendous quantities of information on bird and mammal ranges. It was not until the appearance of Darlington (1957) that Wallace's study was superseded.

Between Wallace, who dealt with the present distribution of birds and mammals, and Darlington, who attempted to evaluate the average pattern of vertebrate distribution and to discuss the major faunal movements of vertebrates, zoogeographers have focused attention on several problems of a fundamental nature. Perhaps the major areas of concern have been with:

(1) elucidation of faunal areas and determination of boundaries for these areas;

(2) concern with the basic geologic stability or instability of land masses through time;

(3) working out the history of major taxonomic units;

(4) analyzing the ecologic factors determining zoogeographic distribution; and

(5) determining the directional movements of faunal migrations.

Early attempts at recognition of faunal boundaries and areas consisted of hand compiled lists of species and distributional limits. Modern use of computors has resulted in such studies as that of Simpson (1964) in which the presence or absence of each North American mammal species was noted for quadrates 150 miles on each side, with species density contours plotted for all areas of North America.

Certain areas were recognized quite early as being zones of transition between major faunistic units. For example, a huge literature exists concerning the importance and/or reality of Wallace's and Weber's lines in separating the Oriental and Australian faunas (*see* Mayr, 1944). The area between Java and New Guinea is one of rapidly shifting faunal dominance, and attempts to delineate exact lines of demarcation are not particularly fruitful or important. The evolving and changing nature of faunas now is universally recognized and in the last 30 years emphasis has shifted to other features.

Of basic importance to any zoogeographical theory concerning the origin and spread of faunas is the stability or instability of the major land areas through geological history and the extent to which dry land *vs.* overseas dispersal is required of organisms. No branch of zoogeography has been more subject to shifting fads and fancies. In the early part of this century, the imaginary building of narrow land bridges, which extended thousands of miles across ocean deeps, was a favored activity. Such a bridge might be "required" to explain the presence of perhaps one or two small insects or tiny land snails on remote oceanic islands. Typical of this genre, but far from being the most extreme, was the proposal of Meyrick (1926, p. 271) who explained the origin of eight Microlepidoptera on Rapa by having a land bridge extend from Fiji to Rapa. In his own words, " A rise of 12,000 feet in the sea-bottom of the South Pacific is required to show these results, but entertain no doubt that such an elevation must have existed since the Eocene period, because it is absolutely the only explanation possible." There was literally no portion of the ocean which had not been repeatedly bridged by proposed land corridors of some zoogeographer. In sharp reaction to this, during the 1930's and 1940's it became suspect for a zoogeographer to suggest changes in land area exceeding the fluctuation of the oceans related to the maximum Pleistocene glaciation.

A major school of zoogeographers considers that the present land masses have been stabilized in their present outline and position throughout the spread of currently extant animal groups. Dispersal to islands was explained through the *dei ex machina* of cyclonic winds and accidental carriage on the feathers of migratory or sea-birds. An occasional land bridge across Bering Strait; one between New Guinea and Australia; and repetitive openings and closings of the Panama land bridge were all that was required for zoogeographic proposals.

A second major school, in vogue during the 1920's and revived in full flower during the late 1950's and 1960's, was the idea of continental drift. This assumes that the major continents were in the past grouped together as one continuous land mass that subsequently broke up into the large continental fragments which slowly, or rapidly, depending on the zoogeographer, drifted to their present position. Considerable geological evidence, particularly coming from palaeomagnetism, indicates that quite possibly the continents were joined together at one time. However, I know of no animal distributions that are more simply explained by continental drift than by stability of continental mass. If drift occurred, then it must have been at a time prior to the movements of any extant families.

Particularly in respect to the mammals, where there is an abundant fossil record, we know a great deal about the history of current biotas. In a delightful book, Simpson (1953) has summarized the major features of historical biogeography as it applies to mammals. For groups in which the fossil record is absent or uninformative, data on past movements must be deduced from a combination of phylogenetic and distributional data. The tremendous effects of ecology on animal distributions have been reviewed by Hesse, Allee, and Schmidt (1951). They are not further considered in this report.

A basic problem continues to be the question of directional faunal movements. Biogeographers traditionally have been divided into two schools. Those resident in Europe and North America, perhaps subconsciously looking "downward" at the distended Southern Hemisphere on their Mercator map projections, have almost universally postulated spread from the Holarctic land mass into the Southern Continents. Biogeographers resident in South America, South Africa, Australia, and New Zealand, recognizing the many faunal elements they have in common, and possessing both a "polar" viewpoint and a sense of isolation, have tended to hypothesize a center of origin and spread from Antarctica into South America, South Africa, and Australia. This subject will be discussed later.

Recent years have seen two new important trends in study. A program of airplane and ship nettings sponsored through the efforts of J. Linsley Gressitt and reported on in various volumes of *Pacific Insects*, issued by the B. P. Bishop Museum, has provided extremely important data concerning the actuality and relative frequency of overseas dispersal in relation to arthropods. Secondly, several individuals have begun to focus on the dynamics of dispersal, colonization, and extinction of individual species in small faunal units. The resulting science of experimental biogeography now is attempting to predict faunal compositions, colonization rates, and to evolve generalized laws of biogeography. A recent summary by MacArthur and Wilson (1967) should be required reading for every potential biogeographer.

MOLLUSCAN DISTRIBUTION

As indicated earlier, the basic systematic and distributional data needed for zoogeographic surveys of mollusks are fragmentary. Any collection from south-east Asia, for example, will provide range extensions of several hundred miles and enable revisions of systematic position for many of the known species. This holds true for most areas of the world, except for much of Europe and North America, north of Mexico. I am currently finishing a revision of the Pacific Island Endodontid land snails. Ignoring Hawaii, in the larger subfamily there are 155 species level taxa. Of these, 103 were previously undescribed. In regard to particular areas, only one of 25 Endodontids found on Rapa Island was previously known and only two of 24 found on Mangareva. The classification of these species was equally poorly understood. Only five of 23 genera had been named previously, and only two of these are being used with their historic limits.

Not only are most areas incompletely explored, but the systematic work has been done from quite different philosophic viewpoints. The Australian land snail fauna has been reviewed by Iredale (1933, 1937 *a*, 1937 *b*, 1938). His concept of genera and families is so much narrower than that utilized by most other malacologists that direct faunistic comparisons on the basis of his publications are impossible (Solem, 1959, pp. 26–28). In many cases reduction of his families to generic level, and equation of his genera with superspecies is necessary for comparative studies.

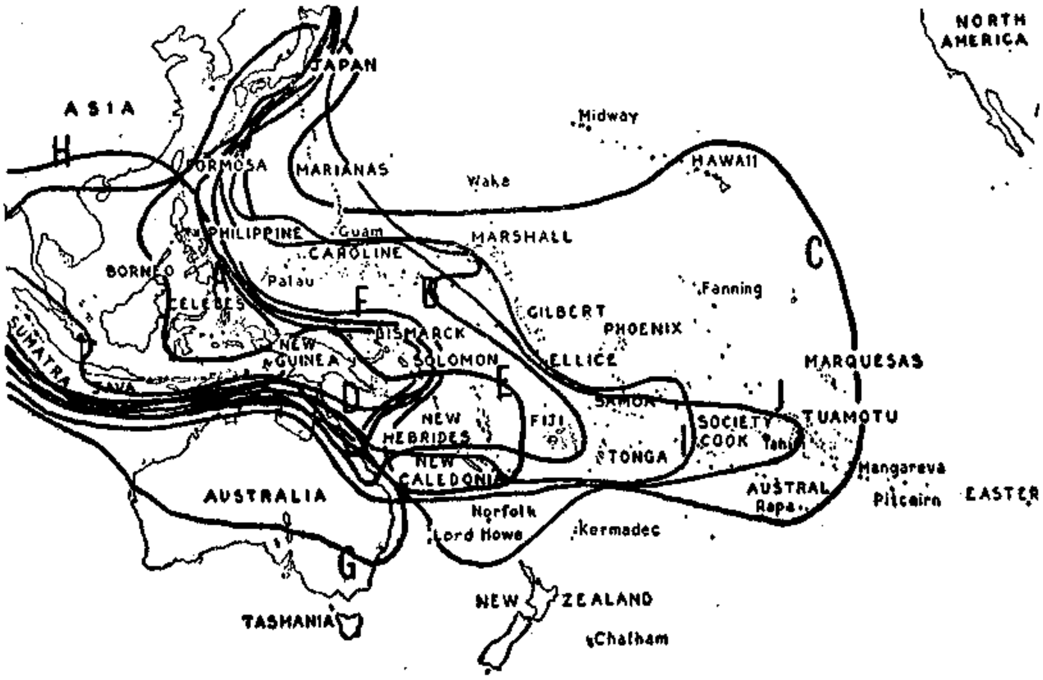


FIG. 1. Distributional limits of land snail families in Pacific region. Adapted from Solem (1959). The families are:

A, Clausiliidae;
B, Pupinidae;
C, Helicinidae;
D, larger Helicarionidae with normal shell development;
E, Enidae;
F, Cyclophoridae;
G, Camaenidae;
H, Rathouisiidae;
I, Diplommatinidae;
J, Trochomorphidae.

Several generations of collecting and faunistic reviews combined with an equal amount of systematic revisionary work will be required before a world land snail geography can be written. Despite this, sufficient information does exist to answer a few questions. I propose to deal with two problems in this report. First, to contrast the land snail distribution in the areas from South-east Asia to the Solomon Islands with that of the terrestrial vertebrates. Secondly, to summarize what data currently available on some southern hemisphere relict land snail families tells us concerning the patterns and directions of land snail migratoins.

WALLACE'S LINE AND LAND SNAILS

Although the terrestrial vertebrates show a sharp to slow transition between the Oriental and Australian faunas, in the area known as "Wallacea" no such transition is evident for vascular plants, insects, and land snails. Fairly comprehensive treatment of the general patterns of land snail distribution on the family level in this area is given in Solem (1959). Here it is proposed merely to summarize that data (Fig. 1), as slightly modified by more recent studies. It is obvious that on the family level, there is a single fauna of land snails that extends from South-east Asia to New Guinea and often on to the Solomon Islands and the tropical coast of Queensland. While some groups are also present on the islands of Polynesia and Micronesia, these consist of the smaller sized species or groups that are arboreal in habitat and therefore more apt to be transported accidentally. The larger Helicarionidae, Cyclophoridae, Camaenidae, and Clausiliidae, *plus* the carnivorous slugs belonging to the Rathouisiidae, are limited to the core area, except for the desert radiations of camaenids found in Australia. Departures from this pattern occur primarily on the generic level. The camaenid genus *Amphidromus* of South-east Asia to the Tenimber Islands is replaced by the *Papuina* complex in the Aru Islands, New Guinea, coastal Queensland, and the Bismarck-Solomon axis (Solem, 1959, p. 274, Fig. 20). Similarly, the helicinid genera *Geophorus* and *Palaeohelicina* (Solem, *op. cit.*, p. 277) replace each other in approximately equivalent fashion.

Very few land snail families depart from this pattern (Fig. 2). The Strobilopsidae are primarily a North American taxon with relict forms being found in the Philippines, Japan, Korea, Northern China, and Western New Guinea. The Streptaxidae are common through much of peninsular South-east Asia, Japan, Formosa, the Philippines, and Borneo, with one or two representatives reaching the Celebes. They are absent from Sumatra, Java, and the rest of Indonesia and New Guinea except for an introduced species. The Polygyracean relict family Corillidae is restricted to the mainland of South-east Asia. Figure 2 gives the distribution of two additional families, the Partulidae (D) which are restricted to the high islands of Micronesia and Polynesia with an apparently secondary invasion into the fringe of Melanesia, and the Poteriidae, found in parts of Micronesia, Melanesia, and Polynesia with their relatives being restricted to tropical Central and South America.

Many students of vertebrate distribution have either been unwilling to accept the reality of such differences, or have failed to appreciate the simple explanation for this phenomenon.

The present distribution of any animal group is the result of a historical process operating over a greater or lesser period of time. There have been terrestrial organisms since the Devonian period. With the imperfection of the fossil record, we have only the most fragmentary information concerning zoogeography of past geological eras. As we approach the present, the record becomes more complete. In regard to the mammals, which are a product of mid to late Tertiary radiations, the record is relatively comprehensive. Despite obvious limitations and inadequacies, the fossil record does show that (1) there has been a definite history of rise, dominance, decline, and extinction of animal groups; (2) many types of organisms abundant today were at one time absent or rare; and (3) some creatures that are rare today formerly were common. By the Upper Carboniferous and Permian there is evidence of a rich fauna of insects, land snails, scorpions, spiders, phalangids, and mites. Not only were these groups established, but they had diversified considerably. Pennsylvanian strata contain at least three families of land snails, and the Permian beds yield 17 orders of insects, 10 of which still exist today. The origins of these invertebrate forms must have considerably predated the Permian and Carboniferous. Most probably the first invertebrates made the transition from freshwater to land in the Early or Middle Devonian.

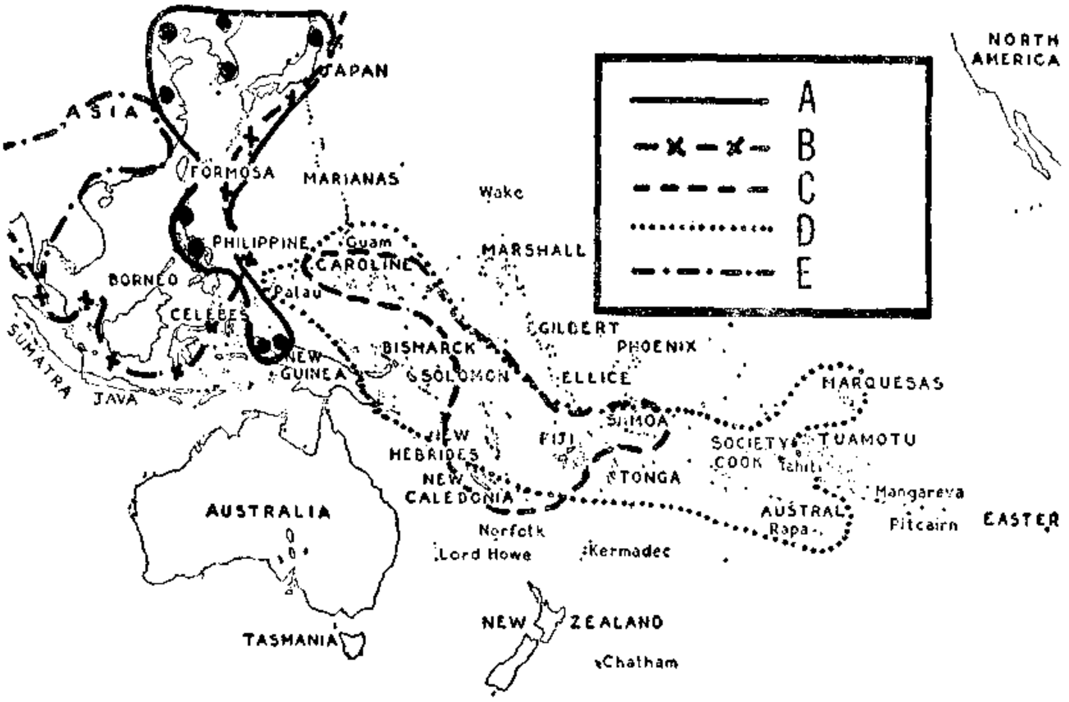


FIG. 2. Land snail families that do not conform to the basic pattern. Data from Solem (1959) and later studies. The families are:

A, Strobilopsidae;
B, Streptaxidae;
C, Poteriidae;
D, Partulidae;
E, Corillidae.

The basic radiation patterns of the higher vertebrates are approximately as follows: the giant amphibians became dominant in the Permian and declined at the end of the same era; reptiles had their first appearance in the late Carboniferous, an early radiation in the Permian and then produced the explosive evolution of the dinosaurs in the Mesozoic. Some time in the late Triassic, small mammals evolved from the Therapsid reptiles, with opossum-like marsupials and primitive placental mammals appearing in the late Cretaceous. Birds evolved in the Jurassic and had their major radiation in the Cretaceous. During the latter period there was the dramatic extinction of the dinosaurs. The Tertiary is characterized by the tremendous radiation of mammals and eventual evolution and rise to dominance of man.

These historical facts are clearly reflected in the differing patterns of current vertebrate distribution. When viewed at the family level, although there is an "average pattern of vertebrate distribution" (Darlington, 1957), the basic type of distribution is not unitary. If we exclude the flying mammals (bats), only a single family of recent mammals shows a disjunctive distribution—the tapirs which are found in South-west Asia and in Central and South America. Fossil tapirs still lived in Europe, Asia, and North America in the Pleistocene, so that this disjunctive pattern is of very recent origin. Otherwise families of mammals show continuous distribution within or between major zoogeographic realms. The essentially tropical nature of birds is emphasized by their distribution patterns, with numerous families showing Pantropical distribution, but are absent or sparsely represented in the temperate regions. Similar disjunctive patterns are extremely common in reptilian families, and in addition they show a few striking examples of relict occurrences. For example, the only Old World iguanas are found in Fiji and Madagascar, while the remarkable Tuatara of New Zealand is the only living member of a major group that was widely distributed in late Mesozoic times, but are absent from fossil beds later than the Lower Cretaceous, about 135,000,000 years ago. When amphibian distribution is analyzed, there are even more striking observations, such as the New Zealand frog *Leiopelma*, whose only relative is in the Pacific North-west of the United States (*Ascaphus*). Presumably the leiopelmids were widely distributed in the past, but now survive only as these cold temperate relicts.

Since the major radiation of these groups occurred at different times in the geologic span, their initial and major radiations did not coincide. While distributional radiations occurring during the last part of the geologic time scale would be the same, barriers and land bridges present in past eras were undoubtedly different. Thus, the Oriental nature of the New Guinea plant, insect, and land snail fauna probably reflects conditions existing in the Mesozoic. Presumably at this time there was essentially dry land connections between South-east Asia and Australia *via* New Guinea. Long-range climatic barriers in Australia undoubtedly prevented most of these forms moving into Australia but there probably was a Mesozoic "highway" enabling colonization. During the Tertiary, the geologic history of Indonesia has been highly complex, with numerous elevations and subsidences occurring. Hence forms of comparatively late evolution and mid to late Tertiary radiations have had to try and filter across various water gaps. Thus the dramatic change in mammal and bird distributions from Java to New Guinea.

The probable nature of this historic difference has been whimsically summarised in Figs. 3 and 4, with due apologies to George Gaylord Simpson, whose earlier efforts inspired these diagrams.

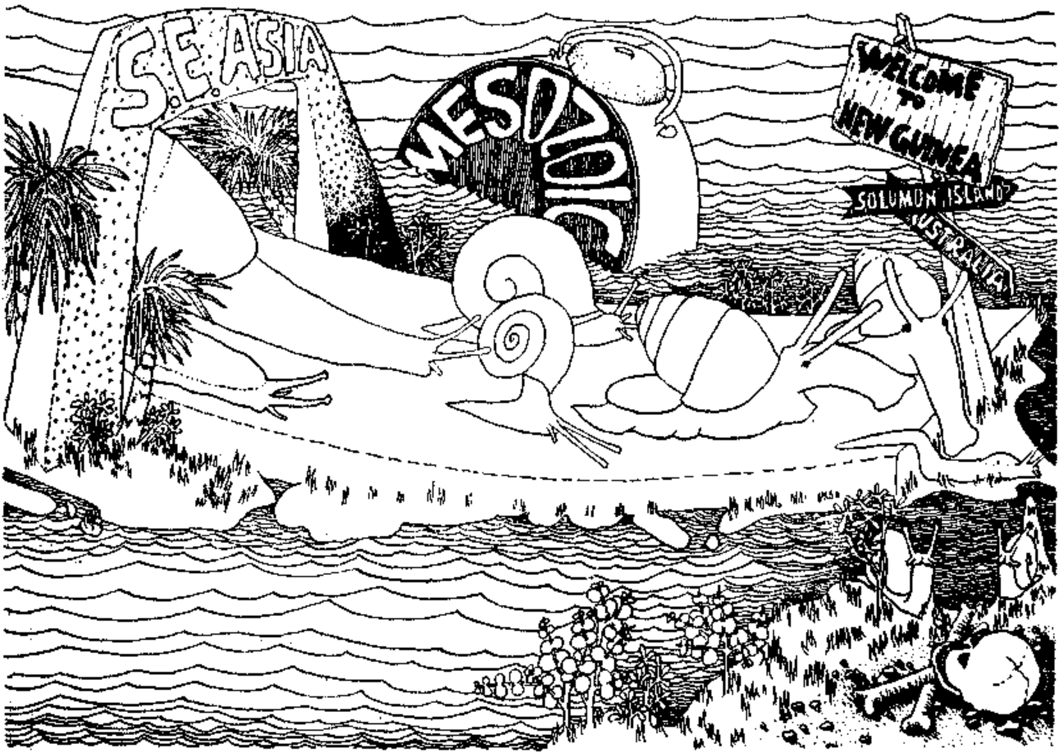


FIG. 3. South-east Asia to Australia dispersal in the Mesozoic. A cartoon by Margaret Ann Moran.

Obviously this is an enormous simplification of incredibly complex historical events, yet a basic radiation of land snails, insects, and plants through the Indonesian Archipelago to New Guinea and the Solomon Islands during the late Mesozoic does explain the vast difference from higher vertebrate distribution, which must have occurred in the presence of water barriers during the late Tertiary.

DIRECTION OF LAND SNAIL MIGRATIONS

The question of Holarctic *vs.* Antarctic origins and distributions have been outlined above. Here it is proposed to review in some detail the scanty information available concerning two superfamilies of land snails—Bulimulacea and Acavacea—that have figured prominently in nearly all Antarctic "origins" and "dispersals".

Before discussing these taxa, it is necessary to emphasize what is the typical dispersal pattern shown by a newly evolved species or group of species. While every taxonomist can point to departures from this pattern, nevertheless it is the most frequently encountered story and less difficulties in interpretation are encountered by use of this axiom. When a species, consisting of many populations, becomes differentiated and is better adapted to conditions than neighbouring species, then it will begin to expand and sooner or later replace the less effective competitors. Then populations on the periphery of the range will be competing against less well-adapted forms and are therefore under no particular selective pressure themselves. In contrast, as the population density builds up near the original center of origin, there will be intraspecific competition which can provide a rela-

FIG. 4. Present higher vertebrate distribution, South-east Asia to Australia. A sociological impression by Margaret Ann Moran.

tively high selection pressure for greater efficiency in use of environmental resources. When continued, this will in time lead to specific level separation. The situation will thus come to resemble the model in Fig. 5 *a*. Given time and sufficient vagility, the original Form "A" will pass over short water or montane barriers, expanding to limits beyond which it cannot pass. If subsequent widening or heightening of intermediate barriers occur, then populations but little changed from the original Form "A" will be preserved around the periphery of distribution (Fig. 5 *b*). Under little selection pressure for change, these populations may closely resemble the primitive state of organization.

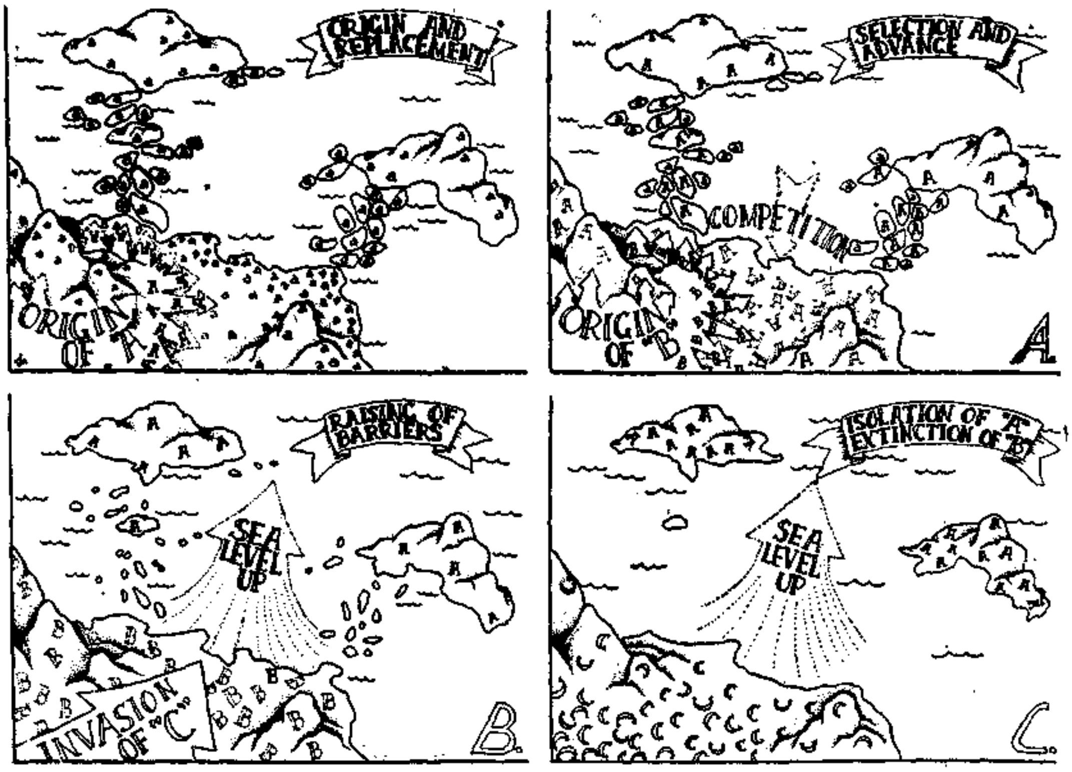


FIG. 5. Hypothetical pattern of origin, dispersal, differentiation, replacement and isolation resulting in a disjunctive relict distribution on islands. Form "A" evolved from "*a*" is more efficient. Form "B" evolved from "A" under conditions of crowding and is more efficient in use of resource space, but has a lower vagility (= ability to cross barriers). Form "C" is an unrelated invader from outside the region, with great efficiency and low vagility.

Given sufficient time, forms derived in the center of evolution, such as Form "B", can, and often have been, replaced by totally unrelated organisms that are represented in Fig. 5 *c* as Form "C". The current distributional pattern will show Form "A" limited to two isolated areas with their replacement, Form "C", occupying most of their original range. Without knowledge of their prior history, most zoogeographers would interpret this distributional pattern as Form "A" having originated in one of the areas and having been transported directly to the other, whereas historical evidence shows that they were independently derived.

Fortunately, most relict groups of organisms have a more complex and phylogenetically restricted present pattern. Under these circumstances, by determining generalized and derived taxa, observing their distributional patterns, and assuming, unless other evidence is present, that the most primitive forms lie on the far limit of distribution with the derived taxa occurring nearer the center of origin, it is possible to deduce the probable direction of migration and areas of origin.

Although phylogenetic data on the families considered below is inadequate from the viewpoint of modern systematics, nevertheless indications are clear enough to give an extremely high probability to their Holarctic origin and subsequent spread into the Southern Hemisphere, although today they are primarily restricted to that region.

Distribution of the family Bulimulidae is shown in Fig. 6. Two little-known genera from Africa, *Aillya* and *Prestonella*, were originally described as bulimulids, but the weight of evidence suggests that the resemblances are convergent and that they are probably highly modified relatives of the Succineidae (*see* Solem, 1959, p. 123).

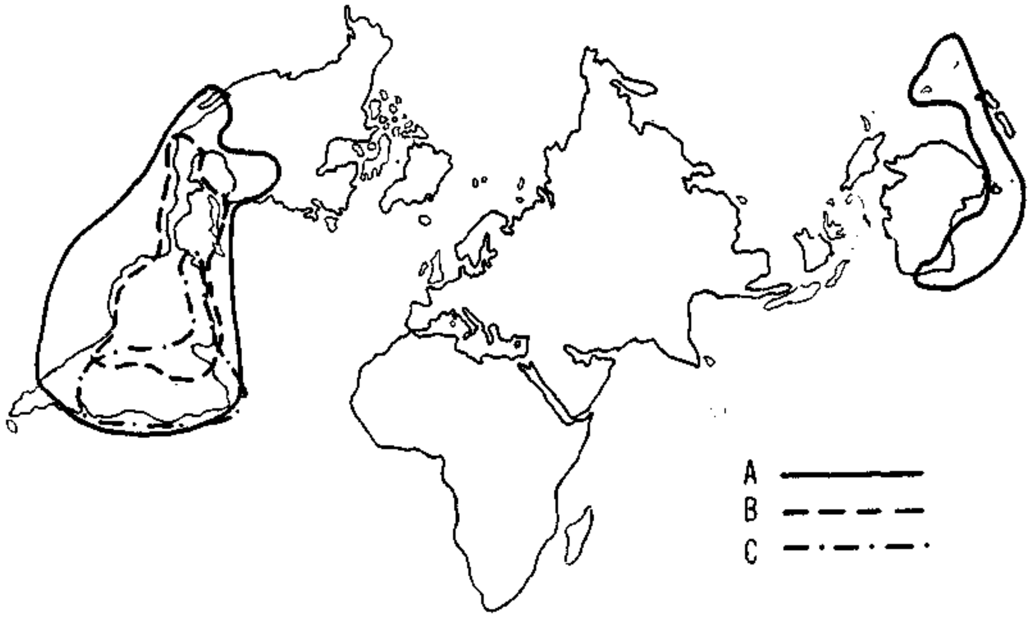


FIG. 6. Present distributional limits of the Bulimulidae. Subfamilies are: A, Bulimulinae; B, Orthalicinae; C, Odontostominae.

Probably 1,300 species of bulimulids have been described. About 110 of these are found in the Pacific area, with the remainder restricted to Neotropica with only a very few forms extending into North America. There is abundant fossil record of South American bulimulids and forms probably referable to that group have been recorded from the Eocene and Pliocene of the Rocky Mountain region. No fossils that are unquestionably bulimulid and of greater than Pliocene age are known from the Pacific region. Some controversy remains concerning major divisions within the family. Iredale (1937 *a*, 1944) placed the Australian-Tasmanian genus *Bothriembryon* in one family, *Placostylus* and its relatives into a second family, both of which he considered separate from the South American bulimulids. Pilsbry (1946), on the basis of dissecting specialized Solomon Island *Placostylus*, gave that group subfamily recognition. My own dissections of several *Placostylus* (unpublished data) indicate that there are no significant anatomical differences between the Austral-Melanesian bulimulids and the more generalized South American taxa. I do not accept Iredale's family level separation.

While there is no doubt that the family Urocoptidae is distinguished from the bulimulids, how to rank the major types of South American bulimulids is uncertain. Zilch (1960, pp. 473-520) recognized the Odontostominae and Orthalicinae as separate families. Both seem to be taxa derived from the more generalized Bulimulinae. What little is known of their anatomy suggests to me that their separation is of subfamily, rather than family nature, but this is a matter of personal opinion.

In South America no bulimulids have been reported south of 46° south latitude in Chile or approximately 39° south near the Atlantic coast of Argentina. The greatest degree of generic diversification is present in Brazil and the Andean region, with a second center of diversity in Northern Central America. Very few species extend into the United States, with three species of the genus *Bulimulus* accounting for nearly all of the North American map range. A few *Drymaeus* occur in Florida. Of the derived taxa, the seemingly less specialized Orthalicinae extends from Florida and Central Mexico south along the Andean chain to Southern Peru and Bolivia, also reaching most of the Amazonian and Orinoco basins. The greatest differentiation is found in the Andean area from Colombia to Southern Peru. A few species of the more specialized Odontostominae occur north of the Amazon, even reaching coastal Venezuela, but they are primarily a group of Southern Brazil and Argentina.

No clear pattern of phylogeny is seen among the South American taxa with the fragmentary anatomical data currently available.

Data on the phylogenetic heirarchy found in the Pacific area bulimulids is presented by Solem (1959, pp. 123–147). Subsequent dissections of many additional species have confirmed basic relationships indicated in that study. The data are insufficient to allow formal taxonomic revisions to be published. Quite surprisingly, on the basis of both anatomy and shell structure the generalized taxa are the Australian genus *Bothriembryon* and the New Hebridean *Diplomorpha*. Both genera show no important qualitative differences from the more generalized South American taxa. They belong unquestionably in the subfamily Bulimulinae. Anatomical variations within *Placostylus* are simple in kind, but complex in distribution. The species from Lord Howe Island, the New Hebrides, Santa Cruz Island, and New Zealand have basically similar anatomical structures. Too few have been dissected to enable meaningful assignment of subgeneric names but they represent the same level of evolution. Species of *Placostylus* from the Loyalty Islands and New Caledonia have altered anatomic structures and seem to be intermediate between the generalized taxa mentioned above, and the very specialized species from the Solomon Islands and Fiji. In the Solomon Islands, *Placostylus* ranges through most of the Archipelago south of Bougainville, while in Fiji the genus is limited to the main groups of islands and does not reach the Lau Archipelago. The Solomon Islands and Fiji species are at a higher level of complexity than the New Caledonian taxa. Again, too few species have been dissected to enable determination of exact relationships.

The basic indications of these relationships are summarized in Fig. 7. Obviously this is a complicated picture and one which is not amenable to simple interpretation. In an early paper, Hedley (1892) hypothesized a "Melanesian continent" to explain the current distribution of *Placostylus*. This was before the relationship of *Bothriembryon* to the bulimulids was known, and before *Diplomorpha* had been removed from the Partulidae. Hedley suggested that *Placostylus* had been derived from the New Guinea region. In subsequent studies Hedley (1899, pp. 398–399) reversed his thinking and derived *Placostylus via* an Antarctic dispersal route. Bulimulids are known as fossils in the South American Paleocene, and almost certainly date from the same period in the Australian-New Zealand area. On the basis of fragmentary phylogenetic data, I would suggest an origin from the Holarctic land mass through the Indonesian Archipelago, with essentially three distinguishable waves of migration deducible. This is summarized in Fig. 8. The initial migratory wave included the ancestors of *Bothriembryon* and *Diplomorpha*. The former remained isolated in the south-western part of Australia, with a secondary radiation spreading northward in Australia and eastward into Tasmania occurring at a later time. Whether the New Hebridean *Placostylus* are direct derivatives from *Diplomorpha*, or whether they represent a secondary invasion from New Caledonia, cannot be determined at present. The second alternative is indicated in Fig. 8, since accidental spread from a New Caledonian base to Lord Howe Island and the Northern tip of New

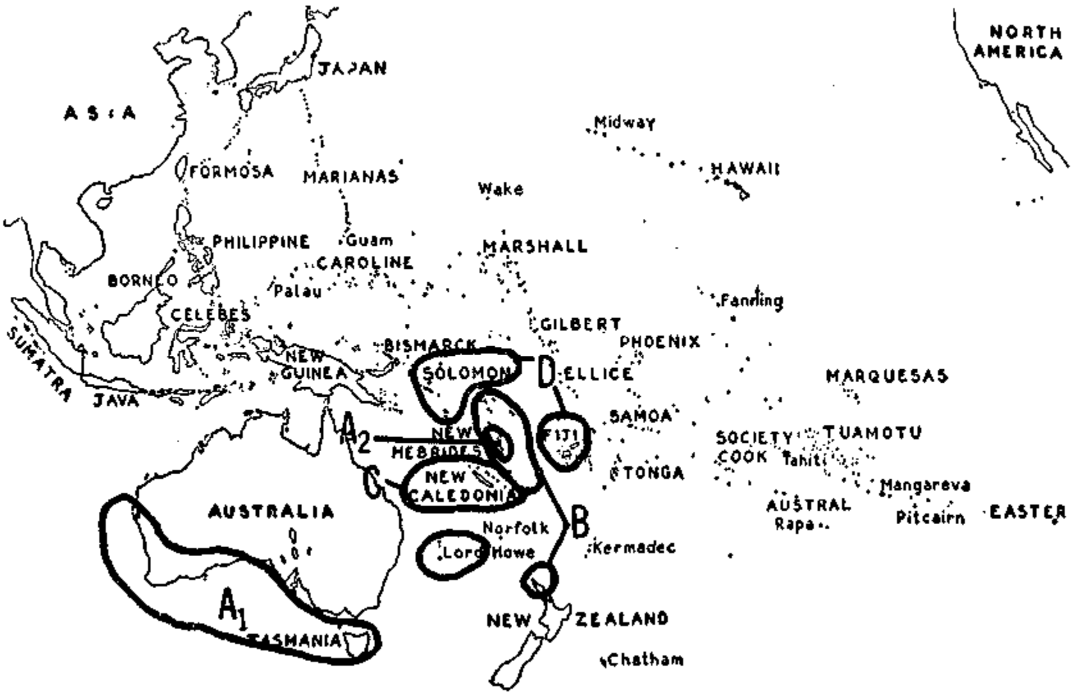


FIG. 7. Present distribution of Pacific area Bulimulinae. Taxa are: A_1—*Bothriembryon*; A_2—*Diplomorpha*; *B*—generalized *Placostylus*; C—*Placostylus* with some specializations; D—specialized *Placostylus*.

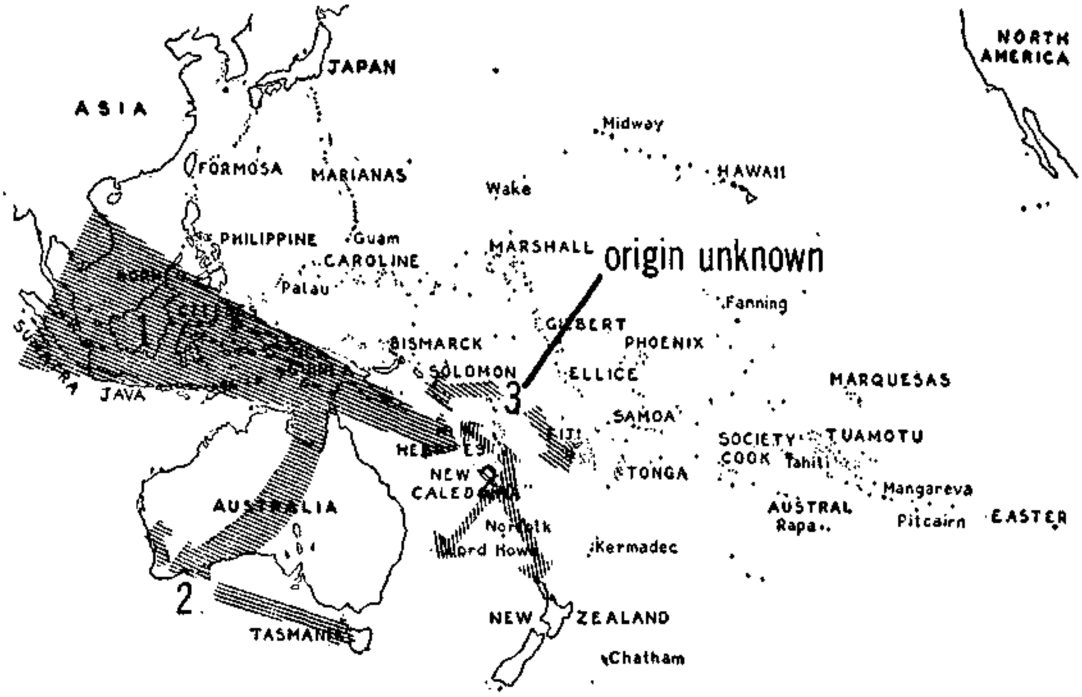


FIG. 8. Hypothesized migration patterns of Pacific area Bulimulinae. Original migration is "1"; secondary spread of *Bothriembryon* and *Placostylus* is "2"; derivation of specialized Fijian and Solomon Island *Placostylus* ("3") is of unknown direction and uncertain place of origin.

Zealand from the New Caledonian area seems most probable. The third major wave of colonization, coming probably from the New Guinea area, resulted in the advanced taxa reaching the Solomon Islands and Fiji. While geographic relationships would suggest a dispersal from the Santa-Cruz-New Hebrides into the Solomon Islands and Fiji independently, I suspect that a more complex derivation is required. Lack of space in Fig. 8 has resulted in an awkward placing of directional movement for this third colonization wave.

The above suggestions of origin and dispersal is admittedly speculative. However, the peripheral distribution of Pacific bulimulids in relation to the main Australian-New Guinea land mass is quite clear. Trying to derive this from an Antarctic origin would be exceedingly difficult.

Although exceedingly diverse in shell form and shape, the 16 genera grouped as the superfamily Acavacea or family Acavidae agree in numerous features of shell and anatomy. Early studies by Semper and Hedley were utilized by Pilsbry (1895, XXXII), together with dissection of new materials, to recognize a subfamily Acavinae. At this time, the South American genera, *Strophocheilus* and *Gonyostomus*, were considered bulimulids. Slightly later, Pilsbry (1900, p. 564) added the Strophocheilinae as a subfamily of the Acavidae. Comparatively little anatomical data have been added since this time. By far the most important paper is that of Watson in Connolly (1915) who dissected a number of South African species and analyzed the phylogenetic relationships of the Acavids. Randles (1900) dissected the Ceylonese genus *Acavus*; von Ihering (1912) gave some anatomical details on two genera that may be Acavids, but whose systematic position remains uncertain (*Macrocyclis* and *Solaropsis*); and Hylton-Scott (1939) studied *Strophocheilus oblongus lorentzianus*.

The data contained in the above papers are sufficient to indicate relative complexity in organization of the taxa, and to indicate direction of phylogeny within each area, with the exception of South America. Much of the following is condensed from Watson's excellent account. Whether the major geographic groupings are considered subfamilies or families is a matter of personal opinion, particularly until many features of the Australian and Madagascaren taxa can be examined.

A Synopsis of Classification

Family ACAVIDAE
- Subfamily STROPHOCHEILINAE (South America)
  - *Strophocheilus* Spix, 1827
  - *Gonyostomus* Beck, 1837
- Subfamily DORCASIINAE (South Africa)
  - *Trigonephrus* Pilsbry, 1905
  - *Tulbaghinia* Melvill and Ponsonby, 1898
  - *Dorcasia* Gray, 1838
- Subfamily CARYODINAE
  - *Caryodes* Albers, 1850 Tasmania
  - *Anoglypta* Martens, 1869 „
  - *Hedleyella* Iredale, 1914 (= *Panda* Martens, 1860 not van Heyden, 1826) + *Pygmipanda*, *Brazieresta*, and *Pandofella* Iredale, 1933
  - *Pedinogyra* Albers, 1860

Subfamily ACAVINAE

Clavator Martens, 1860	Madagascar
Eurystyla Ancey, 1887	„
Helicophanta Férussac, 1821	„
Ampelita Beck, 1837	
Stylodon Beck, 1837	Seychelles
Acavus Montfort, 1810	Ceylon
Oligospira Ancey, 1887	

The treatment given in Zilch (1960, pp. 463–473) differs in considering the Dorcasiinae and Strophocheilinae to belong to a single subfamily; that *Macrocyclis* belongs to the Caryodinae; and that *Solaropsis* is a Camaenid. The published data concerning *Macrocyclis* (von Ihering, 1912, pp. 481–482, Plate XLI, Figs. 5, 6) are insufficient for family placement. Wurtz (1955, p. 101) pointed out that *Solaropsis* does not belong to the Camaenidae, but made no family reference. I suspect this will prove to be an Acavid genus.

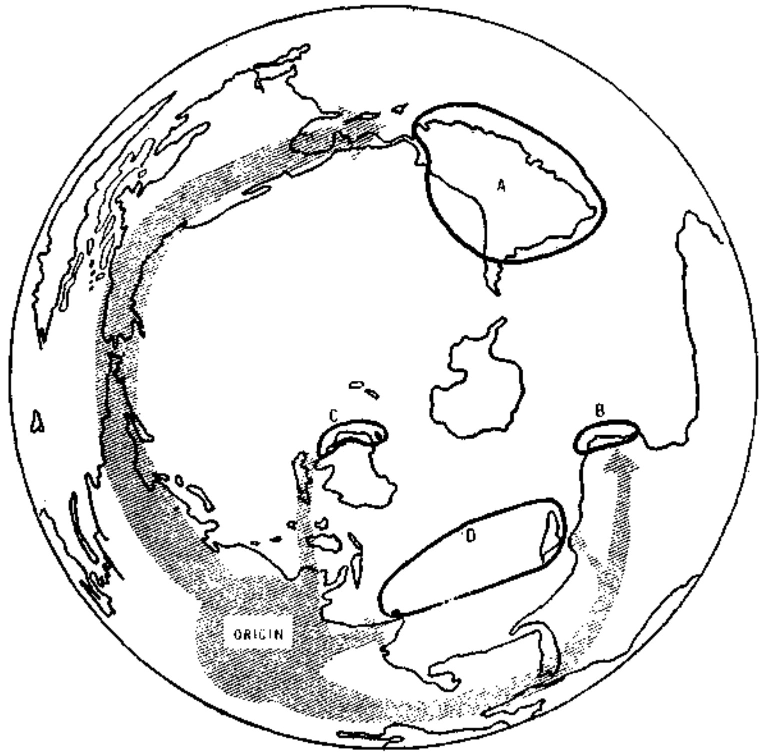


FIG. 9. Distribution and hypothesized dispersal routes of the Acavidae. Subfamilies are: A—Strophocheilinae; B—Dorcasiinae; C—Caryodinae; D—Acavinae. *Solaropsis* and *Macrocyclis* not included.

On the basis of both anatomical and shell features, the Strophocheilinae (Fig. 9, A) are the most generalized. The greatest differentiation occurs in Brazil, but species are found to about 40° south latitude and as far north as the Magdalena Basin of Colombia. One species has been transported by man to some of the West Indian Islands. The Dorcasiinae are restricted to South-west Africa and part of the Cape Province. Almost certainly, the Achatinidae have replaced the Dorcasiinae in the wetter regions of Africa, but they have managed to persist in the highly unfavourable habitats found in their range. Fossil species of both *Dorcasia* and *Trigonephrus* are known from the Eocene. I agree with Watson in Connolly (1915, p. 129) that "the southern genus *Trigonephrus* retains more primitive characteristics than does *Dorcasia*, which is found further north".

Both the Strophocheilinae and the Dorcasiinae are typical Mesurethrans in having the kidney open directly into the pallial cavity, rather than being connected to the pneumostome by a closed ureter. The Australian and Tasmanian Caryodinae are more advanced in anatomical structure, possessing a partly enclosed secondary ureter and with a peculiar appendix on the reproductive system that is absent in the more generalized species. The southern members of Caryodinae, *Caryodes* and *Anoglypta*, restricted to Tasmania, are more generalized in both shell and anatomy than *Hedleyella* of New South Wales and Southern Queensland.

The Acavinae of Ceylon, Seychelles, and Madagascar also have an incomplete secondary ureter, but apparently the genitalia is slightly more complicated in structure than that of the Caryodinae (Randles, 1900, Pl. IX). Although very little is known concerning the anatomy of the Madagascaran genera, available data do suggest that they are more generalized in structure than *Acavus*.

For three of the four subfamilies, utilizing the criteria of generalized *vs.* derived given by Watson, the more generalized genera are found in the southern part of the subfamily range, while the derived occur farther north. Unquestionably the Acavid genera are relicts and have been extant for a considerable period of time, since *Strophocheilus, Dorcasia,* and *Trigonephrus* all have been reported from Eocene beds. When viewed in south polar perspective (Fig. 9) it seems the pattern of spread from a South-east Asian origin to the present relict occurrences in the Southern Hemisphere is exceedingly long and tortuous. However, adoption of an alternative proposal featuring an Antarctic origin and center of dispersal (Fig. 10) requires construction of land bridges over many areas where the ocean's depth exceeds 12,000 feet, or derivation through continental drift in an era far before the Cretaceous. With the presence of generalized genera in the south and derived genera in the north of each subfamily range, it makes far more sense to accept a Holarctic pattern of distribution, with subsequent replacement by more advanced land snail taxa.

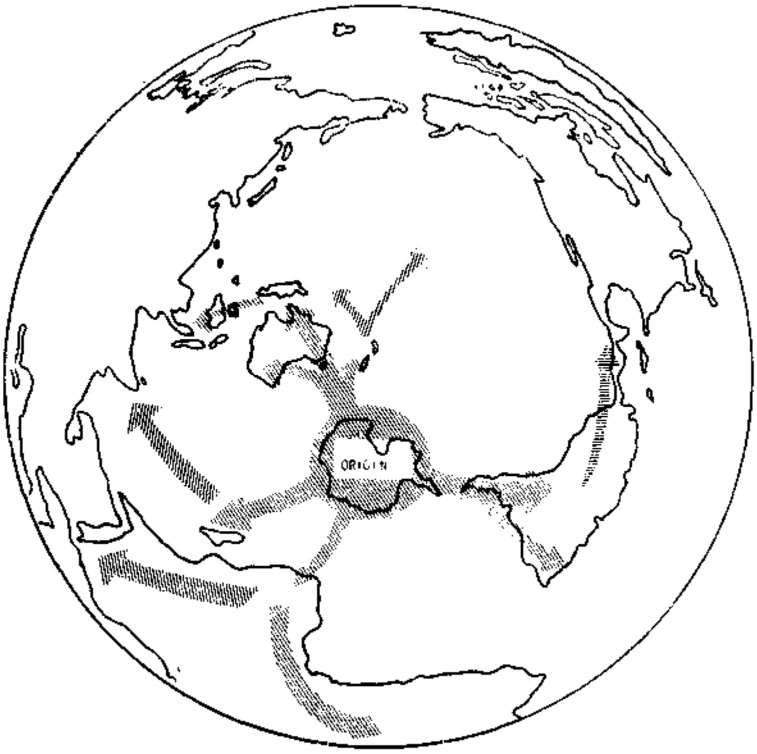


FIG. 10. Hypothesized Antarctic dispersal routes. Following many sources.

The data presented in Connolly (1915) have been subsequently used by Germain (1924) and Boettger (1936) to champion a "Gondwanaland" origin and distribution across the Indian ocean. Such a pattern of origin and dispersal has been suggested for many groups where people have been impressed because of the similarities between the South African and South-east Asian or Indian faunas. Referring to the basic concept of evolution and dispersal outlined above, these similarities could be viewed as relicts from a former continuous spread through the middle Eastern and North African crescent.

The preceding review of phylogenetic trends within the Bulimulacea and Acavidae is not intended as a "formal proof" of derivation from the Holarctic land mass. These are the families that have been cited most frequently as offering proof of an Antarctic origin and dispersal. I have attempted to show that known phylogenetic trends within these groups can be interpreted more logically as indicating a northern origin. Both groups are of unquestionable antiquity, with Eocene fossils recorded. The Achatinidae of Africa and Camaenidae of South-east Asia have replaced the acavids in these areas, but in South America the camaenids are as yet a minor, although successful, constituent of the fauna (Solem, 1966). They are much more highly developed in the West Indies (Wurtz, 1955) but the long persistence of the Panama water gap denied them access to South America until comparatively recent times.

Other families that much more strongly indicate northern origin and dispersal into the southern lands are the Rhytididae and the "Endodontidae", which I am currently revising.

ACKNOWLEDGEMENTS

Preliminary systematic and faunistic studies which have contributed to the above conclusions were accomplished with the aid of National Science Foundation grants G–16419 and GB–3384. The illustrations have been prepared with the assistance of NSF grant GB–6779. I am deeply indebted to Mrs. Jane Calvin for the preparation of Figs. 1, 2, 6–10; and to Margaret Ann Moran for transferring to paper so successfully my ideas expressed in Figs. 3, 4, and 5. Manuscript preparation by Mrs. Lynda Hanke enabled completion of this paper in time for presentation at the symposium.

LITERATURE CITED

BOETTGER, C. R. 1936. Die Verbreitung der Land Schneckenfamilie "Acavidae" und ihre Bedeutung. *Compt. Rend. XII Congr. Internat'l. Zool., Lisbon*, : pp. 1033–1050.

CONNOLLY, M. 1915. Notes on South African Mollusca. III. A monograph of the Dorcasiinae. *Ann. S. African Mus.*, **13** (4): 120–192.

DARLINGTON, P. J. 1957. *Zoogeography*. Wiley & Sons, New York, 675 pp.

GERMAIN, L. 1924. La Distribution Géographique et L'origine des Mollusques de la Famille des Acavidés. *Comptes Rendus de Congrès des Sociétés Savantes de Paris et des Départments*. Section des Sciences, **1924**: 254–269.

HEDLEY, CHARLES 1892. The range of *Placostylus*; A study in ancient geography. *Proc. Linn. Soc. New South Wales*, **7** (2): 335–339.

——— 1899. A zoogeographic Scheme for the Mid-Pacific. *Ibid.*, **24**: 391–417.

HESSE, R., W. C. ALLEE AND K. P. SCHMIDT 1951. *Ecological Animal Zoogeography*. Wiley & Sons, New York, 715 pp.

HYLTON-SCOTT, M. I. 1939. Estudio Anatómico del "*Borus Strophocheilus lorentzianus*". *Revista del Museo de la Plata, N.S., Zool.*, **1**: 217–278.

IREDALE, T. 1933. Systematic notes on Australian land shells. *Rec. Austr. Mus.*, **19** (1): 37–59.

——— 1937 *a*. A basic list of the land Mollusca of Australia. *Austr. Zool.*, **8** (4): 287–333.

——— 1937 *b*. A basic list of the land Mollusca of Australia. Part II. *Ibid.*, **9** (1): 1–39.

——— 1938. A basic list of the land Mollusca of Australia. Part III. *Ibid.*, **9** (2): 83–124.

——— 1944. The land Mollusca of Lord Howe Island. *Ibid.*, **10** (3): 299–334.

MACARTHUR, R. H. AND E. O. WILSON 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, 203 pp.

MAYR, E. 1944. Wallace's line in light of recent zoogeographic studies. *Quart. Rev. Biol.*, **19** (1): 1–14.

MEYRICK, E. 1926. On Micro-Lepidoptera from the Galapagos Islands and Rapa. *Trans. Ent. Soc. London*, **74**: 269–278.

PILSBRY, H. A. 1895. *Manual of Conchology*, 2nd ser., **9**: i–xlviii.

——— 1900. On the zoölogical position of *Partula* and *Achatinella*. *Proc. Acad. Nat. Sci. Philadelphia*, **1900**: 561–581.

——— 1946. Notes on the anatomy of Australian and Galapagos Bulimulidae. *Notulae Naturae, Acad. Nat. Sci. Phila.*, **168**: 1–4.

RANDLES, W. B. 1900. On the anatomy of the genus *Acavus*. *Proc. Malac. Soc. London*, **9**: 103–113.

SCLATER, P. L. 1858. On the general geographical distribution of the members of the Class Aves. *J. Proc. Linn. Soc. (London), Zool.*, **2**: 130–145.

SIMPSON, G. G. 1953. *Evolution and Zoogeography*. Oregon State System of Higher Education. 64 pp.

——— 1964. Species density of North American Recent Mammals. *Systematic Zoology*, **13** (2): 57–73.

SOLEM, A. 1959. Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. *Fieldiana: Zoology*, **43**: 1–359.

——— 1966. The Neotropical land snail genera *Labyrinthus* and *Isomeria* (Pulmonata, Camaenidae). *Ibid.*, **50**: 1–226.

VON IHERING, H. 1912. Analyse der Süd Amerikanischen Heliceen. *Jour. Acad. Nat. Sci., Philadelphia*, 2nd ser., **15**: 473–500.

WALLACE, A. R. 1876. *The Geographical Distribution of Animals*. Macmillan, London, 2 Vols.

WURTZ, C. B. 1955. The American Camaenidae. *Proc. Acad. Nat. Sci., Philadelphia*, **107**: 99–143.

ZILCH, A. 1960. *Euthyneura* in *Handbuch der Paläozoologie*, (6), **2** (3): 401–600.

BEITRÄGE ZUR SYSTEMATIK DER NIEDEREN MOLLUSKEN (CONTRIBUTION TO THE SYSTEMATICS OF THE LOWER MOLLUSCS)

LUITFRIED V. SALVINI-PLAWEN

I. Zoologisches Institut der Universität Wien, Wien I/Austria,
Dr. Karl Lueger-Ring 1

ABSTRACT

Insufficient knowledge of the so-called Aplacophora and their relatively low number of species have led to the opinion that they do not form a mollusc-group *sensu stricto*, which was supported by systematic uncertainties (comp. Fretter and Graham, 1962, p. 9). For a long time only those shell-bearing animals had been regarded as true molluscs, which are seizable within the conchyology: Gastropoda (with Placophora), Scaphopoda, Bivalvia, and Cephalopoda. The new results now vindicate not only the definitive range of the "Aplacophora" among the molluscs unequivocally, but they stress also their morphologic-phylogenetical importance.

On the basis of special morphology, the aplacophoran molluscs divide into the independent and equivalent groups Solenogastres (*sensu nomine*) and Caudofoveata. Only the first group (without ctenidia) is equipped with ventral footfolds, with which the animals creep on a mucus thread upon mud, — while the ctenidia-bearing Caudo-foveata, which must be separated from the former, are burrowing forms in ooze, characterized by a unitary or divided footplate (mouthshield). Phylogenetically the two groups must have evolved independently (which is excellently proved in the studies of S. Hoffman, 1949, and Boettger, 1955), so that the systematic value for both Solenogastres and Caudofoveata requires the taxonomic range of proper classes — equivalent to the class Placophora.

According to this knowledge it is evident that the so-called Aplacophora have to be considered only as a summarizing term for diverse representatives with the same phylogenetical level of organization (*i.e.*, that both groups have not yet developed any shell-like structure): the discussed cognition gives reason to the fact that the "Aplacophora" not only contain the worm-like, shell-less representatives of the recent fauna, but also that within this definition the primitive molluscs, the prototype, have to be included. This reflection sets forth that the aplacophoran molluscs (like all proper "Monoplacophora", the Conchifera) represent a phylogenetic stage-group, but not a systematic relationship-category; the negative term "Aplacophora" therefore has to be dropped.

> Within the former Aplacophora families Lepidomeniidae, Neomeniidae, Proneomeniidae, and Chaetodermatidae (= Crystallophrissonidae), the latter shows now the independent class Caudofoveata, while the remaining 50 genera (comp. Salvini Plawen, 1957 *b*, 1968*c*) continue as Solenogastres *sensu stricto*. The classification of this group in families on the basis of the existence or of the lack of secondary respiration folds has indeed to be abolished, for latest investigations have proven the insufficient correlative value of that characteristic.

Findings of recent representatives of Tryblidiacea clears up a further discrepancy. The few *Neopilina*-species belong, with respect to their anatomy, without any doubt to the monoplacophoran molluscs, to the Conchifera; the nervous system, however, demonstrates primitive characteristics, which are similar to those of the chitons. This fact and the reflective knowledge that neither Solenogastres nor Gaudofoveata show a typical amphineury (according to the definition as two separated pairs of medullary cords), reduces therefore the taxonomic value of the nervous system. On the other hand the mantle, the spicula-bearing integument, demonstrates not only the most obvious difference to the monoplacophoran groups, but it shows also morphologically the best corresponding characteristic in itself. This condition corresponds to the term *Aculifera* (Hatschek, 1891), through which the three classes Selenogastres, Caudofoveata, and Placophora are confronted with the five classes of the *Conchifera*: Tryblidiacea, Gastropoda, Scaphopoda, Bivalvia, and Cephalopoda.

EINLEITUNG

IM ALLGEMEINEN ist wenig über die niederen, bisher als Amphineura zusammengefasten Mollusken bekannt. Nur die Gruppe der Placophora hat die Grenze der reinen wissenschaftlichen Fachkenntnis überschritten. Jene aplacophoren Formen mit wurmartiger Gestalt, unscheinbar-versteckter Lebensweise und geringer Artenzahl hingegen, wurden sowohl anatomisch wie systematisch in ihrer Bedeutung weitgehend vernachlässigt und dem zoologischen Allgemeinwissen vorenthalten. Historisch gesehen erweist sich diese Erscheinung insofern verständlich, als die Wurmmollusken durch ihre Schalenlosigkeit weder für die Konchyologie, noch für die Paläontologie erfassbar waren und auch morphologisch vielfach nicht als vollwertige Weichtiere angesehen wurden. Wenn auch heute die meisten Fachautoren die sog. Aplacophora den Mollusken zurechnen (vgl. H. Hoffmann, 1951; Boettger, 1952, 1955, 1959; Jaeckel, 1955; Fischer-Piette et Franc, 1960; Kaestner, 1965), so folgen neuerdings Fretter and Graham (1962, p. 9) wieder der vorsichtigen, unentschlossenen Haltung von H. Hoffmann (1937) und erkenne nsien icht als vollwertige Weichtiere an.

Diese Unsicherheiten konnten jedoch durch die Studien von S. Hoffman (1949) beseitigt und eindeutig entschieden werden; auch die anfangs spekulativen Ansichten bezüglich der Stellung und Einordnung der recent aufgefundenen Tryblidiacea erweisen sich nun als weitgehend gefestigt (vgl. Boettger, 1959; Ax, 1960; Kaestner, 1965; Vagvolgyi, 1967). Zur Klärung der systematischen Beurteilung und der taxonomischen Klassifizierung ergeben sich daher aus jenen morphologischen Befunden neue Aspekte, deren diskutierte Begründungen schliesslich eine neue Gliederung des Systems der niederen Mollusken erfordern.

1. MOLLUSCA UND "APLACOPHORA"

Versteckte Lebensweise, geringe Artenzahl und wirtschaftliche Bedeutungslosigkeit der rein marinen sog. Aplacophora liessen ihren morphologischen Wert zum Teil bis heute nicht erkennen. In dem Begriff Weichtiere (Mollusca) wurden nur die schalentragenden Gruppen einbezogen,—die Malakologie umfasste daher nur Placophora, Gastropoda, Scaphopoda, Bivalvia und Kephalopoda. Diese auch heute noch weitverbreitete Ansicht entspricht dem Begriff der Konchyologie, welche sich lange Zeit mit dem Inhalt der Weichtierkunde deckte. Selbst die von Lovén 1844 erstmalig entdeckten, 1877 von Koren und Danielssen als Mollusken erkannten "Aplacophora" änderten zunächst an der herrschenden Auffassung nur wenig; zwar wurde die Gruppe 1876 von v. Ihering erstmalig mit den Placophora zusammen als Amphineura eingeordnet (allerdings nicht bei den Weichtieren), doch wiederholte Einsprüche gegen die volle Molluskennatur der sog. Aplacophora (Thiele, 1891, 1895, 1902, 1925; Odhner, 1919; H. Hoffmann, 1937; Fretter and Graham, 1962) machten sie zu einem systematischen Streitobjekt bis in die jüngste Zeit. Diskussionen, Vergleiche und Charakterisierungen (vgl. Kaestner, 1965, pp. 313–318), welche von Mollusken allgemein sprechen, behandeln daher, wie auch die Paläontologie (vgl. Knight, 1965, p. 3), nur allzu häufig allein die schalentragenden Weichtiere, die Conchifera.

Durch die Untersuchungen und Homologie-Nachweise von S. Hoffman (1949) wurde die Molluskennatur der sog. Aplacophora eindeutig nachgeweisen. Die bisherigen Unsicherheiten in der Morphologie und Homologie von Fuss, Pallialraum und Urogenitalapparat gegenüber den Chitonen, wurden durch die Arbeiten von S. Hoffman beseitigt. Nach S. Hoffman, mit dessen Ergebnissen auch die Ausführungen von Heath (1911) übereinstimmen, zeigt sich der Molluskenfuss auf die schmale Ventralfurche der Solenogastrenreduziert, der Pallialraum sowohl auf die Gaudalhöhle eingeschränkt, wie auch teilweise als sog. Laichgänge ("Schalendrüsen") in das Körperinnere verlagert, wo sie zusammen mit den Coelomodukten als Geschlechtsgänge fungieren (eigentliche Gonodukte rückgebildet!). Diese in groben Zügen wiederholte Homologiedarstellung in der Organisation von Wurmmollusken zu Käferschnecken (vgl. S. Hoffman, 1949) wird durch typische Weichtiermerkmale erhöht und gesichert (Mantel mit der Fähigkeit Kalk abzuscheiden, Radula, Herz/Pericard-Anordnung, Nervensystem); sie findet in phylogenetischer Sicht durch die Studi von Boettger (1955) eine Bestätigung.

Die Zugehörigkeit der aplacophoren Weichtiere zum Stamm der Mollusca wird durch diese Befunde ausser Zweifel gestellt, weshalb sie als eigene Gruppe neben den Chitonen eingeordnet werden müssen. Damit kann der Auffassung von Fretter and Graham (1962, p. 9) nicht gefolgt werden. Es sind auch jene Meinungen nicht vertretbar, welche vom Standpunkt der Vereinfachung der Vielfalt, oder der "Popularität" die schalentragenden Formen als die Mollusken schlechthin postulieren (anstatt als Conchifera!) und nur sie allein als echte Weichtiere anerkennen (vgl. Fretter and Graham, 1962, p. 6 ff).

Selbst moderne Autoren vertreten die falsche Ansicht dass ein echter Mollusk eine Schale haben müsste und dass die Käfer-schnecken eine sekundär unterteilte Concha besitzen (vgl. Fretter and Graham, 1962, p. 8; Hedgpeth, 1962, p. 89; Morton and Yonge, 1964, p. 25), wobei diese Auffassungen im Zusammenhang mit dem *Neopilina*-Fund vertreten werden. Eine derartige Ableitung ist theoretisch kaum denkbar (vgl. Boettger, 1959; Vagvolgyi, 1967), ausserdem steht sie in starkem Widerspurch zur Organisation der verschiedenen Weichtierklassen, so, dass die Entwicklung nur von aplacophoren Formen über das polyplacophore Stadium zum monoplacophoren Zustand progressiv erfolgt sein kann. Als Beispiel mag hierfür die zunehmende Konzentrierung der Dorsoventral-Muskulatur angeführt werden: Solenogastres mit zahlreichen Strangpaaren*), Placophora mit 16 Strangpaaren (Stränge I-VIII jedseitig in vorderes und hinteres Bündel geteilt), Tryblidiacea rezent mit 10 Strangpaaren (I & VII sind noch geteilt!) und fossil mit 8–6 Strangpaaren, das fossile Genus *Cyrtonella* Hall mit 3 oder 2 Strangpaaren, Bivalvia fossil mit 8 (*Babinka*), rezent mit 5–0 Strangpaaren (vgl. Yonge, 1953), etc.

Die Anpassung einer Organisation an einen bestimmten Lebensraum, wie die seitliche Abrundung der rezenten Aplacophora zur Wurmgestalt, stellt kein Hindernis für Homologievergleiche dar; im Gegenteil, derartige Verhältnisse erlauben in hohem Masze jene Merkmale aufzudecken, die durch ihr gemeinsames Auftreten in verschiedenen Entwicklungszweigen als ursprünglich zu erkennen sind. Dies gilt bei Placophora und den aplacophoren Weichtieren besonders für das Kutikula-bedeckte, Spikula-tragende Integument; die Schalenlosigkeit ist daher kein Argument, die aplacophoren Formen nicht als echte Mollusken anerkennen zu wollen und die wertvolle morphologisch-phylogenetische Bedeutung der Gruppe zu ignorieren.

2. Solenogastres und Caudofoveata als Stadiengruppe Aplacophora

Schon Odhner (1919, p. 78) weist auf die morphologische Verschiedenheit der bisher als Neomeniida zusammengefassten Gattungen der Solenogastres *sensu nomine* zud den Chaetodermatiden hin, und auch andere Autoren betonen die tiefgreifenden Differenzen in diesen gegenübergestellten Organisationen (vgl. Wirén, 1892; Simroth, 1894; Thiele, 1902; Nierstrasz, 1905, 1909, 1910; Heath, 1911; H. Hoffmann, 1930). Es ist S. Hoffman (1949) zu verdanken, dass durch histologische Untersuchungen und detaillierte Homologievergleiche das Fundament für die Ausführungen von Boettger (1955) gelegt werden konnte. Danach sind jene Formen, welche sich bereits durch den Besitz von echten Ktenidien und durch den Mangel einer Fussfurche deutlich abheben, als eigene Gruppe aus dem Verband der bisherigen Solenogastren herauszulösen. Die solcherart voneinander getrennten Caudofoveata (Schildfüsser) und Solenogastres *sensu stricto* (=*sensu nomine*, syn. Ventroplicida; Furchenfüsser) weisen in ihrer gesamten Anatomie merkmalsreiche Differenzen auf, welche ihrer Organisation jeweils ein charakteristisches Bild zuordnen.

---

* Entgegen der Behauptung von Lemche (1959 *c*), dass bei den Solenogastres keine gut entwickelte Dorsoventral Muskulatur entwickelt sei (p. 429: "Solenogastres, en los que no ha sido posible todavia encontrar ningun musculo bien desarrollado que corresponda, en este grupo, a los retractores pedios" p. 431: "Solenogastres, en los que los musculos dorsoventrales parecen poco desarrollados"), — *entgegen dieser Aussage, tritt dieses Organ-system gar wohl,* und sehr deutlich auf! Die Homologie mit den 16 Paar Dorsoventra-Strängen der Chitonen ist ebenso eindeutig (vgl. H. Hoffmann, 1937; S. Hoffman, 1949, pp. 418–420).

Die herausgelöste, neu zu definierende Gruppe der Caudofoveata umfasst drehrunde, durch Abschnittsbildungen häufig stark untergliederte Grabformen mit durchwegs soliden Spikula in der dünnen Kutikula. Die Rückbildung des ventralen Körperanteiles bei der Umgestaltung flacher Ausgangsformen zum Wurm-Habitus (vgl. Boettger, 1955) führte dazu, dass der Pallialraum auf eine terminale, glockenförmige Höhle eingeschränkt wurde, welche jedoch stets mit einem Paar echten Ktenidien ausgestattet ist (die angeblich " two pairs of gills of a rather primitive structure" bei *Prochaetoderma californicum* nach Schwabl, 1963 p. 267, stellen gemäß einer Nachprüfung an den Originalschnitten nur *ein*, und zwar ganz gegenteilig sehr differenziertspezialisiertes Paar Ktenidien dar, mit blattartig vergrösserten Lamellen! — vgl. Bivalvia). Eine charakteristische, einheitliche oder geteilte Schildplatte als Graborgan in postoraler oder zirkumoraler Lage kann vielleicht als letzter Rest des Molluskenfusses oder einer Mundscheibe angesehen werden. Die distiche, meist aber weitgehend reduzierte Radula ist mit einem divertikellosen Darmschlauch gepaart, welcher letzterer einen meist gut differenzierten, unpaaren und ventralen Verdauungssack aufweist. Die getrenntgeschlechtlichen Tiere geben ihre Genitalprodukte ohne innere Besamung frei in das Wasser ab; die Gonodukte sind hierbei (wie auch bis auf wenige Reste die Dorsoventralmuskulatur) rückgebildet, wodurch Eier und Samen über Perikard und Coelomodukte abgeleitet werden.

Wesentlich vielfältiger erweisen sich durch 50 Gattungen die Solenogastres selbst, welche eine längsverlaufende Ventralfurche als Rest des Molluskenfusses besitzen, der auf relativ stabiler Unterlage mittels einer Schleimbahn als flimmerndes Kriechorgan dient (Lehm, epizoisch; vgl. Salvini Plawen, 1967 *c*, 1968 *b*). Die recht verschieden starke Kutikula ist durch ebenso variierende Kalkkörper gekennzeichnet, welche zumeist als Schuppen oder Hohlnadeln, aber auch als Haken, Rinnenspikula, oder in Schaufelform auftreten; selten fehlen sie. Der Pallialraum entbehrt hier vollkommen echter Ktenidien, zeigt sich aber noch häufig als Fortsetzung der Ventralfurche. Der praeorale Mantelraum findet sich als atriales Sinnesorgan vielfach mit der Mundhöhle verschmolzen vor und dient wohl der chemischen Nahrungsauswahl. Der Verdauungstrakt ist durch die mannigfaltig geformte Radula (bei einem Drittel der Formen reduziert) und durch den, in der Regel mit zahlreichen, seitlichen Ausbuchtungen versehenen Mitteldarm gekennzeichnet, welchem sich das, wohl noch in seiner ursprünglichen Form vorhandene dorsoventrale Muskelsystem anpasst. Alle Arten sind (teils protandrische) Zwitter, und häufig können besondere Begattungsorgane und Kopulationsstacheln, sowie verschiedene Samenbehälter konstatiert werden. Die ebenfalls durch die habituelle Abrundung zur Wurmform rückgebildeten Gonodukte bewirken, das die Geschlechtsprodukte über Perikard, Coelomodukte und (die als Pallialraum-Anteile identifizierten) Laichgänge ausgeleitet werden.

Im Hinblick auf diese skizzierten Organisationen lässt sich schon klar erkennen, das die "Aplacophora" eine reine Stadiengruppe darstellen, welche durch die Schalenlosigkeit als negatives Merkmal definiert sind. Schliesslich muss aber auch die Ausgangsform der Weichtiere, der "Urmollusk", als mit spikulatragendem Integument versehen gefordert werden (Boettger, 1955, 1959), welche Organisation daher ein Aplacophore, aber keinen Wurmmollusk vorstellte. So "ist eine theoretische schalenlose Stammform mit Kriechsohle anzunehmen, von der sich einmal innerhalb einer Klasse Aplacophoren, und zwar unabhängig von einander" Caudofoveata und Solenogastres "mit verschiedenartiger Reduktion der Kriechsohle entwickelt haben, andererseits die Klasse Placophora, die die Kriechsohle beibehalten hat" (Boettger, 1959, p. 387). "Die allein, die Familie Crystallophrissonidae (= Chaetodermatidae) umfassenden Aplacophoren ohne Bauchfurche stellten zweifellos einen selbständigen Zweig der schalenlosen Amphineuren dar, der sich unabhängig von den Aplacophoren mit Bauchfurche aus der gemeinsamen Stammform entwickelt hat" (Boettger, 1955, p. 242). Diese Ausführungen betonen deutlich die unabhängige Differenzierung von Solenogastres, Caudofoveata und Placophora aus einem "Urmollusken", doch fehlt die konsequente Folgerung: drei Entwicklungslinien = drei gleichwertige systematische Gruppen! Mit der Zusammenfassung von zwei eigenen Organisationen allein, in Bezug auf das negative Merkmal von deren schalenlosen Zustand, wird nur eine irreführende Stadiengruppe gebildet, welche den Bemühungen nach einem natürlichen System nicht gerecht wird. Solenogastres und Caudofoveata sind daher als eigene Klassen einzuordnen, gleichwertig der Klasse Placophora!

Die weitere Untergliederung der drei Klassen gestaltet sich entsprechend dem jeweiligen Umfang recht verschieden. Die Einteilung der rund 1000 Placophora-Arten ist zuletzt von Fischer-Piette and Franc (1960, pp. 1776–1783) klar umrissen worden; sie folgt der Schalen-Systematik von Bergenhayn (1955) und gruppiert 13 Familien in die drei Ordnungen Lepidopleurina, Ischnochitonina und Acanthochitonina.

Die neue Klasse Caudofoveata beinhaltet drei Familien mit 49 Arten in sechs Gattungen: *Limifossor* Heath, *Scutopus* Salvini-Plawen und *Metachaetoderma* Thiele als Limifossoridae, — einzig *Prochaetoderma* Thiele als Prochaetodermatidae, — sowie *Chaetoderma* Loven (= *Crystallophrisson* Möbius)* und *Falcidens* Salvini-Plawen als Chaetodermatidae.

Bis vor kurzem wurden die Solenogastres *sensu stricto* in drei Familien aufgespalten, welche Gruppierung allein auf dem Merkmal von sekundären Respirationsfalten der Pallialraumwand basierte. Neue Untersuchungen konnten jedoch zeigen (vgl. Salvini Plawen, 1967 *a*), dass die Ausbildung der Atemfalsten vom Reifezustand der Tiere abhängig ist und sich daher systematisch vollkommen unverlässlich erweist. In der Folge kann also die bisherige Familiengruppierung nicht aufrecht erhalten werden, und die insgesamt 108 Arten verteilen sich auf 50 Gattungen der einrigen Familie Neomeniidae (Salvini Plawen, 1967 *b*, *c*). Auf Grund des noch zu erwartenden Materials grösserer Expeditionen ("Galathea", "Vema", "USARP", "Meteor", etc.) wird auch vorerst noch davon Abstand genommen eine neue, verwandtschaftsgerechtere Systemgruppierung innerhalb der Solenogastres auszuarbeiten.

3. SOLENOGASTRES, CAUDOFOVEATA UND PLACOPHORA ALS ACULEFERA

Das rezente Auffinden von Tryblidiacea-Arten (*Neopilina galatheae* Lemche mit *N.g.* var*i adenensis* Tebble *N. ewingi* Clarke and Menzies, *N. veleronis* Menzies and Layton, *N. bruun.* Menzies, *N. bacescui* Menzies) hat gezeigt, wie sehr einerseits unsere Kenntnis noch teilweise in den Anfängen steckt (die gesamte Tiefsee stellt ja noch weitgehend unerforschtes Neuland dar), wie exakt andererseits aber unsere morphologische Beurteilung durchdacht sein kann: in die Darstellung der Verwandtschaftsbeziehungen der niederen Mollusken durch Boettger (1955) fügt sich *Neopilina* derart bestätigend ein, das keine wesentlichen Abänderungen der Ausführungen notwendig sind (Boettger, 1959, p. 387).

Entgegen den hypothetischen Erörterungen von Lemche (1959 *a*, *b*, *c*) und Lemche and Wingstrand (1959, 1960) über Verwandtschaftsbeziehungen und Metamerie-Vorstellungen, sind die *Neopilina*-Arten eindeutig sehr basal stehende, monoplacophore Conchifera (vgl. Boettger, 1959; Portmann, 1960; Ax, 1960; Steinböck, 1963; Kaestner, 1965; Vagvolgyi, 1967; Salvini Plawen, 1968 *d*) welche sich mit ihrer Entwicklung in manchen Merkmalen von der gemeinsamen Conchiferen-Wurzel entfernt haben. Durch das im Grundkonzept ursprüngliche Nervensystem ist *Neopilina* amphineur und conchifer zugleich (Portmann, 1960, p. 1647) und nimmt hier, sowie in anderen Organen eine gewisse Zwischenstellung ein. Die Kennzeichen einer dreischichtigen Concha (zudem mit spiraliger Embryonalschale), der Statocysten und der Sub-Rectalcommissur, der oralen Tastorgane und des Magen-Fermentstabes sind progressiv erworbene Organisations-Eigenheiten der Schalen-Weichtiere, wogegen der den gesamten Körper überdeckende Mantel, der peripedale Pallialraum, die Marksträngne, und die Getrenntgeschlechtlichkeit konservativ erhaltene Merkmale darstellen; die Dorsoventralmuskulatur, das Subradularorgan, die Zuckerdrüsen und der Mitteldarm vermitteln. Die Klasse der Tryblidiacea ist daher eindeutig zu den Conchifera zu stellen (wodurch die aus der Paläontologie übernommene Bezeichnung "Monoplacophora" sinnlos wird, da alle Schalen-Weichtiere primär monoplacophor sind und der Terminus somit nur als synonymer Stadiengruppen-Begriff fur die Conchifera Verwendung finden kann).

---

* Durch den Entscheid der "International Commission on Zoological Nomenclature" (*Bull. zool. Nomencl.*, **23**: 22–24, 1966) ist der Gattungsname *Chaetoderma* Loven, 1844 voll gültig (neben *Chaetodermis* Swainson, 1839 für eine Fisch-Gattung); *Crystallophrisson* Möbius, 1875, ist daher als Synonym von *Chaetoderma* Loven zu betrachten.

Seit v. Ihering (1876) werden Placophora und "Aplacophora" zusammenfassend mit der Bezeichnung "Amphineura" belegt, was eine deutliche Abtrennung von den Conchifera kennzeichnete. Durch die erhaltene Amphineurie der Tryblidiacea (*Neopilina*) und deren Zuordnung zu den Schalen-Weichtieren wird die Gegensätzlichkeit jedoch durchbrochen und aufgehoben. Das genaue Studium von Caudofoveata und Solenogastres zeigt zudem weiterhin, dass weder dieser, noch jener Gruppe eine volle Amphineurie (zwei Paar getrennte Markstränge) zugesprochen werden kann. Bei Solenogastres sind gewisse laterale (Lateralganglion und Ganglion posterior superior) und ventrale (Ventralganglion und häufig auch Ganglion post. inferior) Anschwellungen die Regel, ebenso wie mehr oder minder seriale, ventrale Ganglienbildungen an den Ansatzpunkten der Konnective und Lateroventral-Kommissuren; vier echte Markstränge konnten bisher nur bei *Gymnomenia pellucida* (vgl. Odhner, 1919) festgestellt werden, und eine Ganglienbildung zugleich mit Zellbelag der Stränge wird auch nur für *Pachymenia abyssorum* (vgl. Heath, 1911), *Rupertomenia fodiens* (vgl. Schwabl, 1955) und *Biserramenia psammobionta* (vgl. Salvini Plawen, 1968 *c*) angegeben. Für die Caudofoveata scheint hingegen der histologische Bau mehr dem Typus echter Markstränge zu entsprechen, wenn auch den meisten Arten eine vordere Ventral-Anschwellung und ein verschmolzen-unpaares Ganglion posterior superior zukommt,—doch aber vereinen sich hier in der kaudalen Körperhälfte die ventralen Bahnen mit den Lateralsträngen, wobei Hand in Hand die verbindenden Kommissuren zurücktreten.

Diesen Ausführungen gemäss erweist sich die Benennung von Solenogastres, Caudofoveata und Placophora zusammen als "Amphineura" wenig glücklich, wenn nicht sogar irreführend. Morphologisch weitaus besser fundiert, und als Gegensatz zu den Schalen-Weichtieren zudem deutlich unterschieden, zeigt sich in den drei Klassen das spikulatragende Integument. Durch die detaillierten Untersuchungen von S. Hoffman (1949) ist daher im Vergleich mit weiteren Studien (Plate, 1902; von Knorre, 1925; zusammenfassend H. Hoffmann, 1930; Fischer-Piette and Franc, 1960) die Gruppen-Bezeichnung Aculifera (Hatschek, 1891; Stachel-Weichtiere)* vorzuziehen und durch ihren Bezug auf ein Mantel-Merkmal als gleichwertiges Kennzeichen den Conchifera gegenüberzustellen.

Portmann (1960, p. 1647) zieht es vor (da *Neopilina* zugleich amphineur und conchifer ist), die Gruppierung der Mollusca in Unterstämme aufzuheben und die Weichtiere allein durch Klassen zu unterteilen, wobei diese Lösung den taxonomischen Schwierigkeiten aus dem Wege geht. In morphologischer Sicht erweist sich ein solcher Schritt aber wenig vorteilhaft, und ausserdem lasst sich eine Folge von acht Klassen weit weniger gut überblicken.

Die Aufteilung in Aculifera und Conchifera stützt sich nicht nur auf die Kennzeichen der Mantelbedeckung allein (Chitin-hältige Kutikula, Epithel samt Papillen, Spikula; dreischichtige Concha). Der Mangel von Schweressinnesorganen, Fühlern und Augen, sowie die Ausbildung der Supra-Rectalcommissur einerseits, die Kephalisation, die Statocysten, die Sub-Rectalkommissur, sowie der einheitliche Bau des Darmtraktus mit dem Vorkommen eines Fermentstabes andererseits, diese deutlich gegensätzlichen Organisationsmerkmale unterstreichen weiterhin die Verschiedenheit der Unterstämme, welche zudem durch die seriologischen Untersuchungen von Leone and Pryor (1954) unterstützt wird.

Zusammenfassend ergibt sich aus den oben diskutierten Erörterungen eine systematische Gruppierung der Weichtiere, welche wie folgt zu gliedern sein wird:

Phylum MOLLUSCA
  Subphylum ACULIFERA
    Classis *Solenogastres*
    Classis *Caudofoveata*
    Classis *Placophora*

---

* vgl. hierzu Nierstrasz und Hoffmann, 1929; Thiele, 1931; Jaeckel, 1954 und 1955.

Subphylum CONCHIFERA
Classis *Tryblidiacea*
Classis *Gastropoda*
Classis *Scaphopoda*
Classis *Bivalvia*
Classis *Kephalopoda*

ZUSAMMENFASSUNG

Auf der Grundlage neuerer morphologich-phylogenetischer Erkenntnisse werden für die niederen Mollusken in der systematischen Beurteilung die Folgerungen diskutiert und dargelegt.

1. Die aplacophoren Weichtiere erweisen sich als vollwertige Mollusken und sind in die zwe gleichwertigen Gruppen *Caudofoveata* und *Solenogastres* (*sensu nomine*) aufzuteilen.
2. Die morphologische Gleichwertigkeit der Gruppen erfordert innerhalb der niederen Mollusken den taxonomischen Rang von drei unabhängigen *Klassen* Solenogastres, Caudofoveata und Placophora.
3. Die negative Bezeichnung "Aplacophora" umfasst lediglich eine *Stadiengruppe* und entspricht daher nicht den morphologisch-systematischen Grundsätzen; sie wird somit fallen gelassen.
4. Die monoplacophore Conchiferen-Natur der rezenten Tryblidiacea (*Neopilina*) mit amphineurem Nervensystem, sowie der Mangel einer typischen Amphineurie bei Solenogastres und Caudofoveata, lassen die Gruppen-Bezeinhnung "Amphineura" irreal erscheinen, und sie ist durch den morphologisch gut fundamentierten Begriff Aculifera (Hatschek, 1891) zu ersetzen.
5. Die Gruppierung der Mollusca erfolgt daher in das Subphylum *Aculifera* mit den drei Klassen der aplacophoren Solenogastres und Caudofoveata, sowie den polyplacophoren Placophora, weiters in das Subphylum *Conchifera* mit den fünf (zumindest primär) monoplacophoren Klassen der Tryblidiacea, Gastropoda, Scaphopoda, Bivalvia und Kephalopoda.

LITERATURVERZEICHNIS

AX, P. 1960. Die Entdeckung neuer Organisatienon im Tierreich. *Neue Brehm-Buckerei*, **258**: 1–116.

BERGENHAYN, J. 1955. Die fossilen Schwedischen Loricaten, nebst einer vorläufigen Revision des Systems der ganzen Klasse Loricata. *Acta Univ. Lundensis, N.S. Lunds Univ. Årsskrift Avd* 2, **51** (8): XX–XX.

BOETTGER, C. 1952. Die Stämme des Tierreiches in ihrer systematischen Gliederung. *Abhdl. Braunschweig wiss. Ges.*, **4**: 238–300.

——— 1955. Beiträge zur Systematik der Urmollusken (Amphineura). *Zool. Anz. Suppl.*, **19**: 223–256.

——— 1959. Diskussionsbeitrag zu: Protostomian Interrelationships in the light of *Neopilina*, by H. Lemche. *Proc. XV Int. Congr. Zool. London*, pp. 386–389.

FISCHER-PIETTE, E. ET A. FRANC 1960. *Classe des Aplacophores et Classe des Polyplacophores.* In: Grassé, *Traité de Zoologie*, **5** (2): 1655–1785.

Fretter, V. and A. Graham 1962. *British Prosobranch Molluscs.* The Ray Society, London, pp. 755.

Hatschek, B. 1891. Aculifera, in Das Integument der Chitonen, von J. Blumrich. *Zeitschr. wiss. Zool.,* **52:** 404–406.

Heath, H. 1911. Reports on the scientific results of the expedition to the Tropical Pacific, XIV. The Solenogastres. *Mem. Mus. Comp. Harvard Coll.,* **45** (1): 1–182.

Hedgpeth, J. 1962. Introduction to seashore life of the San Francisco bay region and the coast of Northern California. *Calif. Nat. Hist. Guides,* **9**: 1–139.

Hoffmann, H. 1930. *Amphineura.* In: Bronn's *Klassen und Ordnungen des Tierreiches,* 3, Abt. 1, Suppl.: 1–453.

——— 1937. Über die Stammesgeschichte der Weichtiere. *Zool. Anz. Suppl.,* **10**: 33–69.

——— 1951. *Mollusca.* In: *Handbuch der Biologie,* von L. .v Bertalanffy, **6** (6), Lg. **36**: 161–208.

Hoffman, S. 1949. Studien über das Integument der Solenogastren. *Zool. Bidr. Från Uppsala,* **27**: 293–427.

Hyman, L. 1966. Further notes on the occurrence of chitin in invertebrates. *Biol. Bull.,* **130** (1): 94–95.

Ihering, H. von 1876. Natürliches System der Mollusken. *Jahrb. Dtsch. Malakozool. Ges.,* **3**: 97–148.

Jaeckel, S. 1954. Aculifera Aplacophora und Aculifera Placophora im Gebiet der Nord- und Ostsee. *Kieler Meeresforsch.,* **10**: 261–271.

——— 1955. Bau und Lebensweise der Tiefsee-Mollusken. *Neue Brehm-Bücherei,* **148**: 1–70.

Kaestner, A. 1965. *Mollusca.* In: *Lehrb. spez. Zool. Jena,* **1** (1), 2. Aufl.: 312–451.

Knight, J. 1952. Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Miscell. Coll.,* **117** (13): 1–56.

Knorre, H. von 1925. Die Schale und die Rückensinnesorgane von *Trachydermon* (*Chiton*) *cinereus* L. und die ceylonischen Chitonen der Sammlung Plate. *Zeitschr. Naturw. Jena,* **61**: 469–632.

Lemche, H. 1959 *a.* Molluscan phylogeny in the light of *Neopilina. Proc. XV Int. Congr. Zool. London,* pp. 380–381.

——— 1959 *b.* Protostomian interrelationships in the light of *Neopilina. Ibid.,* 381–386.

——— 1959 *c.* *Neopilina* (Un molusco actual con caracteres de tipo fosil, y su significado). *Rev. Univ. Madrid,* **8** (29–31): 411–442.

——— and K. Wingstrand 1959. The anatomy of *Neopilina galatheae* Lemche. *Galathea Reports,* **3**: 9–71.

——— 1960. *Classe des Monoplacophores.* In: Grassé, *Traité de Zoologie,* **5** (2): 1787–1821.

Leone, Ch. and C. Pryor 1954. Seriological comparisons among four classes of Mollusca. *Biol. Bull.,* **107** (3): 411–419.

Menzies, R. 1967. New species of *Neopilina* of the cambro-devonian class Monoplacophora from the Milne-Edwards Deep of the Peru-Chile Trench. *Adv. Abstr. Contr. Fish. Aquat. Sci. India,* **1** (3): 42.

——— and W. Layton 1962. A new species of Monoplacophoran Mollusc, *Neopilina* (*Neopilina*) *veleronis* from the slope of the Cedros Trench, Mexico. *Ann. Mag. Nat. Hist., Ser.* 13, **5** (55): 401–406.

Morton J. and C. Yonge 1964. *Classification and Structure of the Mollusca.* In: *Physiology of Molluscs,* by Wilbur and Yonge, **1** (1): 1–58.

Nierstrasz, H. 1905. *Kruppomenia minima* und die Radula der Solenogastren. *Zool. Jahrb. Anat.,* **24**: 655–702.

——— 1909. Die Amphineuren: I. Die Solenogastren. Ergebn. *Fortschr. Zool.,* **1**: 239–306.

——— 1910. Die Amphineuren: III. Die verwandtschaftlichen Beziehungen der Solenogastren und Chitonen. *Ibid.,* **2**: 414–430.

——— and H. Hoffmann 1929. *Aculifera.* In: Grimpe, *Tierwelt der Nord- und Ostsee,* Teil IX *a*: 1–64.

Odhner, N. 1919. Norwegian Solenogastres. *Bergens Mus. Årb.* 1918–19 (3): 1–86.

Plate, L. 1902. Anatomie und Phylogenie der Chitonen. *Teil C. Zool. Jahrb. Suppl.,* **5** (2): 281–600.

Portmann, A. 1960. *Généralités sur les Mollusques.* In: Grassé, *Traité de Zoologie,* **5** (2): 1625–1654.

Salvini Plawen, L. v. 1967 *a*. Neue scandinavische Aplacophora (Mollusca, Aculifera). *Sarsia*, **27**: 1–63.

——— 1967 *b*. Kritische Bemerkungen zum System der Solenogastres (Aculifera, Aplacophora). *Zeitschr. zool. Syst. Evolut. forsch.*, **5** (4): 398–444.

——— 1967 *c*. Über die Beziehungen zwischen den Merkmalen von Standort, Nahrung und Verdauungstrakt bei Solenogastres (Aculifera, Aplacophora). *Zeitschr. Morph. Ökol. Tiere*, **59**: 318–340.

——— 1968 *a*. Über Lebendbeobachtungen an Caudovofeata (Mollusca, Aculifera), nebst Bemerkungen zum System der Klasse. *Sarsia*, **31**: 105–126.

——— 1968 *b*. Über einige Beobachtungen an Solenogastres (Mollusca, Aculifera). *Ibid.*, **31**: 131–142.

——— 1968 *c*. Neue Formen im marinen Mesopsammon: Kamptozoa und Aculifera. *Ann. naturhistor. Mus. Wien*, **71**: 131–145.

——— 1968 *d*. Die 'Funktions-Coelomtheorie' in der Evolution der Mollusken. *Systematic Zoology*, **17** (2): 192–208.

Chwabl, M. 1955. *Rupertomenia fodiens* n.g.n.sp., eine neue Lepidomeniide von der Südwestküste Schwedens. *Österr. zool. Zeitschr.*, **6** (1–2): 90–146.

——— 1963. Solenogaster molluscs from Southern California. *Pacific Science*, **17** (3): 261–281.

Simroth, H. 1894. *Amphineura*. In: Bronn's *Klassen und Ordnungen des Tierreiches*, **3**, Abt. *1*: 128–355.

Steinböck, O. 1963. Über die Metamerie und das Coelom der *Neopilina galatheae*. *Zool. Anz. Suppl.*, **26**: 385–403.

Tebble, N. 1967. A *Neopilina* from the Gulf of Aden. *Nature*, **215** (6101): 663–664.

Thiele, J. 1891. Die Stammesverwandtschaft der Mollusken. *Zeitschr. Naturw. Jena*, **25**: 480–543.

——— 1895. Über die Verwandtschaftsbeziehungen der Amphineuren. *Biol. Centralblatt*, **15**: 859–869.

——— 1902. Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken. *Zeitschr. wiss. Zool.*, **72**: 249–466.

——— 1925. *Solenogastres und Mollusca*. In: *Handbuch der Zoologie, von* Kükenthal, **5** (1): Teil. 1: 1–258.

——— 1931. *Aculifera (nur Loricata). Handbuch der systematischen Weichtierkunde*, **1**: 1–22.

Vagvolgyi, J. 1967. On the origin of molluscs, the coelom, and coelomic segmentation. *Systematic Zoology*, **16** (2): 153–168.

Wiren, A. 1892. Studien über Solenogastres II (*Chaetoderma productum, Neomenia, Proneomenia acuminata*). *Svenska Vetensk. Akad. Handl.*, **25** (6): 1–99.

Yonge, C. 1953. The monomyarian condition in the Lamellibranchia. *Trans. Roy. Soc. Edienbourg*, **57**: 443–478.

NEW DATA ON THE CEPHALOPODA OF THE INDIAN OCEAN

J. A. Filippova

All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, U.S.S.R.

Abstract

This report is based on the extensive collections of cephalopods made from 190 stations in Indian Ocean by the r/v "Vityaz" (1959–67), r/v "Academician Knipovitch" (1966) and by the factoryship "Sovetskaja Rossia" (1966–67).

The region of investigations includes the northern and central parts of Indian Ocean up to 41° S.

The following species are recorded for the first time as occurring in Indian Ocean: *Symplectoteuthis luminosa, Todarodes sagittatus angolensis, Nototodarus sloanei (? gouldi), Thysanoteuthis rhombus, Moroteuthis lonnbergii, Ctenopteryx siculus, Cycloteuthis sirventi, Sandalops melancholicus.*

The existence of a clear latitudinal zonality in the distribution of squids of the family Ommastrephidae in the Indian Ocean is established for the first time. *S. oualaniensis* inhabits the tropical waters only, spreading out to 20° S, being the prevailing species here. From 20 to 37° S *O. bartrami* is the predominant species which replaces *S. oualaniensis* ecologically, together with *T. sagittatus angolensis.* Approximately from 34 to 41° S. (further to the south there are no data) partly overlapping the area of *O. bartrami* in its southern boundary, *T. sagittatus angolensis* becomes the predominant species. Its area appears to extend from the South Atlantic (Adam, 1962; Korabelnikov, 1959) along the southern coast of Africa and eastward in the Indian Ocean upto Amsterdam and Saint Paul Islands. Further to the east it has not been observed.

The presence of *T. rhombus* is recorded in the Indian Ocean for the first time. Hence its area of distribution is sufficiently extensive, including the tropical and subtropical waters of the World Ocean. The area of *O. banksi* too has been extended. The existence of *O. carribaea* in the Indian Ocean is stated.

The wide distribution of two pelagic octopuses—*Tremoctopus violaceus* and *Argonauta hians* in the surface waters of the Indian Ocean is stated and the possibility of their belonging to the pleiston biocenosis is discussed.

The fauna of Cephalopoda of the Indian Ocean have been studied quite insufficiently. There are only a few papers on this subject and most of them deal mainly with the neritic and bottom forms. The available information on the oceanic cephalopods is very scanty and there is much vagueness in such questions as systematic position and distribution of cephalopods.

At the same time it would be wrong to underestimate the importance of cephalopods in the life of the ocean. Their wide distribution, their vast abundance and the fact that they form a favourable food item of many marine inhabitants on the one hand, and that they are themselves active and voracious predators on the other, allow us to consider them to be one of the main members of oceanic cenosis.

The comprehensive study of Indian Ocean during the last decade will increase our knowledge of the biology of cephalopods which is necessary to decide the general problems concerning the ecology and productivity of this ocean.

The present report is based on the extensive collection of cephalopods made by r/v "Vityaz" (1959–1967), r/v "Academician Knipovitch" (1966), d/e "Ob" (1957), w/s "Sovetskaja Rossia" (1966–1968), and "Orlik" (1963–64). We examined the material from 190 stations. The region of investigations includes practically the whole Indian Ocean: from the continent of Asia on the north to 41° on the south and from the African coast on the west to Australia on the east. The materia was collected by nets of different types but the principal part of it has been obtained by a round dip net and pleiston trawl during the night collections. The work at night stations with the use of electric light as a means of attraction and concentration of animals was carried out regularly on the research vessels. Most of the pelagic squids like many other marine animals possess a positive reaction to light. This habit has been taken advantage of for fishery and scientific purposes.

As a result of preliminary examination of the collection of Cephalopoda the following species are recorded for the first time as occurring in Indian Ocean: *Symplectoteuthis luminosa, Todarodes sagittatus angolensis, Nototodarus sloanei, Thysanoteuthis rhombus, Moroteuthis lonnbergii, Ctenopteryx siculus, Cycloteuthis sirventi, Sandalops melancholicus:*

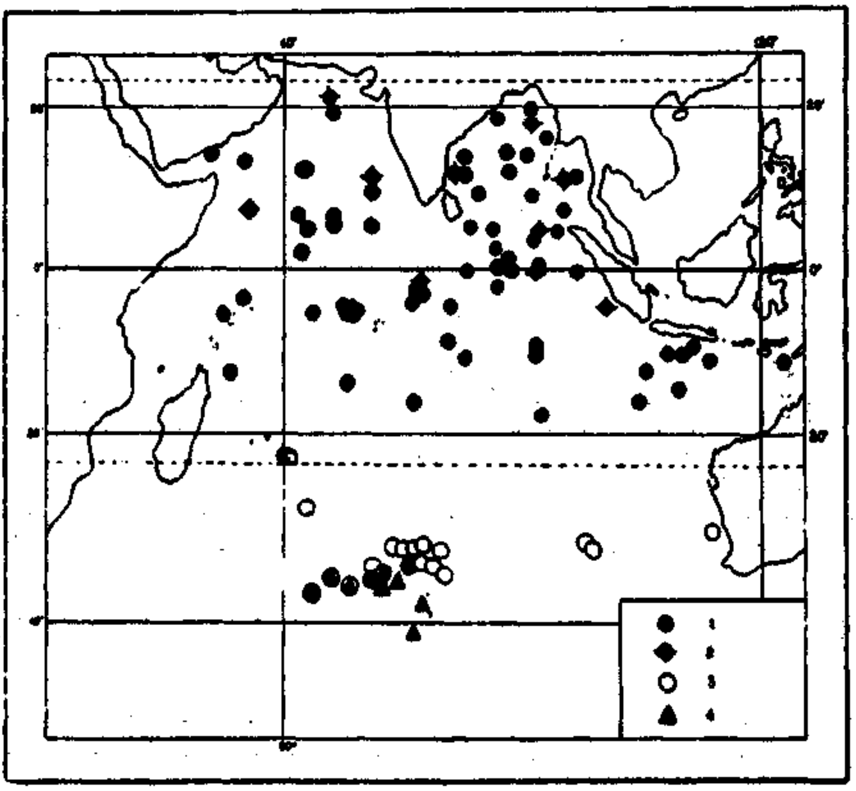


Fig. 1. The distribution of the squids of the family Ommastrephidae in the Indian ocean: 1. *Symplectoteuthis oualaniensis*, 2. of its juveniles, 3. *Ommastrephes bartrami*, 4. *Todarodes sagittatus angolensis*.

Among them there are well-known species widely distributed in other oceans for instance, *Thysanoteuthis rhombus, Ctenopteryx siculus*, and there are the species—*Sandalops melancholicus* and *Cycloteuthis sirventi*, which are known today from single specimens. Besides our material proves the presence of the small epipelagic squid *Onychia carribaea* in Indian Ocean, which Clarke (1966) considered to be doubtful.

Thus the list of cephalopods of Indian Ocean has been increased. At the same time there is no doubt that future investigations will extend it further.

The shelf waters of the investigated region are inhabited abundantly by representatives of the neritic families, Sepiidae and Loliginidae. Among the cuttle fishes *Sepia pharaonis* is the most abundant species.

As for the surface waters of the open ocean the number of species of cephalopods is not so great:

Fam. Ommastrephidae: *Symplectoteuthis oualaniensis, S. luminosa, Ommastrephes bartrami, Todarodes sagittatus angolensis, Nototodarus sloanei* (*? gouldi*).

Fam. Thisanoteuthidae: *Thysanoteuthis rhombus.*

Fam. Onychoteuthidae: *Onychoteuthis banksi, Onychia carribaea.*

Fam. Agronautidae: *Argonauta hians.*

Fam. Tremoctopodiae: *Tremoctopus violaceus.*

Besides the above-mentioned forms which are the constant inhabitants of the oceanic epipel gial the squids of greater depths were taken at the surface at night:

Fam. Enoploteuthidae: *Abralia* sp., *Thelidioteuthis alessandrini.*

Fam. Cranchidae: *Pyrgopsis pacificus, Leachia eschscholtzii.*

In the surface waters of the Indian Ocean as well as the Atlantic and the Pacific the main role belongs to the representatives of the family Ommastrephidae. Our data show that *Symplectoteuthis oualaniensis* is the most abundant and predominant form in the northern and central parts of the Indian Ocean. The pelagic shoaling squid is widely distributed in the tropical part of the Pacific Ocean. In the Indian Ocean it has been recorded in a few places till now: from the Arabian Sea, near Zanzibar and north-west Australia (Clarke, 1966). Recently it has been found in the Gulf of Aden in great numbers (Zuev, 1965).

This squid was caught by our research vessels from 80 stations, situated in northern and central parts of the Indian Ocean approximately up to 20° S. Further to the south it is replaced by the other member of the same family—*Ommastrephes bartrami.*

Although *Symplectoteuthis oualaniensis* is considered to be a well-known species the boundaries of its area have not been determined. Our material allows us to do this in the limits of the Indian Ocean. Thus the southern boundary of *S. oualaniensis* passes along approximately 20° S. It coincides with the zone of subtropical convergence and the area is wholly situated in the limits of the tropical waters. The fact that one specimen of *S. oualaniensis* was taken near the southern end of Africa (Massy, 1925) can be explained by its penetrating there with the warm Agulhas current.

As the plankton studies show, the zone of subtropical convergence (18–20° S.) serves as the southern boundary of distribution of tropical forms of zooplankton also (Vinogradov and Voronina 1962). This zone is the southern boundary of the areas of some tropical epipelagial fishes (Parin, 1968). *S. oualaniensis* shows the same pattern. It, like other oceanic squids, is similar to epipelagic fishes in its ecology. The similarity of distribution of *S. oualaniensis* and the inhabitants of the tropical waters—snake mackerel *Gempylus serpens* may serve as an instance of such relationship (Parin, 1967).

The larvae of *S. oualaniensis* have been collected at 15 stations in the northern and equatorial waters. By analogy with the snake mackerel it is possible to suggest the spawning grounds to be located within the limits of the equatorial waters proper. The feeding ground of adults is situated outside and extends to the southern boundary of the range of *S. oualaniensis.*

The old tropic connection appears to exist between *S. oualaniensis* and *G. serpens*. As the investigations of Parin showed the squids were one of the main food items of the fish. In some cases it was reliably known that the squid was *S. oualaniensis*.

This species has been found to consist of two forms, one with and the other without a light organ on the dorsal surface of mantle. As these forms also differ in size at which they attain maturity, Clarke (1966) opined that they must be considered distinct sympatric species.

Our careful examination of all specimens of *S. oualaniensis* (nearly 150 specimens) confirmed the presence of the two forms mentioned. Most of the squids examined had the accumulations of yellow bodies, the diameter of which was nearly 1 mm., embedded in the dorsal muscles. They form large oval spots, which emit the bluish luminescence in the living animals.

The form with the light organ is larger than the one without. In our material the maximum of the dorsal mantle length of first form was 35 cm., and that of the second was 13 cm. The latter attains maturity at a smaller size than the former. It is true for both males and females. For instance, a male without the light organ with the dorsal mantle length of 9 cm. had a well formed hectocotylus. The males of the larger form attain such degree of maturity at a mantle length of 12-13 cm. only. We noticed that these two forms differ not only in the size and presence or absence of the light organ, but also in the form of body and fins. These differences are so obvious that the two forms can be identified by these external features.

All points mentioned above allow us to agree with Clarke (1966) that the squids which were previously united in a single species *S. oualaniensis*, belong to two distinct sympatric species.

The distinction of two forms of *S. oualaniensis* is possible with the adult animals only. In young squids with a mantle of less than 6 cm. no trace of light organ or any other differences have been discovered. Thus it allows us to assume that the appearance of these features is connected with the beginning of maturity.

South of the Tropic of Capricorn *S. oualaniensis* was replaced by the other member of the family Ommastrephidae—*Ommastrephes bartrami.** There are data on the presence of this species in the equatorial part of the Indian Ocean: Sasaki (1916) and Robson (1921) pointed out that *O. bartrami* was found near Ceylon and Chagos Islands (Clarke, 1966). We consider these data to be erroneous. Clarke refers to them as being doubtful, supposing that *S. oualaniensis* was mistaken for *O. bartrami* due to external similarity. We carefully examined our material and are absolutely sure in the correctness of our identifications.

Thus, *O. bartrami* have been captured at 20 stations in the region between 23 and 37° S. and 60 and 113° E.

At present the data on this species are not sufficient to delineate its area of distribution. However the peculiarities of its distribution in the Indian Ocean, namely, its connection with the subtropical waters and its complete absence in the tropic, but at the same time its presence in the temperate and subtropical waters of northern Pacific (Berry, 1912; Sasaki, 1929; Filippova, unpublished) suggest that *O. bartrami* is distributed in the Pacific in the same way and that, possibly, this squid inhabits the temperate and subtropical waters, avoiding the tropic. Such type of distribution is typical of the swallow fish –*Hirundichthys rondeletii*—which has bipolar (antitropic) distribution (Parin, 1968).

---

* Clarke (1956) doubts about the existence of the species *Ommastrephes bartrami* (Lesueur, 1821) in the Atlantic Ocean; however, he acknowledges the validity of the so-called Pacific *O. bartrami*. He, however, does not consider them to be equal. Having compared the squids from the Indian Ocean with the ones from the north-western Pacific we got assured of their complete identity. Thus, here we shall deal with the so-called Indo-Pacific *O. bartrami*.

In the region from 34 to 41° S. and from 63 to 77° E. *Todarodes sagittatus angolensis* has been discovered. It belongs to the same family Ommastrephidae. Like the first two forms it occurs in vast schools. It was especially abundant in the region between Amsterdam and Saint Paul Islands. The size of the captured squids varied from 18 to 40 cm. in mantle length. At six stations situated from 35 to 37° S. it has been collected together with *O. bartrami*. However, *T. sagittatus angolensis* prevailed by its abundance. From this latitude it becomes a predominant species, and further to the south—the single numerous species, while *O. bartrami* has not been met with here.

The discovery of this species in the Indian Ocean was quite unexpected. This squid has up till now been considered to be amongst the commonest species of the eastern part of the North Atlantic. Recently, Adam (1962) described a new subspecies living in the South Atlantic near the African coast (Angola) and in the region of Tristan da Cunha, according to Korabelnikov (1959). Besides in our collection there is one specimen of *T. sagittatus angolensis*, caught at 46° 22′ S., 5° 29′ W.

Thus, the clear latitudinal zonality in the distribution of the abundant forms of the family Ommastrephidae exists in the Indian Ocean: the tropical waters are the realm of *S. oualaniensis*; subtropical region is inhabited by *O. bartrami*, the area of which is partly overlapped by the area of the third species—*T. sagittatus angolensis*, distributed further to the south.

Onychoteuthis banksi is considered to be a common form of the surface waters of the world ocean. In the Indian Ocean it has been recorded from several places: off southern and eastern coasts of Africa and near Mascarene Islands. We add records in 14 other places (Fig. 2).

Thysanoteuthis rhombus has been known in the North and South Atlantic, in particular, from strandings near the Cape of Good Hope (Barnard, 1947) and Algoa Bay (Bruggen, 1962), in the

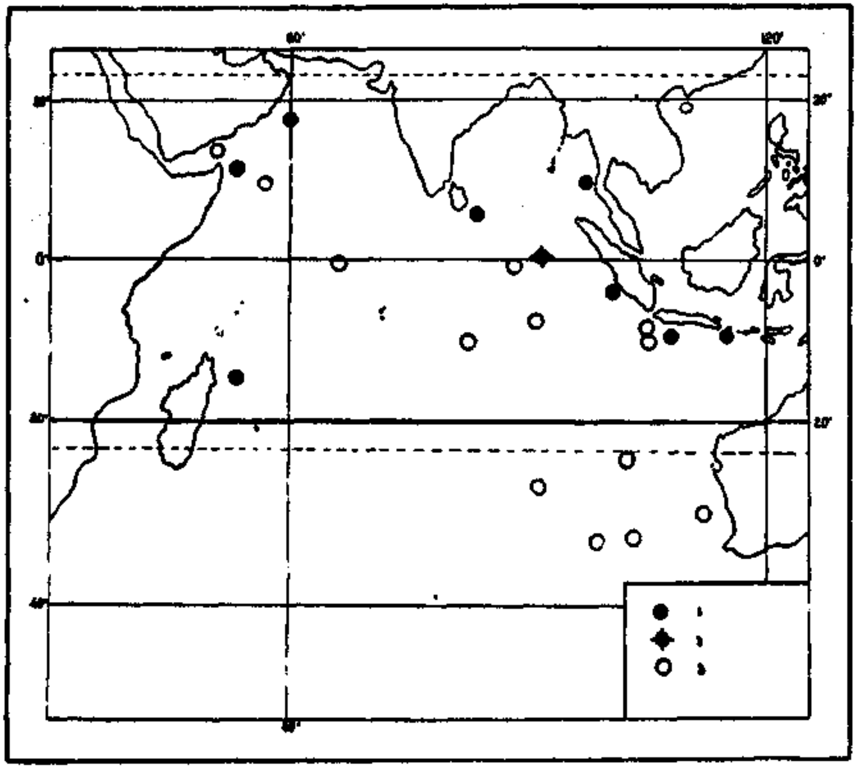


FIG. 2. The distribution of *Thysanoteuthis rhombus* (1) and *Onychoteuthis banksi* (2).

Pacific—off Japan, China and the Bonin Islands (Sasaki, 1929; Pfeffer, 1912; Nishimura, 1964). Now for the first time it has been found in the Indian Ocean at 9 stations. Once a juvenile of this squid was found. This indicates that the reproduction of this squid takes place in the waters investigated. Thus our data destroy the hiatus in the distribution of *T. rhombus*, making it continuous henceforth.

There were doubts with regard to the presence of *Onychia carribaea* in the Indian Ocean (Clarke, 1966). In our collection there are typical representatives of this species caught at 12° 57′ S., 118° 32′ E. and 26° 20′ S. 90° 02′ E.

In the surface waters of the open Indian Ocean pelagic octopuses have been captured—*Tremoctopus violaceus* and *Argonauta hians*. Although both of them are banal enough, the distribution of them in the Indian Ocean has not been elucidated in detail.

T. violaceus has been met with at 14 stations in the tropic zone of the Indian Ocean (Fig. 3). Mainly young females were captured. The more abundant *A. hians* has been obtained from 28 stations. In our collection it was represented by the females with the shells often filled with eggs.

It is interesting to note some peculiarities of pelagic octopuses. If all the squids mentioned above are active and moving animals and belong to nekton, both of the pelagic octopuses in our opinion, should possibly be regarded as belonging to pleiston biocenosis.* Females of *Argonauta* with a shell used as float appears to keep to the surface of the sea, as a rule. There were observations pointing out that *Argonauta* often attach themselves to some pleiston organisms such as *Velella* and jellyfishes, using them for floats (Jones, 1963; Bruun, 1956; David, 1965).

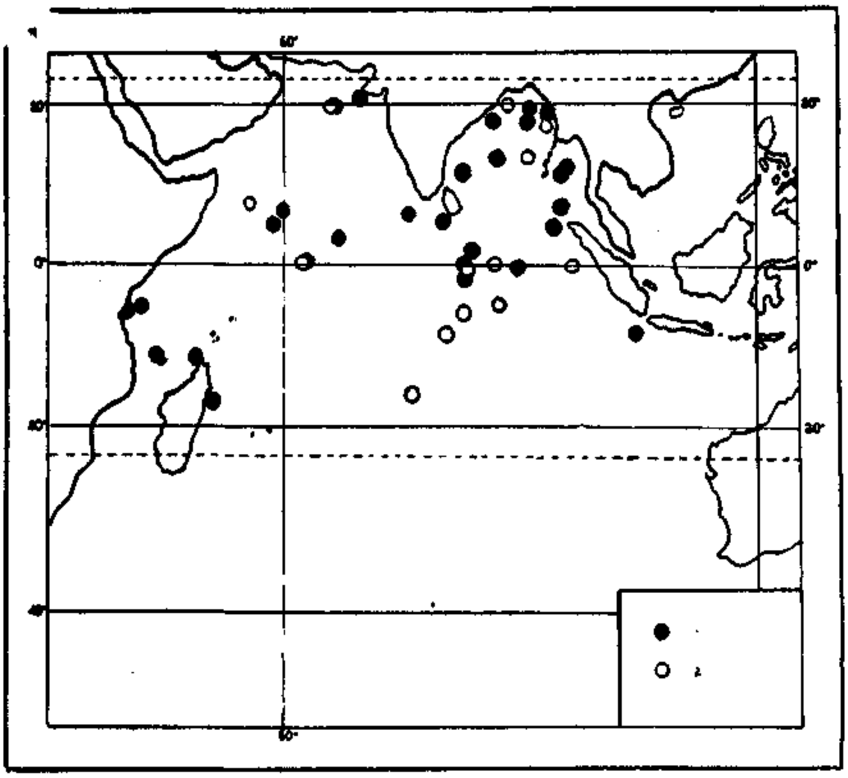


FIG. 3. The distribution of the pelagic octopuses—*Tremoctopus violaceus* (I) and *Argonauta hians* (2).

---

* About the term *see* Savilov (1958).

As is known *T. violaceus* is devoid of shell and appears to be more active. However, it is in need of a constant association with the pleiston organisms, but the reason is different. Young *Tremoctopus* has been observed to use fragments of the tentacles of *Physalia* as defensive and offensive weapons. They cover the oral surface of three pairs of arms (Naef, 1923; Jones, 1963). All the examined specimens (18) of our collections were armed in the same manner. After discharging the batteries of the *Physalia's* tentacles *Tremoctopus* is forced to replace them regularly with new ones. That is why the association of the young octopuses with the fleets of *Physalia* must be constant. The adult octopuses do not appear to be in need of borrowing *Physalia's* tentacles and, seemingly, their connection with pleiston biocenosis is broken.

The investigations carried out by the Soviet ships in the Indian Ocean widen our knowledge in general and on the fauna of Cephalopoda in particular. As a result of these studies the data obtained on the distribution of squids confirm the opinion of Akimushkin (1963) about the absence of endemism in most of oceanic Cephalopoda. It is impossible to point out any oceanic surface species peculiar only to this ocean. This is especially clear for the tropical waters: the distribution of some molluscs is confined to two oceans (Atlantic and Indian or Pacific and Indian) and others are distributed circumtropically. The same pattern has been stated for the epipelagic fishes (Parin, 1968).

ACKNOWLEDGEMENTS

I should like to express my appreciations to Dr. V. A. Tchekunova for the collection of the cephalopods during cruise II of r/v "Academician Knipovitch" and to Mr. A. S. Pervushin for the organization of the regular sampling of squids on the factoryship "Sovietskaja Rossia". I am very grateful to Dr. S. K. Klumov and Dr. N. V. Parin through whose kindness I was able to examine the collection of Cephalopoda of the Institute of Oceanology of the Academy of Sciences, USSR.

LITERATURE CITED

Adam, W. 1939. The Cephalopoda in the Indian Museum, Calcutta, *Rec. Indian Mus.*, **41**: 61–110.

——— 1962. Cephalopodes de l'Archipel du Cap-Vert, de l'Angola et du Mozambique. *Trabalhos do Centro de Biologia Piscatoria*, **32**: 7–64.

Akimushkin, I. I. 1963. The Cephalopoda of the Seas of the USSR. *Izd. Akad. Nauk. SSSR* (in Russian) (Translation in English, Jerusalem, 1965). 223 pp.

Barnard, K. H. 1947. Rare squid at the Cape (*Thysanoteuthis rhombus* Troschel). *J. Conch. Lond.*, **22**: 286 pp.

Berry, S. S. 1912. A review of the cephalopods of western North America. *Bull. Bur. Fish. Wash.*, **30**: 263–336.

Bruggen, A. C. van. 1962. *Thysanoteuthis rhombus* in Algoa Bay. *Ann. of the Natal Museum*, **15**: 267–272.

Bruun, A. *et al.* (Eds.). 1956. *The Galathea Deep-Sea Expedition* 1950–52. Macmillan, New York, 285 pp.

Clarke, M. 1965. Large light organs on the dorsal surfaces of the squids, *Ommastrephes pteropus*, "*Symplectoteuthis oualaniensis*" and "*Dosidicus gigas*". *Proc. malac. Soc. Lond.*, **36**: 319–321.

——— 1966. Review of the systematics and ecology of oceanic squids. *Advances in Marine Biology*, **4**: 91–300.

David, P. M. 1965. The surface fauna of the ocean. *Endeavour*, **24** (92): 95–101.

Goodrich, E. S. 1896. Report on a collection of Cephalopoda from the Calcutta Museum. *Trans. Linn. Soc. Lond.*, Ser. 2 (Zool.), **7**: 1–24.

Hoyle, W. E. 1906. The Cephalopoda. In *The Fauna and Geography of the Maldive and Laccadive Archipelagoes.* 2. Cambridge University Press, Cambridge, 1079 pp.

Jones, E. C. 1963. *Tremoctopus violaceus* uses *Physalia* tentacles as weapons. *Science*, **139**: 764–766.

Korabelnikov, L. V. 1959. The diet of sperm whales in the Antarctic. *Priroda* No. 3 (in Russian), 103–104.

MASSY, A. L. 1916. The Cephalopoda of the Indian Museum. *Rec. Indian Mus.*, **12**: 185–247.

——— 1925. On the Cephalopoda of the Natal Museum. *Ann. Natal Mus.*, **5**: 201–229.

NAEF, A. 1923. Die Cephalopoden. *Fauna Flora Golf. Neapel*, Monograph 35, Tiel 1, Band **1**: 1–863.

NISHIMURA, S. 1966. Notes on the occurrence and biology of the oceanic squid, *Thysanoteuthis rhombus* Troschel, in Japan. *Publ. of the Seto Mar. Biol. Lab.*, **14** (4): 327–349.

PARIN, N. V. 1967. The materials on the distribution and biology of the snake mackerel—*Gempylus serpens* Cuv. (Pisces, Gempylidae) in the Pacific and Indian Ocean. *Vopr. Ichthyology*, **7** (6) (in Russian), 990–999.

——— 1968. The ichthyofauna of the oceanic epipelagial. *Izd.* "*Nauka*" (in Russian). 3–185.

PFEFFER, G. 1912. Die Cephalopoden der Plankton-Expedition. Zugleich eine monographische Übersicht der Oegopsiden Cephalopoden. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, **2**: 1–815.

SASAKI, M. 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *J. Fac. Agric. Hokkaido imp. Univ.*, **20**, Suppl. 10: 1–357.

SAVILOV, A. I. 1958. The pleiston of western part of the Pacific Ocean. *Dokl. Akad. Nauk SSSR*, **122** (6): (in Russian), 1014–1017.

VINOGRADOV, M. E. AND N. M. VORONINA 1962. Some data on the distribution of zooplankton in the northern Indian ocean. *Tr. of the Inst. of oceanol. Akad. Nauk SSSR*, **58** (in Russian), 80–114.

ZUEV, G. V. 1965. The squid from the Aden Gulf. *Rybnoe Khoz.*, No. 1 (in Russian), 22 pp.

A SYNOPSIS OF THE RECENT CEPHALOPODA OF CANADA

M. C. MERCER

Fisheries Research Board of Canada
Biological Station, St. John's, Newfoundland, Canada

ABSTRACT

Records of cephalopods taken in the zone extending from the coasts of Canada to the 1000 fathom contour and also including the West Greenland-Baffin Bay area, are discussed.

The Arctic cephalopod fauna, except for a single endemic sepiolid squid and two octopod immigrants from the Pacific, is composed of North Atlantic post-glacial immigrants. The Arctic-Atlantic fauna comprises 21 teuthoids (all but 1 oegopsid), 4 sepioids (all sepiolids), and 6 octopods.

The Pacific fauna comprises 14 teuthoids (all but 1 oegopsid), 1 sepioid (a sepiolid), and 5 octopods; it is quite distinct from that of the Atlantic and includes at least 6 Pacific boreal endemic autochthons. The Gonatidae is considered to be a North Pacific autochthon, *G. fabricii* in the Atlantic probably being derived by trans-Arctic migration during the Post-Glacial Warm Period.

INTRODUCTION

A LARGE collection of cephalopods has been accumulated during ground fish trawling surveys conducted by the Fisheries Research Board in the past 20 years. Since the cephalopods of Canada have received little attention in the past, these specimens, supplemented by material from other agencies, will form the basis of a series of faunal reports by the author.

This paper is preliminary, the aim being to provide a species list and to discuss briefly the composition and relationships of the fauna. Many new records are reported here. Descriptions, lists of specimens, and taxonomic discussions will be presented elsewhere. Except where indicated the author has examined specimens of all species listed.

For practical (though not zoogeographically meaningful) considerations of the collections examined by the author, the area covered is restricted arbitrarily to the zone extending from the coasts of Canada to the 1,000 fathom contour, but it also includes the West Greenland-Baffin Bay area (Fig. 1). The synopsis of species lists only those which have been taken within this area. In the discussion, pertinent literature records from zoogeographically allied areas are reviewed. Neritic and sublittoral forms have probably been sampled adequately except in the Pacific region and the Beaufort Sea; the oceanic fauna is undoubtedly richer than numbers of species listed here indicate.

As with most pelagic forms, there is a dearth of reliable data on depth distribution of pelagic cephalopods. Most specimens have been taken by trawls without opening-closing devices so that it is impossible to ascertain accurately from what depth they were captured.

Discussion of distribution is further complicated by the considerable taxonomic problems in the group. Several families are in need of revision, and, until such time as synonymies are worked out, the provisional nature of any distributional discussion must be realized. Nevertheless it is hoped that this preliminary review will be of some value.

In discussing the composition of the fauna the author has adopted the classification and terminology of marine environments presented by Hedgpeth (1957). For data on hydrography of the area the reader is referred to Dunbar (1951) for the Canadian Eastern Arctic, Hachey (1961) for the Canadian Atlantic, and Fleming (1955), Doe (1955), Dodimead (1961) and Uda (1963) for the Canadian Pacific.

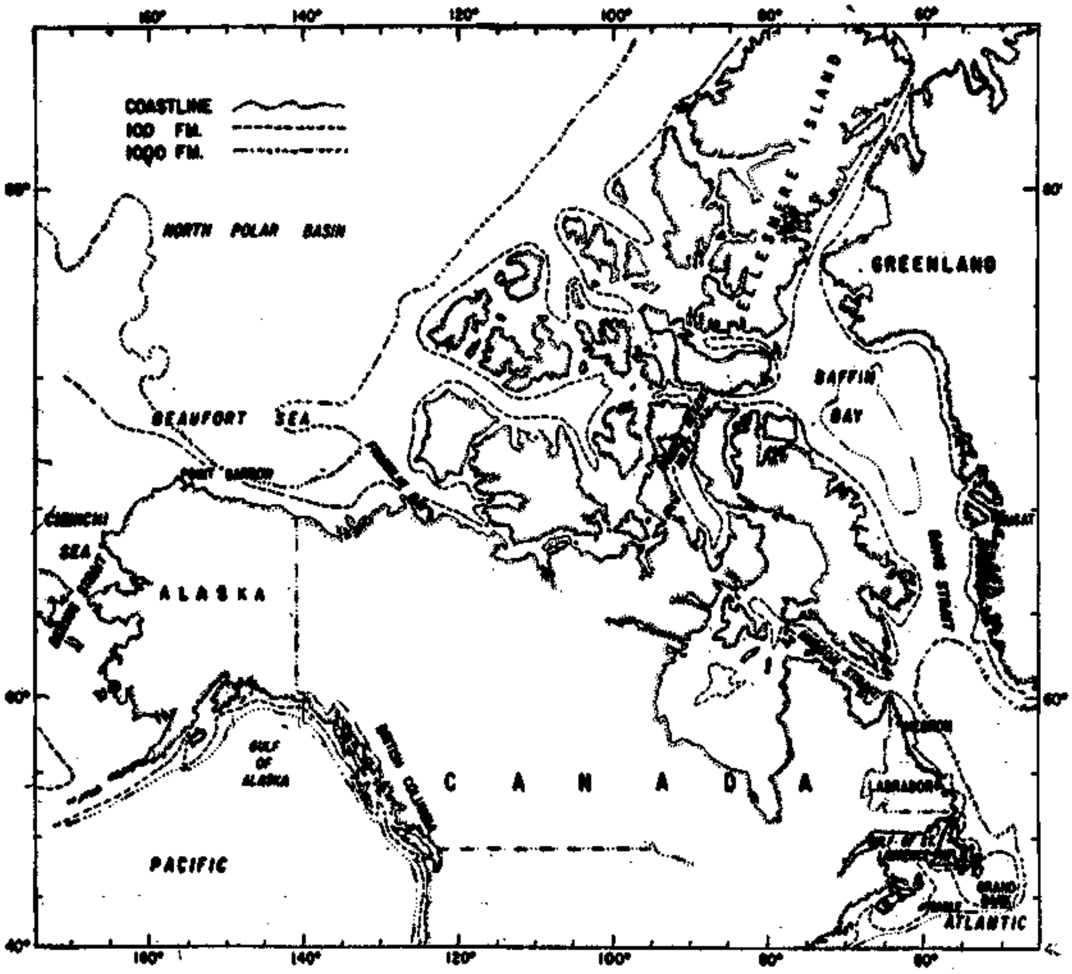


FIG. 1. Map of Canada showing place names mentioned in the text.

THE ATLANTIC-ARCTIC FAUNA

The Arctic cephalopod fauna has been reviewed by Grimpe (1933) and recently by Akimushkin (1963). Berry (1925) presented a bibliography for the cephalopods of the American Arctic. The fauna of the North-West Atlantic has not been reviewed since Verrill (1879-1881).

The Arctic cephalopod fauna is derived principally from North Atlantic post-glacial immigrants; most of these do not penetrate into high Arctic waters, but belong to Ekman's (1953) "Atlantic-Arctic" group, ranging no farther than the Barents Sea in the east and the Davis and Hudson Straits in the west. Akimushkin (1963) attributed the apparent lack of recent incursions of

Pacific forms to a combination of physiographic and hydrographic factors, namely, extreme shallowness, low salinity, and extremely low temperature in the Bering Strait region. He reported only a single immigrant in the Chukchi Sea from the Pacific (*Benthoctopus profundorum*) which apparantly entered during the Littorina Period.

However, MacGinitie (1955) collected a single specimen of *Benthoctopus hokkaidensis*, three specimens of *Gonatus fabricii* (which were washed ashore), and two specimens of an unidentified *Cirroteuthis*, at Point Barrow. (It should be noted that *Cirroteuthis mülleri* has been taken in the Norwegian Basin which communicates with the North Polar Basin by a channel about 1,500 meters deep.)

A single species, *Rossia molleri*, is known to be an Arctic endemic (Mercer MS, 1968).

Because of the relationships just discussed the faunas of the Atlantic and Arctic are considered together. Twenty teuthoids belonging to 11 families are recorded. The only myopsid is the neritic boreal *Loligo pealeii*. The summer range of this species extends to the Nova Scotian area, and it has also been reported from pilot whale stomachs in the Gulf of St. Lawrence (Préfontaine, 1930). No specimens have ever been taken in the Newfoundland area.

The pelagic ommastrephid *Illex illecebrosus* also visits Canadian Atlantic waters as a seasonal migrant. It is fished commercially in the Newfoundland inshore area where annual landings have ranged as high as 23 million pounds. The biology of this species has been dealt with by Squires (1957) and Mercer (MS, 1965, and in preparation).

Rees and Maul (1956) suggested that the giant squid *Architeuthis* sp. and *Taningia danae* probably live pelagically over the continental slope. *T. danae* is here first recorded from the Western Atlantic.

The mesopelagic enoploteuthids, *Pyroteuthi margaritifera* was taken in the warm water of the North Atlantic Current.

Two of the three bathypelagic histioteuthids taken, *Histioteuthis bonellii* and *H. reversa*, also occur in the Indo-Pacific; *H. elongata* is so far known only from the North Atlantic (N. Voss, in press).

The teuthoids (except *Loligo*) are oegopsid species of generally wide distribution although three of these, *Chiroteuthis lacertosa, Brachioteuthis beani*, and *Pyrgopsis lemur*, are presently known only from the Western North Atlantic ; undoubtedly this is due to our inadequate knowledge of these species. The relationship of the bathypelagic *C. lacertosa* to the Eastern Atlantic *C. veranyi* and supposed Pacific "*C. veranyi*" needs to be elucidated. *Pyrgopsis lemur* is known from only three specimens (Mercer, 1966).

Squids of the genus *Mastigoteuthis* are listed in the synopsis. The genus is badly in need of revision ; of the 13 species listed by Clarke (1967) 6 are known from the type only; all but 2 have been reported from the North Atlantic.

Three of the sepioids belong to the genus *Rossia* which has been reviewed by Mercer (MS, 1968). The Arctic endemic *R. molleri* ranges southward only to Hebron Fiord in the east, occurs under high Arctic conditions, and has been taken westwards to Franklin Bay. The Arctic-boreal *R. palpebrosa* occurs southwards to about 32° N in the Western Atlantic and 51° N in Eastern Atlantic ; it has been taken under high Arctic conditions at Ellesmere Island; however it is not recorded farther west than Prince Regent Inlet, the type locality. *R. megaptera* ranges from New England to the south of the Davis Strait Ridge, generally in warmer Atlantic water. *Stoloteuthis leucoptera* is a sublittoral boreal species which ranges northwards to the Gulf of St. Lawrence; it does not occur on the Newfoundland banks.

Records requiring verification are those of Grieg (1896, *fide* Berry, 1925) for *Sepiola rondeletii* from Kraakøskallen and Godøsund, Greenland and Mörch (1857, *fide* Berry, 1925) for (?) *Sepiola atlantica*. Grimpe (1933) attributed these records to *Sepietta scandica*. Posselt (1898, *fide* Berry, 1925) recorded *Spirula* from Vaigat, 69° 44′ N. Likely this was a dead shell as these are widely distributed by surface currents. (I have examined a shell collected on the beach at Sable Island). Live *Spirula* have never been taken in the Greenland-Iceland area and would not be expected to occur there (*see* Bruun, 1943).

Octopods include the Arctic-Atlantic-boreal, bathyal forms *Bathypolypus arcticus* and *Benthoctopus piscatorum*, both of which also occur in the North-East Atlantic as does the deep bathyal *Graneledone verrucosa*. Only *B. arcticus* is reported from Baffin Bay and it has also been taken in Franklin Bay. (This species is eurybiotic, ranging southwards to about 32° N in the west and about 53° N in the east with depth records from continental shelf to 1543 metres.) The meropelagic *Alloposus mollis* is warm water epipelagic as a juvenile, but settles on the continental slope, probably to breed (Thore, 1949). All our specimens were collected on the south-west slope of the Grand Bank.

At least two cirromorphs occur, one of these co-specific with Verrill's *Stauroteuthis syrtensis* (of which the author has examined the holotype). Literature records include *Cirroteuthis mülleri* from West Greenland (reviewed by Robson, 1932) and *Chunioteuthis ebersbachii* from Newfoundland (known only from the type locality 42° 59′ N, 51° 51′ W in 1099 metres—Grimpe, 1916). However, the systematics of cirromorphs is confused and the relationships of these forms are not clear.

Records of single specimens of the Pacific species *Benthoctopus profundorum* and *B. hokkaidensis* from the Chukchi Sea and Point Barrow area have already been noted.

In considering the boreal sublittoral and neritic cephalopod fauna of the Western North Atlantic it is interesting to make comparisons with that of the East. Muus (1963 *a-e*) has recently published keys to the cephalopods north of *ca.* 40° N and briefly reviewed local distributional patterns.

Some of the sepioids listed are warm water Mediterranean species. Three sepiids, all belonging to the genus *Sepia*, are found; none of these range farther north than the northern North Sea—Skagerrak area. Seven sepiolids, belonging to 4 genera, occur but of these only *Rossia palpebrosa* (= *R. glaucopis*—Mercer, MS, 1968) ranges northwards to the Barents Sea. *R. macrosoma* is found in the Norwegian Sea and Muus (1962) has reported a specimen from East Greenland. None of the other species range farther northwards than the Norwegian Sea and none are amphi-Atlantic.

Muus lists 20 teuthoids comprising 16 genera and 9 families. Four myopsids occur, all loliginids; none of these range farther north than the Faroe-Shetland area and none are amphi-Atlantic.

In the Ommastrephidae Muus lists *Ommastrephes bartrami*, and *O. pteropus*; we must also list *O. caroli*. Clarke (1967) has discussed this complex and is not satisfied with our present concepts of synonymies and distributions. Also recorded are *Todarodes sagittatus* and *Todaropsis eblanae*, both Eastern Atlantic endemics. *Illex illecebrosus* (type locality Sandy Bay, Mass.) is generally considered to comprise two subspecies in the North Atlantic (Adam, 1952) although Clarke (1967) considers them separate species. In the Western Atlantic the winter range extends no farther north than Nova Scotia while during the summer and early fall the species occurs considerably farther to the north. There are two 19th century records from West Greenland; however, Paul Hansen (in litt.) is unable to confirm the occurrence of *Illex* in the area. The only Icelandic record is the single specimen reported by Gröndall (1891). The specimen could not be located, and the Marine Research Institute has no further information on this species at Iceland (Jón Jónsson, in litt.). Since the species does not occur beyond the continental slope there is apparently no genetic interchange between populations on both sides of the Atlantic.

The remaining teuthoids are all oceanic species of wide distribution and nearly all have been reported from the Western Atlantic. (The single exception is *Taonidium pfefferi* which is known only from the Eastern Atlantic. The Taoniinae are badly in need of revision and no significance should be attached to this).

Muus listed the octopods *Octopus vulgaris* and *Eledone cirrhosa* (which have pelagic larvae). *O. vulgaris* is also found in the Western Atlantic where it ranges southward from about 40° N ; it is the only recorded discontinuous amphi-Atlantic, boreal form. (Muus also listed 3 cirromorphs; however, as previously noted, the systematics of this interesting group is too confused for consideration of distributions). We have already noted the three bathyal octopods that are common to both sides of the Atlantic, all having a continuous distribution.

As would be expected then, the Arctic-boreal species are common to both sides of the Atlantic while the boreal species are different. This was recognized very early by Lovén (1846, cited from Ekman, 1953) for other mollusc groups.

THE PACIFIC FAUNA

Cephalopods have been reported off British Columbia from the stomachs of sperm whales (Robbins *et al.*, 1937; Pike, 1950). Berry (1912) reported on benthic collections made principally off California and Alaska, and Pearcy (1965) has recently discussed the species composition and distribution of pelagic cephalopods off Oregon.

British Columbia falls within the high boreal, Aleutian, molluscan province as designated by Schenk and Keen (1936). Keen (1940) has shown that less than 2 per cent of the molluscs are amphi-Pacific or discontinuous amphi-Pacific. Akimushkin (1963) discussed the distribution of cephalopods in the area and reported that 27 per cent of all Far Eastern cephalopods occur along the Pacific coast of North America; he included the oceanic species.

The Pacific Arctic-boreal cephalopod fauna is quite distinct from that of the Atlantic and contains a well-developed endemic element. This is hardly surprising since Ekman (1953) has pointed out that during the whole of the Tertiary the North Pacific was more favourable for the development of a cold temperate fauna than was the North Atlantic.

Fourteen teuthoids belonging to 8 families are recorded off British Columbia. The only myopsid is the eastern North Pacific neritic, boreal, endemic *Loligo opalescens*. The remaining species are oegopsids. At least six of these are Pacific boreal endemics: *Moroteuthis robusta, Todarodes pacificus, Gonatus magister, G. berryi* (?), *G. anonychus*, and *Gonatopsis borealis*. *T. pacificus* is an eastern Pacific species whose recorded range extends to the Kronotski Gulf (Kamchatka Peninsula) (Akimushkin, 1963); it is here first recorded from the North-West Pacific. *Histioteuthis dofleini* is thus far recorded only from the North Pacific although members of the bathypelagic Histioteuthidae generally have wide distributions (N. Voss, in press).

The family Gonatidae is undoubtedly a North Pacific autochthon. Atlantic populations of the discontinuous circumboreal *Gonatus fabricii* were derived from Pacific populations by migration through the Arctic ; this most likely occurred during the Post-Glacial Warm Period through the North American Arctic where transport of larvae would be assisted by the Coriolis-driven current. This route was taken by Pacific benthic organisms at the time, as well evidenced by their present distributions (*see* Nesis, 1963). Although Clarke (1967) has suggested that the populations might be continuous through the Arctic we have taken no specimens West of Hudson Strait and Nesis (1965) reported none east of the Barents Sea.

The Antarctic *G. antarcticus*, possibly only a subspecies of *G. fabricii*, is also a Quaternary derivative. Berg (1933) and Hubbs (1952) have attributed most antitropical distributions to communication through the tropics during Pleistocene cooling.

The remaining eurybathic gonatids are endemic to the cold-temperate North Pacific. There may however be more undescribed species, *e.g.* there may be two species confused under the name *G. fabricii* (*see* Akimushkin's—1963—"var. *separata*").

Five species we record off British Columbia are also taken in the Atlantic : *Gonatus fabricii, Octopoteuthis sicula, Taonius pavo, Ommastrephes "bartrami"* (which is probably not co-specific with the Atlantic *O. bartrami*—*see* Clarke, 1967, and *Onychoteuthis banksi* (a warm water epipelagic form which has been referred to a separate species *borealijaponicus* by Okada (1927); it is possibly a subspecies of the Atlantic *O. banksi* from which it differs in having a commissure connecting the visceral photophores).

The arctic-boreal sublittoral *Rossia pacifica* is the only sepioid present; its range is continuous from the north-east coast of Japan and both sides of the Japan Sea to California.

The four recorded octopods are all North Pacific autochthonous endemics. Two of these belong to the genus *Octopus. O. leioderma* is recorded off California and Alaska (Berry, 1912) and in the Eastern Pacific southwards to Paramushiro in depths of 38-1760 metres (Akimushkin, 1963). The giant *Octopus, Octopus dofleini,* ranges from California to Japan ; Pickford (1964), in a paper based on a small series of specimens, recognizes three subspecies. The other species are the pelagic *Japetella heathi* which may be discontinuous amphiboreal (Akimushkin, 1963) and the bathyal cirromorph *Opisthoteuthis californiana,* the known range of which extends from California to the Aleutians in depths of 124–933 metres (Pereyra, 1965).

In addition to the species listed here from British Columbia, Pearcy (1965) also reported *Abraliopsis* sp., *Chiroteuthis veranyi* (?), the cosmopolitan cranchiids *Galiteuthis armata* and *Cranchia scabra, Histioteuthis meleagroteuthis* (= *Meleagroteuthis hoylei*), and the bathypelagic vampyromorph *Vampyroteuthis infernalis* from off Oregon.

SYNOPSIS

Listings of species marked with an asterisk refer to literature records only, no specimens having been examined by the author.

Subclass **COLEOIDEA**
  Order SEPIOIDEA
    Family *SPIRULIDAE*
      Genus *Spirula* Lamarck, 1801
        Spirula spirula (Linnaeus, 1758)[1]
    Family *SEPIOLIDAE*
      Subfamily ROSSIINAE
        Genus *Rossia* Owen 1835
          Rossia palpebrosa Owen, 1835
          Rossia megaptera Verrill, 1881
          Rossia molleri Steenstrup, 1856
          Rossia pacifica Berry, 1911
      Subfamily STOLOTEUTHINAE Berry, 1912
        Genus *Stoloteuthis* Verrill, 1881
          Stoloteuthis leucoptera (Verrill, 1878)

---

[1] dead shell only.

Order TEUTHOIDEA

Suborder **Myopsida**

Family *LOLIGINIDAE*

Genus *Loligo* Lamarck, 1798
Loligo pealeii LeSueur, 1821
Loligo opalescens Berry, 1911

Suborder **Oegopsida**

Family *HISTIOTEUTHIDAE*

Genus *Histioteuthis* Orbigny, 1839
Histioteuthis reversa (Verrill, 1880)
Histioteuthis bonellii (Férussac, 1835)
Histioteuthis elongata (Voss and Voss, 1962)
Histioteuthis dofleini (Pfeffer, 1912)

Family *CRANCHIIDAE*

Subfamily CRANCHIINAE

Genus *Pyrgopsis* Rochebrune, 1884
Pyrgopsis lemur Berry, 1920

Subfamily TAONIINAE

Genus *Taonius* Steenstrup, 1861
Taonius pavo (LeSueur, 1821)

Genus *Megalocranchia* Pfeffer, 1884
Megalocranchia megalops (Prosch, 1849)

Genus *Galiteuthis* Joubin, 1898
Galiteuthis armata Joubin, 1898 *

Family *CHIROTEUTHIDAE*

Genus *Chiroteuthis* d'Orbigny, 1839
Chiroteuthis lacertosa Verrill, 1881
Chiroteuthis sp.

Family *MASTIGOTEUTHIDAE*

Genus *Mastigoteuthis* Verrill, 1881
Mastigoteuthis agassizii Verrill, 1881
Mastigoteuthis grimaldii (Joubin, 1895) *
Mastigoteuthis cordiformis Chun, 1908 *

Family *ENOPLOTEUTHIDAE*

Subfamily ENOPLOTEUTHINAE

Genus *Pyroteuthis* Hoyle, 1904
Pyroteuthis margaritifera (Rüppell, 1844)

Genus *Thelidoteuthis* Pfeffer, 1900
Thelidoteuthis alessandrini (Vérany, 1851)

Family *ARCHITEUTHIDAE*

Genus *Architeuthis* Steenstrup, 1857
Architeuthis dux Steenstrup, 1857

Family *OCTOPOTEUTHIDAE*

Genus *Octopoteuthis* Rüppell, 1884
Octopoteuthis sicula Rüppell, 1844

Genus *Taningia* Joubin, 1931
Taningia danae Joubin, 1931

Family *OMMASTREPHIDAE*

Subfamily OMMASTREPHINAE

Genus *Ommastrephes* d'Orbigny, 1839
Ommastrephes bartrami (LeSueur, 1821)
Ommastrephes pteropus Steenstrup, 1856 *

Subfamily TODARODINAE

Genus *Todarodes* Steenstrup, 1880
Todarodes pacificus Steenstrup, 1880

Subfamily ILLICINAE

Genus *Illex* Steenstrup, 1880
Illex illecebrosus (LeSueur, 1821)

Family *GONATIDAE*

Genus *Gonatus* Gray, 1849
Gonatus fabricii Lichtenstein, 1818
Gonatus magister Berry, 1913
Gonatus anonychus Pearcy and Voss, 1963

Genus *Gonatopsis* Sasaki, 1920
Gonatopsis borealis Sasaki, 1923

Family *BRACHIOTEUTHIDAE*

Genus *Brachioteuthis* Verrill, 1881
Brachioteuthis beani Verrill, 1881
Brachioteuthis riisei (Steenstrup, 1882) *

Family *ONYCHOTEUTHIDAE*

Genus *Onychoteuthis* Lichtenstein, 1818
Onychoteuthis banksi Leach, 1817

Genus *Moroteuthis* Verrill, 1881
Moroteuthis robusta Dall MS (Verrill, 1876)

Order OCTOPODA

Suborder **Cirrata**

Family *STAUROTEUTHIDAE*

Genus *Stauroteuthis* Verrill, 1879
Stauroteuthis syrtensis Verrill, 1879

Family *OPISTHOTEUTHIDAE*

Genus *Opisthoteuthis* Verrill, 1883
Opisthoteuthis californiana Berry, 1949

Genus *Grimpoteuthis* Robson, 1932 (= *Opisthoteuthis*?)
Grimpoteuthis sp.

Suborder **Incirrata**

Family *BOLITAENIDAE*

Genus *Japetella* Hoyle, 1885
Japetella heathi (Berry, 1911)

Family *ALLOPOSIDAE*

Genus *Alloposus* Verrill, 1880
Alloposus mollis Verrill, 1880

Family *OCTOPODIDAE*

Subfamily OCTOPODINAE

Genus *Octopus* Lamarck, 1798
Octopus leioderma Berry, 1911
Octopus dofleini (Wülker, 1910)

Subfamily BATHYPOLYPODINAE

Genus *Bathypolypus* Grimpe, 1921
Bathypolypus arcticus (Prosch, 1849)

Genus *Benthoctopus* Grimpe, 1921
Benthoctopus piscatorum (Verrill, 1879)

Genus *Graneledone* Joubin, 1918
Graneledone verrucosa (Verrill, 1881)

ACKNOWLEDGEMENTS

I am indebted to the scientific and technical staff of the Fisheries Research Board of Canada, St. John's Biological Station, for the collection of the bulk of the material from the Canadian Atlantic. Dr. H. J. Squires, Head of the Division of Invertebrates and Dr. W. Templeman, Director, kindly made the material available for study.

Dr. A. H. Clarke, Curator of Molluscs, National Museum of Canada, loaned the entire Arctic and eastern Canadian cephalopod collections from his institution.

Dr. D. B. Quayle loaned the cephalopod collections of the Fisheries Research Board Nanaimo Biological Station.

For the loan of various other material I wish to thank Dr. Gilbert L. Voss, Chairman of Biological Sciences, Institute of Marine Sciences, University of Miami, Dr. Kenneth J. Boss, Assistant Curator of Molluscs, Museum of Comparative Zoology, Harvard University, Dr. Clyde F. E. Roper, Associate Curator of Molluscs, United States National Museum, Dr. Norman Tebble, Curator of

Molluscs, British Museum (Natural History), Dr. Donald H. Steele, Assistant Professor, Department of Biology, Memorial University of Newfoundland.

Dr. Roper has critically read the manuscript and offered many helpful suggestions.

LITERATURE CITED

ADAM, W. 1952. Céphalopodes. Résultats scientifiques. Expédition océanographique Belge dans les eaux côtières africaines de l'Atlantique Sud. *Rés. sci. expéd. océanogr. Belg.*, 3 (3): 1–142.

AKIMUSHKIN, I. I. 1963. Golovonogie mollyuski morei SSSR Izdatel'stvo Akademii Nauk SSSR. Moskva, 1963. (Cephalopods of the Seas of the U.S.S.R. Israel Program for Scientific Translations. 223 p. Jerusalem, 1965).

BERG, L. S. 1933. Die bipolare Verbreitung der Organismen und die Eiszeit. *Zoogeographica*, **1**: 444–484.

BERRY, S. STILLMAN 1912. A review of the cephalopods of western North America. *U.S. Fish. Doc.* No. 761, pp. 269–336, 18 figs., 25 pls. (reprinted from *Bull. U.S. Bur. Fish.*, **30**: 1910).

——— 1925. The Cephalopoda collected by the Canadian Arctic Expedition, 1913–18. *Rept. Can. Arctic Exped.*, 1913–18, **8** (**B**): 3–8.

BRUUN, ANTON FR. 1943. The biology of *Spirula spirula* (L.). *Dana Rept.*, **24**: 1–44, 2 pls.

CLARKE, MALCOLM, R. 1967. A review of the systematics and ecology of oceanic squids. *Adv. Mar. Biol.*, **4**: 91–300.

DODIMEAD, A. J. 1961. Some features of the upper zone of the sub-Arctic Pacific Ocean. *INPFC Bull.*, **3**: 11–24

DOE, L. A. E. 1955. Offshore waters of the Canadian Pacific coast. *J. Fish. Res. Bd. Canada*, **12** (1): 1–34.

DUNBAR, M. J. 1951. Eastern Arctic waters. *Bull. Fish. Res. Bd. Canada*, **88**: 1-131.

EKMAN, SVEN 1953. *Zoogeography of the Sea.* Sidgwick and Jackson Ltd., London, 417 pp.

FLEMING, RICHARD, H. 1955. Review of the oceanography of the northern Pacific. *INPFC Bull.*, **2**: 1–43.

GRIEG, J. A. 1896. Bidrag til kundskaben om Vestlandets mollusker. *Bergens Museums Aarbog*, **10**: 1–33.

GRIMPE, G. 1916. *Chunioteuthis*—eine neue Cephalopodengattung. *Zool. Anz., Leipzig*, **46**: 349–359.

——— 1933. Die Cephalopoden des arktischen Gebietes. *Fauna Arctica*, **6**: 489–514.

GRÖNDAL, B. 1891. Skýrsla um hió islenzka náttúrufraeóisfélag, félagsárió 1890–1891. Rvik.

HACHEY, H. B. 1961. Oceanography and Canadian Atlantic waters. *Bull. Fish. Res. Bd. Canada*, **134**: 1-120.

HEDGPETH, JOEL W. 1957. Classification of marine environments. *Geol. Soc. America Mem.* 67. *Treatise on Marine Ecology and Paleoecology*, **1**: 17–27.

HUBBS, C. L. 1952. Antitropical distribution of fishes and other organisms. *Proc. 7th Pac. Sci. Congr.*, **3**: 324–329.

KEEN, A. M. 1940. Molluskan species common to western North America and Japan. *Proc. 6th Pac. Sci. Congr.*, **3**: 479–483.

LOVÉN, S. 1846. Malacologiska notiser. Nagra anmärkningar öfver de Skandinaviska Hafs-Molluskernas geografiska utbredning. Övers. K. Svenska Vet.-Akad. Förhandl., Stockholm.

MACGINITIE, G. E. 1955. Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. *Smithsonian Misc. Coll.*, **128** (9): 1-201.

MERCER, M. C. 1965. Contribution to the biology of the short-finned squid, *Illex illecebrosus illecebrosus* (LeSueur), in the Newfoundland area. *Fish. Res. Bd. Canada Manuscr. Rept. (Biol.)*, **834**: 1-36.

——— 1966. First record of *Pyrgopsis lemur* (Cephalopoda: Cranchiidae) from the North-west Atlantic. *J. Fish. Res. Bd. Canada*, **23** (8): 1257–1258, 1 fig.

——— 1968. Systematics and biology of the sepiolid squids of the genus *Rossia* Owen, 1835 in Canadian waters with a preliminary review of the genus. *Mem. Univ. Nfld.* M.Sc. thesis, 96 pp.

MÖRCH, O. A. L. 1857. Fortegnelse over Groenlands Bloeddyr (Mollusca Groenlandica), Naturh. Tillaeg til en Faunistisk og Statistisk beskrivelse af Greenland (H. Rink), 75–100, Kjöbenhavn.

MUUS, BENT J. 1962. Cephalopoda. The Godthaab Expedition 1928. *Medd. om Grønland*, **81** (5): 1–23.

——— 1963 *a*. Cephalopoda, Sub-Order: Sepioidea. *Cons. Perm. Explor. Mer. Fisches d'Identif du Zooplankton*, **94**: 1–5.

——— 1963 *b*. Cephalopoda, Sub-Order: Teuthoidea, Family: Loliginidae. *Ibid.*, **95**: 1–3.

——— 1963 *c*. Cephalopoda, Sub-Order: Teuthoidea, Families: Ommastrephidae, Chiroteuthidae, Cranchiidae. *Ibid.*, **96**: 1–6.

——— 1963 *d*. Cephalopoda, Sub-Order Teuthoidea, Families: Octopoteuthidae, Gonatidae, Onychoteuthidae, Histioteuthidae, Brachioteuthidae. *Ibid.*, **97**: 1–5.

——— 1963 *e*. Cephalopoda, Order Octopoda. *Ibid.*, **98**: 1–3.

NESIS, K. N. 1962. Pacific elements in north-west Atlantic benthos., Soviet Fisheries Investigations in the North-West Atlantic. Israel Program for Sci. Trans., Jerusalem, 1963, 82–99.

——— 1965. The distribution and nutrition of the young of the squid *Gonatus fabricii* (Licht.) in the N.-W. Atlantic and the Norwegian Sea. *Okeanologiya*, **5**: 134–141 (In Russian).

OKADA, Y. K. 1927. Contribution à l'Étude des Céphalopodes luminieux (Notes préliminaries). *Bull. l'Inst. Océanogr.*, **494**: 1–7.

PEARCY, WILLIAM G. 1965. Species composition and distribution of pelagic cephalopods from the Pacific Ocean off Oregon. *Pac. Sci.*, **19** (2): 261–266.

PEREYRA, WALTER T. 1965. New records and observations on the flapjack devilfish, *Opisthoteuthis californiana* Berry. *Pac. Sci.*, **19** (4): 427–441.

PICKFORD, GRACE E. 1964. *Octopus dofleini* (Wülker). *Bull. Bingham Oceanogr. Coll.*, **19** (1): 1-70.

PIKE, GORDON C. 1950. Stomach contents of whales caught off the coast of British Columbia. *Prog. Rept. Fish. Res. Bd. Canada*, **83**: 27–28.

POSSELT, H. J. 1898. Grønlands Brachiopoder og Bløddyr. *Medd. om Grønland*, **23**: 1–298.

PRÉFONTAINE, GEORGES 1930. Notes sur *Globicephala melaena* (Traill). *Rapt. Ann. Soc. Prov.*, 49–66.

REES, W. J. AND G. E. MAUL 1956. The Cephalopoda of Madeira. *Bull. Mus. (Nat. Hist.)*, **3**: 257–281.

ROBBINS, LEWIS L., FRANCES K. OLDHAM AND E. M. K. GEILING 1937. The stomach contents of sperm whales caught off the west coast of British Columbia. *Rept. B.C. Mus.*, 19–20, 1 pl.

ROBSON, G. C. 1932. A monograph of the recent Cephalopoda. Part II. The Octopoda (excluding the Octopodinae). 359 p.

SCHENK, H. G. AND M. KEEN 1936. Marine molluscan provinces of western North America. *Proc. Amer. Philosoph. Soc.*, **76** (6): 921–938.

SQUIRES, H. J. 1957. Squid, *Illex illecebrosus* (LeSueur), in the Newfoundland fishing area. *J. Fish. Res. Bd. Canada*, **14** (5): 693–729.

THORE, S. 1949. Investigations of the "Dana" Octopoda: Part I—Bolitaenidae, Amphitretidae, Vitreledonellidae and Alloposidae. *Dana Rept.*, **33**: 1–85.

UDA, MICHITAKA 1963. Oceanography of the subarctic Pacific Ocean. *J. Fish. Res. Bd. Canada*, **20** (1): 119–179.

VERRILL, A. E. 1879–1881. The cephalopods of the Northeastern coast of America. *Trans. Conn. Acad. Sci.*, **5**: 187–446, 56 pls.

VOSS, N. Revision of the Histioteuthidae (in press).

DISCUSSION

Dr. A. M. Bidder: How does temperature limit the distribution?

Mr. M. C. Mercer: The boreal species invade the northern parts of their distribution during the summer months only when the surface temperatures range upwards to 6°–8° C. They do not breed here. We do not have good data on distribution in relation to temperature for most oceanic species, however, partly because of difficulty in determining in what depth they were captured. For the benthic species, we have good data on distribution in relation to temperature, as I have given here for *Rossia.*

Dr. A. M. Bidder: What are the dominant elements in the cephalopod fauna?

Mr. M. C. Mercer: *Illex* is by far the most abundant species occurring near shore in the North-West Atlantic. The Arctic squid, *Gonatus fabricii,* is also quite abundant in the Labrador Sea. However, since most of sampling has been by otter trawl, we have no good data on comparative abundance of other oegopsids.

CEPHALOPODA OF THE WEST COAST OF INDIA COLLECTED DURING THE CRUISES OF THE RESEARCH VESSEL *VARUNA*, WITH A CATALOGUE OF THE SPECIES KNOWN FROM THE INDIAN OCEAN*

E. G. SILAS‡

Central Marine Fisheries Research Institute, Mandapam Camp, India

ABSTRACT

A comprehensive treatise on the Cephalopoda of the Indian Seas is wanting. The only noteworthy works with specific reference to this area are those by Goodrich (1896: *Trans. Linn. Soc. London*, 7, 1-24), Massy (1916: *Rec. Indian Mus.*, 12: 185-248), and Adam (1939, *Ibid.*, 41: 61-110), based on collections in the Indian Museum. Little attention has been paid to the study of the biology and fishery of Indian cephalopods. The only detailed account we have is the one on *Sepioteuthis arctipinnis* Gould reported on by Rao (1954: *Indian J. Fish.*, 1: 37-66). Other sources of information are stray records or accounts in expedition reports. In the light of these it is evident that there is need for more information on the Cephalopoda of the Indian Seas.

The present account deals with the dibranchiate cephalopods (Decapoda, Vampyromorpha and Octopoda) collected by the author during the research cruises of the Indo-Norwegian Project Research Vessel *VARUNA* from off the west coast of India and the Laccadive Sea. Samples were obtained in the course of the operation of different fishing gears and plankton nets as follows: Over 215 otter trawl collections made from different parts of the continental shelf and the continental slope to a maximum depth of 380 metres; 101 mid-water trawl collections made with the Isaacs-Kidd mid-water trawl from depths between 20 and 350 metres from the south-west coast of India and the Laccadive Sea; 92 drift net collections made in the same area; about 2,363 plankton samples from 0–200 m. and 38 deep-water plankton collections made with the Indian Ocean Standard net from depths from 250 to 1,300 metres. In addition, at night, collections of oceanic squids (Ommastrephidae) were made by dip-netting also using a night light at the side of the ship. Stomach inclusions of some of the pelagic fishes, especially tunas obtained in drift nets, were also examined for cephalopod remains.

The families chiefly dealt with in this account are Ommastrephidae, Sepiolidae, Sepiidae, Loliginidae, Enoploteuthidae, Cranchiidae, Chiroteuthidae, Bolitaenidae and Octopodidae. In addition, to facilitate reference, a list of the Cephalopoda known to occur in the Indian Ocean is included.

INTRODUCTION

A COMPREHENSIVE treatise on the Cephalopoda of the Indian Seas is wanting. The only noteworthy works with reference to this area are those by Goodrich (1896), Massy (1916), and Adam (1938, 1939 *b*). The Cephalopoda around Ceylon was reported on by Winckworth (1926, 1936). Hoyle (1906), and Robson (1921) studied the material from the Laccadive and Maldive Archipelagos.

Noteworthy works on Cephalopoda from other parts of the Indian Ocean are those by Chun (1910, 1914, 1915), Adam (1939 *a*, 1939 *c*, 1954, 1960), Wulker (1920), Massy (1927), Robson (1924 *a*, 1924 *b*, 1929, 1932), Thore (1949), and Adam and Rees (1966). Several important works on the Cephalopoda of the Pacific and Atlantic Oceans also deal with Indian Ocean species and in this connection special mention should be made of the works of Pfeffer (1912), Berry (1912), Sasaki (1929), Hoyle (1886), Verrill (1881, 1882), Pickford (1946, 1949), Roper (1966), and Voss (1956, 1963),

---

* Published with the permission of the Director, Central Marine Fisheries Research Institute, Mandapam Camp.

‡ Present address: C.M.F.R. Substation, Gopala Prabhu Cross Road, Ernakulam, Cochin-11, Kerala.

The classification adopted here is that given by Thiele (1935) with slight modifications as given by Voss (1956, 1963). A list of the nominal species of Cephalopoda, both valid species and synonyms so far recorded or described from the Indian Ocean is given in the second part of this paper to facilitate reference.

MATERIAL

Since January 1962, R. V. *VARUNA* has been carrying out hydrographic work as well as exploratory fishing off the west coast of India and the Laccadive Sea, with a few cruises undertaken as far south as the Equator and in the Bay of Bengal. A total of 2,363 plankton samples (including 138 duplicate hauls) collected during the first 75 cruises of R. V. *VARUNA* were examined for Cephalopoda. Most of the samples are from vertical tows made with the Indian Ocean Standard Net from 200 metres to surface or from 5 metres above bottom (in the continental shelf area) to surface. In addition to these, 45 horizontal surface tows made with the same net for 15 minutes

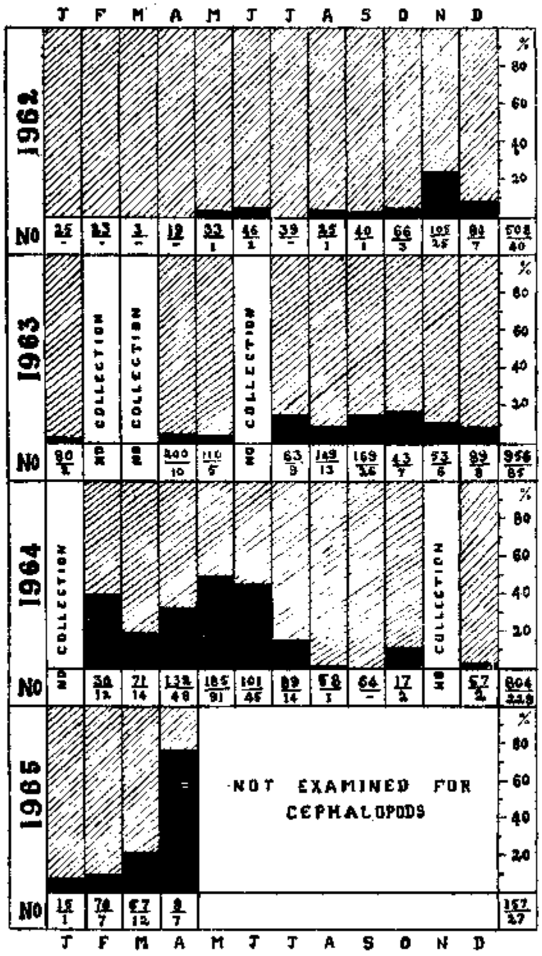


FIG. 1. Percentage of R. V. *VARUNA* plankton tows (vertical upto 200 m to 0 m) with cephalopods in relation to the total number of tows taken during each month for the period January 1962 to April 1965.

duration between 20·00 and 22·00 hours and 38 deep-water open tows from depths upto 1,300 metres were also examined for Cephalopoda. Besides these, cephalopods from 101 Isaacs Kidd Mid-water Trawl collections from various depths from surface to 350 metres taken in the same area also studied. The exploratory fishing were programme of R. V. *VARUNA* included otter trawling from shallow neritic waters to a depth of about 400 metres off the edge of the continental drift-netting from both neritic and oceanic waters. Cephalopods were obtained during fishing shelf and special study was made of the material obtained in drift nets.

CEPHALOPODA OF R. V. *VARUNA* PLANKTON COLLECTIONS

Of a total of 2,363 plankton samples examined for Cephalopoda, 383 (16·21%) (Fig. 1) were found to contain mostly larvae and juveniles of species of the families Sepiidae, Loliginidae, Enoploteuthidae, Histioteuthidae, Bathyteuthidae, Ommastrephidae, Chiroteuthidae, Cranchiidae, Bolitaenidae, Octopodidae and Argonautidae. The species most abundant in the collections are:

Abralia andamanica Goodrich

Abraliopsis gilchristi (Robson)

Thelidioteuthis alessandrinii (Verany)

Bathyteuthis abyssicola Hoyle

Calliteuthis reversa Verrill

Symplectoteuthis oualaniensis (Lesson) (*Rhynchoteuthis* 'Stage')

Larval 'Doratopsis Stage' of *Chiroteuthis* sp.

Liocranchia valdivia Chun

Liocranchia reinhardti (Steenstrup)

Japetella diaphana Hoyle

Larvae of Octopodidae (Several species)

?*Argonauta hians* Solander

Larvae of Sepiidae and Loliginidae (In neritic collections)

The distribution and abundance of Cephalopoda in the net plankton based on Indian Ocean Standard Net collections have been studied. The estimated abundance of cephalopods (all species in the plankton) in 1000^3 metres of water strained is shown for the years 1963 and 1964 in the accompanying Figs. 2 and 3. The quantitative distributions have been shown by contouring the standard contour intervals based on a logarithmic scale to the base 10. Greater abundance is noticeable in the continental shelf, especially off Cochin and in the Wadge Bank area off Cape Comorin during the year 1963. During the same year, cephalopods were very scarce in the neritic collections north of Cochin except off Mangalore. As in 1963, the area immediately south of Quilon was found to be poor in cephalopod larvae in 1964. Greater abundance was noticed in the Wadge Bank and between Quilon and Mangalore, the bulk of the material composed of larvae of Octopodidae, Sepidae, Loliginidae and Enoploteuthidae.

The relative abundance of cephalopods in the day hauls and night hauls both in the neritic (shelf area) and oceanic areas is shown in Table I. It will be noted that the number of specimens taken in night hauls in the neritic and oceanic areas is more or less the same (210 *versus* 211 in 98 and 99 hauls with cephalopods respectively). However, day hauls indicate that a slightly greater number of specimens were captured in the neritic than in the oceanic area (217 *versus* 171 respectively).

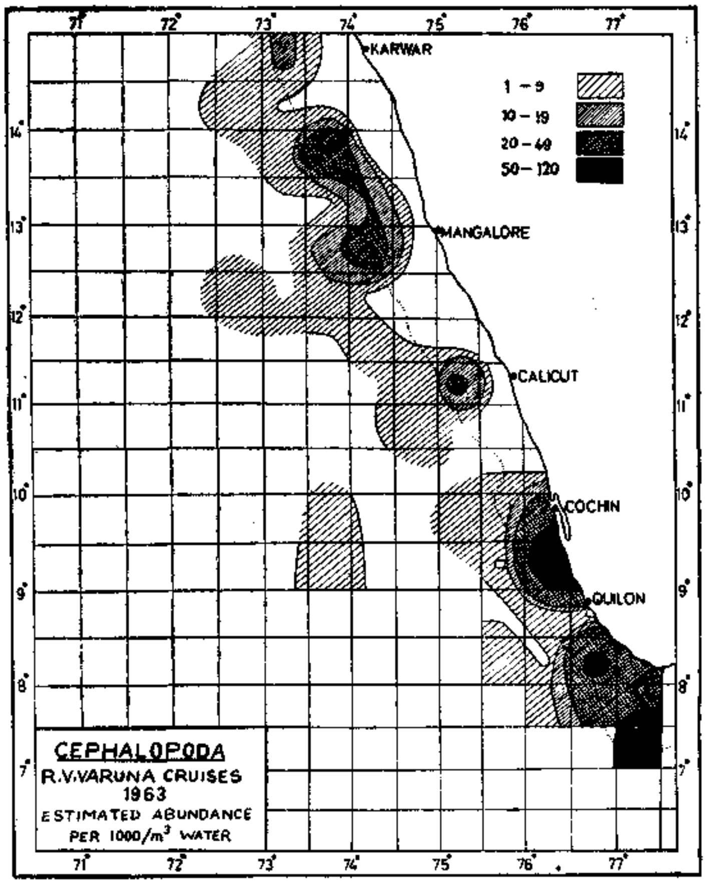


FIG. 2. Estimated abundance of cephalopods in the r 1963.

No closing device was used for the Indian Ocean Standard Net and as such it would be rather difficult to comment on the vertical distribution of the pelagic species, some of which are also known to be mesopelagic and bathypelagic. However, a depth-wise analysis is given (Table II) which may give some idea of the distributional patterns in the neritic area. For instance, there were more samples with cephalopods in hauls taken from 50–0 m. onwards to 100–0 m, while fewer hauls from 10–0 m onwards to 40–0 m contained cephalopods. The reasons for this apparent abundance in the 55 m to 105 m depth zone are not quite clear.

In Tables III to IX, the tows containing cephalopods during each month and the total number of specimens caught are shown for the period January 1962 to May 1965. In Fig. 4, the combined frequency of occurrence of the different species of cephalopods in the net plankton is indicated. From these, the following are evident:

1. The maximum number of cephalopods were taken during the months April to July and in the months November and December.
2. The larvae of *Abralia andamanica* were taken in greater numbers than other species.

3. Larvae of *A. andamanica* were more common in the months June–July (especially in 1964) when compared to *Abraliopsis gilchristi* the largest number of which were taken in the month of May (especially in 1964).

4. *Abraliopsis gilchristi* evinces a more oceanic distribution when compared to *Abralia andamanica* which was well represented in the continental shelf area.

5. Most of the ommastrephid larvae (*Rhynchoteuthis*-type) have been identified as belonging to the species *Symplectoteuthis oualaniensis*. They were more abundant in the months March–April and November-December. Some stages in development are illustrated in Fig. 5.

6. Larvae of Octopoda (all species) were present more abundantly in the months April–May, and they were more frequently taken in the neritic waters.

7. Larval 'Doratopsis stage' of *Chiroteuthis* spp., larvae of Cranchiidae and larvae of *Japetella diaphana* also occurred more frequently in the months April–May and November-December.

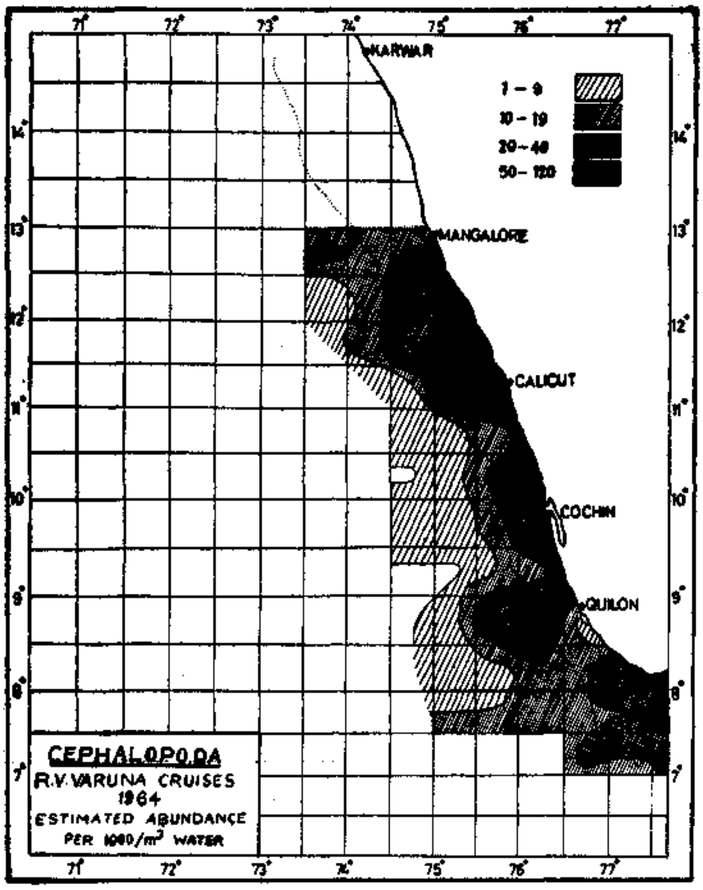


FIG. 3. Estimated abundance of cephalopods in the plankton for the year 1964.

TABLE I

Frequency of occurrence of cephalopods in R. V. VARUNA *plankton collections from the neritic and oceanic areas off the west coast of India and the Laccadive Sea (January* 1962 *to May* 1965)

Particulars	Neritic	Oceanic	Total
No. of plankton hauls	1605	758	2363
No. of samples with cephalopods	207	176	383
Percentage of samples with cephalopods	8·76	7·44	16·20
No. of day hauls with cephalopods	109	77	186
Percentage of day hauls with cephalopods in total number of samples	4·61	3·25	7·87
Percentage of day hauls with cephalopods in relation to total number of samples from neritic and oceanic areas ..	6·79	10·15	
No. of night hauls with cephalopods	98	99	197
Percentage of night hauls with cephalopods in total number of samples	4·15	4·19	8·34
Percentage of night hauls with cephalopods in relation to total number of samples from neritic and oceanic areas ..	6·11	13·06	
Total number and (per cent) of specimens caught ..	427 (52·78)	382 (47·22)	809
No. and (per cent) of specimens in day hauls (% of 388) ..	217 (55·93)	171 (44·07)	388
No. and (per cent) of specimens in night hauls (% of 421) ..	210 (49·88)	211 (50·12)	421

TABLE II

Occurrence of cephalopods in the plankton samples in relation to depth of haul

Depth (M)[1]	Total No. of samples	No. of samples with cephalopods	Percentage of hauls with cephalopods	Day hauls				Night hauls			
				No.	No. with cephalopods	% in total day hauls	No. of specimens	No.	No. with cephalopods	% in total night hauls	No. of specimens
10–0	108	3	2·77	..	..	..	..	58	3	5·17	4
20–0	151	3	1·98	78	2	2·56	2	73	1	1·36	1
30–0	246	19	7·72	124	9	7·25	13	122	10	8·19	10
40–0	183	15	8·19	98	4	4·08	6	85	11	12·94	24
50–0	265	41	15·47	136	21	15·44	33	129	20	15·50	36
60–0	103	17	16·50	61	12	19·67	27	42	5	11·90	14
70–0	58	9	15·51	30	3	10·00	6	28	6	21·42	8
80–0	151	19	12·58	100	15	15·00	35	51	4	7·84	8
90–0	35	9	25·71	13	6	46·15	27	22	3	13·63	3
100–0	107	10	9·34	56	7	12·50	11	51	3	5·88	6
110–0	8	2	25·00	3	1	33·33	1	5	1	20·00	2
120–0	5	..	..	1	..	..	..	4	..	..	..
130–0	5	2	25·00	2	1	50·00	2	3	1	33·33	D*
140–0	2	..	..	2	..	..	..	..	..	..	..
150–0	72	19	26·38	32	4	12·50	5	40	15	37·50	60
160–0	12	5	41·66	7	3	4·28	6	5	2	40·00	3
170–0	17	8	47·05	14	5	35·71	12	3	3	100·00	6
180–0	47	12	25·53	26	7	26·92	12	21	5	23·80	5
190–0	30	14	46·66	20	9	45·00	19	10	5	50·00	20
Total for shelf area	1,605	207	12·90	803	109	13·57	217	752	98	13·03	210
Oceanic 200–0	758	176	23·21	369	77	20·86	171	389	99	25·44	211
TOTAL ..	2,363	383	16·21	1,172	186	15·87	388	1,141	197	17·26	421

[1] All hauls between 11 and 20 metres have been included in the 20–0 m group, and so on.

* Damaged bits of specimens and hence number not indicated.

TABLE III

Occurrence of larvae of Abraliopsis gilchristi *in the IOS Net collections made during the cruises of R. V.* VARUNA *off the west coast of India and the Laccadive Sea (January* 1962 *to May* 1965)*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1962	—	—	—	—	—	—	—	—	—	—	2 (2)	1 (1)
1963	—	—	—	1 (1)	1 (1)	—	—	—	—	—	1 (1)	1 (1)
1964	—	—	1 (1)	4 (4)	16 (27)	—	1 (1)	—	—	—	—	—
1965	—	—	—	—	—							
Combined frequency	—	—	1 (1)	5 (5)	17 (28)	—	1 (1)	—	—	—	3 (3)	2 (2)

* In Tables III to IX the number of positive hauls during each month is indicated followed by the total number of specimens. The area and the period of observations (1962 to May 1965) are the same for the species and larval types given in these tables and hence are not repeated in the titles.

TABLE IV

Occurrence of larvae of Abralia andamanica *in the IOS Net collections*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1962	—	—	—	—	—	—	—	—	—	—	2 (3)	2 (3)
1963	—	—	—	3 (3)	—	—	8 (56)	1 (1)	—	—	2 (7)	1 (1)
1964	—	1 (1)	6 (6)	8 (9)	18 (42)	26 (91)	9 (14)	—	—	—	—	1 (3)
1965	—	1 (1)	1 (1)	—	—							
Combined frequency	—	2 (2)	7 (7)	11 (12)	18 (42)	26 (91)	17 (70)	1 (1)	—	—	4 (10)	4 (6)

TABLE V

Occurrence of larvae of Ommastrephidae (Rhynchoteuthis *larvae*) *in the IOS Net collections*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1962	—	—	—	—	—	—	—	—	—	1 (1)	9 (15)	8 (18)
1963	1 (2)	—	—	3 (4)	—	—	1(1)	—	1 (1)	2 (2)	—	9 (15)
1964	—	5 (7)	11 (17)	11 (13)	17 (28)	—	—	—	1 (1)	—	—	—
1965	—	—	4 (5)	—	—							
Combined frequency	1 (2)	5 (7)	15 (22)	14 (17)	17 (28)	—	1 (1)	—	2 (2)	3 (3)	9 (15)	17 (33)

TABLE VI

Occurrence of larval 'Doratopsis Stage' of Chiroteuthis *spp. in the IOS Net collections*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1962	—	—	—	—	—	—	—	—	—	—	—	1 (1)
1963	—	—	—	—	—	—	—	—	1 (1)	1 (2)	1 (1)	—
1964	—	—	1(1)	1 (1)	3 (3)	1 (1)	1 (1)	—	—	—	—	—
1965	—	—	1 (1)	—	—							
Combined frequency	—	—	2 (2)	1 (1)	3 (3)	1 (1)	1 (1)	—	1 (1)	1 (2)	1 (1)	1 (1)

TABLE VII

Occurrence of Cranchiidae (larvae and adults) in the IOS Net collections

Year	J	F	M	A	M	J	J	A	S	O	N	D
1962	—	—	—	—	—	—	—	—	—	1 (1)	1 (1)	—
1963	—	—	—	—	—	—	1 (1)	2 (2)	—	—	1 (1)	—
1964	—	1 (1)	—	2 (3)	6 (8)	1 (1)	—	—	—	—	—	—
1965	—	2 (2)	—	—	—							
Combined frequency	—	3 (3)	—	2 (3)	6 (8)	1 (1)	1 (1)	2 (2)	—	1(1)	2 (2)	—

TABLE VIII

Occurrence of larvae of Octopoda in the IOS Net collections

Year	J	F	M	A	M	J	J	A	S	O	N	D
1962	—	—	—	—	1 (1)	—	—	—	1 (1)	—	—	2 (2)
1963	—	—	—	2 (2)	2 (2)	—	1 (1)	5 (22)	—	1 (1)	3 (4)	—
1964	—	7 (9)	3 (4)	10 (23)	27 (43)	9 (13)	1 (1)	—	1 (2)	—	1 (1)	1(1)
1965	—	1 (1)	3 (4)	—	—							
Combined frequency	—	8 (10)	6 (8)	12 (25)	30 (46)	9 (13)	2 (2)	5 (22)	2 (3)	1 (1)	4 (5)	3 (3)

TABLE IX

Occurrence of Japetella diaphana *in the IOS Net collections*

Year	J	F	M	A	M	J	J	A	S	O	N	D
1962	—	—	—	—	—	—	—	—	—	—	4 (4)	2 (2)
1963	—	—	—	2 (2)	—	—	—	—	—	—	1 (1)	1 (1)
1964	—	—	—	1 (1)	1 (1)	—	—	—	1 (1)	—	—	—
1965	—	—	—	—	—							
Combined frequency	—	—	—	3 (3)	1 (1)	—	—	—	1 (1)	—	5 (5)	3 (3)

In Figs. 6-11, the occurrence and distribution of these species in the area where R. V. *VARUNA* worked are indicated.

CEPHALOPODS TAKEN IN ISAACS KIDD MID-WATER TRAWL DURING CRUISES OF R. V. *VARUNA*

A three metre (board) Isaacs Kidd Mid-water trawl was used during cruises of R. V. *VARUNA* and 101 samples collected between 1963 and December 1967 were examined for cephalopods. Of these 68 tows (67·4%) contained cephalopods (larvae and adults). Twenty-six of these tows were made during day-time (06·00–18·00 hrs.) yielding 83 specimens, while 42 night tows contained 199 specimens. A depth-wise analysis of the tows and the number of specimens obtained are shown in Table X. As no closing device was used for the net, the hauls have been shown as from 50 metre intervals to surface.

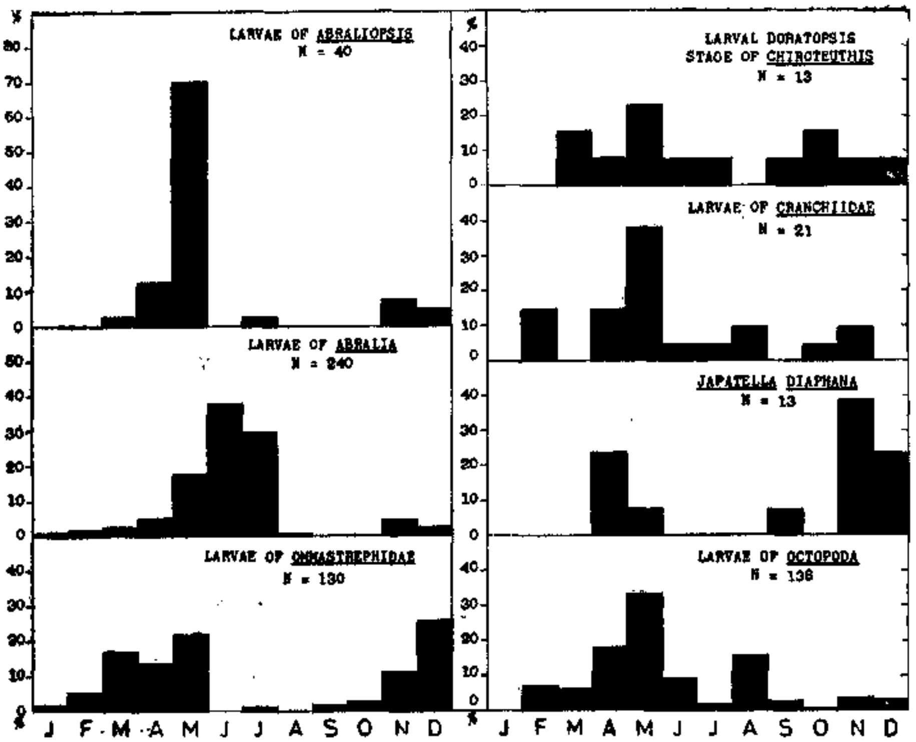


FIG. 4. Monthly occurrence and abundance of seven of the more frequently occurring cephalopod larvae in the IOS Net collections off the south-west coast of India and the Laccadive Sea (May 1962–April 1965).

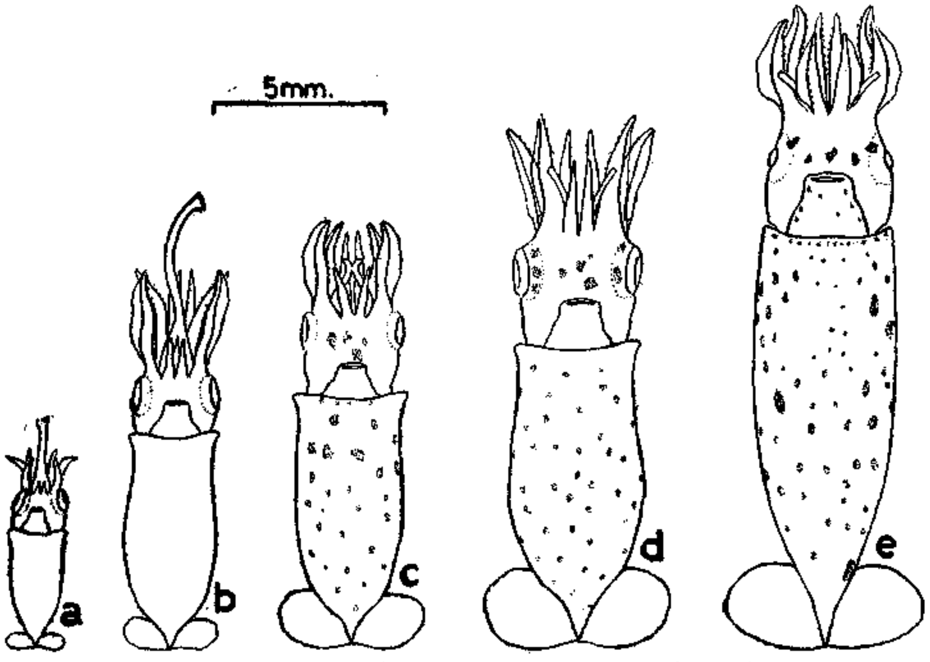


FIG. 5. "*Rhynchoteuthis* larvae" and early juveniles of *Symplectoteuthis oualaniensis* (Lesson) from R. V. *VARUNA* plankton collections.

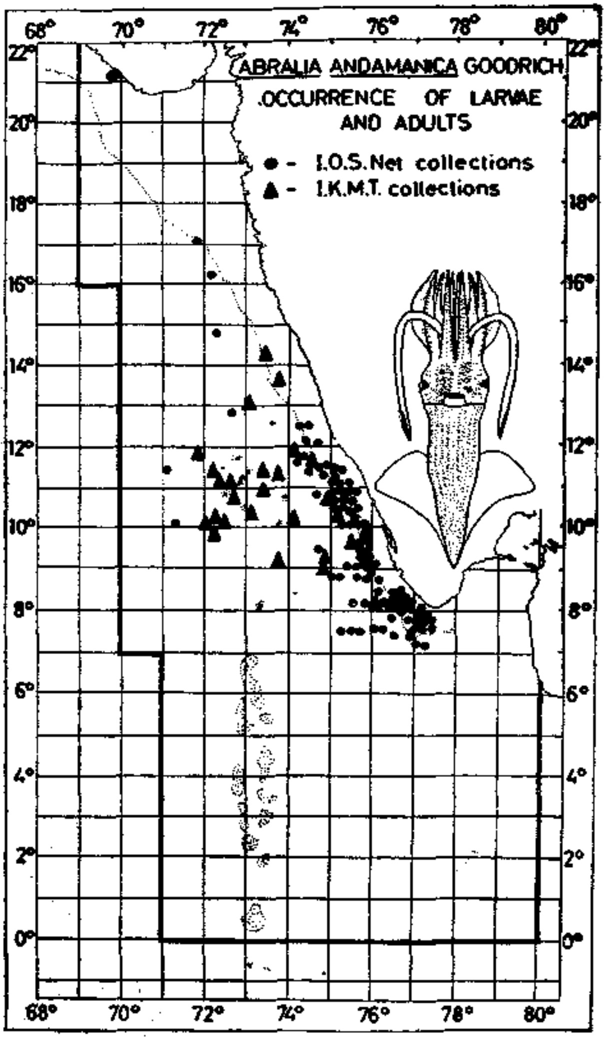


FIG. 6

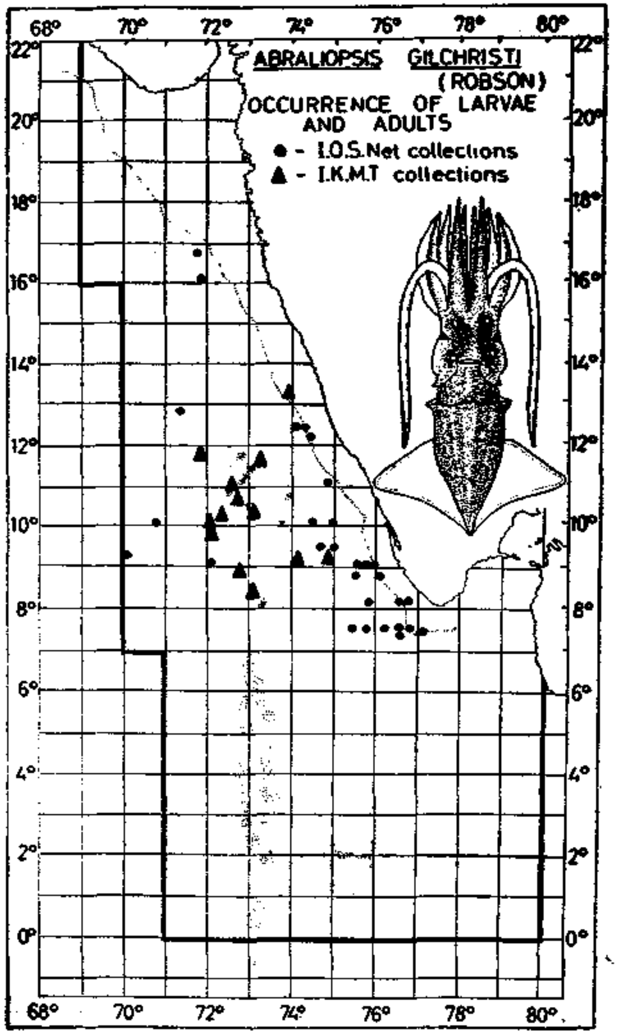


FIG. 7

FIGS. 6–7. Fig. 6. Map showing the places from where larvae and adults of *Abralia andamanica* were collected during R. V. *VARUNA* cruises. In Figs. 6–12, the dark line delimits the area covered during R. V. *VARUNA* cruises. Fig. 7. Map showing the places from where larvae and adults of *Abraliopsis gilchristi* were collected during R. V. *VARUNA* cruises.

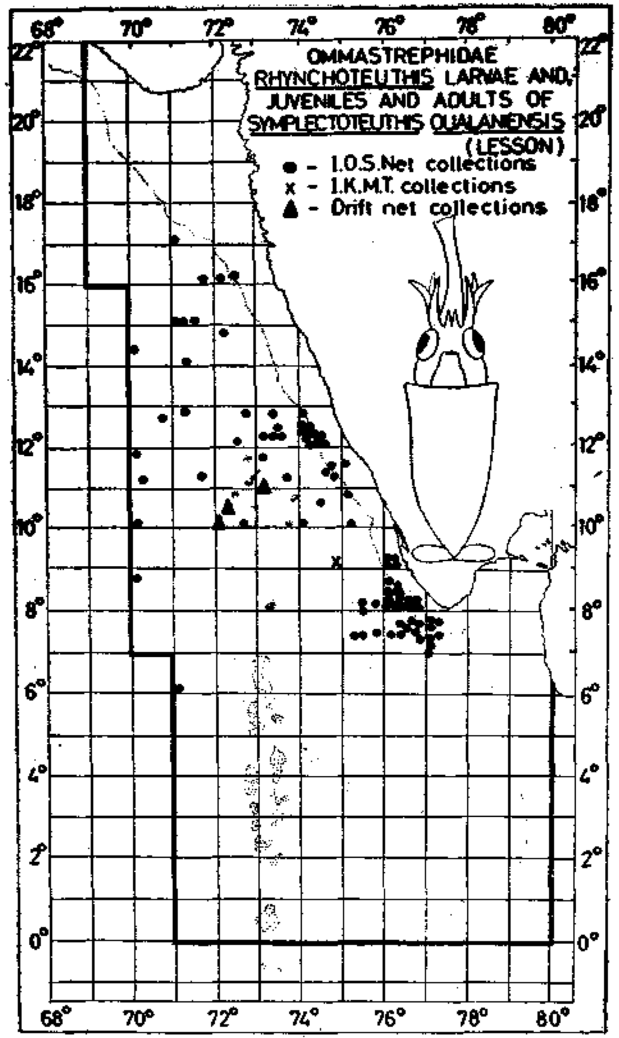


FIG. 8

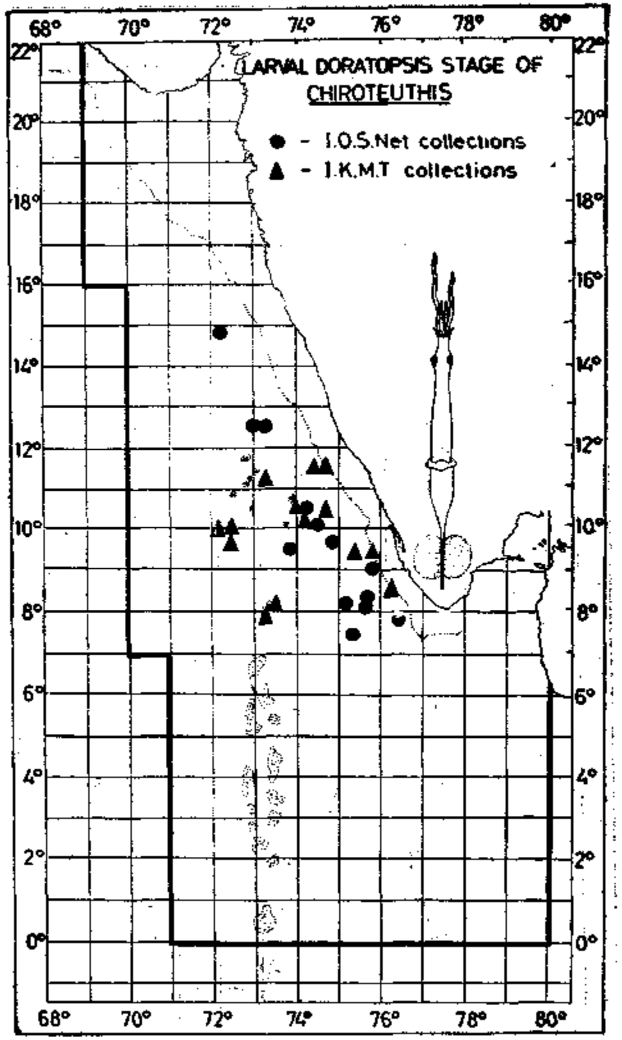


FIG. 9

FIGS. 8–9. Fig. 8. Map showing the places from where "*Rhynchoteuthis* larvae", juveniles and adults of *Symplectoteuthis oualaniensis* were collected during R. V. *VARUNA* cruises. Fig. 9. Map showing places from where larval doratopsis stage of *Chiroteuthis* spp., were collected during R.V. *VARUNA* cruises.

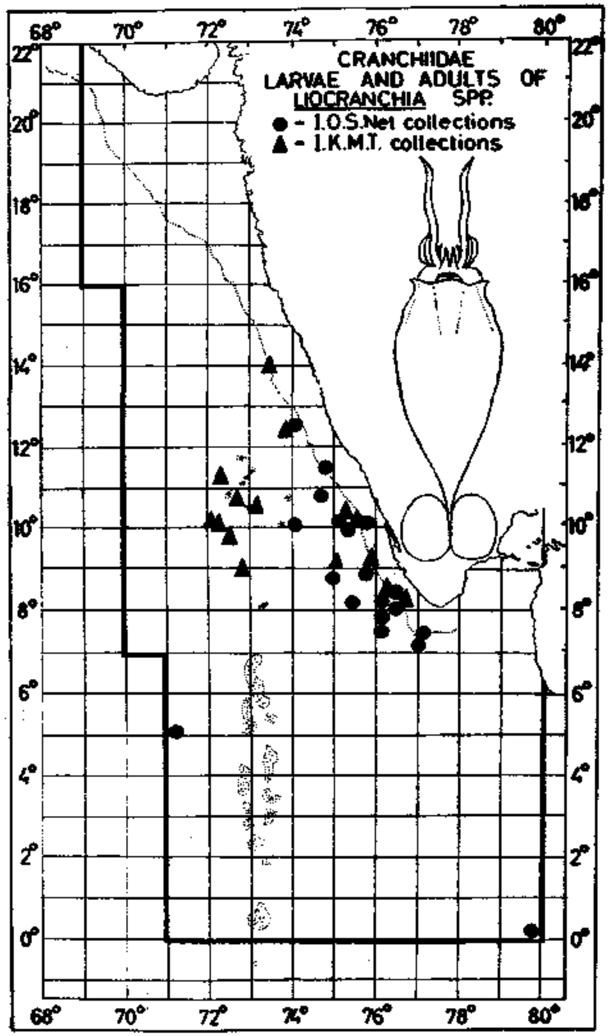


FIG. 10

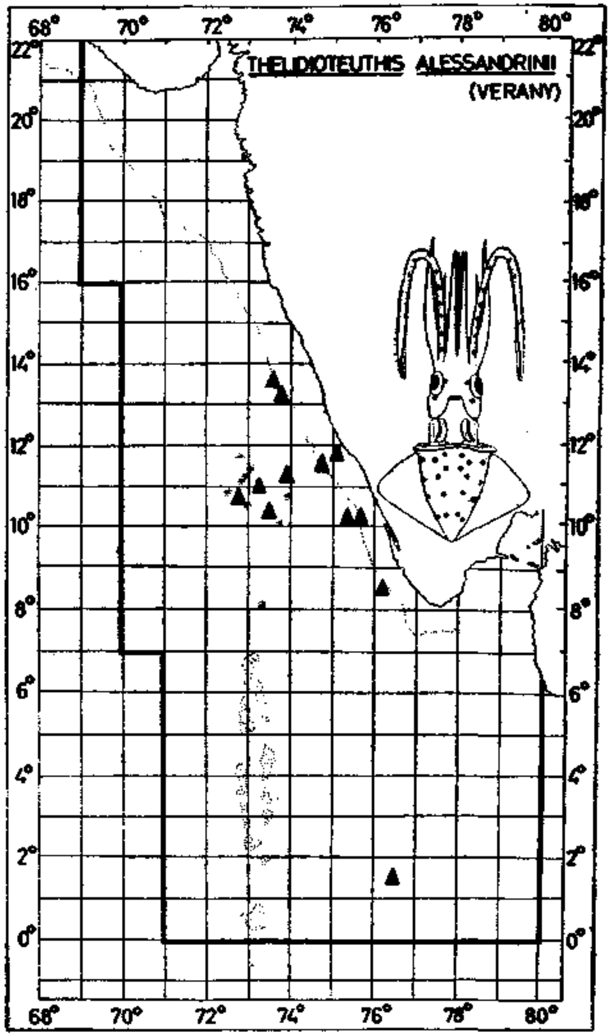


FIG. 11

FIGS. 10–11. Fig. 10. Map showing places from where larval and adult *Liocranchia* (Cranchiidae) were collected during R. V. *VARUNA* cruises. Fig. 11. Map showing places from where *Thelidioteuthis alessandrinii* larvae were collected during R. V. *VARUNA* cruises.

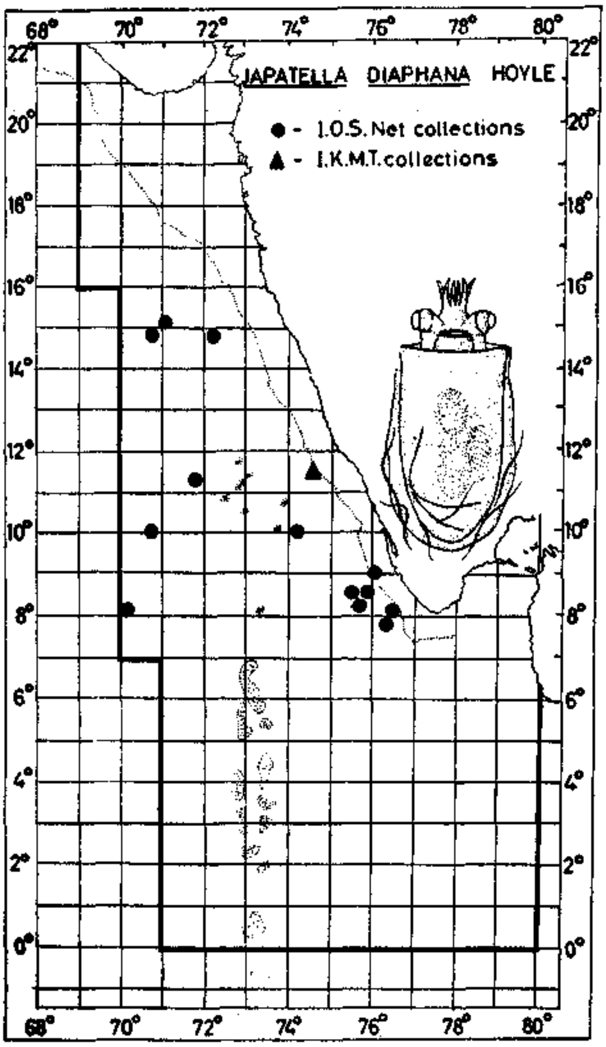


FIG. 12. Map showing places from where *Japetella diaphana* larvae were collected during R.V. ***VARUNA*** cruises.

TABLE X

Cephalopods in Isaacs Kidd Mid-water Trawl collections

Depth Range	Total No. of tows	Tows without cephalopods	Tows with cephalopods	Number of specimens
50–0 m	39	20	19	55
100–0 m	42	11	31	170
150–0 m	14	1	13	40
200–0 m	2	—	2	4
250–0 m	—	—	—	—
300–0 m	2	..	2	11
350–0 m	2	1	1	2
TOTAL ..	101	33	68	282

Besides the species obtained in the IOS Net, one interesting addition is a third representative of the family Enoploteuthidae, namely, *Thelidioteuthis alessandrinii* (Verany). This species is represented by a number of juveniles and three adults in the collections. The distribution of this species is shown in Fig. 11.

CEPHALOPODS IN IOS NET SURFACE TOWS

In some of the surface tows taken with the IOS Net generally between 20·00 and 22·00 hours during R. V. *VARUNA* cruises larvae of *Symplectoteuthis oualaniensis* are well represented, a single haul at Stn. 3365 containing as many as 38 larvae. On the other hand larvae of *Abralia* and *Abraliopsis* which were more frequently seen in vertical tows were relatively scarce.

As will be seen from Table XI, more cephalopod larvae occurred in surface tows taken during February.

TABLE XI

Cephalopods in IOS Net surface tows

Year	Month		Total No. of tows	No. of tows with cephalopods	No. of specimens
1966	February	..	21	12	154
	December		10	1	4
1967	February	..	13	8	35
	March	..	4	2	2
	April	..	3	1	8
	June	..	3	1	1
	September	..	4	2	3
	October	..	3	—	—
	November		5	—	—
	December	..	3	1	1
	TOTAL	..	69	32	208

CEPHALOPODS IN DEEP-WATER OPEN TOWS WITH THE IOS NET

The IOS Net was also used for making 38 deep-water vertical open tows from depths between 250 m to surface and 1,300 m to surface. These collections have not yielded many specimens of cephalopods, probably as the speed of hauling (about 45–50 m/minute) was too slow to capture specimens of cephalopods as compared to 55 to 60 m/minute in vertical tows with the same net from depths upto 200 m reported earlier.

The occurrence of cephalopods in the deep-water collections are shown in Table XII.

TABLE XII

Cephalopods in IOS Net deep-water collections

Year	Month	Total No. of tows	No. of tows with cephalopods	No. of specimens
1963	November ..	8	2	4
	December ..	9	2	3
1964	March	5	3	5
	April ..	1	—	—
	October ..	1	—	—
	December ..	1	—	—
1965	February ..	2	1	1
	March ..	1	—	—
	November ..	2	—	—
1966	February ..	8	—	—
	TOTAL	38	8	13

OTHER COLLECTIONS

1. *Drift net fishing.*—In the course of exploratory fishing with drift nets of varying mesh sizes on a number of occasions specimens of *Symplectoteuthis oualaniensis* have been caught in net sections with mesh size of 3 cm. Very often 15 to 20 specimens are found in a small section of the net indicating the shoaling habit of this species. As the nets are hauled in at dawn, on many occasions live specimens entangled in nets have been caught. Like other ommastrephids, *S. oualaniensis* is also known to leap out of water. On a number of occasions at night whole schools have been seen leaping out of water in pursuit of fish and other planktonic organisms attracted by light to the side of the research vessel. On 7-2-1966, while shooting the drift net, one specimen 23 cm in total length 'flew' and landed on the main deck of the vessel.

2. *Otter trawl collections.*—Material of cephalopods from the trawling grounds have been collected and the following were found to occur more commonly: *Sepia aculeata, Sepia pharaonis, Sepiella inermis, Loligo duvaceli,* and *Octopus macropus.* These collections made from depths upto 400 metres have not been fully worked out.

Figure 13 shows some of the species commonly met with in the IOS Net collections, Isaacs Kidd Mid-water Trawl collections and drift-net collections.

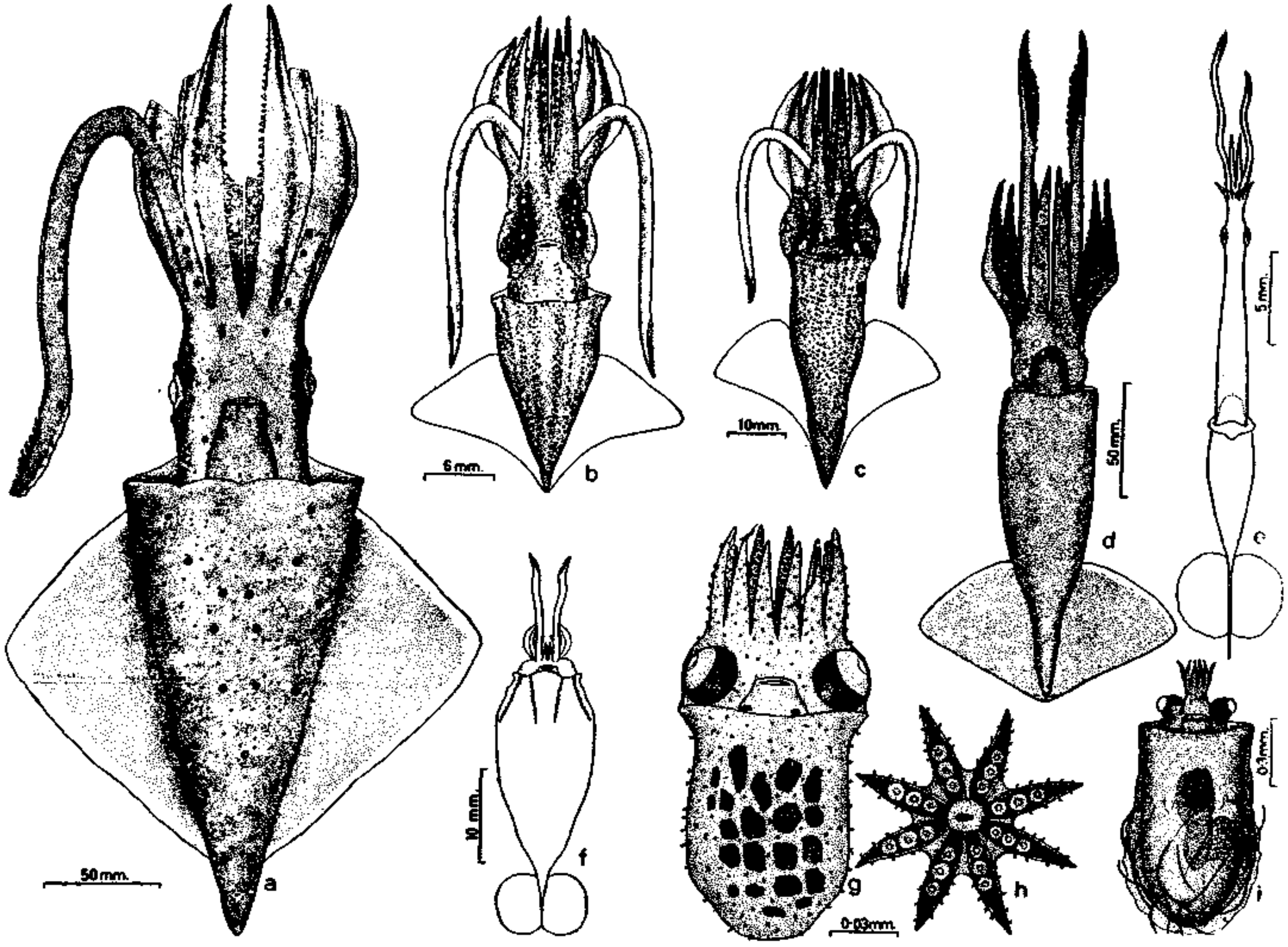


FIG. 13. Some of the more common species of cephalopods occurring in the plankton collections, mid-water trawl collections, and drift net collections off the south-west coast of India and Laccadive Sea. (*a*) *Thelidioteuthis alessandrinii*, adult female; (*b*) *Abraliopsis gilchristi*; (*c*) *Abralia andamanica*; (*d*) *Symplectoteuthis oualaniensis*, adult; (*e*) Larval 'doratopsis stage' of *Chiroteuthis* sp.; (*f*) *Liocranchia reinhardti*; (*g*) Larval *octopus* and (*h*) arrangement of web and suckers in the same; (*i*) Larval *Japetella diaphana*. The thread-like structures seen over the body are not connected to the mantle but are embeded in the gelatinous covering and mucus surrounding the mantle.

PRELIMINARY CATALOGUE OF CEPHALOPODA KNOWN FROM THE INDIAN OCEAN

Up to now no attempt has been made to bring out a catalogue of the Cephalopoda of the Indian Ocean. Several cephalopods, especially the neritic squids and cuttlefishes are economically important as they form seasonal subsistence fishery in some places bordering the Indian Ocean. The same is true of several species of octopuses which are also consumed. Many of the cephalopods are important links in the trophic chain and pelagic cephalopods, especially some of the oceanic squids, are important as forage for pelagic fishes such as tunas, billfishes, lancet fishes, and for the toothed whales. Some of the epipelagic and bathypelagic species are useful indicators of water masses. In spite of their usefulness, the Cephalopoda of the Indian ocean has not received its due share of recognition. There are vast areas which have not been explored for their cephalopod fauna. The present catalogue, in addition to facilitating reference, will also give us a picture as to what is known about this interesting group on an ocean-wide basis. A catalogue of this nature involves a considerable amount of compilation and in this connection, the revisional works cited in the introductory part of this work have been helpful. Due to limitation of space, a complete bibliography is not given here, for which the references given in the papers listed at the end should be consulted. For instance, Adam and Rees (1966: pp. 156-159) have given an exhaustive list of references pertaining to the family Sepiidae.

On the basis of available literature brief remarks are given under each species and important references dealing with the species are cited. I will be most thankful if my attention could be drawn to any omissions or errors.

Class **CEPHALOPODA**

Subclass **NAUTILOIDEA**

Family NAUTILIDAE

Genus *Nautilus* Linnaeus, 1758

1. ***Nautilus pompilius*** Linnaeus, 1758, p. 709 (Type locality: 'Habitat in India'). Shells are widely distributed and may be washed up along coasts far removed from the natural habitat of the animal.

Distribution: Indian Ocean; Western and Central Pacific (Philippines to Australia and Polynesia).

Remarks: The species has been described by Owen (1832), Willey (1902), Griffin (1900) and others and its economic importance and ecology studied by Dean (1901).

Subclass **COLEOIDEA**

Order *SEPIOIDEA*

Family SPIRULIDAE

Genus *Spirula* Lamarck, 1801

2. ***Spirula spirula*** (Linnaeus, 1758), p. 710 (Type locality: 'America').

Synonyms: Nautilus spirula Linnaeus, 1758 (As above); *Spirula australis* Lamarck, 1816; *Spirula prototypos* Peron and Lesueur, 1807; *Spirula peronii* Lamarck, 1822; *Spirula reticulata* Owen, 1848; *Lituus laevis*, Gray, 1849; *Spirula blakei* Lönnberg, 1896; *Spirula australis* Chun, 1914; and *Spirula peronii* Hidalgo.

Distribution: Widely distributed in the different oceans and shells are washed ashore on beaches. The species inhabits depths between 200–1,500 metres.

Remarks: For detailed information on the morphology, anatomy and biology of this species reference is invited to Chun (1914), Kerr (1931), and Bruun (1943).

Family SEPIIDAE

Genus *Sepia* Linnaeus, 1758

3. ***Sepia aculeata*** Ferussac and d'Orbigny, 1835–1848, p. 287 (Type locality: Java).

Synonyms: Acanthosepion aculeatum Rochebrune, 1884, p. 101; *Acanthosepion hasselti*, Rochebrune, 1884, p. 101; *Sepia blainvillei* Ferussac and d'Orbigny, 1848 *nec* Deshayes, 1835; *Sepia indica* Ferussac and d'Orbigny, 1848, p. 281, pl. 21; *Acanthosepion indicum* Rochebrune, 1884, p. 112; *Acanthosepion javanicum*, 1884, p. 110; *Sepia microcotyledon*, Ortmann, 1891, p. 673, pl. 46, fig. 1; and *Sepia esculenta* var.? Robson, 1932, p. 29.

Distribution: Indo-Pacific. Adam and Rees (1966) record this species from the following areas in the Indian Ocean: Bombay, Cochin, Karwar, Mannar, Ennur, Madras, Dighe, Hambantota (Ceylon); Singapore, Penang. Outside the Indian Ocean they record it from Batavia, Sarawak, and Sasaki (1929) reports it from as far north as Formosa.

Remarks: For a description of the species reference is invited to Adam (1939 *c*), and Adam and Rees (1966: pp. 12–14, pl. 4, figs. 20 & 21; pl. 42, fig. 251).

4. ***Sepia acuminata*** Smith, 1916, p. 21, pl. 2, figs. 3 & 4 (Type locality: Port Elizabeth; Tongaat Beach, Natal).

Synonyms: Rhombosepion acuminata Robson, 1924 *a*, p. 643; *Sepia* sp. A. (partim) Robson, 1924, p. 13.

Distribution: South-Western Indian Ocean (Natal coast of Union of South Africa) and doubtfully recorded from Mombasa (Adam and Rees, 1966).

Remarks: For detailed description reference is invited to Adam and Rees (1966: pp. 53–55, pl. 16, figs. 91 & 92; pl. 43, fig. 261).

5. ***Sepia apama*** Gray, 1849, p. 103 (Type locality: Port Adelaide, Australia).

Synonyms: ? *Amplisepia verreauxi* Iredale, 1926, p. 194, pl. 23, figs. 1 & 2; ? *Sepia palmata* Owen, 1881, p. 134, pls. 24 & 25; ? *Amplisepia parysatis* Iredale, 1954, p. 71, pl. 4, figs. 1 & 2; *Sepia* sp. B, Voss, 1962, p. 3.

Distribution: Indian Ocean [Shark's Bay (*A. parysatis*)]. Western Pacific Ocean (Australia from Port Adelaide, Sydney, Hobson's Bay, Melbourne, Port Jackson and Semaphore, S. Australia; Norfolk Island; ? New Zealand).

Remarks: For detailed discussion and description of this species reference may be made to Adam and Rees (1966: pp. 34–38, pl. 12, figs. 64–67, pl. 45, fig. 269).

6. ***Sepia arabica*** Massy, 1916, p. 288, pl. 23, figs. 1–5, pl. 24, fig. 10 (Type localities: Laccadive Sea 11° 14′ 30″ N, 74° 57′ 15″ E from 68 to 148 fathoms; and from Persian Gulf, 26° 20′ N, 53° 54′ E from 54 fathoms).

Distribution: Laccadive Sea, Arabian Sea, Persian Gulf, Gulf of Aden, and Adam and Rees (1966: pp. 96–97, pl. 23, figs. 152–155, pl. 46, fig. 278) also mention of its occurrence in Red Sea. The depth distribution of this species is given by these authors as 97 to 270 metres.

7. ***Sepia australias*** Quoy and Gaimard, 1832, p. 70, pl. 5, figs. 3–7 (Type locality: Agulhas Bank).

Synonyms: Sepia (Doratosepion) australis Massy, 1925, p. 214; *Rhombosepion australe* Rochebrune, 1884, p. 85; *Rhombosepion australis* Massy, 1927, p. 156; *Sepia capensis* d'Orbigny, 1845; *Rhombosepion capensis* Rochebrune, 1884, p. 85; and *Sepia sinope*, Gray, 1849, p. 106.

Distribution: Indian Ocean (Agulhas Bank; Off Cape Natal, Durban; Port Elizabeth; Mossel Bay; Grahamstown, Natal; Port Alfred; Red Sea); South-Eastern Atlantic (Cape of Good Hope; Dassen Island and adjacent areas); Pacific Ocean (? China).

Remarks: For taxonomic discussion reference is invited to Adam and Rees (1966: pp. 89–91, pl. 21, figs. 138–142; pl. 45, fig. 270).

8. ***Sepia brevimana*** Steenstrup, 1875, pp. 475, 497; 1881, pl. 1, figs. 24–26 (Type locality: Indian Ocean).

Synonyms: Sepia rostrata (partim) Ferussac and d'Orbigny, 1848, p. 284 (*nec* 1835, pl. 8); *Acanthosepion rostratum* Rochebrune, 1884, p. 102, pl. 6, fig. 1; *Sepia winckworthi* Adam, 1939 *a*, p. 1, fig. 1, pl. 1 (From Singapore); *Acanthosepion spinigerum* (partim) Rochebrune, p. 103.

Distribution: Indian Ocean (Juhu, Bombay; Mannar; Madras; Puri; Port Blair, Andaman Islands; Hambantota, Ceylon; and Singapore). Western Pacific (Java Sea; Sarawak).

Remarks: For a taxonomic discussion reference is invited to Adam (1939 *a*, 1939 *c* and 1944), and for a redescription Adam and Rees (1966: pp. 5–7, pl. 2, figs. 5–8).

9. ***Sepia burnupi*** Hoyle, 1904, p. 27, pl. 1, figs. 188, 189 (Type locality: Umkomaas, Natal, South Africa).

Synonyms: Sepia (Doratosepion) incerta Massy, 1925, p. 219, pl. 13, figs. 22, 23, 29–36, pl. 14, figs. 40 and 43 (*nec* Smith, 1916); ? *Sepia exsignata* Barnard, 1962, p. 250, fig. 3, *Distribution:* Natal coast of South Africa, from about 40 to 48 metres depth.

Remarks: For a description as well as taxonomic discussion reference is invited to Adam and Rees (1966: pp. 81–83, pl. 20, figs. 127 & 128).

10. ***Sepia confusa*** Smith, 1916, p. 24, pl. 2, figs. 7, 8 (Type localities: Tongaat Beach, Natal; Port Elizabeth, Cape Colony).

Synonyms: Sepia brunupi Hoyle, 1904, p. 27, pl. 1, fig. 192 (partim); *Doratosepion confusa* Massy and Robson, 1923, p. 435, figs. 1–3; *D. confusum* Robson, 1924 *a*, p. 647; *Sepia* (*Doratosepion*) *confusa* Massy, 1925, p. 221, pl. 13, figs. 20, 21, 24–28, pl. 14, fig. 38.

Distribution: South-east coast of Africa (Zanzibar area from 5° 38′ 54″ S 39° 15′ 42″ E to 5° 40′ 18″ S, 39° 17′ 36″ E; Natal coast to Port Elizabeth).

Remarks: For a redescription of the species and taxonomic discussion reference is invited to Adam and Rees (1966: pp. 65–67, pl. 18, figs. 112 & 113, pl. 42, fig. 248).

11. ***Sepia dollfusi*** Adam, 1941, p. 12, pl. 2, fig. 3; 1942, pp. 3, 8; 1959, p. 138, fig. 5, pl. 4, fig. 4; pl. 6, figs. 4, 5; and pl. 7 (Type locality: Perim, Red Sea).

Synonyms: Sepia gibbosa Issel, 1869, p. 238 (partim) (*nec* d'Orbigny); *Sepia lefebrei* Hoyle, 1907, p. 39, figs. 1–7; *Lophosepion lefebrei* Robson, 1927, p. 322 (partim) (*nec* d'Orbigny); *Sepia rouxi* Hoyle, 1907, p. 42 (partim) (*nec* Ferussac and d'Orbigny).

Distribution: Indian Ocean (Red Sea and Suez Canal).

Remarks: For a redescription and taxonomic discussion refer Adam and Rees (1966: pp. 98–99, pl. 24, figs. 156–158; pl. 41, fig. 237).

12. ***Sepia elliptica*** Hoyle, 1885, p. 189; 1885 *a*, p. 293; 1886, p. 131, pl. 19, figs. 14–24 [Type localities: "Challenger" Stations 188 (9° 59′ S, 139° 42′ E) and 190 (8° 56′ S, 136° 05′ E) from 28 fathoms in the Arafura Sea, South of Papua)].

Synonyms: Acanthosepion (*Fiscisepia*) *ellipticum adjacens* Iredale, 1926 *a*, p. 239, pl. 35, figs. 5, 6; and *Acanthosepion ellipticum* Iredale, 1954, p. 77.

Distribution: Indian Ocean (Ganjam coast, Orissa; Arabian Sea); Western Pacific (Arafura Sea, S. of Papua; Queensland; Melville Island, Northern Territory, N.-W. Australia; Pellew Group, Gulf of Carpentaria).

Remarks: For taxonomic discussion refer Adam (1939 *c*), and Adam and Rees (1966: pp. 14–16, pl. 5, figs. 24–27; pl. 43, fig. 258).

13. ***Sepia elongata*** d'Orbigny, 1845, p. 289, pl. 13, figs. 7–10 (Type locality: Near Cosseir, Red Sea).

Synonym: Doratosepion elongatum Rochebrune, 1884, p. 97.

Distribution: Indian Ocean (Red Sea near Cosseir and Gulf of Aqaba).

Remarks: Adam and Rees (1966: pp. 86–87, pl. 21, figs. 132 & 133) have shown that the Australian records of this species should refer to *S. braggi* Verco (1907). Adam (1941 *c*) has described the male of this species till then known only from the shell.

14. ***Sepia gibba*** Ehrenberg, 1831; *vide* Adam, 1941 *b*, p. 7, pl. 2, fig. 2 (Type locality: Red Sea).

Synonyms: *Sepia gibbosa* d'Orbigny, 1845, p. 287; *Lophosepion gibbosum* Rochebrune, 1884, p. 91; *Sepia lefebrei* d'Orbigny, 1845, p. 288, pl. 91; *Lophosepion lefebrei* Rochebrune, 1884, p. 90, pl. 4, fig. 2.

Distribution: Indian Ocean (Red Sea from Eylath, and Suakin, Sudan coast).

Remarks: For a description refer Adam and Rees (1966: pp. 100–102, pl. 25, figs. 159–161).

15. ***Sepia hieronis*** (Robson) 1924 *a*, p. 645, pl. 2, figs. 9–11 (Type locality: From 4 stations from Saldanha Bay to St. Helena Bay area and not off Cape Town, as given by Robson, 1924 *a*).

Synonyms: *Sepia* sp. A., Robson, 1924, p. 13; *Rhombosepion hieronia* Robson, 1924 *a* (As above).

Distribution: Indian Ocean (Natal, Union of South Africa); South-Eastern Atlantic Ocean (Off Cape Town; Saldanha Bay—St. Helena Bay area, Union of South Africa).

Remarks: For a recent description *see* Adam and Rees (1966: pp. 112–114, pl. 30, figs. 187 & 188; pl. 43, fig. 262).

16. ***Sepia insignis*** Smith, 1916, p. 25, pl. 2, fig. 10 (Type locality: Tongaat Beach, Natal, South Africa).

Distribution: Natal Coast.

Remarks: Adam and Rees (1966: p. 114, pl. 31, figs. 189–191) remark that "This species, the animal of which is unknown, does not seem to be related to any other species hitherto described".

17. ***Sepia incerta*** Smith, 1916, p. 23, pl. 2, fig. 6 (Type localities: Tongaat Beach, Natal; Port Elizabeth, Cape Province).

Synonyms: *Sepia burnupi* Hoyle, 1904 (partim), p. 27, pl. 1, figs. 190 and 191; *Sepia (Doratosepion) burnupi* Massy, 1925, p. 215, pl. 12.

Distribution: Indian Ocean (Natal Coast to Port Elizabeth, Union of South Africa).

Remarks: Species is known only from the male, a redescription of which is given by Adam and Rees (1966: pp. 67–70, pl. 19, figs. 114 & 115; pl. 41, fig. 241). They have also shown that the description of a female given by Massy (1925) should refer to *S. burnupi*, Hoyle (1904).

18. ***Sepia joubini*** Massy, 1927, p. 161, pl. 18 (Type locality: Tugela River mouth, Cape Natal).

Distribution: Indian Ocean (Tugela River mouth, Cape Natal, Union of South Africa).

Remarks: A redescription of the male and female is given by Adam and Rees (1966: pp. 70–71, pl. 43, fig. 257). The shell of this species is practically unknown.

19. ***Sepia kobiensis*** Hoyle, 1885, p. 195; 1885 *a*, p. 300; 1886, p. 142, pl. 18, figs. 7–14 (Type locality: Bay of Kobe, Japan).

Synonyms: Sepia andreanoides Hoyle, 1885, p. 193; *Sepia (Doratosepion) andreanoides* Berry, 1912, p. 423; *Sepia (Doratosepion) kobiensis* Berry, 1912, p. 423; *Sepia kobiensis* var. *typica* Sasaki, 1929, p. 206, fig. 111, pl. 19, figs. 1–4; *Sepia kobiensis* var. *andreanoides* Sasaki, 1929, p. 206, figs. 112–114, pl. 1, fig. 7, pl. 19, figs. 5–7; *Sepia kobiensis* var. *toyamensis* Sasaki, 1929, p. 209, fig. 115, pl. 19, fig. 8–12; *Sepia kobiensis* var. *beppuana* Sasaki, 1929, p. 211, fig. 115, pl. 19, figs. 13–15; *Sepia kobiensis* var. *crassa* Sasaki, 1929, p. 213, pl. 19, figs. 16–18; *Sepia kobiensis* var. *albatrossi* Sasaki, 1920, p. 195, pl. 26, figs. 2 and 3.

Distribution: Indian Ocean (All records are doubtful). ? Laccadive Sea, 11° 14′ 30″ N, 74° 57′ 15″ E from 68–148 fathoms (Massy, 1916); ? 13° 36′ N, 47° 32′ N, 130 fms (Massy, 1916); ? South of Ceylon, 6° 2′ 30″ N, 81° 29′ E from 52 to 68 fms (Massy, 1916); ? Persian Gulf, 26° 20′ N, 53° 54′ E, from 53 fms (Massy, 1916); ? Off C. Negrais, Burma from 40 fms (Massey, 1916); ? Kolumadulu Atoll, from 35 fms (Hoyle, 1905). Pacific Ocean (? Poeloe Weh—*see* Adam, 1939 c; Several localities from Japan.

Remarks: Adam and Rees (1966: pp. 71–78, pl. 19, figs. 116–120; pl. 43, fig. 255; pl. 44, fig. 264) have shown that all previous records of this species from the Indian Ocean are doubtful. The varieties described by Sasaki (1929) are from Japanese waters. For detailed taxonomic discussion refer Adam and Rees (1966).

20. ***Sepia latimanus*** Quoy and Gaimard, 1832, p. 68, pl. 2 (Type locality: Port Dorey, Australia).

Synonyms: Sepia rappiana Ferussac, 1835, pl. 10; *Acanthosepion rappianum* Rochebrune, 1884, p. 105; *Sepia hercules* Pilsbry, 1894, p. 144, 1895, p. 2, pl. 1, figs. 1 & 2; *Ponderisepia eclogaria* Iredale, 1926 *a*, p. 239, pl. 35, figs. 7 & 8; *Sepia eclogaria* Adam, 1939 *c*, p. 49; *Sepia harmeri* Robson, 1928, p. 8, figs. 2 & 3; and *Sepia mozambica* Rochebrune, 1884, p. 118.

Distribution: Indian Ocean (Mozambique and Singapore); Western Pacific (Malaya to Fiji and Australia to Japan).

Remarks: For taxonomic discussion reference may be made to Adam (1939 *c*) and Adam and Rees (1966: pp. 33–34, pl. 11, figs. 61–63t pl. 45, fig. 269 A).

21. ***Sepia murrayi*** Adam and Rees, 1966, pp. 63–65, pl. 18, figs. 107–111; pl. 43, fig. 260 (Type locality: John Murray Expedition Station 71, 25° 35′ N, 56° 42′ 18″ E to 25° 43′ N, 56°39′ 18″ E in Gulf of Oman at 106 m depth).

Remarks: The description is based on females and it is likely that it may be more widely distributed in the Indo-Pacific.

22. ***Sepia novaehollandiae*** Hoyle, 1909, p. 266 (Type locality: Kangaroo Island, South Australia).

Synonyms: Sepia australis Ferussac, 1835, pl. 7, fig. 4 (*nec* Quoy and Gaimard, 1832); *Mesembrisepia novaehollandiae* Iredale, 1926, p. 191; *Sepia (Mesembrisepia) novaehollandiae* Cotton and Godfrey, 1940, p. 428, figs. 416–418; ? *Sepia dannevigi* Berry, 1918, p. 264, figs. 51–55, pl. 73, pl. 74, figs. 1 & 2.

Distribution: Indian Ocean (? Western Australia). Western Pacific Ocean (South Australia).

Remarks: Adam and Rees (1966: pp. 48–53, pl. 15, figs. 84–90) have given a very lengthy discussion on this species. They have also commented on the following nominal species which have also been reported from Western Australia (Indian Ocean).

1. *Sepia irvingi* Meyer, 1909
2. *Sepia ostanes* (Iredale), 1954
3. *Sepia chirotrema* Berry (1918).

23. ***Sepia officinalis vermiculata*** Quoy and Gaimard, 1932, p. 64, pl. 1, figs. 1–5 (Type locality: Cape of Good Hope).

Synonyms: Acanthosepion vermiculatum Rochebrune, 1884, p. 113; *Acanthosepion vermiculata* Robson, 1924 *a*, p. 639; ? *Sepia hierredda* Turton, 1932 (? *nec* Rang), p. 2; ? *Sepia jousseaumi* Rochebrune, 1884, p. 117.

Distribution: Indian Ocean (From mouth of Zambesi River southwards at Natal, Delagoa Bay, Isipingo, and Port Elizabeth to Knysna Estuary, Union of South Africa).

Remarks: While giving a description of the subspecies Adam and Rees (1966: pp. 30–32, pl. 10, figs. 55 & 56; pl. 45, fig. 271) have also commented on its affinities to the other subspecies known from the Atlantic and the Mediterranean, *viz.*, subsp. *officinalis* Linneaus (1758), subsp. *hierredda* Rang, subsp. *filliouxi* Lafont, and subsp. *mediterranea* Ninni. Reference is also invited to Adam (1941, 1952 and 1962).

24. ***Sepia omani*** Adam and Rees, 1966, pp. 92–94, pl. 22, figs. 143–147; pl. 41, figs. 242–244 (Type localities: Gulf of Oman from John Murray Exped. Stn. 75, 25° 10′ 48″ N, 56° 47′ 30″ E to 25° 09′ 48″ N, 56° 47′ 30″ E from 201 m.

Remarks: The species is said to show affinities to *S. prashadi* Winckworth (1936) and *S. kobiensis* Hoyle (1885).

25. ***Sepia papillata*** Quoy and Gaimard, 1832, p. 61, pl. 1, figs. 6–14 (Type locality: Cape of Good Hope, South Africa).

Synonyms: Spathidosepion papillatum, Rochebrune, 1884, p. 94; *Sepia tuberculata*, Hoyle, 1910, p. 265, pl. 4 *a*, figs. 4–6 (*nec* Lamarck).

Distribution: Indian Ocean (Port Elizabeth, South Africa). South Eastern Atlantic Ocean (Cape of Good Hope).

Remarks: For a redescription and taxonomic discussion reference may be made to Adam and Rees (1966: pp. 108–109, pl. 28, figs. 175–178).

26. ***Sepia pageora*** (Iredale), 1954, p. 76, pl. 4, figs. 7–9 (Type locality: Keppel Bay, Queensland, Australia).

Synonyms: Sepia indica Gray, 1849, p. 108 (*nec* d'Orbigny, 1848); *Acanthosepion pageorum* Iredale, 1954 (as above).

Distribution: Indian Ocean (Port Cloates, Shark Bay, and Broome, Western Australia. Melville Island, Northern Territory, Australia, and Timor Sea which are on the border line between the Indian Ocean and Western Pacific Ocean may also be mentioned here). Western Pacific Ocean (Queensland).

Remarks: Adam and Rees (1966: pp. 20–22, pl. 7, figs. 36–37; pl. 42, fig. 253) who examined a specimen from Cape Upstart, Australia, remark that if their specimen "really belongs to *S. pageora*, this species is probably identical with *S. smithi* Hoyle."

27. ***Sepia pharaonis*** Ehrenberg, 1831 (Type locality: Tor, Sinai; Massaouah

Synonyms: Sepia rouxii Ferussac and d'Orbigny, 1841, p. 271, pl. 19; *Acanthosepion rouxii* Rochebrune, 1884, p. 108; *Sepia torosa* Ortmann, 1888, p. 652, pl. 23, fig. 2; *Sepia framea* Ortmann, 1891, p. 675, pl. 41, fig. 2; *Sepia singalensis* Goodrich, 1896, p. 3, pl. 1, figs. 4–8; *Ascarosepion singhalensis* var. *foxi* Robson, 1927, p. 325; *Sepia koettlitzi* Hoyle and Standen, 1901, p. 1, pl. 1; *Sepia formosana* Berry, 1912, p. 420, fig. 2, pl. 9, fig. 7; *Crumenasepia hulliana* Iredale, 1926, p. 239, pl. 35, figs. 1 & 2; *Sepia hulliana* Adam, 1939 *c*, p. 65; *Sepia tigris* Sasaki, 1929, p. 168, fig. 167, pl. 28, figs. 13–16; *Crumenasepia ursulae* Cotton, 1929, p. 90, pl. 15, figs. 3 & 4; *Sepia ursulae* Adam, 1939 *c*, p. 66; *Sepia* (*Crumenasepia*) *ursulae* Cotton and Godfrey, 1940, p. 434, fig. 421; ? *Sepia venusta* Pfeffer, 1884, p. 12, figs. 15 and 15 *a* (*nec* Munster, 1837); ? *Sepia venustoides* Hoyle, 1909, p. 266 (= *S. venusta* Pfeffer); *Sepia sinope* Voss, 1962 (*nec* Gray, 1849), p. 3.

Distribution: Indian Ocean (Red Sea; Suez; Suez Canal at Kabret and Port Taufiq; Muscat and Yedda, Arabia; Mukalla, S. Arabia; Mersa Fijab; Gulf of Aden; Berbera, British Somaliland; Colombo, off Point de Galle; Hambantota, Gulf of Mannar; Trincomali; Ceylon; Bombay, Rameswaram, Madras, Ennur, and Puri, India; Cottselow, Rottnest Island, Perth, Western Australia). Pacific Ocean (Howick Island, Northern Queensland, Australia; Hong Kong; Takao, Formosa; Taihoku Market, Formosa; Tokyo Bay, Japan).

Remarks: For taxonomic discussion reference may be made to Adam (1939 *c*), and Adam and Rees (1966: pp. 22–26, pl. 8, figs. 38–43; pl. 41, fig. 240).

28. ***Sepia prashadi*** Winckworth, 1936, p. 16 (Type locality: Madras).

Distribution: Indian Ocean (Madras, India; Mauritius; Madagascar; Gulf of Suez; and Gulf of Oman).

Remarks: A revised description of the species is given by Adam and Rees (1966: pp. 26–28, pl. 9, figs. 44–48; pl. 41, figs. 245 & 246).

For earlier accounts on the species reference is invited to Adam (1939 *c*, 1941 and 1959).

29. ***Sepia savignyi*** Blainville, 1827, p. 285 (Type locality: Red Sea).

Synonyms: Sepia officinalis Audouin in Savigny, 1827, p. 11, pl. 1, fig. 3 (*nec* Linnaeus); *Sepia savigni* Rochebrune, 1884, p. 115).

Distribution: Indian Ocean (Red Sea; Gulf of Aden; and Persian Gulf).

Remarks: For a discussion on the status of the species reference is invited to Adam (1959). The species has been redescribed by Adam and Rees (1966: pp. 10–11, pl. 3, figs. 16 & 17; pl. 4, figs. 18 & 19; pl. 41, fig. 238; pl. 42, fig. 249).

30. ***Sepia recurvirostra*** Steenstrup, 1875, p. 475, 479 (Type locality: South China).

Synonyms: Sepia singaporensis Pfeffer, 1884, p. 10, figs. 13, 13 *a*; ? *Sepia pagenstecheri* Pfeffer, 1884, p. 9, figs. 12, 12 *a*; *Sepia esculenta* Joubin, 1897, p. 102 (*nec* Hoyle, 1885).

Distribution: Indian Ocean (Singapore; Burma); Western Pacific Ocean (South China; Hong Kong; Borneo Bank; Santubong and Buntal, Sarawak; and Java Sea, 6° 36′ 5″ S, 114° 55′ 5″ E).

Remarks: For a taxonomic discussion and description of this species reference is invited to Adam (1939 *c*, 1965) and Adam and Rees (1966, pp. 28–29, pl. 9, figs. 49–52; pl. 10, figs. 53 & 54).

31. ***Sepia sewelli*** Adam and Rees, 1966, pp. 61–63, pl. 17, figs. 104–106; pl. 46, fig. 273 (Type locality: John Murray Expedition Station 27 at 11° 57′ 12″ N, 50° 35′ E to 11° 56′ 42″ N, 50° 39′ 12″ E near Cape Guardafui, Red Sea).

Distribution: Indian Ocean (Near Cape Guardafui, Red Sea; and from John Murray Expedition Stations 105 and 106 close to Zanzibar).

32. ***Sepia simoniana*** Thiel, 1921, p. 436, pl. 52, figs. 5–13 (Type locality: Simon's Bay, Union of South Africa).

Synonyms: Sepia natalensis Massy, 1925, p. 212, pl. 11, figs. 1–11; pl. 14, fig. 17; *Sepia tuberculata* Gray, 1949, pp. 101, 102 (*nec* Lamarck, 1799); *Sepia papillata* Smith, 1916, p. 22, pl. 2, figs. 1 & 2 (*nec* Quoy and Gaimard).

Distribution: Indian Ocean (Cape Henderson, Durban, Port Elizabeth, Grahamstown, off Tugela River, Natal, Isipingo, and 18 miles east of Cape Agulhas, Union of South Africa). South-Eastern Atlantic Ocean (Simon's Bay and Cape of Good Hope, Union of South Africa).

Remarks: Adam and Rees (1966: pp. 109–111, pl. 29, figs. 179–182; pl. 42, fig. 254) have given a redescription of the species.

33. ***Sepia thurstoni*** Adam and Rees, 1966, pp. 2–4, pl. 1, figs. 1–4; pl. 41, fig. 235 (Type locality: Rameswaram Island, Madras State, India).

Synonyms: Sepia rouxii Hoyle, 1904 *a*, p. 198 (*nec* Ferussac and d'Orbigny; *Sepia rostrata* (partim) Winckeworth, 1936, p. 16 (*nec*

Ferussac and d'Orbigny *Sepia* sp. Adam, 1939, p. 80, pl. 3, figs. 1 & 2.

Distribution: Indian Ocean (Rameswaram Island, Madras, India; Off Negombo and Hambantota, Ceylon).

34. ***Sepia trygonina*** (Rochebrune), 1884, p. 97, pl. 5, fig. 1 (Type locality: Red Sea).

Synonym: *Doratosepion trygoninum* Rochebrune, 1884, p. 97, pl. 5, fig. 1.

Distribution: Indian Ocean (Red Sea; Gulf of Aden; Ennur, Madras, India).

Remarks: Adam and Rees (1966: pp. 84–86, pl. 20, figs. 129–131; pl. 37, figs. 220 & 221; pl. 46, fig. 277) have given a detailed description of this species.

35. ***Sepia tuberculata*** Lamarck, 1798, p. 130; 1799, pl. 1, fig. 1 *a-b* (Type locality: Unknown).

Synonyms: *Spathidosepion tuberculatum* Rochebrune, 1884, p. 93, pl. 4, fig. 3; *Hemisepius* (?) *tuberculatus* Smith, 1916, p. 25.

Distribution: The type locality is unknown. Adam and Rees (1966: pp. 106–108, pl. 26, figs. 169 & 170; pl. 27, figs. 171 & 172; pl. 28, figs. 173 & 174; pl. 44, figs. 265 & 268) have recently reported this species from St. James, South Africa.

36. ***Sepia vicellius*** Gray, 1849, p. 100 (Type locality: Unknown).

Remarks: This is a doubtful species. Adam and Rees (1966, p. 32) give the distribution as "? Red Sea (Rochebrune)". They remark that Gray's specimen belongs to *Sepia officinalis* which does not occur in the Red Sea, and Rochebrune's specimens from the Red Sea may be some other form.

37. ***Sepia zanzibarica*** Pfeffer, 1884, p. 9, figs. 11, 11 *a* (Type locality: Zanzibar).

Distribution: Indian Ocean (Mombasa and East Africa; Zanzibar; Madagascar; and Natal).

Remarks: Adam and Rees (1966: pp. 7–8, pl. 2, figs. 9–11; pl. 41, fig. 247) have given the description of the female and the shell of this species which is said to be closely related to *S. thurstoni*.

38. ***Sepia (Hemisepius) typica*** (Steenstrup), 1875, p. 469, pl. 1, figs. 1–10; pl. 2, fig. 1 (Type locality: Table Bay, South Africa).

Synonyms: *Hemisepius typicus* Steenstrup, 1875 (as above); *Hemisepion typicum* Rochebrune, 1884, p. 78, pl. 3, fig. 1; *Hemisepius typicus* var. *chuni* Thore, 1945, p. 50.

Distribution: Indian Ocean (Off Cape Natal, S. Africa). South-Eastern Atlantic Ocean (Hout Bay, False Bay, and Saldahana Bay, Union of South Africa).

Remarks: Adam and Rees (1966: pp. 117–118, pl. 32, figs. 192–195; pl. 33, figs. 196 & 197) have given a description of this species and do not consider var. *chuni* to be different from *S.* (*H.*) *typicus*. Chun (1914) recorded this species from 'Valdivia' Stn. 100 at Agulhas Bank (34° 9′ S, 24° 59′ E).

39. ***Sepia* sp.** Adam and Rees, 1966, p. 111, pl. 30, figs. 183 & 184; pl. 46, fig. 276.

Distribution: Indian Ocean (John Murray Exped., Stn. 27, 11° 57′ 12″ N, 50° 35′ E to 11° 56′ 42″ N, 50° 39′ 12″ E near Cape Guardafui; Stn. 106, 5° 38′ 54″ N, 39° 15′ 42″ E, 5° 40′ 18″ N, 39° 17′ 36″ E, Zanzibar area).

Remarks: Adam and Rees (1966, p. 111) remark that the specimens are closely related to *Sepia simoniana* (= *S. natalensis*), but differing in the structure of the tentacular club.

Genus *Sepiella* Gray 1849

40. ***Sepiella cyanea*** Robson, 1924, p. 13; 1924 *a*, p. 648, figs. 25–27, pl. 2, fig. 6 (Type locality: Natal, South Africa).

Synonyms: ? *Sepiella obtusata* Massy, 1928, p. 95 (*nec* Pfeffer, 1884); *Sepias* p.A, Voss, 1962, p. 3.

Distribution: Indian Ocean (Durban, Natal coast, Port Elizabeth, Algoa Bay, Isipingo, South Africa; Nosy N'Tangam; Ambavanibe, Madagascar).

Remarks: For detailed description *see* Adam and Rees (1966: pp. 122–124, p. 36, figs. 208–215).

41. ***Sepiella inermis*** (Ferussac and d'Orbigny, 1835–1848), 1835, pl. 6 *bis*; 1848, p. 286, pl. 20, figs. 1–9 (Type localities: Batavia, Bombay, Pondicherry, Coromandel Coast).

Synonyms: *Sepia inermis* Ferussac and d'Orbigny (as above); *Sepia* (*Sepiella*) *inermis*, Tryon, 1879, p. 196, pl. 91, fig. 423, pl. 92, figs. 424–429; *Sepiella inermis* Rochebrune, 1884, p. 88; *Sepia* (*Sepiella*) *microcheirus* Gray, 1849, p. 107; *Sepiella microcheirus* Adam, 1939 *c*, p. 105; *Sepiella curta* Pfeffer, 1884, p. 13, figs. 16, 16 *a*; *Sepiella maindroni*, Rochebrune, 1884, p. 89; *Diphtherosepion martini* Rochebrune, 1884, p. 81; *Sepia tourannensis* Eydoux and Souleyet, 1852, p. 33, pl. 3, figs. 6–12; *Rhombosepion touranense* Rochebrune, 1884, p. 84; *Sepia affinis* Eydoux and Souleyet, 1852, p. 35, pl. 3, figs. 13 & 14 (*nec* Ferussac, 1826); *Sepiella affinis* Adam, 1939 *c*, p. 107.

Distribution: Indian Ocean (Red Sea; Aden; Mukalla, South Arabia; Juhu, Bombay, Laccadives, Cannanore, Tellicherry, Palk Bay, Rameswaram Island, Madras, Ennur, Chilka, Puri, Gopalpur, Orissa Coast, Sandheads, River Hooghly, Bengal, Pondicherry, Andamans, India; Penang, Malaya; Sumatra, Java; Singapore; Galle, Pearl Banks, Ceylon; Akyab, Mergui, Hainze Basin, Burma). Western Pacific Ocean; Santubang and Buntal, Sarawak; Rade de Semarang, Java; Banka; Touranne Bay, Vietnam).

Remarks: Adam (1939 *c*) should be consulted for exhaustive list of localities from where this species has been recorded. A description of the species as well as a taxonomic discussion is given by Adam and Rees (1966: pp. 123–128, pl. 38, figs. 222–227, pl. 40, figs. 233 & 234). They have also commented on the close resemblance of *Sepiella melwardi* Iredale (1954) from Condon Bay, Melville Island, Northern Territory, Australia, to *S. inermis*. Adam (1944) may also be referred for nomenclatorial discussion.

42. ***Sepiella ocellata*** Pfeffer, 1884, p. 13, figs. 17, 17 *a-b* (Type locality: Java).

Remarks: This species is known from only a single male, the type of which was redescribed by Adam (1939 *c*). According to Adam and Rees (1966) the shell of this species strongly resembles that of *S. ornata* known from West Africa from Mauritania to Angola.

43. ***Sepiella weberi*** Adam, 1939 *c*, pp. 98–101, 114, pl. 4, figs. 1–2; text-figs. 6–8 (Type localities: Soemba, 119° 56′ E, 10° S; Rade de Koepang, Timor).

Remarks: Adam and Rees (1966: p. 128, pl. 37, figs. 216–219) remark on the strong resemblance of this species to *S. cyanea* from South Africa.

The type localities of *Sepiella ovata* Pfeffer (1884), and *Sepiella obtusata* Pfeffer (1884) are unknown and Adam (1939 *c*) who studied the types considers them as doubtful synonyms of *Sepiella japonica* Sasaki (1929). According to him, the types of the former two species are in poor state which makes it difficult to express a definite opinion regarding their validity. Adam and Rees (1966) have shown that the specimens reported by Massy (1928) from Tongaat Beach, Natal as *S. obtusata* probably belongs to *S. cyanea*. Thus at present four species of the genus *Sepiella* are known to occur in the Indian Ocean, one of which, *S. ocellata* is very poorly known.

Family SEPIADARIIDAE

Genus *Sepiadarium* Steenstrup, 1881

44. ***Sepiadarium kochii*** Steenstrup, 1881, p. 214, p. 11, figs. 1–10 (Type locality: Deep Water Bay, Hong Kong).

Synonyms: Sepiadarium malayense Robson, 1932.

Distribution: Indian Ocean (Andamans, India; Ceylon; Malaya; Western Australia); Pacific Ocean (Australia; Amboina; Hong Kong; Japan).

Remarks: Records from the Indian Ocean are by Goodrich (1896), Robson (1914, 1932 *a*). Recently, Voss (1963) while redescribing the species *S. grasilis* from Philippines has given a taxonomic discussion on the genus and also a key for the identification of five species (pp. 38–40), namely, *S. auratum* Robson (1914), *S. gracilis* Voss (1962), *S. austrinum* Berry (1921), *S. kochii* Steenstrup (1881), and *S. nipponianum* Berry (1932).

Family SEPIOLIDAE

Subfamily SEPIOLINAE

Genus *Sepiola* Leach, 1817

45. ***Sepiola penares*** (Gray, 1849), p. 95 (Type locality: Indian Ocean).

Synonyms: *Fidenas penares* Gray, 1849 (as above); *Sepiola penares* Tryon, 1879, p. 157.

Distribution: Indian Ocean? Singapore.

Remarks: This species is very poorly known. It would appear from Joubin's brief notes on it (Joubin, 1902, p. 95) that many of the diagnostic details are not known for the species.

Genus *Euprymna* Steenstrup, 1887

46. ***Euprymna berryi*** Sasaki, 1929, pp. 143–146, pl. 15, figs. 12 & 13, and text-fig. 88 (Type locality: Not indicated. But Sasaki remarks that this species is the "commonest sepiolid occurring in Japan, being found in both the Japan Sea and the Pacific Ocean.... the northern limit of distribution appearing to be the northern part of Honshu".

Synonyms: *Inioteuthis morsei* Hoyle, 1886 (*nec* Verrill, 1881); Goodrich, 1896; Joubin, 1902; *Sepiola bursa* Pfeffer, 1884; *Eupremna morsei* (*nec* Verrill, 1881) Steenstrup, 1887; Hoyle. 1904 *a*, 1904 , 1905; Sasaki, 1914, 1920.

Distribution: Indian Ocean (Ceylon; Kolumadulu Atoll, Indian Sea, Andamans); Western Pacific Ocean [Japan, Formosa, Hong Kong, Philippines (?)].

Remarks: I have followed Sasaki (1929, pp. 143–146) in listing this species from the Indian Ocean. Sasaki has listed this from numerous localities from Japanese waters as well.

47. ***Euprymna morsei*** (Verrill), 1881, p. 417, footnote (Type locality: Tokyo Bay, Japan).

Synonyms: *Inioteuthis morsei*, Verrill, 1881 (as above); *Euprymna similis* Sasaki, 1913, 1914; *Euprymna morsei* Adam, 1954; ? *Euprymna morsei* Voss, 1963.

Distribution: Indian Ocean (No definite record as yet); Pacific Ocean (Japan, Indonesia, Makassar, Amboina and probably also Philippines, though there is no definite record from the latter area).

Remarks: The type locality of this species is given by Voss (1963) as "Yeddo Bay, Japan". It has been reported from 'Siboga' stations (Adam, 1954) close to the limits of the eastern Indian Ocean and this as well as the confusion regarding the identity of this species from different areas are the main reasons for including it in this list.

48. ***Euprymna stenodactyla*** (Grant), 1833, p. 42 (Type locality: Mauritius).

Synonym: *Sepiola stenodactyla* Grant, 1833 (as above).

Distribution: Indian Ocean (Mauritius). Pacific Ocean (Rangiora, Tuamotus; Faunafuti, Ellice Islands; Tarawa, Gilbert Islands; Arno Atoll, Marshall Islands; Bikini Atoll, Marshall Islands; Tumindao Anchorage; Panabutan Bay, Sulu Sea, Mindanao; Ulugan Bay, Palawan Island; ? Philippines).

Remarks: Voss (1963, pp. 52–56, fig. 8 *a, b*) has redescribed this species and has also given a taxonomic discussion to which reference is invited.

Genus *Inioteuthis* Verrill, 1881

49. ***Inioteuthis japonica*** Verrill, 1881 *c*, p. 418, footnote (Type locality: Tokyo Bay, Japan).

Synonym: Sepiola japonica Joubin, 1902.

Distribution: Indian Ocean (Port Blair, Andamans); Pacific Ocean (Japan; Taiwan).

Remarks: The inclusion of this species is based on Massy's (1916, pp. 16–17) record of three specimens from Port Blair, Andamans, assigned by her to this species.

50. ***Inioteuthis maculosa*** Goodrich, 1896, pp. 2–3, pl. 1, figs. 1–3 (Type locality: Andaman Islands).

Distribution: Indian Ocean (Andaman Islands; 'Investigator' Stn. 556, off Burma Coast; Puri Beach, Orissa Coast; Persian Gulf); Pacific Ocean (Indonesia from four 'Siboga' stations; Cubugao Anchorage, Catanduanes Id.; Ragay Bay, Ragay Gulf, Luzon, Philippines).

Remarks: Reference is invited to a recent redescription of the species by Voss (1963: pp. 59–62, fig. 9).

Subfamily ROSSIINAE

Genus *Rossia* Owen, 1834

51. ***Rossia enigmatica*** Robson, 1924, pp. 635–639, pl. 1. fig. 4 (Type locality: Off Cape Town, South Africa).

Synonym: Semirossia sp. Robson, 1924.

Remarks: This species has been included in this list as there has been some confusion regarding station positions off South Africa, Robson's specimens having come from "Stn. 63 (female), Cape Town, in 220 fathoms; and Stn. 6 (male), Cape, in 151 fathoms". Its listing here is provisional.

52. ***Rossia mastigophora*** Chun, 1914, pp. 405–408, pl. 62, figs. 1–3, pl. 63, figs, 1–6 (Type locality: "Valdivia" Stn. 253, 0° 27′ S, 42° 47′ E in Indian Ocean).

Remarks: Further reference to this species is made by Chun (1915, pl. 63, fig. 5). Sasaki (1920) described *Rossia bipapillata* from Suruga Bay, Japan and remarked that it stands closest to *Rossia mastigophora* Chun. While recording *R. bipapillata* from Philippine waters, Voss (1963: pp. 40–42, figs. 4 *c-e*) again remarks on the close affinities of these two species. He also states that "....inasmuch as the male is unknown, the two species may be identical and if so, Chun's name would have priority".

Subfamily HETEROTEUTHINAE

Genus *Heteroteuthis* Gray, 1849

53. ***Heteroteuthis hawaiiensis*** var. ***dagamensis*** Robson, 1924, p. 11; 1924, pp. 632-635 (Type localities: Natal Coast and Cape Town, South Africa).

Remarks: This is the only known representative of the genus from the Indian Ocean.

Joubin (1902: pp. 113–114) described a species *H. weberi* from the 'Siboga' Expedition Stn. 38 (7° 35′ 04″ S, 117° 28′ 06″ E) from close to the eastern limits of the Indian Ocean.

Order **TEUTHOIDEA**

Suborder *MYOPSIDA*

Family LOLIGINIDAE

Genus *Loliolus* Steenstrup, 1856

54. ***Loliolus investigatoris*** Goodrich, 1896, pp. 8–9, pl. 2, figs. 29–37 (Type locality: Bay of Bengal).

Distribution: Indian Ocean (Orissa Coast; Sandheads, River Hooghly; Near Mud Point, R. Hooghly; off Frazergunge, Sunderbunds; off Hooghly estuary; Karnaphuli River, Chittagong; Mouth of Tavoy River; Mergui Archipelago; Penang). Western Pacific Ocean (Bagan Api Api, Sumatra; Cote Nord d'Atjeh; Deli, Sumatra; Java).

Remarks: The following works may also be referred: Massy (1916), Adam (1939*b* and 1954).

55. ***Loliolus affinis*** Steenstrup, 1881 (Type locality: Tranquebar, India).

Remarks: More information is needed on this nominal species. Adam (1954) has opined that *L. affinis* and *L. investigatoris* may be conspecific.

56. ***Loliolus rhomboidalis*** Burgress, 1967, pp. 319–329 (Type locality: R. V. *ANTON BRUUN* Stn. 47 B at 19° 50′ N, 92° 32′ E, from 22–23 metres).

Distribution: Indian Ocean [From type locality and from *ANTON BRUUN* Stns. 37 (13° 28′ N, 97° 19′ E), and 46 (21° 00′ N, 91° 59′ E)].

Remarks: This is the third species of the genus to be described from the Indian Ocean. The presence of several large globular suckers on the right ventral arm of the male easily distinguishes it from its congeners.

A fourth species, *Loliolus typus* Steenstrup (1856) which was originally inadequately described was redescribed by Grimpe (1932) from Indonesian waters (Panaroekan, East Java, aud Soerabaya) which lie close to the limits of the Indian Ocean in this area.

Genus *Loligo* Lamarck 1798

57. ***Loligo duvauceli*** d'Orbigny, 1835, p. 318, pl. 14, pl. 20, figs. 6–16 (Type locality: ?).

Synonyms: *Loligo indica* Pfeffer, 1884; *Loligo galatheae* Hoyle, 1885; ?*Loligo oshimai* Sasaki, 1929.

Distribution: Indian Ocean (Natal Coast, South Africa; Coast of India, Burma, Andaman Islands; Malaya). Pacific Ocean: Indonesian waters; Philippines to Formosa).

Remarks: For details reference may be made to: Adam (1954), and Voss (1963). This is the most common species of the genus in the Indo-Malayan Region. The genus is badly in need of a revision. Voss (1963) has pointed out that Massy's *Loligo indica* may not be identical with this species though Adam (1954) had placed it in its synonymy. Specimens of *L. duvauceli* from the Philippines are characterised by two light organs buried in the ink sac, as is also the case in *L. oshimai* from Japan, but apparently has not been verified for Indo-Malayan specimens.

The following species of *Loligo* are also reported from the Indian Ocean, but hardly any critical study has been made to evaluate their status:—

58. ***Loligo* sp.** Massy (1916, p. 222) from Madras; Pamban, Ramnad District; Gulf of Mannar, Kilakarai; and from 'Investigator' Stn. 565 at 11° 57′ 30″ N, 98° 19′ E.

59. ***Loligo* sp.** B, Robson, 1924, pp. 653–654 from Natal Coast, South Africa.

60. ***Loligo kobiensis*** Hoyle (1885) and reported from Kolumadulu Atoll, Maldives (Hoyle, 1905) and also mentioned by Sasaki (1929, p. 116).

61. ***Loligo forbesii*** Steenstrup, 1856, p. 5, pl. 1, fig. 2.

A species known along European coast of Atlantic and Mediterranean, it is doubtfully recorded from the Red Sea (Ile Abulat) and Djibouti by Adam (1958: p. 188, pl. 50, fig. 2; 1959: p. 155, fig. 10*bis* A-C).

Genus *Sepioteuthis* Blainville, 1824

On the basis of his critical study of the Indo-Pacific genus *Sepioteuthis* Blainville, Adam (1939) has shown that the many nominal species described under this genus are referable to four species, namely, *S. lessoniana* Lesson, *S. australis* Quoy and Gaimard, *S. loliginiformes* (Ruppell and Leuckart), and *S. sepioidea* Blainville, the last-mentioned species occurring in the Western Atlantic. On the basis of this revision, only three Indo-Pacific species may be recognised, and of these *S. australis* does not occur in the Indian Ocean. *S. lessoniana* is subject to considerable variation, especially in colour from place to place which no doubt has been responsible for the descriptions of at least thirteen nominal species which are considered its synonyms.

62. ***Sepioteuthis lessoniana*** Lesson, 1830, p. 244, pl. 2 (Type locality: "Dorery").

Synonyms: *Sepioteuthis hemprichii* Ehrenberg, 1831, p. (?) (Type locality: Tor, Red Sea); *Sepioteuthis guinensis* Quoy and Gaimard, 1832, p. 72, pl. 3 (Type locality: Nouvelle-Guinee); *Sepioteuthis lunulata*

Quoy and Gaimard, 1832, p. 74, pl. 3, figs. 8–13 (Type localities: Vanikoro; Nouvelle-Guinee); *Sepioteuthis mauritiana* Quoy and Gaimard, 1832, p. 76, pl. 4, figs. 2–6 (Type locality: Ile Maurice); *Sepioteuthis sinensis* Ferussac and d'Orbigny, 1835–1848, p. 304 (Type localities: Japon; Chine); *Sepioteuthis doreiensis* Ferussac and d'Orbigny, 1835–1848, pl.3, fig. 2 (=*S. guinensis* Q. & G. and *S. lunulata* Q. & G.); *Sepioteuthis arctipinnis* Gould, 1852, p. 137, pl. 26, fig. 1 (Type localities: Ile Maui, Ile Sandwich); *Sepioteuthis brevis* Owen, 1881, p. 137, pl. 26, fig. 1 (Japanese Sea); *Sepioteuthis neoguinaica* Pfeffer, 1884, p. 4, fig. (Type locality: Nouvelle-Guinee); *Sepioteuthis indica* Goodrich, 1896, p. 5, pl. 1, figs. 9–19 (Type locality: Andaman Islands); *Sepioteuthis sieboldi* Joubin, 1898, p. 27 (Type locality: Waigeou, Japon); *Sepioteuthis malayana* Wülker, 1913, p. 478, figs. 7 *a-f* (Type localities: Sumatra; Sabang, Poeloe We; Celebes; St. Mathias; Samoa); *Sepioteuthis krempfi* Robson, 1928, p. 28, figs. 3–4 (Type localities: Poelo Condor; Baie de Danon a Port Dayot; Golfe de Siam); ? *Sepioteuthis* sp. Rees and Stuckey, 1952, p. 18, pl. 29, figs. 3–4.

Distribution: One of the most widely distributed loliginids in the Indo-Pacific.

Remarks: References—Sasaki (1929), Adam (1939, 1959), Voss (1963).

63. ***Sepioteuthis loliginiformis*** (Ruppell and Leuckart, 1828), pl. 6 (Type locality: Mohila, Mer Rouge).

Synonyms: Chondrosepia loliginiformis Ruppell and d'Orbigny, 1829 (as above); *Sepia loliginiformis* Ehrenberg, 1831.

Distribution: Indian Ocean (Mohila and Mersa tal Kad Yayah, Red Sea; ? Djeddah; ? Zanzibar).

Remarks: Refer also Adam (1939, 1959).

64. ***Sepioteuthis madagascariensis*** Gray, 1848, p. 80 (Type locality: Madagascar).

Remarks: Subsequent references to this species are by Tryon (1879, p. 152), Hoyle (1886, p. 27), Wulker (1913, p. 408), and Adam (1939). Adam (pp. 25–26) considers this a doubtful species.

Genus *Lolliguncula* Steenstrup, 1881.

65. ***Lolliguncula abulati*** Adam, 1955, p. 185, pl. 50, fig. 1 (Type locality: Ile Abulat, Red Sea).

Remarks: Adam (1959, pp. 152–154) has again given a description of the type material.

Genus *Doryteuthis* Naef, 1912

66. ***Doryteuthis arabica*** (Ehrenberg, 1831), p. (?) (Type locality: 'Ile Ketumbal, entre Gumpuda et Poheca, mer Rouge).

Synonyms: Pteroteuthis arabica Ehrenberg, 1831, p. (?); *Ommastrephes arabicus* Ferussac and d'Orbigny, 1835–1848, p. 353, *Distribution:* Indian Ocean (Red Sea, Gulf of Suez).

Remarks: For descriptions of this species reference is invited to Adam (1941 *d*: p. 2, pl. 1, fig. 2; 1942: pp. 3, 12; 1959: pp. 159-163, figs. 13-16).

67. ***Doryteuthis sibogae*** Adam, 1954, pp. 146–149, text-figs. 16–18; pl. 1, fig. 4 (Type locality: S.-E. Coast of Soemba Id: Holotype is from this locality).

Distribution: Indian Ocean (Soemba Id., Indonesia). Western Pacific (Siboga Stn. 193 at Baie de Sanana, Cote, orientale de Sula Besi; Cote Sud de la partie orientale de Flores, 122° 18′ E).

68. ***Doryteuthis singhalensis*** (Ortmann, 1891), p. 676, pl. 46, fig. 3 (Type locality: Ceylon).

Synonyms: Loligo singhalensis Ortmann, 1890 (as above); *Loligo singhalensis* var. *beryllae* Robson, 1928, p. 15, figs. 4–10.

Distribution: Indian Ocean (Ceylon; Sandheads, River Hooghly, Bengal; Bay of Bengal). Western Pacific (Siboga Stn. 142, and Amboine, Indonesia; Balamban, Negros, Batangas, Cebu, Onol, Mindano, Philippines).

Remarks: Adam (1939) considered *Loligo spectrum* Massy (*nec* Pfeffer) from Arakan coast as a doubtful synonym of this species. Recent descriptions are by Adam (1939, 1954), and Voss (1963). Adam (1954) opines that *D. spectrum*, *D. arabica* and *D. singhalensis* may represent geographical races of one species and on this Voss (1963) comments that much more work must be done before their status can be decided.

It may be mentioned here that at present 7 species of *Doryteuthis* are known from the Indo-Pacific: *D. arabica* (Ehrenberg, 1831); *D. spectrum* (Pfeffer, 1884), *D. singhalensis* (Ortmann, 1891), *D. bleekeri* (Keferstein, 1866), *D. sibogae* Adam, 1954; *D. pickfordi* Adam, 1954; and *D. reesi* Voss, 1962. Of the species not already discussed, *D. spectrum* (Pfeffer) is known from the Marquesas Ids., *D. bleekeri*, from Japan, *D. pickfordi* from "Cote Sud de la partie orientale de Flores, 122° 39′ E and 122° 18′ E", and *D. reesi* from Port Maricaban, Southern Luzon, Philippines.

The genus *Uroteuthis* Rehder (1945) is represented by a single species *U. bartschi* Rehder (1945: p. 22, figs. 1–3). (Type locality: Jolo Harbour, Jolo, Philippines), which has subsequently been recorded by Adam (1954) from Flores Straits (122° 39′ E). Voss (1963) has given a redescription of the type material of this species.

Suborder *OEGOPSIDA*

Family LYCOTEUTHIDAE

Genus *Lycoteuthis* Pfeffer, 1900

69. ***Lycoteuthis diadema*** (Chun, 1900), p. 532 (Type locality: South side of Benguela Current, 31° 21′ S, 15° 58′ E).

Synonym: Enoploteuthis diadema Chun, 1900 (as above). *Thanmatolampus diadema* Chun, 1903.

Distribution: Indian Ocean [This species is included here on the strength of one record indicated by Clarke (1966: p. 192, fig. 37) from th

Southern Indian Ocean close to the zone of subantarctic convergence south of Australia. Its distribution is the Westwind Drift, makes it reasonable to expect more records of the species in the Southern Indian Ocean]. Atlantic Ocean (Benguela Current; Gulf of Mexico). Pacific Ocean (West Coast of South America).

Remarks: I am in no position to comment on the species described by Robson (1924 *a*) as *Lycoteuthis* sp. A, or *Leptodontoteuthis inermis* Robson (1924 *c*) from Natal, South Africa.

Chun (1910, 1914) has given an excellent description and illustrations of this rare squid from 'Valdivia' Stns. 89 and 118 and Voss (1956) has supplemented the description with more details. Chun (1910, p. 59) has also included *Lycoteuthis Jattai* Pfeffer (1900) as a doubtful synonym of this species.

Family ENOPLOTEUTHIDAE

Genus *Enoploteuthis* d'Arbigny, 1839

70. ***Enoploteuthis dubia*** Adam, 1960, pp. 12–16, figs. 2 *a-e* (Type locality: Eylath, Gulf of Aqaba).

Remarks: On account of the partly damaged condition of the specimen Adam (1960) described this as *E. dubia* with a query. However, in a revision of the genus *Enoploteuthis*, Roper (1966) confirms *E. dubia*, as a valid species of the genus, especially as the number and arrangement of ocular light organs and the arrangement of light organs on the ventral mantle, funnel, head, and arms are as for the genus, though in the holotype the tentacles are missing and there is a dorsal attachment to the ventro-lateral buccal connectives.

Genus *Abralia* Gray, 1849

71. ***Abralia andamanica*** Goodrich, 1896, p. 9, pl. 2, figs. 38–45 (Type locality: Andaman Sea).

Synonyms: Asteroteuthis andamanica Pfeffer, 1912; *Abralia* (*Asteroteuthis*) *andamanica* Voss, 1963.

Distribution: Indian Ocean (Andaman Sea; and present records from Arabian Sea and Laccadive Sea). Pacific Ocean (Philippines; Japan and Hawaiian Islands).

Remarks: The disposition of the light organs in this species is very characteristic. There are nine or ten rows on the ventral side of the head. On the ventral periphery of the eye there are five light organs, the three in the centre being smaller (*see* Fig. 13 *c*) and those anterior and posterior to these considerably larger. As the latter two photophores are not clearly visible through the skin they are not indicated in Fig. 13 *c*. In some of the preserved specimens the arrangement of the light organs on the ventral side of the head is irregular, but if carefully examined, nine rows can be made out.

Berry (1912 *c*) has drawn attention to the close affinities of his species *A. trigonura* to *A. andamanica*. Sasaki (1929) has given a good description of *A. andamanica* from Sagami Bay, Japan. While recording and describing this species from the Philippines, Voss (1963, p. 105) remarks that "It appears that *andamanica* may be separable into several subspecies throughout its range, with one form occurring in Japan and another in the Hawaiian Islands". The larvae and adults of this species from the present collections (reported in the earlier part of this paper) are being studied in detail.

72. ***Abralia lucens*** Voss, 1963, pp. 105–111, figs. 22 and 23 (Type locality: Port Dupan, Leyte).

Synonym: Abralia (Stenabralia) lucens Voss, 1963 (as above).

Distribution: Indian Ocean (Clarke, 1967, p. 172, fig. 30) SW of Sumatra and slightly north of Christmas Id.). Western Pacific (Line Islands, Oceania; and Philippines).

73. ***Abralia renschi*** Grimpe, 1931, p. 149, figs. 1–8 (Type locality: Indes equatoriales).

Synonym: Abralia (Stenabralia) renschi Grimpe, 1931 (as above).

Distribution: Indian Ocean (Clarke, 1966, p. 172, fig. 30, has indicated the occurrence of the species off the west coast of Sumatra). Western Pacific (Stat. Koer; and Poeloe Weh of 'Siboga' Exped.).

Remarks: See also Adam (1954, pp. 152–153).

74. ***Abralia steindachneri*** Weindl, 1912, p. 271 (Type locality: Shadwan, Red Sea).

Distribution: Indian Ocean (Shadwan, and l'ile Abulat, Red Sea).

Remarks: Grimpe (1931) has placed this species in the subgenus *Stenabralia*. Adam (1942, pp. 3, 13; 1955, p. 190, pl. 50, figs. 3–4; 1959, pp. 164–165) has added to the description of this species from the Red Sea.

It may be mentioned here that Grimpe (1931) described *Abralia spärcki* from Sawrude Island, Amboina, and a redescription of this has been given by Voss (1963, pp. 112–116, figs. 24 and 25), who also records it from "Bagacay Bay, Escarpada Id., Naranjon between Samar and Masbate" in the Philippines. It will not be surprising if this species is also encountered in the Indian Ocean.

Genus *Abraliopsis* Jouhin, 1896

75. ***Abraliopsis gilchristi*** (Robson, 1924 *a*), pp. 3–4; 1924, pp. 601–606, pl. 1, fig. 1, and text-figs. 6–7 (Type locality: Off Natal Coast, South Africa).

Synonyms: Abralia gilchristi Robson, 1924 *a*; ***Enoploteuthis noezelanica*** Dell, 1959.

Distribution: Indian Ocean (Off Natal Coast, South Africa; Present records from the Arabian Sea and the Laccadive Sea reported in the earlier part of this paper). Pacific Ocean (Off Kahu Rocks, east coast of Wellington, New Zealand).

Remarks: A detailed study of the larvae, juveniles and adults of this species collected during cruises of R. V. *VARUNA* is being carried out, Dell (1959) was wrong in describing the specimen from New Zealand under *Enoploteuthis*. His description and drawings of the specimen (pp. 6–8, figs. 11–13) clearly indicate that he was dealing with a species of *Abraliopsis*. Roper (1966) has also commented on this and he remarks that "According to Voss (personal communication) the species is *A. gilchristi* (Robson)".

76. ***Abraliopsis morisii*** (Verany, 1837), pp. 2, 100, pl. 2 *a*.

Synonyms: *Onchoteuthis morisii* Verany, 1837; *Abralia morisii* Gray, 1849; *Abraliopsis morisii* Adam, 1954.

Distribution: Indian Ocean ['Valdivia' Stns. 254 (0° 29′ S, 42° 47′ E), 256 (1° 49′ N, 45° 29′ E), and 265 (6° 24′ N, 49° 31′ E) from off Somalia Coast, East Africa; and Agulhas Bank, South Africa]. The species is also known from the Atlantic and the Mediterranean, and Adam (1954) records it from 3 'Siboga' stations (210 *a*, 214, 297) from Indonesian waters (Western Pacific).

Remarks: Chun (1914, p. 78) considers *A. hoylei* and *A. lineata* as synonyms of *A. morisii*. Until a revision of the genus on a global basis is carried out, it will be better to list these two nominal species, also known from the Indian Ocean, separately.

77. ***Abraliopsis hoylei*** (Pfeffer, 1884), p. 17, pl. 3, figs. 22, 22 *a*, 22 *b* (Type locality: Mascarenes).

Synonym: *Enoploteuthis Hoylei* Pfeffer, 1884 (as above).

Distribution: Indian Ocean (Clarke, 1966, p. 175, fig. 31 has indicated the two localities in the Indian Ocean, south of the Equator from where this species has been recorded).

78. ***Abraliopsis lineata*** (Goodrich, 1896), p. 10, pl. 3, figs. 46–50 (Type locality: Bay of Bengal).

Synonym: *Abralia lineata* Goodrich, 1896 (as above).

Distribution: Indian Ocean (North of Andamans, and off Orissa Coast, Bay of Bengal).

It should be mentioned here that larval stages and juveniles of *Abraliopsis* have been given specific names by some authors. Chun (1914, p. 78) lists the following: *Teleoteuthis carribbaea* Jatta (1896, pp. 100–102, pl. 13, figs. 35–41); *Micrabralia lineata* Pfeffer (1900, p. 167); and *Compsoteuthis Lönnbergi* Pfeffer (1900, p. 167); Chun (1910, pls. 6 & 7) has illustrated the '*Micrabralia*-Stage' and the '*Compsoteuthis*-Stage'.

Genus *Thelidioteuthis* Pfeffer, 1900

79. ***Thelidioteuthis alessandrinii*** (Verany, 1851), p. 99, pl. 35, figs. *f–h* (Type locality: Mediterranean).

Synonyms: *Loligo alessandrinii* Verany, 1851 (as above); *Enoploteuthis polyonyx* Troschel, 1857; *Abralia megalops* Verrill, 1883; *Enoploteuthis pallida* Pfeffer, 1884; *Calliteuthis alessandrinii* Appellöf, 1889; *Thelidioteuthis polyonyx* Pfeffer, 1900.

Distribution: Indian Ocean ('Valdivia' Stations 218, 223, and 235; Present record from R. V. *VARUNA* collections from the Arabian Sea and the Laccadive Sea). Pacific Ocean (Indonesia; Japan; Polynesia). Atlantic Ocean and Mediterranean.

Remarks: The larvae and adults of this species obtained during R. V. *VARUNA* cruises are being studied in detail.

Descriptions of the species are available in Degner (1926), Sasaki (1929), and Chun (1910, 1914—juveniles).

Genus *Pterygioteuthis* Fischer, 1895

80. ***Pterygioteuthis giardi*** Fischer, 1895, p. 205, pl. 9.

Synonyms: Pterygioteuthis margaritifera Ruppell. juv. Pfeffer, 1900; *Pterygioteuthis* sp. Chun, 1903; *Pyroteuthis* (*Pterygioteuthis*) *giardi* Pfeffer, 1912.

Distribution: Indian Ocean ['Valdivia' Stns. 215 (7° 1' N, 85° 56' E), 217 (4° 56' N, 78° 15' E), and 218 (2° 29' N, 76° 47' E); and from Agulhas Bank area—*See* Clarke, 1966, p. 181, fig. 33]. Pacific Ocean, Atlantic Ocean and Mediterranean Sea.

Family OCTOPODOTEUTHIDAE

Genus *Octopodoteuthis* Ruppell, 1884.

I have not been able to consult Ruppel's work in original, but note that Chun (1910, 1914), Sasaki (1929), and Thiele (1935) have used the generic name *Octopodoteuthis* Ruppell and not *Octopodoteuthis* Krohn 1845, for the species *Octopoteuthis sicula* Ruppell. I have followed Thiele (1935) in placing this species under the genus *Octopodoteuthis*, though recently Adam (1952), Voss (1936) and Clarke (1966) have treated it as *Octopoteuthis sicula* Ruppell.

81. ***Octopodoteuthis sicula*** (Ruppel, 1844), p. 135 (Type locality: Messina).

Synonyms: Octopoteuthis sicula Ruppell, 1844 (as above); *Verania sicula* Krohn, 1847; *Onychoteuthis* (*Verania*) *sicula* Verany, 1851; *Octopodoteuthis* Chun, 1910.

Distribution: Worldwide from warm and temperate seas. In Indian Ocean larvae have been recorded from four 'Valdivia' stations: 102 (34° 31' S, 26° 0' E, Agulhas Current), 190 (0° 58' S, 99° 43' E west of Sumatra), 215 (7° 1' N, 85° 56' E Indian North Equatorial Current), and 271 (13° 2' N, 46° 41' E, Gulf of Aden).

Genus *Octopodoteuthopsis* Pfeffer, 1912

82. ***Octopodoteuthopsis* sp.** Robson, 1924 *a*, p. 4; 1924 *b*, pp. 606-607, pl. 1, fig. 2, text-fig. 3.

Distribution: Known from SS 'Pickle' Stn. 347 off Cape Town, South Africa.

Remarks: Robson (1924 *b*) has pointed out that his specimen differs from *Octopodoteuthopsis megaptera* Verrill, and *Cucioteuthis*,

Genus *Taningia* Joubin, 1931

83. ***Taningia danae*** Joubin, 1931 (Type locality: Atlantic at 14° 52′ N, 28° 04′ W),.

Synonyms: ? *Enoploteuthis molinae* Harting, 1861 (*nec* d'Orbigny); *Cucioteuthis unguiculatus* Joubin.

Distribution: Indian Ocean and Atlantic Ocean.

Remarks: Records from the Indian Ocean are by Harting (1861) and by Clarke (1966) from off Durban, South Africa.

The genus *Cucioteuthis* Steenstrup (1882) which is also a representative of the family Octopodoteuthidae is represented by a single species *C. molinae* (d'Orbigny, 1845) (= *C. unguiculata* Steenstrup, 1882) may have a cosmopolitan distribution, as it has been recorded from the Pacific by Hoyle (1886) and Mediterranean by Joubin (1900). Specimens have been obtained from the stomach contents of whales.

Family ONYCHOTEUTHIDAE

Genus *Onychoteuthis* Lichtenstein, 1818

84. ***Onychoteuthis banksii*** (Leach, 1817), p. 141 (Type locality: ?).

Synonyms: *Loligo banksii* Leach, 1817 (as above; 1818, p. 13), pl. 18, fig. 7; *Onychoteuthis aequimanus* Gabb, 1868; *Onykia angulatus* Lesueur, 1821; *Loligo angulatus* Ferussac, 1823; *Onychoteuthis angulata* d'Orbigny, 1826; *Loligo bartlingii* Lesueur, 1821; *Onychoteuthis bartlingii* Gray, 1849; *Onychoteuthis bergii* Lichtenstein, 1818; *Loligo bergii* Blainville, 1823; *Onychoteuthis bergii*, Middendrof, 1849; *Loligo bianconii* Verany, 1846; *Ommastrephes bianconii* Gray, 1849; *Onychoteuthis borealijaponicus* Okada, 1927; *Teleoteuthis caroli* Joubin, 1900; *Loligo felina* Blainville, 1823; *Onychoteuthis felina* d'Orbigny, 1826; *Onychoteuthis fleuryi* Renaud, 1830; *Onychoteuthis fusiformis* Gabb, 1862; *Onychoteuthis krohnii* Verany, 1846; *Teleoteuthis krohnii* Carus, 1889; *Teleonychoteuthis krohnii* Pfeffer, 1900; *Ancistroteuthis lichtensteinii* (partim) Jatta, 1896; *Loligo lessonii* d'Orbigny, 1826 (*nomen nudum*); *Onychoteuthis lessonii* Lesson, 1830; *Onychoteuthis lobipennis* Dall, 1872; *Enoploteuthis margaritifera* (partim) Jatta, 1896; *Onychoteuthis molinae* Lichtenstein, 1818; *Onychoteuthis raptor* Owen, 1881; *Onychoteuthis rutilus* Gould, 1852; *Teleonichoteuthis rutilus*, Jatta, 1904; *Loligo uncinata* Quoy and Gaimard, 1824; *Onychoteuthis uncinata* d'Orbigny, 1826; *Onychoteuthis* sp. Hoyle, 1906, Robson, 1921.

Distribution: Cosmopolitan. The up-to-date records of this species from the Indian Ocean has been shown by Clarke (1966: p. 142, fig. 19).

Remarks: As would be seen from the list of synonyms, this species has been dealt with by several authors. For detailed synonymy reference is invited to Adam (1952), who has also given a description of the species. Recent descriptions are also given by Voss (1956, 1963). Records from the Indian Ocean are by Goodrich (1896), Pfeffer (1912) and Rees (1949).

Genus *Onychia* Lesueur, 1821 (as *Onykia*)

85. ***Onychia caribaea*** Lesueur, 1821, p. 98 (Type locality: ?).

Synonyms: *Onykia carribaea* Lesueur, 1821 (as above); *Teleoteuthis* (*Onychia*) *agilis* Verrill, 1885; ? *Loligo laticeps* Owen, 1836; ? *Ommastrephes laticeps* d'Orbigny, 1835–1848; ? *Onychia cardioptera* Gray, 1849; ? *Loligo plagioptera* Eydoux and Souleyet, 1852.

Distribution: Cosmopolitan in tropical and temperate seas. In the Indian Ocean, Pfeffer (1912) records this species from off Zanzibar and from the northern part of the Bay of Bengal. Clarke (1966: p. 150, fig. 22) indicates an additional record from the Agulhas Bank area off South Africa.

Remarks: Voss (1956) has shown that *T.* (*O.*) *agilis* which was considered by Pfeffer (1912) to be distinct from are conspecific. Pfeffer (1912) listed two other species under the genus, namely, *O. intermedia* and *O. appellöfi*.

It may also be mentioned here that Robson recorded (1921) *Onychoteuthis* sp. (young specimens) from between Maldives and Chagos; and Salomon and Diego Garcia, Chagos, remarking that "These examples are very immature, but they exhibit considerable resemblance to young examples of this species figured by Pfeffer". He also records *Teleoteuthis* sp. from six examples, two of which were taken from Amirante Bank, but remarks that these ".... examples have been referred to this genus with much hesitation". As no drawings or descriptions of these specimens are given, their systematic position remains uncertain.

Genus *Moroteuthis* Verrill, 1881

86. ***Moroteuthis lönnbergii*** Ishikawa and Wakiya. 1914, p. 445, pls. 15, 16 (Type locality: Misaki, Japan).

Distribution: Indian Ocean (Northern and Central Indian Ocean), Pacific Ocean (Sagami Bay, Japan).

Remarks: For a detailed description of this species reference is invited to Sasaki (1929: pp. 235–237, pl. 20, fig. 13, text-fig. 119). It is recorded by Filippova (1967) from the Indian Ocean.

87. ***Moroteuthis robsoni*** Adam, 1962

Synonym: *Moroteuthis* sp. A. Robson, 1924 *a*, p. 2; 1924 *b*, pp. 595–599, figs. 1, 2.

Distribution: Indian Ocean (Off South Africa).

Remarks: Robson (1924) obtained one adult from S.S. 'Pickle' Stn. 530 off Cape Town, which was given a specific name by Adam (1962). Clarke (1966: p. 146, fig. 21) records this species as an important item in the diet of the sperm whales caught off Durban, S. Africa.

88. ***Moroteuthis robusta*** (Verrill, 1876), p. 236 (Type locality: Off Alaska).

Synonyms: *Ommastrephes robusta* Verrill, 1876 (as above); *Onychoteuthis robusta* Verrill, 1880; *Lestoteuthis robusta* Verrill, 1880; *Ancistroteuthis robusta* Steenstrup, 1882.

Distribution: Indian Ocean (Doubtful. *See* Remarks). Pacific Ocean (South of Tsugaru Straits and off Abashiri and Muroran, Hokkaido; Bering Sea; Northern parts of North Pacific and California Current).

Remarks: According to Clarke (1966) "A large squid identified from a description of this species was seen off South India" by Baccialona, 1919. La calmar a griffes. *Riviera Scient.*, **6** (2): 104–105.

Genus *Tetronychoteuthis* Pfeffer, 1900

89. ***Tetronychoteuthis dussumieri*** (d'Orbigny), 1839 (Type locality: North of Mauritius, obtained from stomach of dolphin).

Synonyms: *Tetronychoteuthis* sp. Robson, 1926 *c*; ? *Tetronychoteuthis massaye* Pfeffer, 1912 (probably young of this species).

Distribution: Indian Ocean (North of Mauritius and off South Africa). Atlantic Ocean (Off Cape Town; and from 48° N, 15° W).

Remarks: Clarke (1966) has obtained a number of specimens from the stomachs of sperm whales caught off Saldanha Bay and Durban, South Africa.

The family Gonatidae is presently known from two genera, *Gonatus* Gray (1849) and *Gonatopsis* Sasaki (1920) and the known species are subarctic or circumpolar (Northern Hemisphere) in distribution. However, recently Dell (1959) has recorded *Gonatus fabricii* (Lichtenstein, 1818) from New Zealand waters. This species is known to occur in the northern parts of North Pacific, Bering Sea, Southwards from Alaska to California, North Atlantic and the Mediterranean. It is not unlikely that members of this family may be represented in the Indian Ocean sector of the Antarctic.

Adam (1950) described a new family Pholidoteuthidae, with a new genus and species, *Pholidoteuthis boschmai* from 'Snellius' Station 192 (5° 58′ N, 121° 32′ E). A second new species of the genus has been described by Voss (1956) as *Pholidoteuthis adami* from the Upper Gulf of Mexico east of the Mississippi Delta and off the coast of Texas. The family is likely to be represented in the Indian Ocean as well.

Family ARCHITEUTHIDAE

Genus *Architeuthis* Steenstrup, 1857

90. ***Architeuthis sancti-pauli*** Velan, 1877 (Type locality: St. Paul Island, Southern Indian Ocean).

Distribution: Indian Ocean (St. Paul Island).

91. ***Architeuthis*** sp. Clarke, 1966, p. 98.

Remarks: Clarke (1966) records this from the stomachs of sperm whales caught near Durban Bay and Saldanha Bay, South Africa.

A number of species of *Architeuthis* have been described from the different oceans under different generic names (*Megaloteuthis* Kent, 1874; *Dinoteuthis* More, 1875; *Megateuthis* Hilgendrof, 1880; *Plectoteuthis* Owen, 1881; and *Dubioteuthis* Joubin, 1900), and Bruun (1945) made an attempt to bring together all information known about these giant squids and gave it under one specific name, *Architeuthis dux* Steenstrup, the genotype. In addition to strandings, Clarke (1966) reports on material taken from the stomach-contents of sperm whales. Much remains to be known about these giant squids.

Family HISTIOTEUTHIDAE

Genus *Histioteuthis* d'Orbigny, 1839

92. ***Histioteuthis bonelliana*** (Ferussac, 1835), taf. 66 (Type locality: Western Mediterranean at Nice).

Synonyms: *Cranchia Bonelliana* Ferussac, 1835 (as above); *Histioteuthis Ruppellii* Verany, 1851; *Histioteuthis collinsi* Verrill, 1879; *Histioteuthis atlantica* Hoyle, 1885.

Distribution: Indian Ocean (S.S. 'Pickle' Stations 343 and 542 off South Africa; South of Madagascar; South-west Australia). Atlantic and Mediterranean.

Remarks: Specimens were described from South African waters by Robson (1924 *b*, 1926 *c*), and the Southern Indian Ocean by Thiele, 1921 (p. 452 from South of Madagascar); and Dell, 1959.

The nomenclature and status of several of the histioteuthid squids are steeped in confusion and this has been repeatedly drawn attention to by various authors (Chun, 1910; Pfeffer, 1912; Dell, 1952; Voss, 1956, 1963). Pfeffer's (1912) monographic review gives a diagnosis of what may be considered the typical *Calliteuthis* which has three rows of light organs on the ventral arms, a large broad row lodged ventrally and with one row of light organs in the remaining arms. Attempt at further subdivision of the genus into two groups (on the nature of the rings of the arms and the tentacular suckers) *Calliteuthis* and *Stigmatoteuthis* has been an artificial one leading to considerable confusion. As Dell (1951) has pointed out "Practically every new species obtained requires a new generic name". According to Voss (1956), the many specimens referred to *Calliteuthis* and *Stigmatoteuthis* by different workers may well belong to a single variable species showing geographical speciation. Voss (1963) opined that *Meleagroteuthis* Pfeffer (1900) should be placed in the direct synonymy of *Calliteuthis* Verrill (1880) which has priority. He further points out that "It is even possible that future study may show that all should be united under the genus *Histioteuthis*, but this step does not seem advisable at present". Until such time that a revision of the family could be undertaken, the listing of the species of *Calliteuthis* given below can be only considered provisional.

Genus *Calliteuthis* Verrill, 1880

93. ***Calliteuthis hoylei*** (Goodrich, 1896), p. 15, pl. 4, figs. 62–71 (Type locatliy: Andaman Islands).

Synonyms: *Histiopsis hoylei* Goodrich, 1896 (as above); *Stigmatoteuthis Hoylei* Pfeffer, 1900.

Distribution: Indian Ocean (Andaman Sea and Indian Ocean South Equatorial Current, Amiranti at 4° 34′ S, 53° 42′ E).

Remarks: I wish to cite here the extract from Voss's (1963) discussion pertinent to this species. He states that "Whether *Meleagroteuthis* is considered a synonym of *Calliteuthis* or a subgenus, several changes must take place. The only one pertinent to this study, however, is the specific name *hoylei*, which was first used by Goodrich for his species *Histiopsis hoylei* Goodrich, 1896. Pfeffer (1900) has shown that this species is *Stigmatoteuthis hoylei* (now *Calliteuthis hoylei*). In the erection of the genus *Meleagroteuthis* he designated (by monotypy) the type of his new genus as *hoylei*. Chun, however, in 1910 had renamed this *Calliteuthis* (*Meleagroteuthis*) *meleagroteuthis* because of the submersion of both *Stigmatoteuthis* and *Meleagroteuthis* as subgenera. Chun's nomenclature must now stand, and unfortunately the well-known *Meleagroteuthis hoylei* is ground into oblivion.... it now seems unavoidable that we call this species by the name *Calliteuthis meleagroteuthis*...." *Calliteuthis meleagroteuthis* Chun (1910) has a wide distribution in the Pacific Ocean and Eastern Atlantic.

94. ***Calliteuthis reversa*** Verrill, 1880, p. 393.

Remarks: Goodrich (1896, p. 16) has given ? *Calliteuthis reversa* Verrill. It is highly unlikely that this species occurs in the Indian Ocean as Voss (1956) mentions that it would appear to be restricted to the Northern and Western North Atlantic and the Gulf of Mexico. Chun (1914, p. 174) records 1 juv. from 6° 19′ S, 73° 18′ E, the specific status of which needs re-examination.

95. ***Calliteuthis japonica*** (Massy, 1916) (*nec* Pfeffer, 1912).

Remarks: Massy (1916, pp. 242–243) described a specimen of *Calliteuthis* from the 'Investigator' collections, Stn. 374 (Andaman Sea, 11° 37′ N, 95° 57′ E) as *Stigmatoteuthis japonica* Pfeffer. Its status is uncertain.

96. ***Calliteuthis miranda*** Berry, 1918

Remarks: Originally described from Off Victoria, Australia. A record of this is available from Southern Indian Ocean (Dell, 1959 *a*).

Genus ? *Histiochromius* Pfeffer, 1912

97. ***Histiochromius chuni*** Pfeffer, 1912 from Indian Ocean based on '*Brachioteuthis*' from Indian Ocean South Equatorial Current given by Chun (1910). *See* Thiele (1935, p. 970).

Family PARATEUTHIDAE (= ALLUROTEUTHIDAE)

Genus *Parateuthis* Thiele, 1921

98. ***Parateuthis tunicata*** Thiele, 1921

Remarks: This species is included in the list as it was described from the Indian Ocean Sector of the Antarctic (64° 29′ S, 85° 27′ E and 65° 15′ S, 80° 00′ E). The description is based on apparently juvenile specimens.

Genus *Alluroteuthis* N. Odhner, 1923

99. ***Alluroteuthis antarcticus*** Odhner, 1923

Remarks: This species was originally described from 63° 25′ S, 45° 39′ W and 64° 1′ S, 50° 30′ W. It was recorded from the Indian Ocean Sector of the Antarctic by Dell (1959 *a*) from 64° 32′ S, 75° 55′ E; 66° 35′ S, 61° 13′ E; and 63° 51′ S, 54° 16′ E. Clarke (1966) opines that *Parateuthis tunicata* Thiele (1921) may represent the juvenile stage of this species.

Family BRACHIOTEUTHIDAE

Genus *Brachioteuthis* Verrill, 1881

100. ***Brachioteuthis riisei*** (Steenstrup, 1882)

Synonyms: *Tracheloteuthis riisei* Steenstrup, 1882; *Verrilliola gracilis* Pfeffer, 1884; *Verrilliola nympha* Pfeffer, 1884; *Entomopsis velaini* Rochebrune, 1884; *Entomopsis clouei* Rochebrune, 1884; *Tracheloteuthis?* sp. Hoyle, 1886 *a*; *Entomopsis alicei* Joubin, 1900; and *Brachioteuthis riisei* Greg, 1924.

Remarks: There are four records of this species from the Indian Ocean by Hoyle (1905) and Pfeffer (1912). *See* Clarke (1966: p. 163, fig. 26).

101. ***Brachiteuthis picta*** Chun, 1910 *a* (Type locality: Benguela Current at 5° 6′ N, 9° 58′ W).

Remarks: Dell (1959 *a*) has recorded this from the Southern Indian Ocean from 43° 19′ S, 93° 56′ E. Detailed drawings of this species are given by Chun (1910, pp. 207–212, pl. 29, fig. 11; pl. 30, figs. 4 & 5; pl. 31, figs. 1–3, 5, 7 & 8; pl. 32).

Family BATHYTEUTHIDAE

Genus *Bathyteuthis* Hoyle, 1885

102. ***Bathyteuthis abyssicola*** Hoyle, 1885, p. 272, fig. 108 (Type locality: Between Morion Island and Isles Crozets; Southern Indian Ocean).

Synonyms: *Benthoteuthis megalops* Verrill, 1885

Distribution: Indian Ocean [‘Valdivia’ Stations 207 (5° 23′ N, 94° 48′ E), 217 (4° 56′ N, 78° 15′ E), and 221 (4° 5′ S, 73° 24′ E); ‘Investigator’ Stations 393 (7° 21′ 6″ N, 85° 7′ 15″ E), and 426 *a* (9° 8′ N, 87° 25′ E) from the Bay of Bengal; and three R.S.S. ‘Discovery’ records (South of Agulhas Bank off South Africa; South-east of Madagsacar; and off Somali Coast, E. Africa] given by Clarke (1966: p. 168, fig. 28). Atlantic Ocean (East Coast of United States; Gulf of Mexico; Gulf of Panama).

Remarks: On the basis of the date of publication of the descriptions of *B. abyssicola* Hoyle and *B. megalops* Verrill, Chun (1910, p. 186) considered the latter to have priority as it was published in ‘April 1885’ and Hoyle's account in May 1885’. Later authors have considered *B. abyssicola* Hoyle as valid. Voss (1956) who had examined the type of Verrill's *Benthoteuthis megalops* could not find any light organs present in the species, while this has been reported for some of the Indian Ocean material (Chun, 1910; Massy, 1916). Hoyle's description also does not mention any light organs. Apparently, as Voss (1956) has pointed out, two species may be confused in literature as the presence or absence of light organs may be considered to be of at least specific importance.

Genus *Ctenopteryx* Appellof, 1889

103. ***Ctenopteryx sicula*** (Verany), 1851, p. 75, pl. 27 (Type locality: Messina, Mediterranean).

Synonyms: Sepioteuthis sicula Verany, 1851 (As above); *Chtenopteryx fimbriatus* Appellof, 1889; *Chtenopteryx cyprinoides* Joubin, 1894; *Calliteuthis neuroptera* Jatta, 1896; *Ctenopteryx sicula* Pfeffer, 1900; *Ctenopteryx cyprinoides* Joubin, 1900; *Ctenopteryx neuroptera* Jatta, 1904.

Distribution: Indian Ocean (Northern and Central parts); Mediterranean and N. Atlantic.

Remarks : Refer also Chun (1910, pp. 199–201, pl. 27, figs. 9–11); Degner (1926, pp. 5–7, fig. 1), and Adam (1967, p. 72). Filippova (1967) records this species from the Indian Ocean.

Genus *Indoteuthis* Grimpe, 1922

104. ***Indoteuthis minima*** (Robson, 1921), p. 432, pl. 65, fig. 2 (Type locality: One example, sex indeterminate from between Alphonse and Providence Island from 900 fathoms).

Synonym: Chunoteuthis minima Robson, 1921 (as above).

Distribution: Indian Ocean (Known only from Type locality).

Remarks: Robson's genus *Chunoteuthis* (Robson, 1921, p. 432) is preoccupied by the Octopoda genus *Chunioteuthis* Grimpe (1916) and as such *Indoteuthis* was proposed for it by Grimpe (1922). The systematic position of the species itself is highly problematic. At first sight, the illustrations of the species given by Robson would appear to be that of a juvenile specimen, but he remarks that 'The adult condition is testified by the length of the arms, both sessile and tentacular'. The description is wanting in specific details as "it arrived in a very shrivelled up condition, apparently having suffered desiccation at some time, and in consequence a good many of its external features have been obliterated". Its placement under the family Benthoteuthidae is thus provisional and only the rediscovery of the species will help to settle this problem.

Family OMMASTREPHIDAE

Subfamily ILLICINAE

Genus *Illex* Steenstrup, 1880

105. ***Illex illecebrosus coindeti*** (Verany, 1837), p. 94, pl. 4; 1851, p. 110, pl. 36.

*Synonyms: **Loligo coindetii*** Verany, 1837 (as above); *Ommastrephes coindetii* Tryon, 1879; *Ommastrephes* (*Illex*) *coindetii* Girard, 1890;

Illex coindetii Steenstrup, 1880; *Illex coindeti* Carus, 1890; *Illex illecebrosus coindeti* Grimpe, 1921; *Ommastrephes sagittatus* (partim) d'Orbigny, 1845; Ferussac and d'Orbigny, 1848; Gray, 1849; *Ommatostrephes sagittatus* (partim) Jeffreys, 1862; *Loligo sagittata* (partim) Blainville, 1825; *Loligo brogniartii* Blainville, 1823; *Loligo pillae* Verany, 1851; *Todaropsis veranyi* (male) Jatta, 1896.

Distribution: Indian Ocean (Red Sea). Mediterranean and Eastern Atlantic.

Remarks: Illex illecebrosus (Lesueur, 1821) and *Illex coindeti* (Verany, 1837) have been considered by some workers as two distinct species. I have followed Adam (1952) in considering the latter as a subspecies of *I. illecebrosus*, and the typical form is known from Northern Europe as far south as the English Channel; East Coast of United States; Gulf of Mexico and Cuba. A second subspecies, *I. illecebrosus argentinus* is known from the S-W. Atlantic.

Adam (1942, pp. 3, 13; 1959, pp. 165–168, figs. 17,18) recorded and described *Illex illecebrocus coindeti* from the Red Sea. There have been no subsequent records of it from the Indian Ocean. For detailed synonymy and description of this subspecies from different parts of its distributional range, reference is invited to Adam (1952: pp. 80–94, figs. 32–40) wherein he has also given a detailed comparison of the two subspecies, *I. i. illecebrosus* and *I. i. coindeti.*

Genus *Todaropsis* Girard, 1890

106. ***Todaropsis eblanae*** (Ball, 1841), p. 363, figs. 1–7 (Type locality: Dublin Bay, Irish Sea).

Synonyms: Loligo eblanae Ball, 1841 (as above); *Ommastrephes eblanae*, Gray, 1849; *Ommatostrephes eblanae* Steenstrup, 1892; *Illex eblanae* Hoyle, 1892; *Loligo sagittata* (partim) Verany, 1851; *Todaropsis veranyi* Girard, 1880; *Ommastrephes* (*Todaropsis*) *veranyi* Girard; and *Todaropsis veranii* Nobre, 1936.

Remarks: Robson (1924, p. 5; 1924, pp. 614–617) has recorded this species from South African waters off Cape Town. Subsequently, it has also been recorded from Cape Point, by Thore (1945). It is widely distributed in the Eastern Atlantic and the Mediterranean. The species is included in this list, as it is a borderline case, which could occur in the Indian Ocean Sector of South Africa as well.

Subfamily TODARODINAE

Genus *Todarodes* Steenstrup, 1880

107. ***Todarodes sagittatus*** (Lamarck, 1799)

Synonyms: Loligo sagittatus Lamarck, 1799; *Loligo todarus* Verany, 1851; *Ommastrephes sagittatus* Pfeffer, 1912; *Todarodes sagittatus* Rees and Maul, 1956.

Distribution: Indian Ocean (East Africa, off Durban, South Africa), North-Eastern Atlantic and Mediterranean.

Remarks: Clarke (1966) identified this species from the stomach-contents of sperm whales caught off Durban, South Africa. For the distribution of the species in the Indian Ocean, Clarke (1966: p. 128, fig. 13) may be referred to.

108. ***Todarodes pacificus*** Steenstrup, 1880, pp. 83, 90, fig. 1 (Type locality: Hakodate, Japan).

Synonyms: Ommastrephes pacificus Appellof, 1886; *Ommatostrephes sagittatus* var. *sloani*? Wulker, 1910; *Ommastrephes sloani* Berry, 1912; *Ommatostrephes sloani pacificus* Pfeffer, 1912; *Ommastrephes sloani pacificus* Sasaki, 1929.

Distribution: Indian Ocean (One record from west of Australia shown by Clarke (1966: p. 128, fig. 13). Pacific Ocean, especially from Japanese waters from Southern Kyushu northwards to Okhotsk Sea.

Remarks: The name *Ommastrephes sloani pacificus* is widely used in Japanese literature to indicate this species, which nomenclaturally is incorrect. This problem has been discussed at length by Voss (1963: pp. 132–133). He has shown that *sloani* is referrable to the genus *Nototodarus* for which "There appears to be a distinct cline within the species of *N. sloani*, following a curve from New Zealand through Australia, the Philippines and Hawaii. Along this curve are *sloani sloani* in New Zealand, *sloani gouldi* in Australia, *sloani philippinensis* in the Philippines and *sloani hawaiiensis* in the Central Pacific and Hawaii". At present the genus *Todarodes* is known from only two species, *T. sagittatus* and *T. pacificus.*

Genus *Nototodarus* Pfeffer, 1912

109. ***Nototodarus sloani gouldi*** (McCoy, 1888) (Type locality: Off Victoria and New South Wales, Australia).

Synonyms: Ommastrephes gouldi McCoy, 1888; *Ommastrephes sloani* (partim) Pfeffer, 1912.

Remarks: Berry (1918) records this from the Indian Ocean Sector off Western Australia. There appears to be no definite records of this from the Indian Ocean since then.

The genus *Ornithoteuthis* of the subfamily Todarodinae presents the most interesting pattern of distribution. It is represented by two species, *O. volatilis* (Sasaki, 1915: described by Sasaki as *Ommastrephes volatilis*) from Sagami Bay, Japan, and by *O. antillarum* Adam, first described as a subspecies of *O. volatilis* from the island of Guadeloupe, in the Antilles (Adam, 1957). The latter has been shown to be specifically distinct from *O. volatilis* by Voss (1957), based on material from the Bahama Islands. It is most likely that this genus may also be represented in the Indian Ocean.

Subfamily OMMASTREPHINAE

Genus *Ommastrephes* d'Orbigny, 1839

110. ***Ommastrephes bartrami*** (Lesueur, 1821), pp. 90–92, pl. 7 (Type locality ?)

Synonyms: Loligo bartramii Lesueur, 1821 (as above); *Stenoteuthis bartrami* Verrill, 1880.

Distribution: More or less cosmopolitan being known from the tropical and warm temperate waters of the Indo-Pacific and the Mediterranean. Voss (1956) remarks that no specimens of this species have been obtained from Florida or the Gulf of Mexico.

Remarks: Records of this species from the Indian Ocean are by Pfeffer (1912) from South Africa, and (?) Robson (1921) from Chagos Islands. Its congener, *O. pteropus* Steenstrup (1885), is known from the Atlantic Ocean. A description of *O. bartrami* from the Indian Ocean based on good series of material is wanting.

The description of *Stenoteuthis bartrami* given by Robson (1921) is very incomplete and his specimens could very well have been *Symplectoteuthis oualaniensis* (Lesson).

Genus *Symplectoteuthis* Pfeffer, 1900

111. ***Symplectoteuthis oualaniensis*** (Lesson, 1830), p. 240, pl. 1, fig. 2 [Type locality: Oualan (= Kusaie, Caroline Islands)].

Synonyms: *Loligo oualaniensis* Lesson, 1830 (as above); *Loligo vanicoriensis* Quoy and Gaimard, 1832; *Loligo brevitentaculata* Quoy and Gaimard, 1832; *Ommastrephes oualaniensis* d'Orbigny, 1835; *Ommastrephes oceanicus* Ferussac and d'Orbigny, 1835–1848; *Ommatostrephes oualaniensis* Steenstrup, 1880; *Symplectoteuthis oualaniensis* Pfeffer, 1900.

Distribution: Indo-Pacific. From Indian Ocean (Red Sea; Arabian Sea; Laccadive Sea (Present collections reported in earlier part of this paper); Bay of Bengal, East of Ceylon; Off Natal coast, South Africa; off East Africa; Cocos Island; and West of Australia. The general distribution is shown by Clarke (1966: p. 114, fig. 9). Pacific Ocean (Japan, Okinawa, Taiwan, Philippines, South Seas, and west coast of South and Central America).

Remarks: Weindl (1912) first recorded this species from the Red Sea, and subsequent records of it from the Red Sea are by Adam (1942, pp. 3, 14; 1959, pp. 168–169; 1960, pp. 8–11, fig. 1). Adam (1954, p. 157) records this species from nine 'Siboga' Expedition Stations from Indonesia. Recent descriptions of this species from the Pacific Ocean are by Sasaki (1929), Voss (1963).

Roper (1963) has shown that *S. oualaniensis* bears subcutaneous photophores of the same type and in the same positions as are found in *Ommastrephes pteropus* and *Dosidicus gigas*. As its name implies, the only other recognised species of the genus, *S. luminosa* Sasaki (1915) known from the Japanese Seas, is also characterised by subcutaneous photophores, but of a smaller size than those in the species mentioned above.

112. ***Symplectoteuthis luminosa*** Sasaki, 1915, p. 144, pl. 4, figs. 7–13, text-fig. 4 (Type locality: Off Misaki, Japan); 1929, pp. 293–295, pl. 24, figs. 4 & 5, text-fig. 140.

Synonyms: *Symplectoteuthis oualaniensis* Watase, 1906 (*nec* Lesson, 1830); *Eucleoteuthis luminosa* Berry, 1916.

Distribution: Indian Ocean (Northern and Central parts); Pacific Ocean (Japanese Sea).

Remarks: Roper (1963) has commented on the light organs (subcutaneous photophores) in this species. The species is recorded from the Indian Ocean by Filippova (1967).

Genus *Dosidicus* Steenstrup, 1857

113. ***Dosidicus gigas*** (d'Orbigny, 1835)

Synonyms: Ommastrephes gigas d'Orbigny, 1835–1848; *Ommastrephes giganteus* d'Orbigny, 1835–1848; *Dosidicus Eschrichtii*, Steenstrup, 1857; *Dosidicus Steenstrupii* Pfeffer, 1884.

Remarks: This species which is known from the west coast of South America is included here only on account of a record of it from Perim Island, Red Sea by Brazier (1892), which is highly doubtful.

Rhynchoteuthis Larvae

Chun (1910) has given drawings of *Rhynchoteuthis* larvae of Ommastrephidae from the following 'Valdivia' Stations from the Indian Ocean: 125, 173, 175, 215, 228 and 236. More than one species may be present in the 'Valdivia' material of *Rhynchoteuthis* illustrated by Chun. *Rhynchoteuthis* was first described as a genus by Chun (1903) and as the name was preoccupied (*Rhynchoteuthis* d'Orbigny, 1847) Pfeffer (1908) proposed *Rhynchoteuthion* for the former. *Rhynchoteuthis chuni* Hoyle (1904) also represents *Rhynchoteuthis* stage of an Ommastrephid.

The *Rhynchoteuthis* larvae obtained during the R. V. *VARUNA* cruises from the Arabian Sea and Laccadive Sea are under sudy.

Family THYSANOTEUTHIDAE

Genus *Thysanoteuthis* Troschel, 1857

114. ***Thysanoteuthis rhombus*** Troschel, 1857, p. 70, pl. 4, fig. 12; pl. 5, figs. 1–4 (Type locality: Mediterranean).

Synonym: ? Thysanoteuthis nuchalis Pfeffer, 1910.

Remarks: The known distribution of the species would lead one to surmise that this is a cosmopolitan species of warmer waters. Voss and Erdman (1959) have given details of the distribution of this species in the Atlantic and Pacific Oceans. Very few adults have been examined and one was stranded at the Cape of Good Hope and reported on by Barnard (1934). In view of this record so close to the Indian Ocean Sector of South Africa and on account of the otherwise known distribution of the species it is included in this catalogue. Voss and Erdman (1959) remark that "Despite the paucity of records of adult specimens, this is almost certainly a common pelagic species. A preliminary examination of the cephalopods collected by the *Dana* expeditions in the North Atlantic has revealed numbers of thysanoteuthid larvae and the lack of capture of adults is probably due to their size and speed."

Genus *Cirrobrachium* Hoyle, 1904

115. ***Cirrobrachium filiferum*** Hoyle, 1904 (Type locality: Eastern Pacific at 0° 50′ N, 137° 54′ W).

Remarks: Thiele (1921) refers one specimen from the Indian Ocean collected at 25° S, 57° 7′ E to this species. However, in 1935 (p. 974) he has listed the genus *Cirrobrachium* with a query (?).

Family CHIROTEUTHIDAE

Subfamily CHIROTEUTHINAE

Genus *Chiroteuthis* d'Orbigny, 1839

Subgenus *Chirothauma* Chun, 1910

116. ***Chiroteuthis* (*Chirothauma*) *imperator*** Chun, 1910, pp. 240, 241, 281, pl. 38; pl. 39, figs. 1–10; pl. 40, figs. 2–5, 7; pl. 41; pl. 42, figs. 1–4, pl. 43, and and pl. 44, figs. 3, 6–16 (Type locality: 'Valdivia' Station 194, West of Sumatra at 'Nias-Sud-Kanal', 0° 15′ N, 98° 8′ E).

    Distribution: Indian Ocean [In addition to the type locality: 'Investigator' Stations 281 (Bay of Bengal, 11° 15′ 15″ N, 8° 7′ E), 297 (Gulf of Oman, 25° 11′ 30″ N, 57° 15′ E), and 366 (Arabian Sea, 24° 45′ N, 63° 50′ 15″ E). Pacific Ocean (Japan, Philippines and Amboine)].

    Remarks: Joubin (1924) discussed the close affinities and the status of the three species *C. picteti* Joubin (1894), *C. macrosoma* Goodrich (1896), and *C. imperator* Chun (1910). Voss (1963) has also suggested that there is a great possibility that *C. macrosoma* and *C. imperator* may be synonyms of *C. picteti*, but only an examination of the types will help to settle this problem. Hence *C. macrosoma* is listed separately in this account.

117. ***Chiroteuthis* (*Chirothauma*) *macrosoma*** Goodrich, 1896, p. 12, pl. 3, figs. 51–57 (Type locality: 12° 50′ N, 81° 30′ E in the Bay of Bengal).

118. ***Chiroteuthis pellucida*** Goodrich, 1896, p. 14, pl. 4, figs. 58–61 (Type locality: Bay of Bengal).

Larvae of *Chiroteuthis*:

1. ***Planctoteuthis***—Stage: Pfeffer, 1912; Robson, 1924, as *Chiroteuthis, Doratopsis* Stage A from Durban, South Africa.
2. ***Doratopsis sagitta*** Chun, 1908 from North Atlantic and Indian Ocean (30° 6′ S, 87° 50′ E).
3. ***Doratopsis exophthalmica*** Chun, 1908; 1910, p. 290 from Southern Indian Ocean at 34° 13′ S, 80° 30′ E; Robson, 1921, p. 434, from between Peros and Salomon, Chagos Islands, Indian Ocean.

The family Valbyteuthidae was created by Joubin (1931) to accommodate an unusual squid he described from the Bay of Panama as *Valbyteuthis danae* in 1931. The family has been listed by Thiele (1935). However, recently Roper and Young (1967) have shown that *Valbyteuthis* does not warrant inclusion in a separate family, but should be placed in the Chiroteuthidae *sensu stricto*. At present *Valbyteuthis* is known from the Atlantic Ocean and the Eastern Pacific. The larval stages of *Valbyteuthis* and the 'doratopsis' type of larvae of *Chiroteuthis* resemble each other very closely. It is not unlikely that *Valbyteuthis* may be found to have a wider distribution than known at present.

Subfamily MASTIGOTEUTHINAE

Genus *Mastigoteuthis* Verrill, 1881

119. ***Mastigoteuthis cordiformis*** Chun, 1908, p. 88 (Type locality: South of Pulo Nias, Sumatra).

Distribution: Indian Ocean ('Valdivia' Station 194, South of Pulo Nias, Sumatra, 0° 15′ N, 98° 8′ E). Pacific Ocean (Java Sea; Philippines; and Suruga Bay, Japan).

Remarks: For descriptions of the species reference may be made to Chun (1910), Sasaki (1929), Adam (1954), and Voss (1963).

120. ***Mastigoteuthis glaukopsis*** Chun, 1908, p. 88; 1910, p. 233, pl. 33, figs. 1, 2; pl. 35, figs. 2, 15, 16; pl. 37, fig. 1 (Type locality: 'Valdivia' Station 261 from Indian Ocean at 4° 63′ N, 48° 37′ E). The distribution of *M. cordiformis* and *M. glaukopsis* (= *M. glaucopsis*) has been shown by Clarke (1966, p. 207, fig. 42).

121. ***Mastigoteuthis sp.*** A. Robson, 1924, p. 5; 1924, pp. 617–619, fig. 13.

Remarks: One specimen obtained from S.S. 'Pickle' Station No. 277 was described by Robson (1924), who remarks that the specimen is in a very poor condition and some of the details seen indicates its affinities to *M. flammea* Chun (1910), a species known from the South-Eastern Atlantic (Benguela Current and Guinea Current).

Family CRANCHIIDAE

Subfamily CRANCHIINAE

Genus *Cranchia* Leach, 1817

122. ***Cranchia scabra*** Leach, 1817, p. 140 (Type locality: Off the Congo, Africa).

Synonyms: Philonexis eylais d'Orbigny, 1839; *Cranchia tenuitentaculata* Pfeffer, 1884; *Cranchia hispida* Pfeffer, 1884.

Distribution: Indian Ocean ('Valdivia' Station 217 at 4° 56′ N, 78° 15′ E; Off Natal Coast, South Africa; and other records given by Pfeffer (1912) and Thiele (1921). This species has a cosmopolitan distribution being also known from tropical to warm temperate waters of the Mediterranean, Atlantic Ocean and Pacific Ocean. *See* also Clarke (1966, p. 218, fig. 46).

Remarks: Robson (1924), Sasaki (1929), Voss (1956, 1963) have given good descriptions of this species.

Genus *Liocranchia* Pfeffer, 1884

123. ***Liocranchia gardineri*** Robson, 1921, pp. 434–435, pl. 65, fig. 1; text-figs. 1 & 2 (Type locality: From off Desroches Atoll, Indian Ocean).

124. ***Liocranchia intermedia*** Robson, 1924, pp. 6–8; 1924, pp. 623–624, pl. 1, fig. 5 (Type locality: Off Natal Coast, South Africa).

Remarks: In the second paper mentioned above, Robson has added to the description of the species.

125. ***Liocranchia reinhardti*** (Steenstrup, 1856), p. 200 (Type locality: Azores, Atlantic Ocean).

Synonyms: *Leachia reinhardti* Steenstrup, 1856 (as above); *Loligopsis* (*Perotis*) *reinhardti* Tryon, 1879; *Cranchia reinhardti* Brock, 1882; *Perothis reinhardtii* Rochebrune, 1884; *Liocranchia brockii* Pfeffer; 1884; *Liocranchia* cf. *reinhardti* Pfeffer, 1884; *Cranchia brockii* Joubin, 1894; *Liocranchia reinhardti* Pfeffer, 1900; *Cranchia* (*Liocranchia*) *globosa* Berry, 1909.

Distribution: Cosmopolitan in all tropical and temperate seas. Records from the Indian Ocean are by Chun (1910) from 'Valdivia' Stations 215 (7° 1′ N, 85° 56′ E), and 217 (4° 56′ N, 78° 15′ E); from Natal, South Africa given by Robson (1924, p. 622); present records from R. V. *VARUNA* collections are given in the earlier part of this paper. *See* also Clarke (1966, p. 220, fig. 47).

126. ***Liocranchia valdiviae*** Chun, 1906, p. 84 (Type locality: Indian Ocean. First mentioned 'Valdivia' Station 182, at 10° 8′ S 97° 14′ E). Chun (1910, pp. 337–342, pl. 48, figs. 3 & 4; pl. 51, figs. 1–4, 8–14; pl. 60, figs. 7–11. In addition to 'Valdivia' Station 182 mentioned above, it is also taken from the following stations: 221 (4° 5′ S, 73° 24′ E), 226 (4° 5′ S, 70° 1′ E), 237 (4° 45′ S, 48° 58′ E), 239 (5° 42′ S, 43° 36′ E), and 258 (2° 58′ N, 46° 50′ E).

Remarks: Sasaki (1920, 1929) has recorded this species from off Kii Province, Japan. Comparing the bathymetric distribution of *L. reinhardti* and *L. valdiviae*, Robson (1924, p. 622) remarks that though both species are found in the same area, the former is found generally in depths under 1000 metres.

Genus *Pyrgopsis* Rochebrune, 1884.

According to Clarke (1966), *Pyrgopsis* is characterised by several larval characters, such as the very short arms, an elongated 'rostrum' to the head and protruding eyes. While it is likely that species of *Lechia* and *Drechselia* pass through a *Pyrgopsis*-like stage, Sasaki (1929, p. 330, pl. 27, fig. 12) has shown the presence of a hectocotylus on a male of *P. pacifica* which suggests that all species of *Pyrgopsis* are not larval forms.

127. ***Pyrgopsis pacificus*** (Issel, 1908), p. 223, pl. 10, figs. 33–44 (Type locality: Between Tahiti and Pango-Pango, South Pacific).

Synonyms: *Zygaenopsis pacifica* Issel, 1908 (as above); ? *Loligopsis zygaena* Verany, 1851; ? *Zygocranchia zygaena* Hoyle, 1909; *Euzygaena pacifica* Chun, 1910.

Distribution: Indian Ocean (Natal, South Africa). Pacific Ocean (Sagami Bay and Misaki, Sagami Province, Japan; Between Tahiti and Pango-Pango; Off Three Kings Ids; Off North Island, New Zealand). Atlantic (0° 29′ N, 18° 57′ W).

Remarks: Robson (1924, pp. 619–622) has given a brief description of the single specimen obtained off Natal, South Africa and discussed the systematic position of *P. pacifica* with the other known species of the genus. Earlier, Chun (1910) considered *Loligopsis xygaenae* Verany, *Pyrgopsis rhynchophorus* Rochebrune (1884), and *Loligopsis schneehagenii* Pfeffer (1884) as doubtful synonyms of *Euzygaena pacifica*. Pfeffer (1912, p. 657) has tried to separate these four species giving an artificial key. In view of the uncertainty as to their systematic position, one more species described under this genus from the Indian Ocean is included in this list.

128. ***Pyrgopsis rhynchophorus*** Rochebrune, 1884, p. 17, pl. 2, figs. 1–6 (Type locality: Agulhas Bank, South Africa).

Synonym: *Zygaenopsis zygaena* Pfeffer (1900).

Distribution: Indian Ocean (In addition to the type locality, also reported by Pfeffer, 1912, from St. Paul).

Remarks: As already mentioned, this species may be a synonym of *P. pacificus* (Issel, 1908).

Genus *Lechia* Lesueur, 1821

129. ***Lechia cyclura*** Lesueur, 1821, p. 90, pl. 6 (Type locality: *See* under Remarks).

Synonyms: *Loligopsis cyclurus* Ferussac, 1832; *Loligo leachii* Blainville, 1823; *Perothis pellucida* Rathke, 1832; *Loligopsis cyclura* d' Orbigny 1835–1848; and *Lechia ellipsoptera* Steenstrup, 1861.

Remarks: Lesueur (1821) mentions the habitat of this species as "Inhabits the Pacific Ocean" and adds that "This description is taken from a drawing made by Mr. Petit, from a specimen obtained in the Pacific Ocean, in lat. 37° South, and long. 33° East". This places the type locality in the south-western Indian Ocean off South Africa and not in the "Pacific Ocean". d'Orbigny (1835–1848), Gray (1849), and Steenstrup (1861) refer to its occurrence in the Indian Ocean. However, while recording two specimens of *L. cyclura* obtained from the stomach of the lancet fish *Alepisaurus ferox* from Madeira, Rees and Maul (1956) mention that "This species has rarely been captured in the Atlantic, and since it was described from the Atlantic coast of N. America by Lesueur (1821)...." There appears to be some confusion about the type locality. Other records of the species from the Atlantic Ocean are by Joubin (1920), and Voss (1960). Strangely, there appears to be no definite record of this species from the Indian Ocean, since its original description.

Genus *Sandalops* Chun, 1906

130. ***Sandalops melancholicus*** Chun, 1906, p. 86 (Type locality: South Atlantic, north of Tristan da Cunha).

Distribution: Indian Ocean (North and Central parts); South Atlantic.

Remarks: Refer also Chun (1910, p. 379, pl. 56, figs. 6–8). Filippova (1967) records this species from the Indian Ocean.

Subfamily TAONIINAE

Clarke (1966) has pointed out that most of the genera of Taoniinae may be based on various larval stages and as such the status of the genera *Taonius* Steenstrup (1861), *Megalocranchia* Pfeffer (1884), *Desmoteuthis* Verrill (1881) (Given as synonym of *Taonius* by Thiele, 1935, p. 980), and *Heliocranchia* Massy (1907) (Given as subgenus of *Hensenioteuthis* Pfeffer by Thiele, 1935, p. 982) are not settled. Adam (1962), Muus (1956), and especially Voss (1960) may also be referred to].

Genus *Crystalloteuthis* Chun, 1906

131. ***Crystalloteuthis glacialis*** Chun, 1906, p. 85; 1910, p. 272, pl. 53, figs. 2–9; pl. 54, fig. 18 (Type locality: Indian Ocean Sector of the Antarctic from 'Valdivia' station. 145, at 59° 16′ S, 40° 13′ E—West Wind Drift).

Remarks: Dell (1959) has recorded this species from the Southern Indian Ocean and the Australian Sector of the Antarctic from 44° S and 65° S respectively.

A second species of the genus, *C. behringiana* Sasaki (1920) is known from the Alleutians; La Perouse Strait; off Bering Island and off Hokkaido in the north North Pacific.

Genus *Corynomma* Chun, 1906

132. ***Corynomma speculator*** Chun, 1906, p. 85; 1910, p. 367, pl. 55; pl. 60, figs. 13–16 (Type locality: First record listed as 'Valdivia' Station. 32 at 24° 43′ N, 17° 1′ W South of Canary Islands, North Atlantic).

Distribution: Indian Ocean ('Valdivia' Station 237 at 4° 45′ S, 48° 58′ E).

Remarks: Chun (1910) considered *Liguriella podophthalma* Issel a synonym of *C. speculator*. Massy (1925) has also recorded this species from South Africa.

Voss (1960) described a new genus and species, *Carynoteuthis oceanica* from off Bermuda and remarked on the possibility of this being the adult of *Corynomma speculator*, which has been incompletely described by Chun. A graded series of specimens which may help to throw light on changes associated with growth may help to solve this problem. Incidentally, Voss (1960) has given reasons for considering *Megalocranchia abyssicola* Joubin (1924) (*nec* Goodrich, 1896) from Azores as a synonym of *Carynoteuthis oceanica*.

Genus *Teuthowenia* Chun, 1910

133. ***Teuthowenia antarctica*** Chun, 1910, pp. 376–379, pl. 54, figs. 1–5; pl. 57, figs. 3–7 (Type locality: 'Valdivia' Station 136 at 55° 57′ S, 16° 14′ E).

Synonym: '*Owenia* n. sp.' Chun, 1903.

Remarks: The inclusion of this species in the present list is only on the presumption that it could occur close to the subtropical convergence. Dell (1959) has recorded this from 64° 21′ S, 116° 02′ E; and 65° 10′ S, 109° 32′ E.

Genus *Toxeuma* Chun, 1906.

134. ***Toxeuma belone*** Chun, 1906, p. 86; 1910, pp. 380–382, pl. 56, fig. 10; pl. 58, figs. 1–5 (Type locality: 'Valdivia' Station 182 at 10° 8′ S, 97° 14′ E).

Synonym: *Cranchiidarium* Chun, 1903.

Distribution: Indian Ocean (Known from type locality only).

Genus *Megalocranchia* Pfeffer, 1884.

135. ***Megalocranchia abyssicola*** (Goodrich, 1896), p. 17, pl. 5, figs. 72–80 (Type locality: Laccadive Sea).

Synonym: *Taonius abyssicola* Goodrich, 1896 (as above).

Distribution: Indian Ocean (Laccadive Sea).

Remarks: This species is based on a single specimen, the type of which (In the Indian Museum, Calcutta) is said to be in such poor condition that nothing of value could be determined from it (Voss, 1960). Joubin's record of *Megalocranchia abyssicola* from the Azores (Joubin, 1924) is based on mis-identification as discussed by Voss (1960, p. 437).

136. ***Megalocranchia maxima*** Pfeffer, 1884, p. 24, figs. 32, 32 *a* (Type locality: Cape of Good Hope).

Synonyms: *Taonius maximus* Hoyle, 1886; *Desmoteuthis maxima* Pfeffer, 1900.

Remarks: This is included in the list as a doubtful record. *M. maxima* is known to also occur in the Japanese Seas west of Osumi Group, Kiushiu (Sasaki, 1920 and 1929, pp. 322–323, pl. 25, figs. 7–9, and text-fig. 148).

Genus *Anomalocranchia* Robson, 1924

137. ***Anomalocranchia impennis*** Robson, 1924, pp. 9–10; 1924, pp. 628–632, pl. 1, fig. 3, and text-figs. 17–20 (Type locality: Off Cape of Good Hope).

Remarks: Nothing has been added to the description of this species since it was first described from a single specimen.

Genus *Henseniotenthis* Pfeffer, 1900

138. ***Henseniotenthis joubini*** Pfeffer, 1912, pp. 747–748, pl. 48, figs. 12–16 (Type locality: 31° 7′ N, 43° 6′ W, Sargasso Sea, Atlantic Ocean).

Synonyms: *Teuthowenia* (*Henseniotenthis*) *joubini* Pfeffer, 1912 (as above); Massy, 1916, p. 245.

Distribution: Indian Ocean ('Investigator' Station 462 *a* at 9° 8′ N, 87° 25′ E in the Bay of Bengal), Atlantic Ocean.

Remarks: Massy's record of the species from the Bay of Bengal is based on a partly damaged specimen in which the tentacles are mutilated, but she has identified it on the nature of the chromatophores and the very distinctive eyes.

Genus *Taonius* Steenstrup, 1861

139. ***Taonius pavo*** (Lesueur, 1821), p. 96 (Type locality: Sandy Bay, Mass., U.S.A.).

Synonyms: Loligo pavo Lesueur, 1821 (as above); *Loligopsis pavo* d'Orbigny and Ferussac, 1839; *Desmoteuthis hyperborea* Verrill, 1881).

Distribution: It has been taken from the stomach of the Albatros *Diomedea fulginosa* at 'Valdivia' Station 146 (58° 52′ S 43° 0′ E) (Chun, 1910, p. 366). In the Pacific Ocean it is known from Northern Mindoro, Philippines and near Kashiki, Kiushiu, Japan. In the Atlantic Ocean in addition to the type locality it has been recorded from the Gulf Stream, and Madeira.

Remarks: This species has been included in this list on account of its wide distribution in the Atlantic and the Pacific and the lone record from the Indian Ocean Sector of the Antarctic. Its occurrence in other areas of the Southern Indian Ocean may be expected. For descriptions and notes on the species reference is invited to Chun (1910), Joubin (1900), Sasaki (1929), Rees and Maul (1956), and Voss (1963).

Genus *Galiteuthis* Joubin, 1898

140. ***Galiteuthis armata*** Joubin, 1898, p. 279 (Type locality: Nizza).

Distribution: Robson (1924, p. 8; 1924, pp. 627–628) reported on a specimen from off Cape Town, South Africa. In the Atlantic Ocean the species is known from the Guinea Current; and in the Mediterranean from Messina and Nizza; In the North Pacific it is known from the Kurile Chain, Bering Sea and west coast of North America.

Synonyms: Galiteuthis (*Taonidium*) *suhmii* Chun, 1910; *Galiteuthis phyllura* Berry, 1911; ? *Taonius pavo* Akimushkin, 1954.

Remarks: In view of its distributional pattern and occurrence in South Africa, this species is included in this list.

Order *OCTOPODA*

Suborder *VAMPYROMORPHA*

Family VAMPYROTEUTHIDAE

Genus *Vampyroteuthis* Chun 1903

141. ***Vampyroteuthis infernalis*** Chun, 1903, p. 88, text-fig. (Type locality: 'Valdivia' Station 65 at 1° 56′ 7″ S, 7° 40′ 6″ E from Guinea Basin, Atlantic Ocean).

Synonyms: Pickford (1949) has shown that *Danateuthis schmidti* Joubin (1929, 1937); *Hansenoteuthis lucens* Joubin (1929, 1937); *Melanoteuthis anderseni* Joubin (1931, 1937); *Melanoteuthis lucens* Joubin (1929, 1937); *Melanoteuthis schmidti* Joubin (1929, 1937) and *Retroteuthis pacifica* Joubin (1929, 1937) based on 'Dana' material represent different developmental stages of *Vampyroteuthis infernalis* Chun. So also are the types of *Cirroteuthis macrope* Berry (1911) [= *Hymenoteuthis macrope* Thiele (1916); Robson (1932)]; and *Watasella nigra* Sasaki (1920, 1929). Robson (1932) placed *Laetmoteuthis lugubris* Berry (1913, 1914) [= *Chiroteuthis* (?) sp. Berry, 1909] under a separate subfamily Laetmoteuthinae of the family Vampyroteuthidae on account of differences in the structure of the radula and other characters. Pickford (1949) remarks that "*Laetmoteuthis lugubris* is not a Vampyromorph, but the condition of the specimens discourage further attempts at identification".

Distribution: Pickford (1959) has mapped the known distribution of *V. infernalis* in all the oceans. According to this there are fifteen records from the Indian Ocean. It has been collected from several more stations in the Atlantic Ocean, but fewer stations in the Pacific Ocean. From the Indian Ocean the records are: 'Investigator' Stn. 107; 'Dana' 1928–30 Exped. Stns. 3828 V, 3909 II, 3917 IV, 3904 II, and 3933 I; 'Discovery' Stns. 1578, 1739, 1764; and 'Galathea' Stns. 190, 279, 301, 314, 318, and 471.

Remarks: Pickford (1949) has considered "*Hymenoteuthis macrope* Berry" recorded by Massy (1916) from Indian Seas (off Gulf of Mannar) as a synonym of *V. infernalis*, representing probably stage IV of this species. For detailed work on this species reference may be made to Pickford (1939 *a, b*; 1940; 1946; 1948; 1949; 1950; 1952; and 1959).

Suborder *CIRROMORPHA*

Family STAUROTEUTHIDAE

Genus *Grimpoteuthis* Robson, 1932

142. ***Grimpoteuthis grimaldii*** (Joubin), 1896, p. 247, text-fig. 7 (Type locality: N.N.W. Fayal, Azores, and Gulf of Gascony—45° 09′ N, 30° 18′ W).

Synonyms: ? *Cirroteuthis Caudani* Joubin, 1896; *Cirroteuthis grimaldi* Joubin, 1903 (As above); ? *Cirroteuthis grimaldi* Massy, 1916.

Distribution: Indian Ocean ('Investigator' Stns. 233 (13° 17′ N, 93° 10′ 25″ E); 332 (10° 21′ N, 92° 42′ 15″ E) from Andaman Sea; 333 (6° 31′ N, 79° 38′ 45″ E, S.-W. of Ceylon); 361 (13° 9′ 27″ N, 46° 45′ 15″ E from Arabian Sea); and 381 (18° 8′ N, 93° 40′ E, off Akyab, Burma). Atlantic Ocean.

Remarks: Robson (1932) is of the opinion that Massy's specimens are not correctly identified. He has drawn attention to several differences between the Indian Ocean and Atlantic material (typical form). It is likely that Massy's specimens may be specifically different from *G. grimaldii*.

Thiele (1935) considers *Grimpoteuthis* Robson a synonym of *Cirroctopus* Naef (1923).

Robson (1924, p. 690, figs. 49–50 and p. 682, fig. 51) described *Cirroteuthis* "A", and *Cirroteuthis* "B" from off Cape Town, South Africa, which he later (1932, pp. 155–156) placed under the genus *Grimpoteuthis*. Although several species have been described or assigned to the genus *Grimpoteuthis*, it is clear that the genus is badly in need of revision.

Robson (1924) also described *Cirroteuthis gilchristi* based on a single specimen from off Cape Town, South Africa, and later (Robson, 1932, pp. 158–160) he has relegated this under the genus *Chunioteuthis* Grimpe (1916).

Hoyle (1885, p. 233) described *Cirroteuthis magna* from 'Challenger' Station 146 at 46° 46′ S, 45° 31′ E between Prince Edward Id., and Crozets. Robson (1932, p. 162) doubts the generic identity of the holotype and has designated the species as *Cirroteuthis* (?) *magna* Hoyle.

Family OPISTHOTEUTHIDAE

Genus *Opisthoteuthis* Verrill, 1883

Subgenus *Teuthidiscus* Berry, 1918

143. ***Opisthoteuthis* (*Teuthidiscus*) *extensa*** Thiele, 1915, p. 573, pls. 94 and 95 (Type locality: 'Valdivia' Stn. 189 at 0° 57′ S, 99° 51′ E off west coast of Sumatra).

Synonyms: *Opisthoteuthis* sp., Chun (1903); *Opisthoteuthis extensa* Thiele (1915) (as above).

Distribution: Indian Ocean (as type locality).

144. ***Opisthoteuthis* (*Teuthidiscus*) *medusoides*** Thiele, 1915, p. 538, pls. 94 and 95 (Type locality: 'Valdivia' Stn. 243 at 6° 39′ S, 39° 30′ E off Dar-es-Salaam, E. Africa).

Synonym: *Opisthoteuthis medusoides*, Thiele (1915) (as above).

Distribution: Indian Ocean (From type locality).

Suborder *INCIRRATA*

Family BOLITAENIDAE

Genus *Japetella* Hoyle, 1885

145. ***Japetella diaphana*** Hoyle, 1885, p. 232 (Type locality: North of Papua, 147° E, 42′ S).

Synonyms: *Eledonella diaphana* Hoyle, 1886; *Boiltaena diaphana* Chun, 1911; *Chunella diaphana* Sasaki, 1920, 1929; *Iapetella diaphana* Robson, 1932; ? *Eledonella sheardi* Alan (1945).

Distribution: Cosmopolitan in deep water from tropics to warm temperate waters. In Indian Ocean (Four 'Valdivia' Stations—182, 217, 231, and 232; 'Investigator' Stn. 273 (Massy, 1916); 'Investigator' Stns. 293, and 462 *a* (Thore, 1949); 'Dana' Stations 3814 I, 3817 II, II, 3824 VI, 3828 V, IX, 3829 II, 3830 V, 3847 I, II, 3850 I, 3860 XVII, XX, 3869 V, VI, 3894 I, 3903 II, 3904 I, III, V, 3905 II, 3906 I, II, IV, 3908 II, 3909 I-V, 3912 II, 3913 I, II, 3914 II, 3915 II, 3917 II, IV, VI; 3918 III, 3919 III; 3920 IV, VII, VIII; 3921 I, II; 3922 III; 3924 II; 3925 II; 3926 I; 3928 I; and 3933 I. (Nos. in Roman indicate number of positive haul); Present records from R. V. *VARUNA* collections from the Arabian Sea and Laccadive Sea reported in earlier part of this paper.

Remarks: Thore's (1949) excellent and exhaustive work should be consulted. He has shown that Massy's (1916) one specimen from 'Investigator' station 315 South of Andaman islands (10° 6′ N, 92° 29′ E) to be *Eledonella pygmaea* and two of the three specimens she has given as *Eledonella* sp. (pp. 214–215 from 'Investigator' Stns. 293 and 462 *a*) to be *J. diaphana*. The third specimen given by Massy (1916, p. 214) as *Eledonella* sp. (Reg. No. M 8110/1 from Arabian Sea, 947 fatohms) is considered by Thore (1949) to be a specimen of *Vitreledonella richardi* Joubin. Dell (1952, p. 75) finds that *E. sheardi* Allan is superficially close to *J. diaphana*, but its position needs reviewing.

Genus *Eledonella* Verrill, 1884

146. ***Eledonella pygmaea*** Verrill, 1884, p. 145, pl. 32, fig. 2 (Type locality: 'Albatross' Stn. 2949 at 37° 12′ 20″ N, 69° 39′ W).

Synonyms: Japetella prismatica Hoyle, 1885; *Eledonella diaphana* (partim) Massy, 1916; *Eledonella massyae* Robson, 1924; (?) *Bolitaena massyae* Robson, 1932; *Bolitaena massyae* subsp. *purpurea* Robson, 1930; and *Eledonella ijimai* Sasaki, 1929.

Distribution: Cosmopolitan species known from warm and temperate seas. In the Indian Ocean is known from 'Investigator' Stn. 315 (10° 06′ N, 92° 29′ E); 'Valdivia' Stn. 190 (0° 58′ 2″ S, 99° 43′ 2″ E); and 'Dana' Stns. 3909 I, III (5° 31′ N, 80° 38′ E), 3915 I (3° 14′ N, 75° 21′ E) and 3920 (1° 06′ N, 62° 25′ E).

Remarks: For detailed description and distribution of the species reference is invited to Thore (1949, pp. 39–49, figs. 30–41).

Family AMPHITRETIDAE

Genus *Amphitretus* Hoyle 1885

147. ***Amphitretus pelagicus*** Hoyle, 1885, p. 235 (Type locality: 'Challenger' collection from 29° 55′ S, 178° 14′ W off Kermadec Island).

Synonyms: ?'*Amphitretus pelagicus* Hoyle' Thiele, 1915; *Amphitretus thielei* Robson, 1930.

Distribution: Cosmopolitan (?) from tropical to cool temperate seas. In Indian Ocean from 'Valdivia' Stn. 102 at 34° 31′ 2″ S, 26° 02′ E, from Agulhas Stream; 'Dana' Stns. 3817 III (2° 15′ S, 98° 55′ 5″ E), 3828 V (1° 42′ N, 96° 05′ E), 3903 (5° 50′ N, 93° 28′ E), 3908 III (4° 28′ N, 82° 13′ E), 3918 III (0° 35′ N, 66° 09′ E), and 3921 III, VI (3° 36′ S, 58° 19′ E).

Remarks: For detailed information on the taxonomy and distribution of this species reference is invited to Thore (1949). His studies show that except for the 'Discovery' specimen described by Robson (1930) from off Cape of Good Hope, this species is thus far known only from the Indo-Pacific. This species is rare in collections and in addition to the seven records from the Indian Ocean listed above Thore (1949) refers to five other records (2 of 'Dana' Exped., and 3 earlier records) of this species from the Pacific Ocean.

Family VITRELEDONELLIDAE

Genus *Vitreledonella* Joubin, 1918

148. ***Vitreledonella richardi*** Joubin, 1918, p. 1, text-figs. (Type locality: Monaco Exped., 1912, Stn. 3223 at 30° 50′ N, 25° 43′ E).

Synonyms: Vitreledonella Alberti Joubin, 1924; *Vitreledonella Ingeborgae* Joubin, 1929; *Vitreledonella translucida* Robson, 1930; *Vitreledonella richardi* Thore, 1949.

Remarks: This species known from the Atlantic Ocean (Joubin, 1918, 1929; Robson, 1932; Thore, 1949), and the Pacific Ocean (Thore, 1949, Dell, 1952) is listed here as Thore (1949) has indicated that one of the specimens described by Massy (1916, p. 214) as *Eledonella* sp. from the Arabian Sea belongs to *Vitreledonella richardi* Joubin. Thore's (1949) work thus indicates the occurrence of this species in all the three major oceans.

Family OCTOPODIDAE

Subfamily OZENINAE

Genus *Eledone* Leach, 1817

149. ***Eledone moschatus*** (Lamarck, 1798), p. 130 (Type locality : ? Mediterranean).

Remarks: Robson (1932) remarks that there is a specimen from the Red Sea in the Paris Museum and Wulker (1920, p. 52) records a dubious form from the Red Sea, which he is inclined to regard as *cirrosa.* In the list of synonyms on p. 259, Robson (*l.c.*) mentions this as "? *Moschites moschata* or *cirrosa* Wulker". Rees (1956) notes that *E. moschatus* is a Mediterranean species with a few rare records outside the Mediterranean from the Bay of Cadiz (Fisher and Joubin, 1907) and African Coast at Baie du Levrier, Port-E'tienne, Mauritania (Adam, 1941). However, Adam (1967, p. 74) reviewing the cephalopoda of the Mediterranean mentions that *E. moschatus* is found only in the Mediterranean and records of it from the Red Sea and the Atlantic are doubtful. In view of the uncertainty of its occurrence in the Red Sea, this species is included in the present list.

Genus *Velodona* Chun, 1915

150. ***Velodona togata*** Chun, 1915, pp. 479–485, pls. 75 & 76, text-figs. 47–50 (Type locality: 'Valdivia' Stn. 249 (?) just north of Zanzibar, East Africa).

Distribution: Indian Ocean (as type locality).

Remarks: Robson (1932, pp. 284–285) may be seen for more details.

151. ***Velodona togata*** subsp. ***capensis*** Robson, 1924, p. 655, text-figs. 30–32 (Type locality: Natal Coast, South Africa from 'Pickle' Stns. 99, 162 and 396).

Synonyms: Velodona togata var. a Robson, 1924, p. 206, fig. 207; *Velodona togata* var. *capensis* Robson, 1924 (as above).

Subfamily OCTOPODINAE

Genus *Octopus* Lamarck, 1798

Subgenus *Octopus* sensu stricto

152. ***Octopus (Octopus) aegina*** Gray, 1849, p. 7 (Type locality: ?).

Synonyms: Octopus kagoshimensis Ortmann, 1888; *Polypus granulatus* Sasaki (*nec* Lamarck) 1929; *Polypus boscii* (Lesueur) Hoyle (partim), 1904; *Octopus rugosus* Adam (*nec* Bosc), 1942; ? *Octopus dollfusi* Robson, 1928.

Distribution: Indian Ocean (Red Sea; Gulf of Suez; Karachi Coast, West Pakistan). Pacific Ocean (Kagoshima, Japan; China; Amoy; Thailand).

Remarks: Refer also Robson (1928, p. 113) and Adam (1954, pp. 166–168, fig. 30, pl. 2, figs. 2–3; 1959, pp. 171–172).

153. ***Octopus (Octopus) arborescens*** (Hoyle, 1904), p. 189, pl. 2, figs. 8, 9, and 12; pl. 3 (Type locality: Cheval Pearl Bank and Periya Paar, Gulf of Mannar, Ceylon).

Synonyms: Polypus arborescens Hoyle, 1904 (as above); *Octopus (Octopus) arborescens* Robson, 1929, pp. 151–152.

Distribution: Indian Ocean (In addition to type locality; Hulule, Mahe Atoll; Felidu Atoll, Maldives; Fadifolu Atoll; South Male Atoll, Maldives; Zanzibar Harbour; Cargados Atoll; and Ross Island, Port Blair, South Andamans).

Remarks: Refer also Hoyle (1907, p. 107); Massy (1916, p. 207); Robson (1921, p. 438, pl. 66, fig. 3; 1925, p. 104); Winckworth (1926, p. 328), and Adam (1938, pp. 11–14, fig. 4; figs. 5 B, C). Adam (1954, p. 178) records this species from 'Siboga' Stn. 282 (Nusa Besi et la pointe N.E. de Timor, 8° 25′ 2″ S—127° 18′ 4″ E) and from Sanguisiapo, Indonesian waters.

154. ***Octopus (Octopus) areolatus*** d'Orbigny, 1835–1848, p. 65 (Type locality: Japan).

Synonyms: Octopus rugosus (partim) Robson (*nec* Bosc), 1929, p. 64.

Distribution: Indian Ocean [Massy (1916) records this species from the gulf of Martaban)] Most of the records of this species are from the Pacific Ocean (Japan: Polynesia; New Guinea; Banda; Hong Kong).

Remarks: Adam (1954, pp. 177–178) considers a female specimen Robson (1929, p. 64) listed from the Birtish Museum Collections under *O.* (*O.*) *rugosus* from 'Amirante Atoll' as "var. *ovulum*" of *O. areolatus*. *Polypus ovulum* was described by Sasaki (1917) from the Tokyo Fish Market and Robson (1929, pp. 123–124, pl. 2, fig. 2) relegated it as a distinct variety of *O. areolatus*. Relevant details of the variety are:

155. ***Octopus* (*Octopus*) *areolatus*** var. ***ovulum*** (Sasaki), 1917, p. 364 (Type locality: Japan).

Distribution: Indian Ocean (Amirante Atoll; Vargat Reef, East Africa) Pacific Ocean (Japan; Macclesfield Bank, China).

Remarks: Refer also Robson (1929, pp. 123–124); Adam (1941, pp. 1–5; 1954, pp. 177–178). Robson (1929) has given a long list of synonyms, for *O.* (*O.*) *areolatus*, the status of many of which are doubtful. Voss (1963, p. 161) remarks that Dr. Pickford in her unpublished monograph on Indo-Malayan octopods considers *O. ovulum* tentatively as a synonym of *O. membranaceus* Quoy and Gaimard (1832).

156. ***Octopus* (*Octopus*) *berenice*** Gray, 1849, p. 11 (Type locality: ?).

Synonyms: Octopus berenice Gray, 1849 (as above); *Octopus rugosus* Adam (*nec* Bosc), 1934.

Remarks: It is one of the insufficiently characterised species, the type locality of which is 'unknown'. Robson (1929, p. 110) remarks that "It is practically impossible to discuss this form with any profit, as the type is in such bad condition. It seems to have affinity with *O. rugosus*, though for a young *rugosus* the web is very short. The web is more like that of *O. horridus*. The size and order of the arms differ from those of *O. horridus* and the funnel organ and locking ridge are unlike those of both *O. horridus* and *O. rugosus*. Recently, however, Adam (1954, pp. 169–170, pl. 1, fig. 7; pl. 2, figs. 4 and 5) has given a description of this species from several 'Siboga' stations and other localities from Indonesian waters from which it would appear that the species is quite common in the area and may also occur in the adjacent Indian Ocean Sector.

157. ***Octopus* (*Octopus*) *cyaneus*** Gray, 1849, p. 15 (Type locality: ? Coast of New Holland).

Synonyms: Octopus cyanea Gray, 1849 (as above); *Octopus cyaneus* Adam, 1938; *Octopus vulgaris* Goodrich (*nec* Lamarck) 1896; *Polypus cyanea* Massy, 1916; *Polypus herdmani* (*nec* Hoyle) 1916; *Octopus marmoratus* Sasaki, 1929; *Octopus horsti* Joubin, 1898; *Polypus horsti* Hoyle, 1907.

Distribution: Indo-Pacific. In Indian Ocean it is known from several localities in the Red Sea (Djeddah; Suakim; Senafir, Sherm Sheik; Ile Abulat); Zanzibar; Coetivy Atoll, Indian Ocean; Ceylon; Madras; Akyab, Burma; Port Blair, S. Andamans; Aves Id., N. Andamans; and west of Sumatra. In the Pacific Ocean it is known from Indonesian waters; and Australia to Japan; ? Hawaii.

Remarks: Refer also Robson (1929, pp. 94–98, text-figs. 21–23); and Adam (1938, pp. 5–7, fig. 2; 1954, pp. 171–172; and 1959, pp. 172–173). Robson (1929) described one variety of this species from India.

158. ***Octoptus (Octopus) cyanea*** var. ***gracilis*** Robson, 1929, p. 98 (Type locality: Madras, India).

Remarks: The variety is based on a single female which is said to differ from the *forma typica* in the very narrow oblong mantle, the width-length index of which is 46; and the colouration, which in the arms appear as unbroken sinuous lines due to the confluence of the ventral spots. In addition, the funnel is freer and the eyes more prominent.

159. ***Octopus (Octopus) defilippi*** Verany, 1851, p. 30, pl. 2, figs. D, E (Type locality: Nice, Mediterranean).

Remarks: In addition to giving a long list of synonyms, mostly pertaining to earlier descriptions of the species from the Mediterranean, Robson (1929, pp. 135–136, text-figs. 45–49) has also included in the list *Polypus defilippi* Massy (1961, p. 196), *Octopus defilippi* Winckworth (1926, p. 321), two specimens from Calcutta and one from, Masquat, Arabia. He agrees with Massy's identification of the specimens from Mergui as belonging to this species, while Winckworth's record gives very few details. He has referred the two specimens from Calcutta (male and female) to this species with great hesitation while he finds the specimens from 'Aden' very much like the Mediterranean *O. defilippi*. Robson concludes that he is inclined to believe that the species occurs in the Indian Ocean "though it is very remarkable that there are so few records of its occurrence outside the Mediterranean". The problem is not so simple, as recently Adam (1967, p. 75) considers the occurrence of *O. defilippi* in the Indian Ocean as doubtful.

160. ***Octopus (Octopus) filamentosus*** Blainville, 1826, p. 188 (Type locality: ? Mauritius).

Synonyms: ? *Octopus (Octopus) filamentosus* d'Orbigny, 1826; *Octopus aranea* d'Orbigny, 1840; *Polypus aranea* Wulker, 1913.

Distribution: Indian Ocean (Mauritius; Mozambique). Pacific Ocean (Celebes Id.; Adelaide, Australia).

Remarks: Refer also Robson (1929, p. 143). Speaking of another species, *O. niveus* Lesson, he remarks (p. 141) that "it is very closely allied to *O. filamentosus* and it may be necessary to treat it as a synonym of the latter, especially as Wulker....has obtained specimens of *filamentosus* with cirrous skin". Recently, however, Adam (1959, pp. 176–178, text-fig. 21) has considered *Octopus niveus* Ferussac (1826) *et* Lesson (1830) as a doubtful synonym of *Octopus horridus* Ferussac (1826). In view of the dubious status of *O. niveus*, and its reported widespread occurrence in the Indo-Pacific, it is listed separately in this catalogue.

161. ***Octopus (Octopus) fusiformis*** Brock, 1887, p. 601, pl. 16, figs. 1 & 2 (Type locality: Amboina).

Synonyms: *Octopus fusiformis* Brock, 1887 (as above); *Octopus pisiformis* (sic) Hoyle, 1897; *Polypus fusiformis* Massy, 1916.

Distribution: Indian Ocean (Palk Strait, S. India). Pacific Ocean (Amboina, Indonesia).

Remarks: Refer also Massy (1916, p. 203), and Robson (1929, p. 132). This species poses a nomenclatural problem. In general facies it is *Loligo*-like without fins which led Massy (1916, p. 204) to doubt whether the species may not be identical with the specimen of '*Cistopus indicus*' (d'Orbigny), the species description of which is based on two different species. Robson points out that this possibility is remote as neither of the specimens of *Cistopus* illustrated by d'Orbigny is narrow enough to suggest identity.

162. ***Octopus (Octopus) gardineri*** (Hoyle, 1905), p. 976, figs. 144 & 145 (Type locality: Hulule, Male Atoll).

Synonyms: *Polypus gardineri* Hoyle, 1905 (as above); *Octopus gardineri* Robson, 1925.

Distribution: Indian Ocean (Hulule, Male Atoll; Minicoy, Laccadives; Coetivy Island; Ceylon). Pacific Ocean (? Rotuma, Fiji).

Remarks: Hoyle (1905) suggested that *O. gardineri* could be the juvenile of either *O. fontanianua* or *O. tonganus* which view according to Robson (1929) is untenable. Regarding the Pacific record of the species Robson (1929, p. 167) remarks that "I am a little inclined to be skeptical concerning Hoyle's specimen from Rotuma (near Fiji). Seeing that *gardineri* is, as far as we know, a distinctive species, it was an astonishing coincidence that in the sets of material concurrently studied Hoyle should have obtained representatives of the same new species from two places as remote from each other as the Maldives and Rotuma!"

163. ***Octopus (Octopus) globosus*** Appellöf, 1886, p. 7, pl. 1, figs. 4 & 5 (Type locality: Japan).

Synonyms: *Octopus globosus* Appellöf, 1886 (as above); *Octopus (Octopus) globosus* Robson, 1929.

Distribution: Indian Ocean (Straits of Malacca; Kabusa Islands, Nicobar Islands; Port Blair, S. Andaman; Mergui, Burma; Bombay; ? Madras; Gopalpore, Orissa; Ceylon). Pacific Ocean (Ternate; Amboine; Batavia; Nagasaki, Japan).

Remarks: Refer also Robson (1929, pp. 93–94, fig. 20), and Adam (1938, pp. 3–5, fig. 5 A; 1954, pp. 170–171).

164. ***Octopus (Octopus) hardwickei*** Gray, 1849, p. 8 (Type locality: Indian Ocean ? Singapore).

Synonym: *Octopus hardwickei* Gray, 1849 (as above).

Distribution: Indian Ocean. Known only from the Type locality.

Remarks: Robson (1929, p. 115) has pointed out that Gray's original description of the species is defective and it has not been redescribed or recorded until Robson (*l.c.*) gave a description based on 2 specimens (male and female) from the Indian Ocean.

165. ***Octopus (Octopus) herdmani*** Hoyle, 1904, p. 187, pl. 1 (Type locality: Ceylon)

Synonyms: Polypus herdmani Hoyle, 1904 (as above); *Octopus herdmani* Winckworth, 1926.

Distribution: Indian Ocean (Galle; Periya Paar and Cheval Paar, and Pearl Banks, Gulf of Mannar, Ceylon; and Zanzibar).

Remarks: Robson (1929, p. 87) has stressed on the very close resemblance of this species to *O. cyanea*. He feels that as the type specimen of *O. herdmani* is not traceable 'the only satisfactory means of deciding whether *herdmani* should be included in the synonymy of *cyanea* are not available'. Fresh collections of topotypes to settle this question should not be difficult.

166. ***Octopus (Octopus) horridus*** Ferussac, 1826 *in* d'Orbigny, 1826, p. 144 (Type locality: Red Sea).

Synonyms: Octopus horridus Ferussac, *in* d'Orbigny, 1826 (as above); *Polypus horridus* Hoyle, 1907; *Octopus argus* Krauss, 1848; *Octopus fimbriatus* Ferussac and d'Orbigny 1835–1848 (Ruppell MS); ? *Octopus aculeatus* Ferussac and d'Orbigny, 1835–1848; ? *Octopus macropus* Goodrich (*nec* Risso; partim), 1896; *Octopus harmandi* Rochebrune.

Distribution: Indo-Pacific. Indian Ocean (Several records from the Suez Canal, Gulf of Suez and Red Sea (Savigny, 1827; Wiendl, 1912; Ferussac and d'Orbigny, 1835–1848; Ehrenberg, 1831; Issel, 1869; Robson, 1927; Boone, 1938; Hoyle, 1907; Wulker, 1920; Vaillant, 1865; Robson, 1929; Gruvel, 1936; Rees and Stuckey, 1952; Adam, 1955, 1959, pp. 176–178, fig. 21); Zanzibar (Hoyle, 1907); South Africa (Krauss, 1848); Amarantie (Robson, 1921); Maldives (Hoyle, 1905); Ceylon (Hoyle, 1904; Winckworth, 1926, 1936); Ross Id., Port Blair, S. Andaman (Adam, 1938). Pacific Ocean [(? Viet Nam (*O. harmandi*); Philippines (Voss, 1963)].

Remarks: Robson (1929) has given a taxonomic discussion on this species to which the observations made on this species by Adam (1959) may also be considered. I have not included *O. niveus* as a doubtful synonym of this species for reasons mentioned elsewhere [*see* Remarks under *O.* (*O.*) *filamentosus* Blainville]. Voss (1963, p. 163) mentions that in an unpublished monograph, Dr. Pickford has made a detailed study of the relationships of *O. horridus*, *O. filamentosus* and *O. niveus* and places the latter two in synonymy. We shall look forward for an early publication of this monograph clarifying the formidable taxonomic problems relating to *O. horridus* and other nominal species.

167. ***Octopus (Octopus) macropus*** Risso, 1826, p. 3 (Type locality: Mediterranean).

Synonyms: Octopus macropus Risso, 1826 (as above); *Polypus macropus* Hoyle, 1907; *Octopus cuvierii* d'Orbigny (? 1826) and *Octopus Leche-*

naultii d'Orbigny (? 1826) *in* Ferussac and d'Orbigny, 1835–1848, p. 18, pl. 4 and pl. 1 respectively; *Octopus macropodus* Sangiovanni, 1829; *Octopus alderii* Verany, 1851.

Distribution: Tropical and warm temperate seas throughout the world. Indian Ocean (For the several records from the Red Sea and Gulf of Suez, reference is invited to Adam (1959, pp. 174–175); Persian Gulf, East Africa; Mauritius; Ceylon; Pondicherry; Penang; Malayasia). For records from the Pacific and Atlantic Oceans and Mediterranean reference is invited to Robson (1929, p. 105).

Remarks: For further details *see* Robson (1929), Adam (1954; 1959), and Voss (1963).

168. ***Octopus (Octopus) medoria*** Gray, 1849, p. 14 (Type locality: ?).
Synonym: *Octopus medoria* Gray, 1849 (as above).

Remarks: This is one of the insufficiently characterised species and is said to be very likely *O. macropus* (Robson, 1929). Adam (1954, p. 172) has placed this tentatively as a synonym of *O. macropus*. This species is mentioned in this list on account of its unknown locality and uncertain taxonomic status.

169. ***Octopus (Octopus) membranaceus*** Quoy and Gaimard, 1832, p. 89 (Type locality: New Guinea).

Synonym: *Octopus membranaceus* Quoy and Gaimard, 1832 (as above).

Distribution: Indo-Pacific. Indian Ocean (Red Sea; East Africa). Pacific Ocean (Amboina; New Guinea; Philippines; Central Pacific and Japan).

Remarks: Robson (1929, p. 122) tentatively placed this as a synonym of *O. areolatus*. However, Adam (1941) and more recently Voss (1963) consider this as a valid species. According to Voss, Dr. Pickford in her monographic revision of the Indo-Malayan octopods (unpublished) considers this as a valid species with *O. ovulum* as a probable synonym.

170. ***Octopus (Octopus) microphthalmus*** Goodrich, 1896, p. 20, pl. 5, figs. 83 & 84 (Type locality: Port Blair, Andamans).

Synonyms: *Octopus microphthalmus* Goodrich, 1896 (as above); *Polypus microphthalmus* Massy, 1916.

Distribution: Indian Ocean (Port Blair, Andamans; Karnaphuli River, Chittagong, East Pakistan).

Remarks: Also refer Massy (1916, p. 205), and Robson (1929, pp. 89–90, fig. 17).

171. ***Octopus (Octopus) nierstrazi*** Adam, 1938, pp. 14–18, figs. 6 A, 7 A-B, 8 & 9 (Type locality: Aves Island, North Andamans).

Synonym: *Octopus nierstraszi* Adam, 1938 (as above).

Distribution: Indian Ocean (Andamans).

172. ***Octopus (Octopus) niveus*** Lesson, 1830, p. 329, pl. 1, 1*bis* (Type locality: Bora Bora Island).

Synonyms: *Octopus niveus* Ferussac *in* d'Orbigny, 1826, p. 144 (nomen nudum); *Octopus aculeatus* Goodrich (*nec* Ferussac and d'Orbigny), 1896; *Octopus macropus* (partim) Goodrich, 1896; *Polypus aculeatus* Massy, 1916.

Distribution: Indo-Pacific (Red Sea, Indian Ocean, and eastwards to Gilbert Islands and Fiji Islands).

Remarks: As discussed earlier under *O. horridus*, this species along with *O. filamentosus* may be conspecific with *O. horridus*. *See* for further remarks Voss (1963, p. 163).

Adam (1939, pp. 89–96) has also commented on the very close resemblance of specimens he described as *O. niveus* and *O. horridus* as known from literature.

173. ***Octopus* (*Octopus*) *pallida*** Hoyle, 1885, p. 223 (Type locality: New South Wales and Bass Straits, Australia).

Distribution: According to Robson (1929, p. 126) it is known from the Indo-Pacific. Hoyle (1904) records this from the Pearl Banks of Ceylon, and Massy (1916) from Persian Gulf; west of Ceylon; Palk Strait; and Madras.

Remarks: This is yet another species of *Octopus*, the taxonomy of which is steeped in utter confusion. Robson (1929) has attempted a clarification, but the status of this species in the System needs more detailed investigation.

174. ***Octopus* (? *Octopus*) *prashadi*** Adam, 1939, pp. 103–105, pl. 2, figs. 1–3, text-fig. 24 (Type locality: Port Blair, Andamans).

Synonym: *Octopus prashadi* Adam, 1939 (as above); *Polypus levis* (*nec* Hoyle) Massy, 1916.

Distribution: Indian Ocean (Andamans).

Remarks: The species is based on two specimens described by Massy (1916) as *Octopus levis* (*nec* Hoyle), which on account of the reported absence of an ink-sac, Robson (1929) placed in the genus *Benthoctopus*. Adam (1939) who had occasion to re-examine Massy's specimens found well-developed ink-sacs in the specimens which would automatically separate it from *Benthoctopus levis* (Hoyle). Adam (1939) remarks that *O. prashadi* shows several abyssal characters, but as the male is unknown, it is not possible to discuss its exact generic or sub-generic position. Hence its placement here may also be considered tentative.

175. ***Octopus* (? *Octopus*) *robsoni*** Adam, 1941, pp. 1–5 (Type locality: Gulf of Suez).

Synonyms: *Octopus robsoni* Adam, 1941 (as above); ? *Octopus areoplatus* Weindl (*nec* Ferussac and d'Orbigny), 1912.

Distribution: Indian Ocean (Gulf of Suez, Red Sea).

Remarks: Refer also Adam (1942, pp. 4, 16; 1959, pp. 178–179, pl. 9, fig. 1; text-fig. 22).

176. ***Octopus* (*Octopus*) *rugosus*** (Bosc, 1792), p. 24, pl. 5, figs. 1& 2 (Type locality: Senegal, West Africa).

Synonyms: *Sepia rugosa* Bosc, 1792 (as above); *Octopus granulatus* Lamarck, 1798; *Octopus granulatus* (partim) Goodrich, 1896; *Polypus granulatus* Hoyle, 1907.

Distribution: Cosmopolitan in tropical to warm temperate waters. From the Indian Ocean (Red Sea; Persian Gulf; Mauritius; Grand Comoros; along the Indian Coast from Kerala Coast; Rameswaram, Sandheads, River Hooghly; Madras; Andamans; Mergui; Gulf of Martaban; Makassar; Malacca Strait; Great Cocos Island).

Remarks: Pickford (1955) has shown that specimens earlier identified from Natal, S. Africa as *O. rugosus* are *O. vulgaris*. There has been confusion in the identity of these two species and it is quite likely that as experienced by Pickford (1955) in the Atlantic, there may be mis-identifications from some of the localities mentioned above. For further details reference may be made to Robson (1929, pp. 64–72), Adam (1939, 1959) and Pickford (1955).

177. ***Octopus* (*Octopus*) *taprobanensis*** Robson, 1926, p. 165, fig. 7 (Type locality: Pearl Banks, Periya Paar, Gulf of Mannar, Ceylon).

Synonyms: *Octopus taprobanensis* Robson, 1926 (as above); *Octopus* sp. Winckworth, 1926.

Distribution: Indian Ocean (Known from the type locality and Port Blair, Andamans).

Remarks: Refer also Robson (1929, p. 108, pl. 6, fig. 2), and Adam (1938, pp. 7–9, figs. 5 D-E, and fig. 3).

178. ***Octopus* (*Octopus*) *tonganus*** Hoyle, 1885, p. 225.

Synonyms: *Octopus tonganus* Hoyle, 1885 (as above); *Polypus tonganus* Massy, 1916.

Distribution: Indian Ocean (Maldives and Arabian Sea). Pacific Ocean (*see* Robson, 1929, p. 77).

Remarks: The species closely resembles *O. rugosus* and according to Robson (1929) it may be a variety of that species.

179. ***Octopus* (*Octopus*) *vulgaris*** Lamarck, 1798, p. 130 (Type locality: ?).

Synonyms: For detailed list of synonyms *see* Robson (1929, pp. 57–58).

Distribution: Cosmopolitan in all but cold seas. In the Indian Ocean it has been recorded from the Red Sea; South Africa; Mauritius; St. Paul Island; and Andaman Islands.

Remarks: Refer also Goodrich (1896), Wulker (1920), Thiele (1915) and Adam (1959).

Subgenus *Macrotritopus* Robson, 1928

180. ***Octopus* (*Macrotritopus*) *bandensis*** (Hoyle, 1885), p. 227 (Type locality: Banda, Indonesia).

Synonyms: *Octopus bandensis* Hoyle, 1885 (as above); *Polypus bandensis* Massy, 1916.

Distribution: Indian Ocean (S.-W. of Colombo from 'Investigator' Stn. 152). Western Pacific (Banda; ? Ternate).

Remarks: Refer also Massy (1916) and Robson (1929).

181. ***Octopus* (*Macrotritopus*) *elegans*** **Brock, 1887**, p. 597.

Synonyms: *Octopus elegans* Brock, 1887 (as above); *Octopus* (*Macrotritopus*) *elegans* Robson, 1929; ? *Octopus amboinensis* Brock, 1887.

Distribution: Indian Ocean (Ross Island and Port Blair, South Andamans; Avis Island, North Andamans; Soemba, Indonesia); Western Pacific (Amboina; Cream; Indonesia).

Remarks: For more details reference is invited to Robson (1929, p. 171, figs. 61 & 62), Adams (1938, pp. 18–22, figs. 10 & 11; 1954, pp. 175–177, pl. 2, fig. 7 and text-fig. 31).

Robson (1929) recognised three other subgenera of genus *Octopus*, namely, *Tritaxeopus* Owen, 1881; *Marcroctopus* Robson, 1928; and *Enteroctopus* Rochebrune and Mabille, 1889. However, these have not been recorded from the Indian Ocean.

There are a few instances where unidentified species are listed as *Octopus* sp., or *Polypus* sp., *e.g.*, Massy (1916: as *Polypus* sp. 3 forms), Adam (1938: as *Octopus* sp. A and *Octopus* sp. B), Adam (1939: as *Octopus* sp. 2 forms), etc. These are not listed here separately.

Genus *Eledonenta* Rochebrune, 1884

182. ***Eledonenta microsicya*** Rochebrune, 1884, p. 158 (Type locality: Clos-Bay, Red Sea).

Synonyms: *Eledonenta microsicya* Rochebrune, 1884 (as above); *Moschites* (*Eledone*) sp., Wulker, 1920; *Eledonenta* (? *Eledone*) *microsicya* Robson, 1929.

Distribution: Indian Ocean (Red Sea).

Remarks: Robson (1929) who re-examined the type of this species concluded that "*microsicya* is in all probability a specimen of *Eledone*, though the only specimens being female it is impossible to make certain to what species we should refer it". The smooth skin led him to suggest that it may be the same as *E. moschata*. The systematic position of the species in the System is doubtful and tentatively it is retained here under *Eledonenta*, the genotype of which *E. filholiana* Rochebrune (1884) was shown by Robson (1929) to be a species of *Octopus*. Though he suggested that *Eledonenta* be abandoned and *microsicya* be placed in *Eledone*, he himself did not do this, as may be noted from the synonym given above.

Genus *Cistopus* Gray, 1849

183. ***Cistopus indicus*** (d'Orbigny, 1840), p. 24, pl. 26 (Type locality: Celebes)

Synonyms: *Octopus indicus* d'Orbigny, 1840 (as above).

Distribution: Indian Ocean (From Bombay southwards along Indian Coast; Gulf of Mannar; Mozambique). Pacific Ocean (Poulo Condore, Vietnam; Celebes; China; Philippines).

Remarks: See Robson (1929, pp. 182–184, fig. 70), and Voss (1963, pp. 165–166). The latter author (p. 164) mentions that Dr. Pickford in her Indo-Malayan octopods (unpublished) considers *Octopus teuthoides* Robson as the young of *Cistopus indicus*.

Genus *Robsonella* Adam, 1938

184. ***Robsonella fontaniana*** (d'Orbigny, 1835), p. 28, pl. 2, fig. 5 (Type locality: Subantarctic and antiboreal region of South America).

Synonyms: *Octopus fontanianus* d'Orbigny, 1835 (as above); *Polypus fontanianus* Robson, 1921; *Joubinia fontanian* Robson, 1929; *Robsonella fontaniana* Adam (1938).

Remarks: Massy (1925) described a specimen from Natal, South Africa, which has been considered by Robson (1929) to be a local variety. Pickford (1955) after re-examining the specimens in the British Museum collections has given a lengthy discussion of the status of the genus *Robsonella* as well as its species.

185. ***Robsonella fontaniana*** var. ***africana*** (Massy), 1925 (Type locality: Natal' South Africa).

Synonyms: *Polypus fontaniana* var. *africana* Massy (As above); *Joubina fontaniana* var. *africana* Robson, 1929.

Distribution: Indian Ocean (Natal Coast, South Africa).

Genus *Scaeurgus* Troschel, 1857

186. ***Scaeurgus unicirrhus*** d'Orbigny, 1840, p. 70.

Synonyms: Refer list given by Robson (1929, p. 192).

Distribution: Mediterranean; tropical and subtropical Atlantic; Indo-Pacific.

Remarks: Refer also Adam (1967, p. 76).

Genus *Macrochlaena* Robson, 1929

187. ***Macrochlaena winckworthi*** (Robson, 1926), p. 161, figs. 1–6 (Type locality: Tuticorin, Gulf of Mannar, India).

Synonym: *Octopus winckworthi* Robson, 1926 (as above).

Distribution: Indian Ocean (Known only from Type locality).

Remarks: Refer also Robson (1929, pp. 193–195, figs. 75 & 76).

Genus *Paroctopus* Naef, 1923

188. ***Paroctopus hongkongensis*** (Hoyle, 1885), p. 224 (Type locality: Hong Kong).

Synonyms: *Octopus hongkongensis* Hoyle, 1885 (as above); *Polypus hongkongensis* Massy, 1916.

Distribution: Indo-Pacific. Indian Ocean (Andaman Sea; S. of Ceylon; Tamblegam and Venkali Reef, Ceylon; Gulf of Mannar). Pacific Ocean (Hong Kong; Inoshima Islands, Japan; Aburatsubo; Kamschatka).

Remarks: Refer also Massy (1916, p. 197), Winckworth (1926, p. 326), Channappayya (1927, p. 109), and Robson (1929, pp. 197–201, figs. 80 & 81).

Genus *Hapalochlaena* Robson, 1929

189. ***Hapalochlaena fasciata*** (Hoyle, 1886), p. 96, pl. 8, fig. 3.

Synonyms: *Octopus pictus* var. *fasciata* Hoyle, 1886 (as above); Goodrich, 1896 (p. 19, pl. 5, fig. 82); *Hapalochlaena maculosa* (partim) Robson, 1929, p. 211.

Distribution: Indo-West Pacific. Indian Ocean (Mulaku Atoll; ? Ceylon). Pacific Ocean (Australia; Ternate; Lombok; Japan).

Remarks: Adam (1939, pp. 98–100, figs. 20 & 21) has given reasons for treating *fasciata* considered by some early workers as a variety of *Octopus pictus* (= *Hapalochlaena maculosa*) as a distinct species.

Genus *Berrya* Adam, 1939

190. ***Berrya hoylei*** (Berry, 1909), p. 407, fig. 1 (Type locality: Hawaii).

Synonyms: *Polypus hoyle* Berry, 1909 (as above); 1914, p. 296, pls. 47, 48 & 55; Massy, 1916, p. 207; *Octopus hoylei* var. *annae* Robson p. 219, fig. 89.

Distribution: Indo-Pacific. In Indian Ocean ('Investigator' Stn. 379 at 28° 59′ N, 50° 3′ E from Persian Gulf; Stn. 360 at 13° 36′ N, 47° 32′ E from Arabian Sea; Stn. 464 at 6° 2′ 30″ N, 81° 29′ E South of Ceylon; and 13° 17′ 15″ N, 93° 10′ 25″ E from Andaman Sea). Pacific Ocean (Hawaii).

Remarks: Although Robson (1929) found Massy's specimens of *Polypus hoylei* to be sufficiently different from the description of Berry's specimens from Hawaii, Adam (1939, pp. 100–103, figs. 22 & 23) found that the creation of a special name for the Indian Ocean material was not necessary. However, Robson's opinion that Massy's specimens may belong to a distinct genus has found agreement with Adam, who has placed it under *Berrya*, which seems to be closely related to Bathypolypodinae.

191. ***Berrya keralensis*** Oomen, 1966, pp. 51–60, figs. 1–6 (Type locality : From 200 to 400 m dep.h off Kerala Coast, India).

Distribution : Indian Ocean (Known from deeper waters off the south-west coast of India).

Family BATHYPOLYPODINAE

I have followed Thiele (1935) in placing the following genera known from the Indian Ocean under this subfamily.

Genus *Benthoctopus* Grimpe, 1921

192. ***Benthoctopus thielei*** Robson, 1932, pp. 233–235, figs. 37–39 (Type locality: Gazelle Harbour, Kerguelen Island).

Synonyms: "*Polypus levis,* Hoyle" Thiele, 1915; (?) *Polypus levis* Theile, 1920.

Distribution: Known from only the type locality.

Remarks: Robson (1932) has given sufficient reasons to show that Thiele's specimens are different from *B. levis* (Hoyle). Both species are, however, known from very inadequate material. Perhaps, more material may throw light on their proper generic position as well. This species is included in this list as it occurs in the Indian Ocean Sector of the Antarctic close to the limits of the Southern Indian Ocean.

193. ***Benthoctopus profundorum*** Robson, 1932, pp. 237–241, pl. 4, fig. 1; text-figs. 33, 42 (Type locality: Yokohama, Japan).

Synonyms: *Octopus januarii* (partim) Hoyle, 1885; *Polypus januarii* (partim) Berry, 1912; *Benthoctopus januarii* (partim) Robson, 1929 (p. 14); ? *Polypus januarii* (partim) Massy, 1916.

Distribution: Indo-Pacific. In Indian Ocean (10° 21′ N, 92° 46′ E) and 13° 27′ N, 93° 14′ E in Andaman Sea). Pacific Ocean (Off Yokohama; Bungo Suido, Japan; Off Kii Province; Aleutian Ids.)

Remarks: The grouping of specimens from the Pacific and the Indian Ocean under this species by Robson is an artificial one. Perhaps more than one species is involved and good series of material from the different areas should help to solve this puzzle. Reference is invited to the discussion given by Robson (1932: pp. 236–237) as well.

Adam (1954, pp. 184–188) has recorded *Benthoctopus* sp. A, B, C and D from Indonesian waters. Some of the species, especially from the Indo-Pacific described under this genus are based on very inadequate material.

Genus *Teretoctopus* Robson, 1929

194. ***Teretoctopus indicus*** Robson, 1932, pp. 249–251, pl. 3, fig. 2; text-fig. 46 (Type locality: Arabian Sea, 24° 45′ N, 63° 50′ E. This is the first locality mentioned by Robson).

Synonyms: "*Polypus pricei* Berry" Massy, 1916, p. 209, pl. 28, figs. 7–8, in error; "? *Octopus pricei* (Berry)" Winckworth, 1926; "*Polypus pricei* (?)" Robson, 1929, pp. 41, 218–219; *Teretoctopus indicus* Robson, 1929, p. 608.

Distribution: Indian Ocean (Type locality from where Massy's specimens were obtained; ? Pearl Banks, Ceylon).

Remarks: Robson (1932), p. 251 has given reasons for considering Massy's specimens (*Polypus pricei* Massy) as deserving the status of a new genus and species.

195. ***Teretoctopus alcocki*** Robson, 1932, pp. 251–253, pl. 3, fig. 3; text-fig. 47 (Type locality: Andaman Sea. First mentioned locality by Robson).

Synonyms: ? *Octopus januarii* Goodrich, 1896; *Polypus januarii* (partim) Massy, 1916.

Distribution: Indian Ocean (? Andaman Sea; Bay of Bengal; and Gulf of Oman at 25° 11′ N, 57° 15′ E, and 23° 46′ N, 58° 31′ E).

Remarks: Refer also Robson (1932, pp. 240, 251–253).

Genus *Bathypolypus* Grimps, 1921

196. ***Bathypolypus valdiviae*** (Thiele, 1915), p. 485, pl. 80, text-figs. 52 & 53 (Type locality: Agulhas Bank, South Africa).

Synonyms: ? *Octopus capensis* Eydoux and Souleyet, 1852; *Polypus valdiviae* Thiele, 1915 (as above); *Bathypolypus* ? *valdiviae* Robson, 1924; *Bathypolypus grimpei* Robson, 1924; *Bathypolypus valdiviae* Massy, 1926; "Undetermined Polypods", Robson, 1924.

Distribution: Indian Ocean (Aghulas Bank; Coast of Natal and off Cape Town; Cape Point—just outside Indian Ocean limits).

Remarks: Robson (1932) has added to the description of this species and has also given a taxonomic discussion on it.

Family TREMOCTOPODIDAE

Genus *Tremoctopus* Della Chiaje 1830

197. ***Tremoctopus violaceus*** Della Chiaje, 1830, pl. 70 (Type locality: Mediterranean).

Synonyms: Robson (1932, pp. 206–208 has given a long list of synonyms.

Distribution: Cosmopolitan, known from all warm and temperate seas.

Remarks: Robson (1932, p. 208) has examined two specimens from Muscat in the British Museum Collections. Wulker (1920) found it at Cosseir in the Red Sea. Adam (1959, pp. 184–186, fig. 25) has given a description of this species from the Red Sea.

Family ARGONAUTIDAE

Genus *Argonauta* Linnaeus, 1758

198. ***Argonauta argo*** Linnaeus, 1758, p. 708 (Type locality: "Pelago, M. Indico, Mediterraneo."

Synonyms: A long list of synonyms is given by Robson (1932, pp. 181–184).

Distribution: Cosmopolitan, in warm and temperate seas.

Remarks: In the Indian Ocean it has been recorded from the Red Sea (Wulker, 1920; Adam, 1959); Cape Agulhas and Simon's Bay, South Africa (Robson, 1932). The distribution data given by Robson (1932) is provisional as he mentions that "....it is naturally uncertain if the world-wide distribution given.... is correct."

199. ***Argonauta bottgeri*** Maltzan, 1881, p. 163 (Type locality: ?).

Synonyms: Reference may be made to Robson (1932, p. 195).

Distribution : Indo-Pacific. Records from the Indian Ocean are from the Andaman Sea (Massy, 1916), Mauritius and Chagos Islands (Robson, 1932).

200. ***Argonauta hians*** Solander, 1786, p. 46 (Type locality: ?).

Synonyms: Robson (1932, pp. 192–193) gives an exhaustive list of synonyms.

Distribution: Cosmopolitan in warm and temperate seas. It occurs in the R.V. *VARUNA* plankton collections reported in the earlier part of this paper. Other records from the Indian Ocean are: Red Sea (Woodward, 1856, Robson, 1932; Adam, 1959); Perisan Gulf (Robson, 1932); Masquat (Robson, 1932).

201. ***Argonauta nodosa*** Solander, 1786, p. 96 (Type locality: ?).

Synonyms: Robson (1932, pp. 198–199) has given an exhaustive list of synonyms.

Distribution: Indo-Pacific. ? Atlantic.

Remarks: Records from the Indian Ocean are from the Mozambique and "Les Grandes Indes" (d'Orbigny, 1826; Robson, 1932).

ACKNOWLEDGEMENT

I wish to extend my sincere thanks to the undermentioned who have helped me with literature locally not available to me, without which it would not have been possible for me to complete this work: Dr. Tucker Abbott, Academy of Natural Sciences, Philadelphia; Dr. W. Adam, Bruxelles; Dr. R. K. Dell, Wellington, New Zealand; Dr. G. E. Maul, Madeira; Dr. Grace, E. Pickford, Bingham Oceanographic Laboratory, Yale University; Late Dr. W. J. Rees, London; Dr. Clyde F. E. Roper, Smithsonian Institution, Washington D.C.; and Dr. Gilbert L. Voss, Institute of Marine Sciences, Miami, Florida. I am also thankful to Mr. N. K. Prasad for his help in the preparation of the drawings.

LITERATURE CITED

ADAM, W. 1934. Cephalopoda. Result. Sci. Voy. Ind. Orient. Neerl., **2**, 16. *Mem. Mus. Roy. Hist. Nat. Belg.* (Hors Serie).

——— 1938 *a*. *Robsonella* nom. nov. 'für. *Joubinia* Robson 1929 (Cephalopoda, Octopoda). *Zool. Anz.*, **121**: 223.

——— 1938 *b*. Sur quelques cephalopodes octopodes des iles Andamans. *Bull. Mus. Hist. Nat. Belgique*, **14** (7): 1–25.

——— 1939 *a*. Notes sur les Cephalopodes. 13. Sur une nouvelle espèce de Sepia. *Sepia winckworthi* sp. nov. *Bull. Mus. r. Hist. nat. Belg.*, **15** (32): 1–11.

——— 1939 *b*. The Cephalopoda in the Indian Museum, Calcutta. *Rec. Indian Mus.*, **41**: 61–110.

——— 1939 *c*. Cephalopoda. Pt. I. Le genre *Sepioteuthis* Blainville, 1824. *Siboga Exped. Monographie*, **55** *a*: 1–33.

——— 1939 *d*. Les Cephalopodes de l'expedition du *Siboga*. Pt. II. Revision des espèces Indo-Malaises du genre *Sepia* Linné, 1758. Pt. III. Révision du genre *Sepiella* (Gray) Steenstrup, 1880. *Ibid.*, **55** *b*: 35–122.

——— 1941 *a*. Notes sur lés Céphalopodes, 16. Sur une nouvelle espéce de Céphalopode (*Octopus robsoni* sp. nov.) de la mer Rouge. *Bull. Mus. r. Hist. nat. Belg.*, **17** (52): 1–5.

——— 1941 *b*. Notes sur lés Céphalopodes, 18. Sur les espéces de Cephalopodes de la mer Rouge décrités par C. G. Ehrenberg en 1831, et sur une nouvelle espèce de *Sepia* (*Sepia dollfusi* sp. nov.). *Ibid.*, **17** (62): 1–14.

Adam, W. 1941 *c*. Notes sur les Céphalopodes. 19. A propos de *Sepia elongata* Ferussac et d'Orbigny, 1835–1848. *Ibid.*, **17** (65): 1–4.

——— 1942. Les Céphalopodes de la mer Rouge. *Bull. Inst. Océanogr. Monaco*, **822**: 1–20.

——— 1944. Révision de l' "Etude monographique de la famille des Sepiadae" d'A.T. de Rochebrune (1884). *Mem. Mus. natn. Hist. Nat. Paris, N.S.*, **18** (6): 219–242.

——— 1952. Cephalopodes. In *Exped. Oceanogr. Belg. eaux Cotières Afr. Atl. Sud.*, 1948–1949, **3** (3): 1–142.

——— 1954. Cephalopoda. Partie III & IV. Cephalopodes à l'exclusion des genres *Sepia*, *Sepiella* et *Sepioteuthis*. *Siboga Exped. Monographie*, **33** *c*: 123–193.

——— 1959. Les Céphalopodes de la mer Rouge. *Res. Sci. Mission R.P. Dollfus en Egypte* (3), **28**: -125–193.

——— 1960 *a*. Cephalopoda from the Gulf of Aquaba. Contr. Knowl. Red Sea. 16. *Bull. Sea-Fish. Res. Stn. Israel*, **26**: 3–26.

——— 1960 *b*. Notes sur les Cephalopodes. 24. Contribution a la connaissance de l'hectocotyle chez les Ommastrephidae. *Bull. Inst. r. Sci. nat. Belge*, **33** (7): 1–10.

——— 1962 *c*. Céphalopodes de l'Archipel du Cap-Vert, de l'Angola et du Mozambique. *Mems. Jta. Invest. Utramar.* (2 *a*), **33**: 1–64.

——— 1967. Cephalopoda from the Mediterranean Sea. *Bull. Sea-Fish Res. Sta. Haifa*, **45**: 65–78.

——— and W. T. Rees 1966. A review of the Cephalopod family Sepiidae. *John Murray Exped. Sci. Rept.*, **11** (1): 1–165.

Allan, J. K. 1945. Planktonic cephalopod larvae from the Eastern Australian Coast. *Rec. Aust. Mus.*, **21** (6): 317–350.

Appellöf, A. 1889. Teuthologische Beitrage. I. *Bergens Mus. Aarsbr.*, No. 3: 1–34.

Audouin, J. V. 1828–29. *Explication sommaire des planches dont les dessins out ele fournis par M.J.C. Savigny pour l'histoire naturelle de ourrage. See* J. C. Savigny 1817.

Ball, R. 1841. On a species of *Loligo* found on the shore of Dublin Bay. *Proc. R. Irish Acad.*, **1**: 362–364.

arnard, K. H. 1962. New species and records of South African marine Mollusca from Natal, Zululand and Mozambique. *Ann. Natal. Mus.*, **15**: 247–254.

Berry, S. S. 1909. Diagnoses of new cephalopods from the Hawaiian Islands. *Proc. U.S. Nat. Mus.*, **37**: 407–419.

——— 1911. Preliminary notices of some new Pacific cephalopods. *Ibid.*, **40**: 589–592.

——— 1912. The Cephalopoda of the Hawaiian Islands. *Bull. U.S. Bur. Fish.*, **32**: 257–362.

——— 1913 *a*. Notes on some west American cephalopods. *Proc. Acad. Nat. Sci. Philadelphia*, 1913, pp. 72–77.

——— 1913 *b*. Some new Hawaiian cephalopods. *Proc. U.S. Nat. Mus.*, **45**: 563–566.

——— 1914. Notes on a collection of cephalopods from the Kermadec Islands. *Trans. N.Z. Inst.*, **46**: 134–149.

——— 1916. Cephalopoda of the Kermadec Islands. *Proc. Acad. Nat. Sci. Philadelphia*, 1916, pp. 45–66.

——— 1918. Report on the Cephalopoda obtained by the F.I.S. "Endeavour ' in the Great Australian Bight and other Southern Australian localities. *Zool. (biol.) Results Fish. Exped. "Endeavour '*, 1909–1914. **4** (5): 203–298.

——— 1921. A review of the cephalopod genera Sepioloidea, *Sepiadarium* and *Idiosepius*. *Rec. South Aust. Mus.*, **1**: 347–364.

———. 1932. Cephalopods of the genera *Sepiolidea*, *Sepiadarium* and *Idiosepius*. *Philippine J. Sci.*, **47** (1): 39–53.

Blainville, H. D. de 1923. *Loligo*. *Dict. Sci. Nat.*, **27**: 126–148.

——— 1824. Memoire sur lès espéces de genre Calmar (*Loligo*, Lamarck). *J. Phys. Paris*, **96**: 116–133.

——— 1826. *Dict. Sci. Nat.*, **48**: 188.

——— 1827. *Sepia. Ibid.*, **48**: 283–285.

Bosc, L. A. 1792. Observation sur la *Sepia rugosa* (*O. rugosus* Fer.). *Act. Soc. H.N. Paris*, **1**: 24.

Brock, J. 1882. Zur Anatomie und Systematik der Cephalopoden. *Zeitschr. Wiss. Zool.*, **36**: 543–610.

Brock, J. 1887. Indische Cephalopoden. *Zool. Jb. Syst.*, **2**: 591–614.

Bruun, Anton F. 1943. The biology of *Spirula spirula* (L.). *Dana Rept.*, **24**: 1–42.

——— 1945. Cephalopoda. *The Zoology of Iceland*, 4 (64): 1–15.

Burgress, L. A. 1967. *Loliolus rhomboidalis* a new species of loliginid squid from the Indian Ocean. *Bull. Mar. Sci.*, **17** (2): 319–329.

Chiaje, S. Delle 1830. *Memoire sulla storia e notomia degli animali senza vertebre del regno di Napoli.* 5 (Napoli).

Hun, C. 1900. *Die Tiefe des Weltmeeres.* Jena, G. Fischer.

——— 1903 *a*. Ueber Leuchtorgane und Augen von Tiefsee Cephalopoden. *Verh. Dtsch. Zool. Ges.*, **13**: 67–91.

——— 1903 *b*. Rhynchoteuthis. Eine merkwurdige Jugendform von Cephalopoden. *Zool. Anz.*, **26**: 716–717

——— 1906. System der Cranchien. *Ibid.*, **31**: 82–86.

——— 1910. Die Cephalopoden. I. Teil: Oegopsida. *Wissenchaftliche Ergebnisse deutschen Tiefsee-Expedition 'Valdivia'* 1898–1899. **18**: 1–402, and Atlas of 61 pls.

——— 1915. Cephalopoda. II. Teil: Myopsida, Octopoda. *Ibid.*, **18**: 405–552, Pls. 62–95

Clarke, M. R. 1966. A review of the systematics and ecology of oceanic squids. *Advances in Mar. Biol.*, **4**: 91–300.

Cotton, B. C. 1929. Contributions to the fauna of Rottnest Islands. 4. Western Australian Sepiidae. *J. Proc. R. Soc. West. Aust.*, **15**: 87–94.

———, and F. K. Godfrey 1940. *The Mollusca of South Australia. Pt. 2. Scaphopoda. Cephalopoda, Aplacophora and Crepipoda.* Adelaide, pp. 317–600.

Dall, W. H. 1872. Descriptions of sixty new forms of Mollusks from the west coast of North America and the North Pacific Oceans, with notes on others already described. *Amer. J. Conch.*, **7**: 93–160.

Dean, B. 1901. Notes on living Nautilius. *Amer. Nat.*, 35 (418): 818–837.

Degner, E. 1926. Cephalopoda. *Rep. Danish Oceanogr. Exped.*, 1908–10. **2 C**, *Biol.*, 1: 1–94.

Dell, R. K. 1951. A new species of squid, *Histioteuthis cookiana*, from New Zealand waters. *Publ. Zool. Victoria Univ. Coll.*, No. **14**: 1–6.

——— 1952. The recent Cephalopoda of New Zealand. *Dominion Mus. Bull. Wellington*, No. **16**: 1–157.

———. 1959. Some additional New Zealand cephalopods from Cook Strait. *Publ. Zool. Victoria Univ. Coll.*, No. **25**: 1–12.

Ehrenberg, C. G. 1831. *Symbolae Physicae*, Evertebrata. I. Mollusca.

Eydoux, J. F. T. and F. L. A. Souleyet 1852. *Voyage autour du monde exécuté pendant les années* 1836 *et* 1837 *sur la corvette la Bonite, Commandée par M. Vaillant, Zoologie*, Paris, **2**: 7–36.

Ferussac, A. de 1826. *In* d'Orbigny, Tableau méthodique de la classe des céphalopodes. *Ann. Sci. Hist. Nat.*, Paris, **7**: 96–169.

——— and d'Orbigny, A. 1835–1848. *Histoire naturelle generale et particuliere des Cephalopodes acetabuliferes vivants et fossiles.* Paris, pp. i–lvi, 1–361 and Atlas, 144 pls.

Filippova, J. A. 1967. New Data on the Cephalopoda of Indian Ocean. *Advance Abstracta*, **1** (4): 36 (Also in *Abstracts*, Symposium on Mollusca, Cochin, Jan. 1968: 9–10).

Fisher, H. 1895. Note preliminarie sur le *Pterygioteuthis Giardi*, cephalopode nouveau recuelli dans le cours de l' expedition Scientifique du Talisman (1883). *Jour. de Conch.*, **43**: 205–211.

Gabb, W. M. 1862. Description of a new species of Cephalopod from the coast of California. *Proc. Acad. nat. Sci. Philadelphia*, **14**: 483.

——— 1868. Description of a new species of cephalopod from the Southern Pacific. *Amer. J. Conch.*, **4**: 23.

Girard, A. A. 1890 *a*. Nota sobre os Cephalopodes de Portugal. *J. Sci. Ac. Lisboa*, Ser. 2, **3**: 200–205.

——— 1890 *b*. Revision des Mollusques du Museum de Lisbonne. I. Cephalopodes. *Ibid.*, Ser. 2, **4**: 233–268.

———. 1890 *c*. Revision des Mollusques du Museum de Lisbonne. II. Additions aûx Cephalopodes. *Ibid.* Ser. 2, **5**: 33–44.

Goodrich, E. S. 1896. Report on a collection of Cephalopoda from the Calcutta Museum. *Trans. Linn. Soc. London*, **7**: 1–24.

Gould, A. A. 1852. *United States Exploring Expedition, etc., under the command of Charles Wilkes.* 12. *Mollusca and Shells.* Philadelphia, pp. i–xv, 1–510, and Atlas of 52 pls.

Grant, R. E. 1833. On a new species of *Septola* (*Sep. stenodactyla*) from the Mauritius, presented by C. Tilfair, Esq. *Proc. Zool. Soc. London*, 1833, pt. 1: 42–43.

Gray, J. E. 1849. *Catalogue of the Mollusca in the Collection of the British Museum. I. Cephalopoda antepedia.* London, pp. i–viii, 1–164.

Griffin, L. E. 1900. The anatomy of *Nautilus pompilus. Mem. Nat. Acad. Sci.*, **8** (5): 1–197.

Grimpe, G. 1916. Chunioteuthis—eine neue Cephalopodéngattung. *Zool. Anz.*, **46**: 349–359.

———. 1921. Teuthologische Mitteilungen. VII. Systematische Ubersicht der Nordsee Cephalopoden. *Ibid.*, **52**: 297–305.

——— 1922. Systematische Uebersicht der europäischen Cephalopoden. *SB. naturf. Ges. Lpz.*, **45–48**: 36–52.

——— 1931. Teuthologische Mitteilugen. 13. Uber die Cephalopoden der Sunda-Expedition Rensch. *Zool. Anz.*, **95**: 149–174.

Gruvel, A. 1936. Contribution a l'etude de la bionomie generale et de l'expedition de la faune du Canal de Suez. *Mem. Inst. Egypte*, **29**: 1–255.

Hidalgo, J. G. 1905. *Catlogo de los Moluscos testaceous de las Islas Filipinas. Jolo Y Marianas. I. Moluscos marinos Revista de la Real Academia de Ciencias*, Madrid, t. i-ii- pl. 1–16, pp. 1–408. June 1904–July 1905.

Hilgendorf, F. 1880. Uber einen riesigen Tintenfisch aus Japan, *Megateuthis martensii* n.g. & n.sp. *Spitzb. naturf. Fr. Berlin*, 1880: 65–67.

Hoyle, W. E. 1885 *a*. Brief notice of the 'Challenger' Cephalopoda. Narrative of the Voyage of the Challenger. *Rep. Sci. Res. Voy. 'Challenger'*, 1873–76., **1**: 1–657.

——— 1885 *b*. Diagnoses of new species of Cephalopoda collected during the cruise of H.M.S. 'Challenger'. Part I. The Octopoda. *Ann. Mag. Nat. Hist.*, Ser. 5, **15**: 222–236.

——— 1885 *c*. Id., Part II. The Decapoda. *Ibid.*, Ser. 5, **16**: 181–203.

——— 1885 *d*. Preliminary report on the Cephalopoda collected by H.M.S. 'Challenger'. Part I. The Octopoda. *Proc. Roy. Soc., Edinburgh*, **13**: 94–114.

———. 1885 *e*. Id., Part II. The Decapoda. *Ibid.*, **13**: 281–310.

———. 1886. Report on the Cephalopoda collected by H.M.S. 'Challenger' during the years 1873–1876. *Rept. Sci. Res. Voy. 'Challenger', Zool.*, **16**: i–vi, 1–246, pls. 1–33.

——— 1891–92. Note on a British Cephalopod, *Illex Eblane* (Ball). *J. mar. biol. Ass.*, **11** (n.s.): 189–192.

——— 1904 *a*. *Sepia burnupi* n. sp. from Natal. *J. Conch. London*, **11**: 27–28.

——— 1904 *b*. Reports on the dredging operations off the west coast of Central America by the 'Albatross'. VI. Reports on the Cephalopoda. *Bull. Mus. Comp. Zool., Harvard*, **43** (1): 1–71.

——— 1904 *c*. A diagnostic key to the genera of recent dibranchiate Cephalopoda. *Mem. & Proc. Manchesterr Literary and Philos. Soc.*, **48** (21): 1–20.

——— 1904 *d*. Report on the Cephalopoda collected by Prof. Herdman at Ceylon, 1902. *Rep. Ceylon Pearl Oyster Fish.*, 2, Suppl. **14**: 185–200.

——— 1905 *a*. The Cephalopoda. In S. Gardiner. *Fauna Maldive Laccadive Archipel.*, 2, Suppl. **1**: 575–988.

———. 1905 *b*. On specimens of *Tracheloteuthis* and *Cirroteuthis* from deep water off the west coast of Ireland. *Ann. Rept. Fish. Ireland*, 1902–03. Pt. 2, App. 3 (1905): 93–98.

——— 1906. Biscayan Plankton. Pt. 8. The Cephalopoda. *Trans. Linn. Soc. London*, **10**: 156–162.

——— 1907 *a*. Reports on the marine biology of the Sudanese Red Sea. 6. On the Cephalopoda. *J. Linn. Soc.* (*Zool.*), **31**: 35–43.

——— 1907 *b*. The Cephalopoda. The marine fauna of Zanzibar and East Africa from collections made by Cyril Crossland in 1901–1902. *Proc. Zool. Soc. London*, 450–461.

——— 1909. A catalogue of recent Cephalopoda. 2. Suppl. 1897–1906. *Proc. Roy. Phys. Soc. Edinburgh*, **17**: 254–299.

——— 1910. Mollusca. Cephalopoda. In *Schultze Zool. Anthropol. Ergebn. Forsch. im West und zentr. Südafrika*, 1903–1905, 4 (1): 261–268.

HOYLE, W. E., AND R. STANDEN 1901. On a new species of *Sepia* and other shells collected by Dr. R. Koettlitz in Somaliland. *Mem. Proc. Manchester. litt. Phil. Soc.*, **45**: 1–3.

IREDALE, T. 1926. The cuttle-fish 'Bones" of the Sydney Beaches. *Aust. Zool.*, **4**: 186–196.

——— 1954. Cuttle-fish "Bones" again. *Ibid.*, **12**: 63–82.

ISHIKAWA, C. AND Y. WAKIYA 1914. Note on a gigantic squid obtained from the stomach of a sperm whale. *Journ. Coll. Agr. Tokyo*, **4**: 435–443.

ISSEL, A. 1869. *Malacologia del Mar Rosso.* pp. 1–387. Pisa.

ISSEL, R. 1908. Raccolte Planctoniche fatta dalla R. Nave Liguria. IV. Malluschi. Pt. 1. Cefalopodi Planctonichi. *Publ. R. Ist. di. Studi. Superiori, Firenze*, pp. 201–243.

JATTA, G. 1896. I Cephalopodi viventi nel Golfo di Napoli (Sistematica). *Fauna und Flora des Golfes von Naepel. Monogr.*, Berlin **23**: 1–268, pls. 1–31.

——— 1904. A proposito di alcuni Cefalopodi del Mediterraneo. *Bull. Soc. Nat. Napoli*, Ser. 1, **17**: 193–207.

JOUBIN, L. 1894. Note Preliminaire sur les Céphalopodes provenant des Campagnes du yacht l' 'Hirondelle'. *Mém. Soc. Zool. France*, **7**: 211–215.

——— 1896. Cephalopodes (Campagne du Caudan). *Result Scientif. Camp. Caudan*, pp. 247–250.

——— 1897. Observations sur divers Céphalopodes. Troisieme note: Cephalopodes du Musee Polytechnique de Moscou. *Bull. Soc. Zool. France*, **22**: 96–104.

——— 1898. Sur quelques Céphalopodes du Musée royal de Leyde et description de trois espèces nouvelles. *Not. Zool. Mus. Leyden*, **20**: 21–28.

———. 1898. Note sur une nouvelle famille de Céphalopodes. *Ann. Sci. Nat. Zool.*, **6**: 279–292.

——— 1900. Céphalopodes provenant des campagnes de la Princesse-Alice (1891–1897). *Result des Camp Scientif. Prince de Monaco*, 1889, **27**: 1–135.

——— 1902. Revision des Sépiolides. *Mém. Soc. Zool. France*, **15**: 80–145.

——— 1903. Sur quelques Cephalopodes recueillis pendant les dernieres campagnes de S.A.A. le Prince de Monaco (1901–1902).

——— 1918. Etudes preliminaries sur les cephalopodes recueillis au cours des croisieres de S.A.S. Le Prince de Monaco. 6 Note. *Vitreledonella Richardi* Joubin. *Bull. Inst. Oceanogr. Monaco*, **340**: 1–40.

——— 1924. Contribution à l'étude des céphalopodes de l'Atlantique nord. *Rés. Camp. Sci. Monaco*, **67**: 1–113.

——— 1929. Notes preliminaries sur les cephalopodes des Croissieres du Dana (1921–1922). Octopodes. Pt. 1. *Ann. Inst. Oceanogr. Paris*, **6** (4): 363–394.

——— 1931. Notes preliminaries sur les cephalopodes des Croissieres du Dana (1921–1922). Pt. 4. *Ibid.*, n.s., **10** (7): 167–211.

——— 1937. Les Octopodes de la Croissiere du "Dana" 1921–1922. *Dana Rept.*, **11**: 1–49.

KEFERSTEIN, W. 1862–66. Weichthiere (Malacozoa). Bronn's *Klassen und Ordnungen des Thierreichs.* bd. I–II, 1862–1866. Leipzig und Heidelberg. (Cephalopoda on pp. 1307–1464, pls. cx-cxxxvi).

KERR, J. G. 1931. Notes upon the 'Dana' specimens of *Spirula* and upon certain problems of cephalopod morphology. *Danish 'Dana' Exped.* 1920–21, *Rept.*, No. **8**: 1–36, pls. 1–20.

KROHN, A. 1847. Nachtrage zu den Aufsatzen uber Tiedemannia, Octopodoteuthis und Aciopa. *Arch. Naturg.*, **13**: 36.

LAMARCK, J. B. 1798. Extrait d'un mémoire sur les genres de la Sèche, du Calmar et du Poulpe, vulgairement nommé, Polypes de mer. *Bull. Soc. Philomath. Paris*, **2**: 129–131.

——— 1799. Id., *Mem. Soc. Hist. nat. Paris*, **1**: 1–25.

——— 1822. *Histoire Naturelle des Animaux sans Vertèbres*, Vol. 7.

LEACH, W. E. 1817. Synopsis of the orders, families and genera of the class Cephalopoda. *Zoological Miscellany*, 3 (30): 137–141.

LESSON, R. P. 1830. Mollusques. In *Voyage autour de monde execute sur la corvette de S.M. 'La Coquille' pendant les annles* 1822–1825, etc., 200 logie, **2** (1): 239–246.

LESUEUR, C. A. 1821. Descriptions of several new species of cuttle-fish. *J. Acad. nat. Sci. Philadelphia*, **11**: 86–101.

LICHTENSTEIN, K. M. H. *1818*. Onychoteuthis, Sepien mit Krallen. *Isis*, *1818*, pp. 1591–1592.

LINNAEUS, C. VON 1758. *Systema Nature*, ed. **10**, 1 : 1–874.

MALTZAN, H. VON 1881. Description de deux espéces nouvelles. *J. de Conch.*, **29**: 162–163.

MASSY, A. L. 1907. Preliminary notice of some new and remarkable cephalopods from the south-west coast of Ireland. *Ann. Mag. nat. Hist.*, Ser. 7, **20**: 367–384.

——— 1916. The Cephalopoda of the Indian Museum. *Rec. Indian Mus.*, **12**: 185–247.

——— 1925. The Cephalopoda of the Natal Museum. *Ann. Natal. Mus.*, **5** (2): 201–229.

——— 1927. The Cephalopoda of the South African Museums. *Ann. S. Afr. Mus.*, **25**: 151–167.

——— 1928. On the Cephalopoda of the Natal Museum. 2. *Ann. Natal. Mus.*, **6** (1): 89–96.

——— AND G. C. ROBSON 1923. On a remarkable case of sex dimorphism in the genus *Sepia*. *Ann. Mag. nat. Hist.*, Ser. 9, **12**: 435–442.

McCOY, F. 1888. Natural History of Victoria. *Prodromus of the Zoology of Victoria and Descriptions of the Living Species of all Classes of the Victorian Indigenous Animals.* Decade **17**: 225–257.

MEYER, W. TH. 1909. Cephalopoda. *Fauna Südwest-Australia*, **2** (19): 329–335.

MIDDENDORF, A. TH. 1849. Bietrage zu einer Malacozoologia Rossica. *Mem. Acad. Petersbourg*, **6**: (6) 67–215, 330–516 and 517–596.

MORE, A. G. 1875. Gigantic squid on the west coast of Ireland. *Ann. Nat. Hist.*, **16** (4): 123.

NAEF, A. 1912. Teuthologische notizen. 4. Die Gattungen der Loliginidae. 5. Die Arten der Gattung Teuthis· *Zool. Anz.*, **39**: 741–749.

——— 1921–22. Die Cephalopoden. *Fauna Flora Golfo Napoli*, **35**: 1–863.

NOBRE, A. *Moluscos marinhos de Portugal*, II (Porto).

ODHNER, N. H. 1923. Contribution to the marine molluscan faunas of South and West Africa. *Göteborgs Vetensksamh. Handl.*, **26** (7): 1–40.

OKADA, Y. K. 1927. Contribution a l'etude des cephalapodes lumineux. (Notes preliminaries). *Bull. Inst. Oceanogr. Monaco*, No. **394**: 1–16.

OKUTANI, T. 1967. Preliminary Catalogue of Decapodan Mollusca from Japanese waters. *Bull. Tokai Reg. Fish. Lab.*, No. **50**: 1–16.

OOMEN, P. V. 1966. The Octopoda of the Kerala Coast. I. A new species of the genus *Berrya* Adam, 1943. *Bull. Dept. Mar. Biol. Oceanogr., Univ. Kerala*, **2**: 51–60.

ORBIGNY, A. D' 1826. Tabelau methodique de la classe des Cephalopodes. *Annls. Sci. nat.*, **7**: 95–169.

——— 1845–47. *Mollusques vivants et fossiles.* Paris, pp. 1–605 and Atlas of 36 pls.

ORTMANN, A. 1888. Japanische Cephalopoden. *Zool. Jb. Syst.*, **3**: 639–670.

——— 1891. Cephalopoden von Ceylon. *Ibid.*, **5**: 669–678.

OWEN, R. 1832. *Memoir on the Pearly Nautilus* (*Nautilus pompilus* Linnaeus), London, pp. 68, 8 pls.

——— 1836. Description of some new and rare Cephalopoda. *Proc. Zool. Soc. London*, **4**: 19–24; *Trans. Zool. Soc. London*, **2**: 103–130 (1881).

PFEFFER, G. 1884. Die Cephalopoden des Hamburger Naturhistorischen Museums. *Abh. naturw. ver. Hamburg*, **8**: 1–30.

——— 1900. Synopsis der œgopsiden Cephalopoden. *Mitteilungen aus dem Naturhistorischen Mus. Hamburg* **17**: 147–198.

——— 1912. Die Cephalopoden der Planktonexpedition. Zugleich eine monographische Ubersicht der Oegopsiden Cephalopoden. *Ergebnisse Planktonexpedition der Humboldt-Stiftung*, bd. **2**: i-xxi, 1–815, and Atlas of 48 pls.

PICKFORD, G. E. 1939 *a*. The Vampyromorpha. A new order of dibranchiate Cephalopoda. *Vestnik Cs. Zool. Spol. Praze*, **6-7**: 346–358.

——— 1939 *b*. A revision of the types of *Vampyroteuthis infernalis* Chun. *Zool. Jahrb. Syst.*, **73**: 47–62.

PICKFORD, G. E. 1946 *a*. A review of the littoral Octopoda from Central and Western Atlantic Stations in the collections of the British Museum. *Ann. Mag. nat. Hist.*, Ser. 11, **13**: 412–429.

——— 1946 *b*. *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. I. Natural history and distribution. *Dana Rept.*, No. **29**: 1–40.

——— 1949 *a*. Id., II. External anatomy. *Dana Rept.*, No. **32**: 1-132.

——— 1949 *b*. Distribution of the eggs of *Vampyroteuthis infernalis* Chun. *J. Mar. Res.*, **8** (1): 73–83.

——— 1952. The Vampyromorpha of the Discovery Expeditions. *Discovery Repts.*, **26**: 197–210.

——— 1955. A revision of the Octopodinae in the collections of the British Museum. *Bull. Brit. Mus. (nat. Hist.)*, **3** (3): 151–167.

——— 1959. Vampyromorpha. *Galathea Rept.*, **1**: 243–253.

PILSBRY, H. A. 1894. Notices of new Japanese Molluska. *Nautilus*, **7**: 143–144.

QUOY, J. R. C. AND J. P. GAIMARD 1832. *Zoologie du voyage de l'Astrolabe, pendant les annees* 1826–1929. 2. Paris.

REES, W. J. 1949. Note on the hooked squid, *Onychoteuthis banksii*. *Proc. Mal. Soc.*, **28**: 43.

——— 1956. Notes on the European species of Eledone—with special reference to eggs and larvae. *Bull. Brit. Mus. (nat. Hist.), Zool.*, **3**: 283–293.

——— AND G. E. MAUL 1956. The Cephalopoda of Madeira. *Ibid.*, **3**: 257–281.

——— AND A. STUCKEY 1952. Mollusca. The Manihine Expedition to the Gulf of Aqaba, 1948–1949. *Ibid.*, **1** (8): 182.

REHDER, H. A. 1945. A new genus and species of squid from the Philippines. *Proc. Biol. Soc. Washington*, **58**: 21–26.

RISSO, A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale*, Vol. 4.

ROBSON, G. C. 1914. Cephalopoda from the Monte Bello Islands. *Proc. Zool. Soc. London*, pp. 677–680.

——— 1921. On the Cephalopoda obtained by the Percy Sladen Trust Expedition to the Indian Ocean in 1905. *Trans. Linn. Soc. London*, **17** (2): 429–442.

——— 1924 *a*. Preliminary report on the Cephalopoda (Decapoda) procured by the S.S. 'Pickle'. *Rep. Fish. mar. biol. Surv. Union S. Afr.*, 3, *Spec. Rept.*, **9**: 1–14.

——— 1924 *b*. On the Cephalopoda obtained in South African waters by Dr. J. D. F. Gilchrist in 1920–1921. *Proc. Zool. Soc. London*, pp. 589–686.

——— 1926 *a*. Notes on the Cephalopoda. No. 1. Descriptions of two new species of *Octopus* from Southern India and Ceylon. *Ann. Mag. nat. Hist.*, Ser. 9, **17**: 159–167.

——— 1926 *b*. The Cephalopoda obtained by the S.S. 'Pickle' (Supplementary Report). *Fisheries and Marine Biological Survey Report, No.* 4 *for the year* 1925, pp. 1–6.

——— 1927. Zoological Results of the Cambridge Expedition to the Suez Canal, 1924. 19. Report on the Mollusca (Cephalopoda). *Trans. Zool. Soc. London*, **22** (3): 321–329.

——— 1928. Cephalopodes des mers d'Indochine. *Serv. Océan. Pêches Indochine*, **10**: 1–53.

——— 1929. *A Monograph of the Recent Cephalopoda.* Part I. *Octopodinae*, **1**: 1–236 (Issued by Birt. Mus. nat. Hist.).

——— 1930. Cephalopoda: Octopoda. In *'Discovery' Rept.*, **2**: 371.

——— 1932 *a*. Report on the Cephalopoda in the Raffles Museum. *Bull. Raffles Mus.*, **7**: 21–33.

——— 1932 *b*. *A Monograph of the Recent Cephalopoda.* Part II. *The Octopoda, excluding the Octopodinae.* **2**: 1–359. (Issued by Brit. Mus. nat. Hist.).

ROCHEBRUNE, A. T. DE 1884. Etude monographique de la famille des Loligopsidae. *Bull. Soc. Philom. Paris*, **8** (7): 7–28; Sepiadae. *Ibid.*, **8** (7): 74–122.

——— AND J. MABILLE 1889. Mollusques. In *Mission Scientifique du Cap Horn*, 1882–83, **6** (2): 1–143 (Cephalopoda on pp. 1–10, pl. 1).

ROPER, C. F. E. 1963. Observations on bioluminescence in *Ommastrephes pteropus* (Steenstrup, 1855), with notes on its occurrence in the family Ommastrephidae (Mollusca: Cephalopoda). *Bull. Mar. Sci. Gulf Carib.*, **13** (2): 343–353.

Roper, C. F. E. 1966. A study of the genus *Enoploteuthis* (Cephalopoda: Oegopsida) in the Atlantic Ocean, with a redescription of the type species, *E. leptura* (Leach, 1817). *Dana Rept.*, **66**: 1–46.

—— and R. E. Yong 1967. A review of the Valbyteuthidae and an evaluation of its relationship with the Chiroteuthidae (Cephalopoda: Oegopsida). *Proc. U.S. Nat. Mus.*, **123** (3612): 1–8.

Ruppell, W. P. E. 1844. *Intorno and alcuni cefalopodi del mare di Missina lattera*, pp. 1–7.

—— and E. S. Leuckart 1828. *Neue wirbellose Thiere des rothen Meeres.*

Sasaki, M. 1913. Decapod Cephalopods found in Japan: Sepiolidae. *Zool. Mag. Tokyo*, **25**: 247–252, 397–403.

——— 1914. Notes on Japanese Myopsida. *Ann. Zool. Jap.*, **8**: 587–629.

——— 1915. On three interesting new oegopsids from the Bay of Sagami. *J. Coll. Agri. Tohoku Univ.*, **6** (6): 131–150.

——— 1917. Notes on the Cephalopoda. 1. On the male *Amphitretus pelagicus* Hoyle. 2. Diagnoses of four new species of *Polypus*. *Ann. Zool. Jap.*, **9**: 361–367.

——— 1920. Report on the Cephalopods collected during 1906 by the United States Bureau of Fisheries Steamer "Albatross" in the North-Western Pacific. *Proc. U.S. Nat. Mus.*, **57**: 163–204.

——— 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *J. Coll. Agric. Hokkaido imp. Univ.*, 20. Suppl.: 1–357, with 30 pls.

Savigny, J. C. L. de 1817. *Description de l'Egypte. Historie Naturelle Mollusques Cephalopodes.* 2.

Smith, E. A. 1916. On the shells of the South African species of Sepiidae. *Proc. Malac. Soc. London*, **12**: 20–26.

Solander, D. C. 1786. *A Catalogue of the Portland Museum.*

Steenstrup, J. J. 1855. Kjaeber af en kolassal Blaecksprutte (*O. pteropus*). *Overs. danske Vidensk. Selsk. Forh.*, pp. 73–110.

——— 1856. Hectocotyldannelsen hos Octopodslaegterne *Argonauta* og *Tremoctopus*, oplyst ved Iagttagelse af lignende Dannenlsen hos Blaeksprutterne i Almindelighed. *Danske Vidensk. Selsk. Skrift.*, Ser. 5, 4: 187–216.

——— 1861 *a*. Overblick over i Kjobenhavn Museer opbevarede Blaeksprutter fra det aabne Hav. (1860–61). *Overs. vid. Danske Selskabs Forhandlinger*, pp. 69–86.

——— 1861 *b*. Bemarkninger om de enkelte Arter, fornemlig efter det Veranyske Cephalopod. *Vark. Overs. Vid. Mode Nat. Foren. Kjobenhavn*, 1960, pp. 332–333.

——— 1875. *Hemisepius*, en ny Slaegt af *Sepia*—Blaeksprutternes Familie. *K. danske. Selsk. Skr. Nat. Afd.*, Ser. 5, **10** (7): 465–482.

——— 1881. *Sepiadarium* og *Idiosepius* to nye Slaegter af Sepiernes Familie. *Ibid.*, Ser. 6, **1** (3): 211–242.

——— 1882 *a*. En ny blaeksprutters laegt Tracheloteuthis. *Vid. med. den Naturhist. Fore. Kjobenhavn*, Ser. 4, **3**: 293–294 (1881).

——— 1882 *b*. Notae teuthologicae. *Hv. Overs. Dansk Vid. Selsk. Forh.*, pp. 143–168.

——— 1887. Notae teuthologicae. 6. Species generis Sepiolae Maris Mediterranei. *Oversigt Danske Vid. Selsk. Forh.*, 1887, pp. 47–66.

Thiele, J. 1915. In Chun, C. *Wiss. Ergebn. Deutsche Tiefsee Exped.*, Bd. 18, pt. 2.

——— 1916. Bemerkungen uber die Systematik der achtarmigen Cephalopoden. *Zool. Anz.*, **48**: 3–4.

——— 1920. Die Cephalopoden. *Dt. Sdpolar-Exped.*, **16**: 433–465.

——— 1935. *Handbuch der Systematischen Weichtierkunde*, **2** (3): 779–1154.

Thore, S. 1945. On the Cephalopoda of Professor O. Carlgren's Expedition to South Africa in 1935. *K. fysiogrs Sällsk. Lund.*, **15**: 49–57.

——— 1949. Investigations on the Dana Octopoda. *Dana Rept.*, **33**: 1–85.

Troschel, F. H. 1857. Bemerkungen uber die Cephalopoden von Messina. *Archiv. fur. Natur. Jahrg.*, **23** (1): 41–76.

Tryon, G. W. 1879. *Manual of Conchology.* 1. *Cephalopoda*, Philadelphia, pp. 1–316.

Turton, W. H. 1932. *The Marine Shells of Port Alfred, S. Africa*, Oxford and London, Verany, J. B. 1837. Mémoires sur deux nouvelles espéces de Céphalopodes, trouves dans l'ocean. *Mém. Acad. Torino*, **1**: 99–101.

——— 1846. Catalogo degli animali invertebrati del Golfo di Genova e Nizza (Guida di Genova).

——— 1851. Mollusques Méditerranées observés, décrites, figurés et chromolithographiés d' aprés le vivant. I. Cephalopodes de la Méditerranée. Gênes.

Verco, J. C. 1907. Notes on South Australian marine Mollusca with descriptions of new species. 6. *Trans. Roy. Soc. S. Aust.*, **31**: 213–214.

Verrill, A. E. 1876. Note on gigantic Cephalopods, a correction. *Amer. Journ. Sci.*, **12** (3): 236.

——— 1879. Notice of recent additions to the marine fauna of the eastern coast of North America. No. 7. Brief contributions to Zoology from the Museum of Yale College, No. 44, *Ibid.*, **18** (3): 468–470.

——— 1880. Synopsis of the Cephalopoda of the north-eastern coast of America. *Ibid.*, **19** (3): 284–295.

——— 1880–81. The Cephalopods of the north-eastern coast of America. Part 2. The smaller cephalopods including the squids and the Octopi, with other allied forms. *Trans. Conn. Acad. Sci.*, **5**: 259–446, pls. 26–56, June, 1880, December 1881, New Haven.

——— 1881. Reports on the results of dredging....On the east coast of the United States....by the ...... 'Blake'. 10. Report on the cephalopods and some additional species dredged by the U.S. Fish Commission Steamer "Fish Hawk" during the season of 1880. *Bull. Mus. Comp. Zool.*, **8**: 99–116.

——— 1882. Report on the Cephalopods of the north-eastern coast of America. *Report U.S. Commission Fish. and Fisheries*, 1879, pp. 211–455 (1–245), with pls. 1–46, Washington.

——— 1883. Supplementary report on the "Blake" cephalopods. *Bull. Mus. Comp. Zool.*, **11**: 105–115.

——— 1885. Third Catalogue of the Mollusca, etc. *Trans. Conn. Acad. Arts & Sci.*, **6** (2): 395–452.

Voss, G. L. 1956. A review of the Cephalopods of the Gulf of Mexico. *Bull. Mar. Sci. Gulf. Carib.*, **6** (2): 85–178.

——— 1957. Observations on *Ornithoteuthis antillarum* Adam, 1957, an ommastrephid squid from the West Indies. *Ibid.*, **7** (4): 370–378.

——— 1960. Bermudan Cephalopods. *Fieldiana*, **39** (40): 419–446.

——— 1962 *a*. List of the types and species of cephalopods in the collections of the Academy of Natural Sciences of Philadelphia. *Notul. Nat.*, **356**: 1–7.

——— 1962 *b*. Six new species and two new subspecies of cephalopods from the Philippine Islands. *Proc. biol. Soc. Washington*, **75**: 169–176.

——— 1962 *c*. South African cephalopods. *Trans. R. Soc. S. Afr.*, **36**: 245–272.

——— 1963. Cephalopods of the Philippine Islands. *Bull. U.S. Nat. Mus.*, **234**: 1–180.

——— and D. S. Erdman 1959. *Thysanoteuthis rhombus*, a large cephalopod new to the Western Atlantic. *Mar. Lab. Univ. Miami, Nautilus*, **73** (1): 23–25.

Watase, S. 1906. On luminous Cephalopods. *Zool. Mag. Tokyo*, **18**: 195–196.

Weindle, Th. 1912. Vorläufige Mitteilung über die von S.M. Schiff, 'Pola' im Roten Meer gefundenen Cephalopoden. *Anz. Akad. Wiss. Wien.*, **48**: 270–275.

Willy, A. 1902. *Contribution to the natural history of the pearly nautilus. Part 6. Of Zoological Results based on material from New Britain, New Guinea, Loyalty Islands.* No. **34**, Cambridge.

Winckworth, R. 1926. A list of Cephalopoda in the Colombo Museum. *Spolia Zeylan.*, **13**: 323–331.

——— 1936. Marine Mollusca from South India and Ceylon. 4. A new Indian *Sepia*. *Proc. Malac. Soc. London*, **22**: 16–23.

Wülker, G. 1910. Ueber Japanische Cephalopoden. *Abh. bayer. Akad. Wiss.*, **3** (Suppl. 1): 1–71.

——— 1913. Cephalopoden der Aruund Kei-Inseln. Anhang: Revision der Gattung Sepioteuthis. *Abh. Senckenb. naturforsch. Ges.*, **34**: 451–488.

——— 1920. Ueber Cephalopoden des Roten Meeres. *Sneckenbergiana*, **2**: 48–58,

Discussion

Mr. M. J. Sebastian: Do you think that the plankton collection made could give a realistic picture of abundance?

Dr. E. G. Silas: As you are probably aware, we have yet to design the perfect sampler for capturing all planktonic organisms when towed. In our investigation, we have used the Indian Ocean Standard Net in open tows, which has certain limitations. We have also used the Isaacs-Kidd Mid-water Trawl for obtaining samples of juveniles and adults of fast-moving organisms. Several of the oceanic squids are very quick in movement and could easily avoid capture by these nets. However, many are susceptible to capture, especially the larval stages on which most of the present investigation is based. Moreover, as these investigations have been carried out regularly over a period of 5 years, a reasonable picture could be given.

Dr. M. C. Mercer: Was any closing device used in the Isaacs-Kidd Mid-water Trawl?

Dr. E. G. Silas: No.

STUDIES ON THE HEART OF GASTROPOD MOLLUSCS: *PILA GLOBOSA* SWAINSON AND *APLYSIA FIMBRIATA* ADAM AND REEVE

S. C. BHARGAVA

Department of Zoology, University of Jodhpur, Jodhpur, India

ABSTRACT

Krijgsman and Divaris (1955) made an excellent review of the earlier literature on the various aspects of molluscan heart. Notable contributions, thereafter, on the heart of various gastropods are of Ghose (1958, 1964), Kawaguti (1963) and Andrews (1965). There, however, seems to be no agreement regarding the type of muscle fibres that constitute the heart in gastropods. The author has studied in detail the anatomy and histology of heart in Indian types: *Pila globosa* and *Aplysia fimbriata.*

The heart in *P. globosa* and *A. fimbriata* has a single atrium and a ventricle, in the former the ventricle is posterior to the atrium while in the latter the position is reverse. In both, the wall of the atrium is thin and transparent while that of ventricle is thick and spongy. The valves of different types are present at the atrioventricular and ventriculoaortic junctions; in *Aplysia* a bulbous swelling occurs at the origin of the aorta. The epicardium is thin and consists of a single layer of flat epithelial cells. The atrial myocardium has scanty muscle fibres in comparison to that of ventricle. The atrial and ventricular myocardial fibres are of non-striated type.

The specialized conducting tissue is not present in the heart of gastropods studied. The absence of nerve or ganglion cells has led the author to believe in the myogenic initiation of the cardiac rhythm. The neurogenic initiation of cardiac rhythm appears to be a remote possibility.

INTRODUCTION

THE heart in Gastropoda usually consists of a single atrium and a ventricle. However, such forms as Rhipidoglossa (except the Helicinidae) possess two atria and a ventricle which is traversed by the intestine as in most of the lamellibranchs.

Studies on the heart of the various gastropods have been carried out by a number of researchers for which a reference may be made of the review by Krijgsman and Divaris (1955). Subsequent notable contributions were made by Kawaguti (1963), Ghose (1964), Andrews (1965), and Hill and Welsh (1966). However, there seems to be no agreement regarding the type of muscle fibres that constitute the heart in gastropods. Hence, an attempt has been made to study in detail the anatomy and histology of the heart and to find out the nature of cardiac fibres in two Indian types: *Pila globosa* and *Aplysia fimbriata.*

Krijgsman and Divaris (1955) and Hill and Welsh (1966) reported uncertainty on the occurrence of nerve cells in the gastropod heart. The specialised tissue for the conduction of cardiac impulse has been reported only in the heart of gastropod *Murex trunculus* (Morin and Jullien, 1930*a*, *b*, 1932). Both these aspects are of considerable interest and consequently an endeavour has been made here to study them.

MATERIAL AND METHODS

Collections of live *Pila globosa* were made from the tanks in Ghana Sanctuary, Bharatpur (Rajasthan), and of *Aplysia fimbriata* at seacoast in Bombay. The specimens were narcotized with menthol and by chilling method. The heart in each case was taken out and fixed separately in 10% formol, Bouin's fluid, and 10% neutral formol.

After dehydration and clearing, the material was embedded in paraffin wax. Serial sections (6 to 10 micra thick) were cut in the transverse, longitudinal, and sagittal planes with reference to the anteroposterior or long axis of the heart. The sections were stained with Delafield's haematoxylin and eosin, Heidenhain's iron-haematoxylin with and without counterstaining with eosin, and Mallory's triple connective tissue stain.

To study nerve cells and fibres, Bielschowsky's (modified by Beech and Davenport, 1933) and Bodian's (1936, 1937) methods were employed. In Bodian's method the protargol (Silver albumose) used was obtained from Winthrop Chemical Co., N.Y., as suggested by McClung (1961).

To examine striations of the muscles, Bromo-phenol blue technique, as advanced by Menzies (1961), was followed.

OBSERVATIONS

In *P. globosa*, the heart is enclosed in an ovoidal pericardial chamber and lies between the respiratory organ (pulmonary sac) and renal organ. The heart comprises an atrium and a ventricle, the former being anterior to the latter (Fig. 1). The two aortic arches and the aortic ampulla are also enclosed in the pericardium.

In *A. fimbriata*, the heart lies in a tough pericardial sac which is much larger than the heart itself. It has two chambers, an atrium and a ventricle, the ventricle projects slightly anterior to the atrium Fig. 2) and both lying anterior to the ctenidium, as in other opisthobranchs.

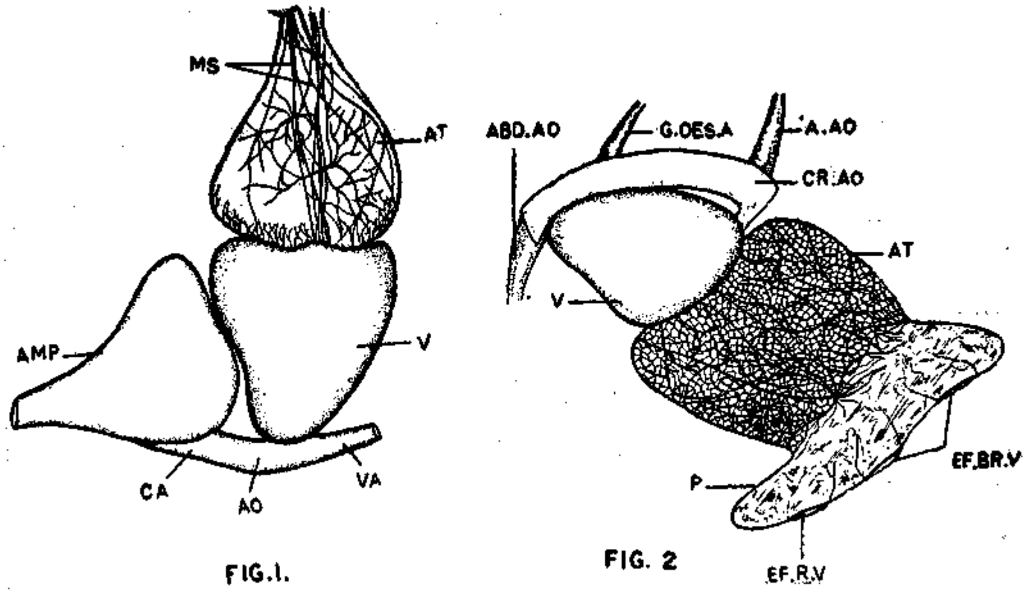


FIG. 1.

FIG. 2

Figs. 1-2. Fig. 1. Dorsal view of the heart and aortic ampulla of *P. globosa*, ×15. Fig. 2. Dorsal view of the heart of *A. fimbriata*, ×8 (Magnifications approximate).

The Atrium

The atrium in *P. globosa* is a thin-walled, transparent and pear-shaped structure with the broader portion towards the ventricle. The muscular strands traversing its walls are disposed in longitudinal, transverse, and oblique planes. These strands are connected with each other by smaller branches, thus, forming a mesh-work as reported in the atrium of *Achatina fulica* and *Macrochlamys indica* (Ghose, 1964) and *Pomacea canaliculata* (Andrews, 1965). A few of the muscular strands are very conspicuous and run anteroposteriorly (Fig. 1). They are distributed at irreguar intervals into the lumen of the atrium. These conspicuous strands, at the posterior end of the atrium, are inserted at the base of the ventricle. Anteriorly, they converge at the narrow region which receives efferent veins.

In *A. fimbriata*, the atrium is thin-walled, transparent, and reticulate but roughly spherical sac which is flat at the coronary sulcus (Fig. 2). Because of its more transparent wall, the atrium, in diastolic condition clearly reveals the disposition of the myocardial fibres. A few conspicuous, thick muscular strands run across the atrial lumen anteroposteriorly as in *P. globosa*. The thin strands run in between and cross the former set of thick strands in different directions in the atrial lumen. The thick and thin sets of strands ramify on the dorsal and ventral surfaces of the atrium just as they do in its lumen. Moreover, a few prominent muscular strands traverse the entire width of the atrium and unite with other strands on the dorsal and ventral surfaces. Thus, a very complex interlacing network of muscle strands is formed. Of the two surfaces, the dorsal one shows more ramifications of the muscular strands than the ventral; this is in harmony with the observations of Jullien *et al.* (1961) in *Aplysia depilans*.

The atrioventricular junction

The posterior wall of the atrium in *P. globosa* is continuous into the cranial wall of the ventricle and forms a conspicuous atrioventricular funnel which contains the atrioventricular orifice (Figs. 3 and 4). The ventricular muscle strands, that lie on either side of the atrioventricular orifice, assume the structure of the atrioventricular valves. The atrioventricular valves are strong, muscular and hang downwards into the lumen of the ventricle (Figs. 3 and 4). Two atrioventricular valves occur in *Helix pomatia* (Nold, 1924; Baecker, 1932), *Haliotis tuberculata* (Skramlik, 1929) and *Ferrissia shimekii* (Boer and Lever, 1958), however, a single conical atrioventricular valve has been reported in *Laevapex fuscus* (Basch, 1959).

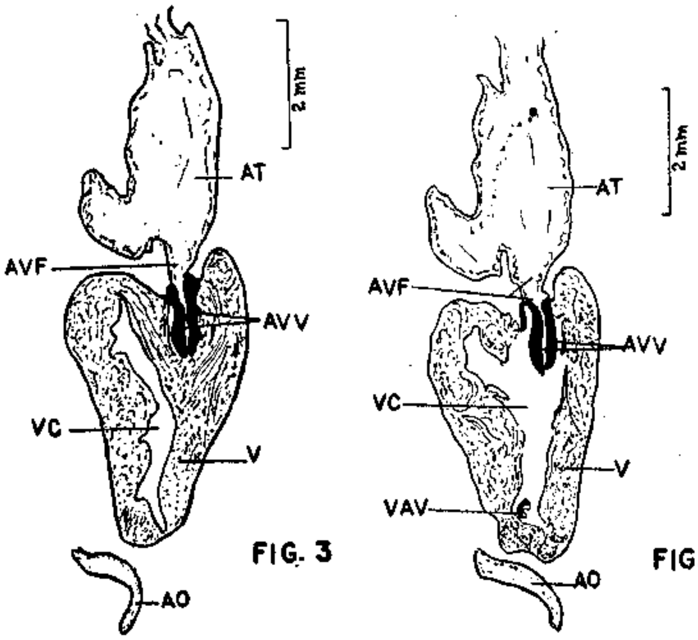
The atrioventricular junction in *A. fimbriata* is very different from that of *P. globosa*. The atrioventricular opening is a transverse long slit guarded by a pair of semicircular membranous flaps functioning as valves (Fig. 5). On either side of this opening are present transversely disposed myocardial fibres that effectively regulate the size of the orifice for the blood to pass from the atrium to the ventricle.

The ventricle

The ventricle in *P. globosa* is a thick-walled, pear-shaped muscular structure. The wider portion of the ventricle lies towards the atrium while posterior narrow one is continuous with the aorta.

A study of sagittal sections reveals that ventricular lumen in *P. globosa* is for the most part tubular (Fig. 3). A little ventrally this tubular lumen splits into an anterior wider portion corresponding to the relatively broad anterior end of the ventricle, where lie the atrioventricular valves (Fig. 4).

A study of the sagittal sections further reveals that the ventricular myocardium is disposed into two main types of strands: the large muscular strands and smaller muscular strands. The large strands form distinct enclosures and contain the smaller strands (Photomicrograph 1). Thus the musculature of the ventricle is broken up into a number of small, irregularly shaped compartments that are confluent with each other. A number of myocardial fibres radiate from a common centre situated near the base of the ventricle in the vicinity of the atrioventricular valves (Photomicrograph 2). These fibres run longitudinally towards the apex of the ventricle and are joined at places by smaller transversely running fibres. This arrangement of fibres in *P. globosa* resembles that of *Murex trunculus* (Morin and Jullien, 1930 *a*, *b*; Brunet and Jullien, 1936 *a*, *b*, *c*). However, the muscle fibres that extend from the atrioventricular border to some extent into the atrium in *Helix pomatia* (Jullien and Vairel-Blanc, 1937) are not observed in *P. globosa*.



Figs. 3–4. Fig. 3. Sagittal section of the heart of *P. globosa* showing the atrioventricular funnel. Fig. 4. Sagittal section of the heart of *P. globosa* showing the atrioventricular valves and ventricular cavity.

The ventricle in *A. fimbriata* is roughly triangular and has spongy walls. The ventricular myocardial fibres run nearly in all directions and at places are seen to radiate from certain points. Three such radiating centres are seen in sagittal sections which are: (1) on the posteriodorsal wall of the ventricle near the atrioventricular junction (Photomicrograph 3), (2) on the posterioventral wall of the ventricle also near the atrioventricular junction (Photomicrograph 4) and (3) at the anterior end (near the apex) of the ventricle (Photomicrograph 5). Possibly, these radiating centres are the points from where the systolic phase of the ventricle is transmitted to the rest of the ventricular myocardium. Jullien (1937 *a*, *b*), in the ventricle of *Aplysia fasciata*, described two main types of fibres, longitudinal and transverse, which are interwoven with each other. The longitudinal fibres extend like a 'fan' from the atrioventricular border on both ventral and dorsal surfaces. These fans on the dorsal and ventral surfaces very much correspond to the radiating centres at the posterioventral and posteriodorsal wall of the ventricle mentioned above in *A. fimbriata*.

The aorta

The interlacing muscle fibres of the apical region of the ventricle in *P. globosa* and *A. fimbriata* lay the beginning of the aorta. The apical region of the ventricle shows numerous anastomosing fibres that have thinner calibre than the rest of the myocardium (Photomicrograph 6).

In *P. globosa* a single aorta emerges from the apex of the ventricle (Fig. 1). The ventriculoaortic opening has a single valve. The ventriculoaortic valve originates from the left wall of the aorta at the ventriculoaortic junction and coils in the region of the ventriculoaortic opening (Photomicrograph 6). The free end of the valve is visible in the lumen of the aorta. The aortic trunk, soon after its origin from the ventricle, divides into a cephalic and a visceral aorta (Fig. 1). There are no valves at the entrances of these vessels or at any point along them as Andrews (1965) reported in certain pilid gastropods.

In *P. globosa*, lying at the root of the cephalic aorta soon after its origin is a bulbous outgrowth, the aortic ampulla (Fig. 1). The ampulla is pyramidal in shape with its broad base in close proximity with the ventricle. The outer surface appears to be uniformly white and is not mottled, as described by Andrews (1965) in certain pilid gastropods. The inner surface of the ampulla has a reticulate arrangement formed by irregularly disposed connective tissue fibres. The lumen of the ampulla has no traversing muscular strands.

In *A. fimbriata*, the aortic trunk, known as crista aorta, arises from the anteroventral portion of the ventricle (Fig. 2). The ventriculoaortic opening is guarded by a pouch-like thin and membranous valve (Fig. 6). The valve is attached to the entire border of the ventriculoaortic opening except at the anterior one, thus, leaving a transverse slit-like passage for the blood to flow from the ventricle into the aorta. A few conspicuous strands of muscle fibres originate from the dorsal ventricular wall near the ventriculoaortic junction and run anteriorly over the membranous valve to terminate in the form of an inverted 'T' (Fig. 6). Obviously, these muscle strands serve the same role as chordae tendineae of the vertebrate heart for the opening and closing of the ventriculoaortic orifice. The crista aorta in *A. fimbriata* as in *A. punctata* (Eales, 1921) and *Dolabella* (Ma'sui, 1945) leads to three arterial trunks: (1) anterior aorta, (2) gastro-oesophageal artery and (3) abdominal aorta (Fig. 2). These arterial trunks distribute blood to the various parts of the body.

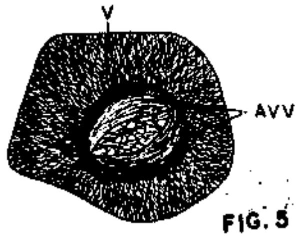


FIG. 5

FIG. 6

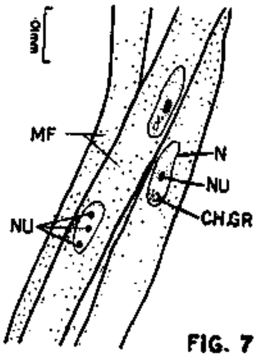


FIG. 7

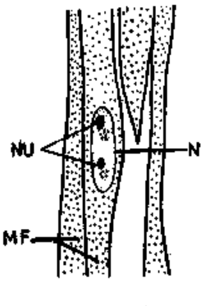


FIG. 8

FIGS. 5–8. Fig. 5. Atrioventricular valves in the heart of *A. fimbriata* as seen after removal of the atrium, ×8 Approx. Fig. 6. Ventriculoaortic valve in the heart of *A. fimbriata*, ×15 Approx. Fig. 7. Camera lucida diagram of a part of a longitudinal section of the heart of *P. globosa* showing ventricular muscle fibres (under oil immersion). Fig. 8. Camera lucida diagram of a part of a longitudinal section of the heart of *A. fimbriata* showing ventricular muscle fibres (under ilo immersion).

Histologically both in *P. globosa* and *A. fimbriata* the atrial as well as the ventricular wall is composed of the following layers:

(1) *Epicardium*—The epicardium is the outermost covering of the heart which is composed of a single layer of flat epithelial cells (Photomicrographs 7 and 8). The epicardium in *A. fimbriata* is thinner, the cell outlines are indistinct in comparison to that of *P. globosa*. The cells in both cases possess conspicuous nuclei.

In *P. globosa* the epithelial cells of the ventricle at places are contiguous with the myocardial fibres, thus, establishing continuity between the epicardium and myocardium (Photomicrograph 8).

(2) *Connective tissue layer*—Underlying the epicardium is a delicate layer of connective tissue, more distinct in *A. fimbriata* and stains deep blue with Mallory's triple. In *P. globosa*, this layer in the atrial wall is uniformly developed while in the ventricle it is broken so that the myocardial fibres are in contact with the epicardium. A perusal of the accessible literature shows that there is no record of the presence of connective tissue layer in between the epicardium and myocardium in the heart of any gastropod studied.

(3) *Myocardium*—This innermost layer is composed of a large number of muscular strands which run in different directions. The atrial myocardium has scanty muscle fibres. The atrial as well as ventricular myocardial fibres are non-striated and exhibit no anastomosing.

In *P. globosa* the nuclei of the fibres are variously shaped: round, oval, or elongated. The larger nuclei of some fibres show one to three nucleoli (Fig. 7). In *A. fimbriata* the nuclei are oval, the large ones display one or two nucleoli (Fig. 8).

There is no trace of endocardium in *P. globosa* and *A. fimbriata*, the blood apparently is in direct contact with the muscle fibrils. Barring Seshaiya's (1930) report on the presence of endocardium, in the heart of *Mysorella costigera*, the absence has been recorded in the heart of *Aplysia punctata* (Eales, 1921), *Helix pomatia* (Baecker, 1932), *Kalinga ornata* (Rao, 1936), *Okadaia elegans* (Baba, 1937), *Achatina fulica* (Ghose, 1958), and Mollusca in general (Hill and Welsh, 1966).

Conducting system

After employing specific techniques for the study of nerve or ganglion cells in the heart of *P. globosa* and *A. fimbriata*, a careful examination has shown their absence. Taking the specialised conducting tissue into consideration, the author has failed to find such a tissue in the heart of *P. globosa* and *A. fimbriata*. Its presence was reported by Morin and Jullien (1930 *a*, *b*; 1932) in the heart of *Murex trunculus*.

DISCUSSION

The cardiac muscle in gastropods presents a wide range of structure. The fibres are cross-striated, branched, and anastomosed (Nold, 1924), but without anastomoses (Baecker, 1932) in *Helix pomatia*. Ghose (1964) described cardiac muscle as smooth and called it highly specialized on account of ramifications and anastomoses in *Achatina fulica* and *Macrochlamys indica*. In contrast, the cardiac muscle of *P. globosa* and *A. fimbriata* displays a simpler structure. The muscle fibres are ramified in *A. fimbriata*, show a little or no ramification in *P. globosa*, but do not anastomose in both types. The atrial and ventricular fibres both in *P. globosa* and *A. fimbriata* are non-striated. Suzuki (1935), as well, observed non-striated fibres in the heart of *Janthina janthina*, *Hipponyx pilosus* and *Cypraea tigris*. On the other hand, Darwin (1876), Marceau (1905), Spillmann

(1905), Plenk (1923, 1925), Morin and Jullien (1930 *a*, 1932) reported striated cardiac fibres in the various gastropods. Andrews (1965) described atrial fibres as non-striated and ventricular fibres striated in certain pilid gastropods. Kawaguti (1963), on the basis of electron microscopic observations on the heart muscle of the snail, *Euhadra hickonis*, stated that cross-striated pattern is rarely perceptible except in a thick section and further added that auricular muscle shows somewhat different features from that of the ventricle. The aforesaid discussion lends no support to the statement of Ghose (1964) that the occurrence of cross-striated muscle fibres in the gastropod heart is a rare phenomenon.

The aorta, as it emerges from the apex of the ventricle in some gastropods, becomes dilated so as to assume the appearance of a separate chamber. It has been given different names in various gastropods: pseudo-chamber in *Patella* (Davis and Fleure, 1903); aortic bulb in *Patella* (Pelseneer, 1906); truncus arteriosus in *Mysorella costigera* (Seshaiya, 1930) and *Struthiolaria* (Morton, 1954); bulbous arteriosus in Haliotidae (Fleure, 1904). Spillmann (1905), however, contradicted the presence of bulbous arteriosus. Recently, Ghose (1964) described the union of the bases of the two aortae as aortic ampulla in *Achatina fulica* and *Macrochlamys indica* and Andrews (1965) considered the aorta as bulbus aortae in certain pilid gastropods. In *P. globosa* an intra-pericardial aortic ampulla, as described by Prashad (1925, 1932) and Andrews (1965), is present at the base of cephalic aorta. However, the aorta at its emergence from the ventricle does not form a bulbous structure. In my viewpoint, this bulbous structure is not essential either in *P. globosa* or any other pilid gastropod. The large rhythmically contractile aortic ampulla at the base of the cephalic aorta in pilid gastropods is capable of pumping the blood with more force in the cephalic aorta which has to carry blood for the major part of the body.

The back-flow of blood from the aorta into the ventricle in *P. globosa* is prevented by a single valve (Andrews, 1965) and not by a pair of valves (Prashad, 1925, 1932). A single valve in the aorta is present in *Helix pomatia* (Schmidt, 1916; Nold, 1924) and *Haliotis tuberculata* (Skramlik, 1929). However, no such valve was noticed in *Bythinella* and *Paludestrina* (*see* Rao, 1936). Ghose (1964) described a thick ring-like muscular band serving as a sphincter to prevent the back-flow of the blood from aortic ampulla into the ventricle in *Achatina fulica* and *Macrochlamys indica*. My observations confirm Andrews' (1965) findings on the occurrence of a single valve in *P. globosa*. Among opisthobranchs, a single valve at the opening of ventricle into the crista aorta is present in *Aplysia punctata* (Eales, 1921), *Kalinga ornata* (Rao, 1936), and *Dolabella* (Matsui, 1945). In these, none of the authors mentioned the presence of muscular strands by which the valve is attached to the ventricular wall and which play an important role in the efficient functioning of the valve as found in *A. fimbriata*. Whether the existence of such muscular strands has escaped their attention or they are not present, is difficult to state.

Regarding the nerve cells or ganglion cells, in the gastropod heart, positive and negative reports on their occurrence have appeared. Dogiel (1887, 1894) reported the existence of nerve cells in the heart of *Helix*. Ransom (1884) and Argaud and Mougeot (1935) found ganglion cells in the heart of snails. On the contrary, Darwin (1876), Foster and Dew-Smith (1877), Morin and Jullien (1932) and Zubkov (1934 *a*, *b*) could not locate the nerve or ganglion cells in the heart of *Helix*. Haller (1884) found a nerve cell network in the atrial wall of prosobranchs *Fissurella costaria* and *Turbo rugosus*. Carlson (1905) and Rijlant (1931) described a ganglion at the ventriculoaortic junction in *Fulgur*. However, Spillmann (1905) denied the presence of any nerve cell in the prosobranch heart and stated that the earlier workers had mistaken connective tissue cells for nerve cells. On the other hand, Rijlant (1931) stated that the aortic ganglion in the heart of *Fulgur* is a true neurogenic pacemaker. Morin and Jullien (1930 *a*, *b*) found nerve cells in the heart of *Murex trunculus*. Suzuki (1934) stated the presence of ganglion cells in the gastropods *Janthina janthina*, *Lementina imbricata*, and *Cypraea tigris*. Divaris and Krijgsman (1954) noticed a white spot at the aortic junction of the heart in *Cochlitoma* (= *Achatina*) but they could not find any nervous elements either in the white spot or elsewhere in the myocardium. Hill and Welsh (1966) hold the opinion that the occurrence of nerve cells in the molluscan heart is still questionable. The author has failed to observe the nerve or ganglion cells in the heart of *P. globosa* and *A. fimbriata*. The absence of these cells led me to believe that the intrinsic automatism of the heart in gastropods is myogenic as previously reported for Mollusca in general by Krijgsman and Divaris (1955) and Welsh (1966).

In the present investigation no specialised tissue for the conduction of cardiac impulse could be found. Only Morin and Jullien (1930 *a*, *b*, 1932) reported the existence of specialised conducting tissue in the heart of *Murex trunculus* amongst Mollusca. The author agrees with Krijgsman and Divaris (1955) that the findings of Morin and Jullien need confirmation.

ACKNOWLEDGEMENTS

I am deeply grateful to Dr. P. N. Mathur, Principal, Government College, Ajmer, for guiding the work. Thanks are due to Dr. S. D. Misra, Professor and Head, Department of Zoology, University of Jodhpur, for encouragement. I am also thankful to my colleagues Dr. B. G. Kapoor for critically going through the manuscript and Dr. S. Johnson for his help in preparation of illustrations.

LITERATURE CITED

ANDREWS, E. B. 1965. The functional anatomy of the mantle, kidney and blood system of some pilid gastropods (Prosobranchia). *J. Zool.*, **146**: 70–94.

* ARGAUD, R. AND A. MOUGEOT 1935. Jadis considéré comme préparation purement musculaire, le ventricule isolé de l'escargot represente en realitè un myoneurone. *Arch. Mal. Coeur*, **28**: 226.

BABA, K. 1937. Contribution to the knowledge of a nudibranch, *Okadaia elegans* Baba. *Jap. J. Zool.*, **7**: 147–190.

BAECKER, R. 1932. Die Mikromorphologie von *Helix pomatia* und einigen anderen Stylommatophoren. *Z. ges. Anat.* 3. *Ergebn. Anat. EntwGesch.*, **29**: 449–585.

BASCH, P. F. 1959. The anatomy of *Laevapex fuscus*, a freshwater limpet (Gastropoda: Pulmonata). *Misc. Publ. Mus. Zool. Univ. Mich.*, **108**: 1–56.

BEECH, R. H. AND H. A. DAVENPORT 1933. The Bielschowsky staining technic. A study of the factors influencing its specificity for nerve fibres. *Stain Techn.*, **8**: 11–30.

BODIAN, D. 1936. A new method for staining nerve fibres and nerve endings in mounted paraffin sections. *Anat. Rec.*, **65**: 89–97.

———. 1937. The staining of paraffin sections of nervous tissues with activated protargol. The role of fixatives. *Ibid.*, **69**: 153–162.

BOER, H. H. AND J. LEVER 1958. On the anatomy of the circulatory system in *Ferrissia shimekii* (Ancylidae—Pulmonata); especially on the blood supply of the central nervous system. *Proc. ned. Akad. Wet. Amst.*, **62** (C): 76–83.

BRUNET, R. AND A. JULLIEN 1936 *a*. De l'architecture du coer chez *Murex trunculus*. Préliminaire à l'étude de la genèse et de la propagation de la contraction cardiaque chez cette espece. *C.R. Soc. Biol., Paris*, **122**: 596–597.

———. 1936 *b*. De l'architecture du coeur chez l'huître portugaise (*Gryphaea angulata*) et le *Murex* (*Murex trunculus*). *Bull. Soc. zool. Fr.*, **59**: 302–307.

———. 1936 *c*. De l'architecture comparée du coeur chez quelques Mollusques gastéropodes. *C.R. Acad Sci., Paris*, **203**, 1016-1018.

CARLSON, A. J. 1905. Comparative physiology of the invertebrate heart. II. The function of the cardiac nerves in molluscs. *Amer. J. Physiol.*, **13**: 396–426.

DARWIN, F. 1876. On the structure of the snail's heart. *J. Anat. Physiol.*, **10**: 506–510.

DAVIS, J. R. A. AND H. J. FLEURE 1903. *Patella*. L.M.B.C., *Mem.*, *Liverpool*, **10**: 1–84.

DIVARIS, G. A. AND B. J. KRIJGSMAN 1954. Investigations into the heart function of *Cochlitoma* (= *Achatina zebra*). *Arch. intern. Physiol.*, **62**: 211–233.

Dogiel, J. 1887. Die Muskeln und Nerven des Herzens bei einigen Mollusken. *Arch. mikr. Anat.*, **14**: 59–64.

———. 1894. Beitrag zur vergleichenden Anatomie und Physiologie des Herzens. *Ibid.*, **43**: 223–238.

Eales, N. B. 1921. *Aplysia.* L.M.B.C. *Mem., Liverpool,* **24**: 1–92.

*Fleure, H. 1904. Zur Anatomie und Phylogenic von *Haliotis. Jenaische zeitschr. f. Naturw.*, 39.

Foster, M. and A. G. Dew-Smith 1877. Die Muskeln und Nerven des Herzens bei einigen Mollusken. *Arch. mikr. Anat.*, **14**: 317–321.

Ghose, K. C. 1958. Histology of the heart and pericardium of *Achatina fulica. Proc. Indian Sci. Congr.*, **45** (3): 345–346 (Abst.).

———. 1964. The structure of the heart of *Achatina fulica* and *Macrochlamys indica* and pacemaker mechanism and refilling of the auricle in *A. fulica*, with a discussion on the same in gastropods. *Philippine J. Sci.*, **93** (2): 219–229.

*Haller, B. 1884. Untersuchungen über marine Rhipidoglossen. *Morphol. Jahrb.*, **9**: 1–98.

Hill, R. B. and J. H. Welsh 1966. In *Physiology of Mollusca* (K. M. Wilbur and C. M. Yonge, eds.), Vol. 2, Academic Press, New York, pp. 126–174.

Jullien, A. 1937 *a*. L'action diastolisante de l'acétylcholine appliquér á l'etude de l'architecture et de l'automatism cardiaque chez *Aplysia fasciata. C.R. Soc. Biol., Paris,* **124**: 650–652.

———. 1937 *b*. De l'automatisme des lambeaux cardiaques et des rapports entre la structure et les fonctions du coeur chez *Aplysia fasciata. Arch. int. Physiol.*, **45**: 189–204.

——— and H. Vairel-Blanc 1937. L'activité automatique cardiaque et la propagation de la contraction en rapport avec la structure du coeur chez *Helix pomatia. J. Physiol.* et *Path. gen.*, **35**: 673–674.

Jullien, A. *et al.* 1961. De l'architecture du coeur, monte in toto, chez les mollusques gastéropodes des genus: *Murex, Helix* et *Aplysia. Bull. Soc. Hist. Nat. Doubs.*, **63** (1): 19–23.

Kawaguti, S. 1963. Electron microscopy on the heart muscle of a snail. *Biol. Jour. Okayama Univ.*, **9** (3–4): 140–148.

Krijgsman, B. J. and G. A. Divaris 1955. Contractile and pacemaker mechanism of the heart of molluscs. *Biol. Rev.*, **30**: 1–39.

Marceau, F. 1905. Recherches sur la structure du coeur chez les Mollusques. *Arch. Anat. micr. Paris,* **7**: 496–588.

Matsui, K. 1945. Physiological studies on the heart of a marine mollusca, *Dolabella* sp. *Sci. Reports Tokyo Bunrika Daigaku,* Sec. B., **104**: 55–73.

McClung, R. 1961. *Hand-book of Microscopical Technique,* 3rd ed., Hafner, New York., p. 374.

Menzies, D. K. 1961. Bromo-phenol blue as a stain for muscle striations. *Stain Technology*, **36** (5): 285–287.

Morin, G. and A. Jullien 1930 *a*. Sur la structure du coeur chez *Murex trunculus. Bull. Histol. Tech. micr.*, **7**: 79–96.

———. 1930 *b*. Sur quelques particulariés histologiques en rapport avec le fonctionnement du coeur chez *Murex trunculus. C.R. Soc. Biol., Paris,* **103**: 263–265.

———. 1932. Recherches sur l'automatisme du coeur insolé de *Murex trunculus. Arch. int. Physiol.*, **35**: 143–145.

Morton, J. E. 1954. The vascular and nervous system *Struthiolaria* (Prosobranchia, Mesogastropoda). *Trans. Roy. Soc. N.Z.*, **83**: 721–743.

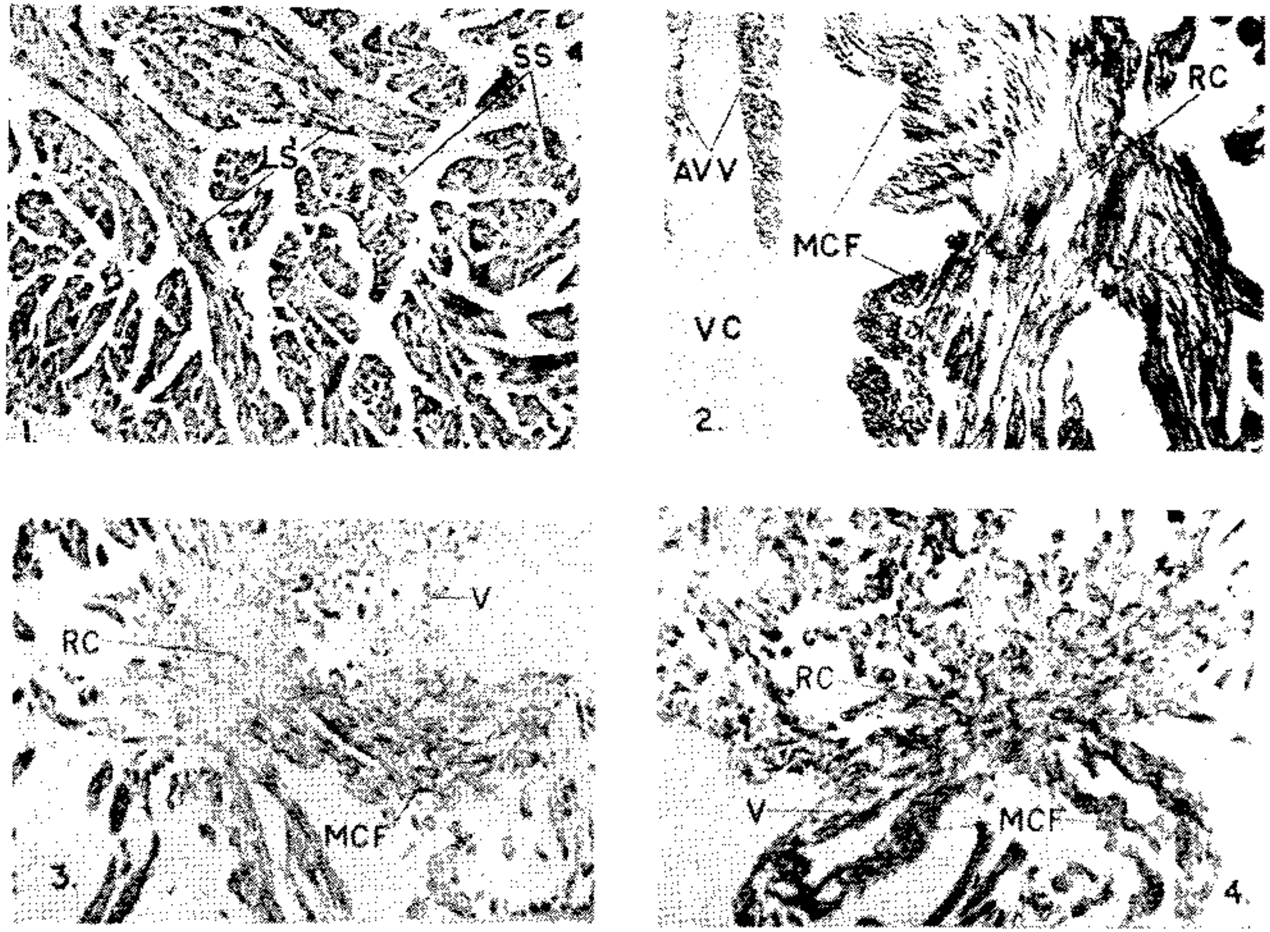
Nold, R. 1924. Die Histologie der Blutgefässystems und der Herzens Von *Helix pomatia. Z. wiss. Zool.*, **123**: 375–430.

Pelseneer, P. 1906. *A Treatise on Zoology* (Ray Lankester, ed.), Part 5, *Mollusca,* Adam and Charles Black, London, pp. 97–101.

Plenk, H. 1923. Die Muskelfasern der Schnecken. Zugleich eine kritische Studie über die sogenannte Schrägstreifung. *Z. wiss. Zool.*, **122**: 1–78.

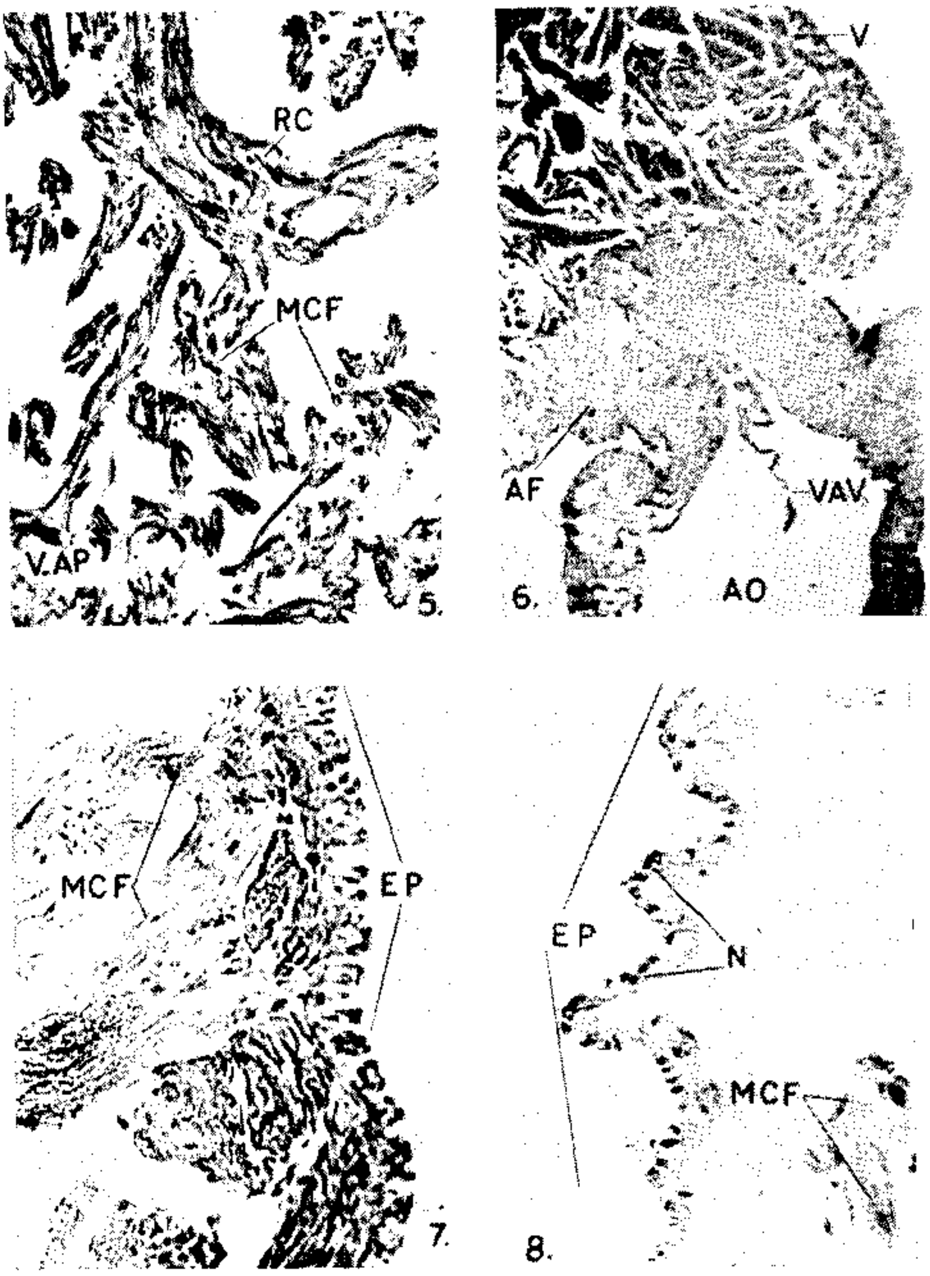
———. 1925. Zum Bau der Muskelfasern von *Anodonta. Ibid.*, **125**: 265–270.

S. C. Bhargava



PHOTOMICROGRAPHS 1–4. 1. Photomicrograph of a sagittal section of the ventricle of *P. globosa* to show large muscular strands forming enclosures that contain the smaller strands, ×300 Approx. 2. Photomicrograph of a longitudinal section showing the radiating centre in the vicinity of atrioventricular valves in the heart of *P. globosa*, ×300 Approx. 3. Photomicrograph of a sagittal section showing radiating centre at the posteriodorsal wall of the ventricle in the heart of *A. fimbriata*, ×300 Approx. 4. Photomicrograph of a sagittal section showing radiating centre at the posterioventral wall of the ventricle in the heart of *A. fimbriata*, ×300 Approx.

Plate I



Photomicrographs 5–8. 5. Photomicrograph of a sagittal section showing radiating centre near the ventricular apex in the heart of *A. fimbriata*, ×300 Approx. 6. Photomicrograph of a sagittal section of the heart of *P. globosa* showing thin anastomosing fibres at the ventricular apex, and ventriculo-aortic valve, ×100 Approx. 7. Photomicrograph of a longitudinal section showing epicardial cells in the ventricle of *P. globosa* and their contact with the myocardial fibres, ×1,200 Approx. 8. Photomicrograph of a longitudinal section showing a part of epicardium in the ventricle of *A. fimbriata*, ×1,200 Approx.

PRASHAD, B. 1925. Anatomy of the common Indian apple-snail *Pila globosa*. *Mem. Indian Mus.*, **8**: 91–154.

———. 1932. *Pila* (The apple-snail). *Indian Zool. Mem.* Methodist Publishing House, Lucknow, **4**: 1–83.

*RANSOM, W. B. 1884. On the cardiac rhythm of Invertebrata. *J. Physiol. London*, **5**: 261–341.

RAO, K. V. 1937. Morphology of *Kalinga ornata*. *Rec. Indian Mus.*, **38**: 41–79.

RIJLANT, P. 1931. L'automatisme du coeur des Gastéropodes: *Fulgur carica* et *Fulgur canaliculatum*; *Polynices*. *Compt. rend. soc. biol.*, **108**: 1150–1152.

*SCHMIDT, G. 1916. Blutgefässystem und Mantelhöhle der Weinbergschnecke (*Helix pomatia*). *Z. wiss. Zool.*, **115**: 201–261.

SESHAIYA, R. V. 1930. Anatomy of *Mysorella costigera*. *Rec. Indian Mus.*, **32**: 1–28.

SKRAMLIK, E. 1929. Untersuchungen über das Kreislaufsystem bei den Weichtieren. I. *Z. vergleich. Physiol.*, **10**: 1–19.

SPILLMANN, J. 1905. Zur Anatomie und Histologie des Herzens und der Hauptarterien der Diotocardier. *Jena. Z. Naturwiss.*, **40**: 537–588.

SUZUKI, S. 1934. On the innervation of the heart of limpets. *Sci. Rep. Tôhoku Univ.*, IV, **9**: 117–121.

———. 1935. The innervation of the heart of molluscs. *Ibid.*, IV, **10**: 15–27.

ZUBKOV, A. A. 1934 *a*. Studies on the comparative physiology of heart. The pacemaker of the heart of the snail (*Helix pomatia*). *Probl. Comp. Physiol.*, U.S.S.R., p. 47.

——— 1934 *b*. Materialien zur vergleichenden Physiologie des Herzens. I. Die Anatomie des Herzens der *Helix pomatia*. *Fiziol. Z.*, **17**: 293–298 (English summary).

* Not consulted in original.

ABBREVIATIONS

A.AO, Anterior aorta; ABD.AO, abdominal aorta; AF, anastomosing fibres; AMP, ampulla; AO, aorta; AT, atrium; AVF, atrioventricular funnel; AVV, atrioventricular valve; CA, cephalic aorta; CH.GR, chromatin granules; CR.AO, crista aorta; EF.BR.V, efferent branchial vein; EF.R.V., efferent renal vein; EP, epicardium G.OES.A, gastro-oesophageal artery; LS, large muscular strands; MCF, myocardial fibres; MF, muscle fibres; MS, muscular strands; N, nucleus; NU, nucleolus; P, pericardium; RC, radiating centre; SS, small muscular strands; V, ventricle; VA, visceral aorta; VAO, ventriculoaortic orifice; V.AP., ventricular apex; VAV, ventricular aortic valve; VC, ventricular cavity; VW, ventricular wall.

SOME FACTORS CONCERNING THE DRILLING APPARATUS AND THE FEEDING AND PREDATION OF PROSOBRANCHIATE GASTROPODS ESPECIALLY ON OTHER MOLLUSCS

GORDON GUNTER

Gulf Coast Research Laboratory, Ocean Springs, Mississippi, U.S.A.

ABSTRACT

Prosobranchiate gastropods are among the most numerous of all aquatic animals. The anatomy and mechanics of their radular mechanism would be a small question, except that it concerns some of the most inveterate predators on earth. The radula also has evolutionary significance because it is found in the cephalopods.

Cuvier (1817), Lacaze-Duthiers (1856), Geddes (1879), Amaudrut (1898), and Simthroth (1901) all stated that the radula did not move over the odontophore. This was an erroneous concept which, however, was given some credence by Galtsoff, Prytherch and Engle as late as 1937. On the other hand, Huxley (1853), Wegman (1884), Herrick (1906), Dakin (1912), Gunter (1936), and Carriker (1955) stated that the radula moves over the odontophore. Earlier papers were based on anatomical considerations, but later ones were based on direct observations. Gunter (*op. cit.*) analyzed radular movement and showed that there were three individual speeds given to radular teeth, which explains their efficient boring mechanism.

Prosobranchiate gastropods have an efficient drilling apparatus which acts as a drum covered with spikes. It will continuously bore through shell and other organic materials (Jensen, 1951 and Gunter, 1952). It seems to be aided by acids or enzymes under some conditions, but these are not necessary for drilling. Certain gastropods that have an efficient drilling mechanism seldom use it after they become adults, but seem to poison their prey by the injection of fluid at the moments when the molluscan prey opens its shell. Recent unpublished works consisting of movie films made by the Louisiana Wild Life and Fisheries Commission demonstrate remarkable plasticity in the movement of the prosobranchiate proboscis, the odontophoral apparatus and the radular mechanism.

INTRODUCTION

THERE are thousands of species of prosobranch gastropods and many of them are predators upon other molluscs, especially the Bivalvia. Probably there is no clam or oyster bed on Earth that is not subject to predation from some gastropod from time to time. The Virginia oyster of North America, *Crassostrea virginica*, suffers extensively from attacks by the drill, *Urosalpinx cinerea*, on the Atlantic coast and the oyster borer, *Thais haemastoma*, a muricid, on the Gulf of Mexico coast.

Some gastropods, such as *Pleuropocra gigantea*, are not well known as predators but are recognized carrion feeders, even though we must say that the food habits of this large conch are imperfectly known at best. Molluscs are not the only food of prosobranch predators, of course, and they are known to drill into elasmobranch eggs (Jensen, 1951), to kill and devour crabs that have lost their chelipeds (Powell and Gunter, in press), and to prey upon heart urchins and sand dollars (Moore, 1956).

AVOIDANCE OF PREDATORS BY SALINITY OR HABIT PREFERENCE

The salinity limits of the Virginia oyster and its predators do not coincide, but overlap, and the oysters can survive at lower salinities. However, during dry, high salinity years the prosobranchs invade and I have seen them wipe out oyster reefs in Apalachicola Bay, Florida, and in Carancahua Bay, Texas.

Several authors have mentioned the fact that oysters of the genus *Crassostrea* have invaded low salinity waters to avoid enemies (*cf.* Gunter, 1955). One of the earlier writers on this subject was Grave (1905). Nelson (1938) gave a clear exposition of this thesis and showed that *Crassostrea* is also antomically fitted to cope with the turbid waters of low salinity areas. In view of the decline in numbers of species with the falling salinity gradient in estuaries (*cf.* Pearse and Gunter, 1958), this assumption seems to be reasonable.

In certain areas oysters have become acclimated to extremely low salinity waters, and can reproduce there. One such area is Redfish Bay in Louisiana, lying between the numerous smaller mouths of the Mississippi River, and which is subject to freshwater overflow for months at a time. The writer made a dozen trips to this bay between June, 1952, and October, 1956, and made salinity determinations over the whole area each time. Unpublished reports of mine show that in 1952 the average salinity was 5·7 *per mille*. Geyer (1955) found that from 5 May 1953 to 4 July 1953 the salinity range in this bay was 3·6 to 8·7 *per mille*. It is generally stated that salinities below 10 parts per thousand affect gonadal development and in general are harmful to oysters. However, this is not true of low salinity oysters in such places as Redfish Bay. There, in certain places, the bottom was paved with live oysters so embedded in the reef that they could not be removed singly. During the higher stages of the tide the salinity approached 10·0 parts per thousand. The only gastropod present was *Neritina reclivata*. In October, 1956, the writer found the highest salinities that had been recorded in five years, a range of 8·2 to 19·8, with an average of 12·8.

These facts are presented to show that some oysters of the genus *Crassostrea* can live and reproduce at salinities below what is commonly accepted as the range or limit for this genus. Possibly they take in salts at high levels of the tide. But even the commonly accepted salinity ranges for oysters are below the ranges tolerated by *Thais*. The so-called "conch line" in Louisiana, for instance, is at a salinity of 15 g./kg. (St. Amant, 1938). Very small conchs go beyond this line into the lower salinity waters, but not the adults. This corresponds to the observation (Gunter, 1961) that the young of euryhaline or semi-euryhaline species go into lower salinity waters than larger specimens.

In any case, certain bivalves such as the oyster, *Crassostrea*, the mussels *Brachidontes, Mytilus*, and *Congeria*, and the clams, *Rangia* spp. avoid gastropod predators by living in part in waters of lower salinity than the predators can tolerate. If it is true that these marine bivalves invaded low salinity waters to avoid predation, then it would seem that some predators are following them in.

METHODS PROSOBRANCHS USE IN OPENING OR PENETRATING BIVALVES

Prosobranch gastropods open bivalves in at least four different ways. These different ways of entering bivalves demonstrate a rather peculiar idea. Drilling or shell boring is not as important as we have been led to believe, and quite possibly, or even probably, the radula with its band-over-a-pulley movement did not originate as a boring mechanism at all but as a feeding mechanism at the end of a soft tube. If we may be permitted to return to this discussion later, things may be clarified first by a discussion of a prosobranch's way of devouring bivalves. These are discussed under the various following headings.

A. *Prying or opening shells by leverage or wedging*

Colton (1908) reported that the relatively large gastropods *Busycon carica*, and *B. canaliculatum* of the Middle and North Atlantic coasts of the United States insert their shell margins between the edges of the closed shells of the quahog, *Mercenaria*, a very large, strong clam, and chip away until they have an opening. (I shall always remember my initial doubts about this matter, and how well the observations have been verified since.) *Busycon* has a hard flint-like shell, which becomes quite thin and blade-like at the edge. These blade-like edges become chipped themselves, but they do perform in opening clams and oysters and other bivalves, so that the proboscis can be introduced. No hole is bored or drilled but an opening for the proboscis is made. Colton (*op. cit.*) stated that *Busycon* could also wedge its shell between those of the bivalve without chipping.

The large gastropods, with large probosces, such as *Strombus* or *Pleuropocra gigantea,* are not known to leave large-bored holes in any mollusc. Yet they have strong flinty, sharp-edged shells similar to *Busycon.* Wells (1958 *a*) has shown that *Fasciolaria hunteria* opens bivalves by wedging their shells open. The same author (Wells, 1958 *b*) has shown that the relatively small *Murex fulvescens* opens *Mercenaria* by chipping and grinding. In any case it would not be surprising to find more large gastropods that hold their bivalve prey with the foot and open the valves with their own shells.

B. *Fast intromission of the proboscis*

The crown conch, *Melongena corona,* of Florida is one of the most aggressive of all gastropod predators. It attacks and overcomes other whelks much larger than itself, such as *Busycon,* and has been reported to attack live horse-shoe crabs, *Limulus.* Smaller specimens of its own species are eaten when no other food is available. Gunter and Menzel (1957) reviewed what is known of the food habits of this snail and described its attack. In the case of bivalves it examines its prey carefully and then suddenly the proboscis shoots "out as rapidly as the flick of a finger, between the open valves...."

These animals sometimes gnaw on the edge of oyster shells in the laboratory, but they are not known to bore holes, and apparently they wait until the oyster opens momentarily and then introduce the proboscis quickly. They wave the proboscis about and expose it readily when feeding. This is in contrast to *Thais* which keeps the proboscis covered with the foot and behaves as if the organ were very sensitive, delicate, and easily injured.

And so we may conclude that certain gastropods, possibly many species, use the proboscis as a weapon of attack, but the radula is not used as a drilling mechanism for boring through shell.

C. *The injection of a poison between the valves*

Colton (1908) in speaking of *Busycon* stated that, in addition to the wedging and chipping it does on bivalve shells, "it may pour a secretion between the valves which kills the clam;....". This statement has been doubted, but subsequent observations of my own are quite similar and indicate that Colton's ideas, based as they must have been on some observation he did not describe, were in all probability correct.

There is no doubt in the world about the fact that *Thais haemastoma* bores through the shells of oysters and devours the oyster through this hole. However, this action is confined chiefly to small specimens of *Thais.* The larger animals merely sit on the opening of the oyster away from the hinge. The following remarks are taken from an unpublished report submitted by the author to the United States Bureau of Commercial Fisheries in 1935.

"If the animals are hungry they will attack oysters in thirty minutes after being placed in a jar or tank with them. The time taken for a *Thais* to kill and completely devour an adult oyster is around twenty-four hours. The attack is always made on the bill edge where the shell is thin and practically always on the upper bill edge. Sometimes the animal gets on top of the shell facing forward, but most of the time it was observed to face the oyster with the upper part of the foot folded over the upper bill edge. The foot is folded around the proboscis and the latter is never seen.

"All attacks are not successful and some animals were seen to relinquish their position and return three times in several days before being successful. Generally a small semi circular hole or a long roughly rectangular hole is bored on the bill edge in the thin new shell. Significant points noted were that no perfectly round holes were bored, no holes were bored except on the bill edge and coinciding with its margin on one side, and all holes were comparatively small. No hole was seen that could have possibly admitted the entrance of the proboscis while the shell was closed. This is contrary to the methods of most boring gastropods which bore a hole large enough to admit the proboscis. This fact seems to indicate that *Thais* uses the small hole as the entrance for some powerful anaesthetizing or paralytic agent which forces the oyster to open. Federighi (1931, p. 100), states that oysters drilled by *Urosalpinx* are often killed although the drill is removed before the oyster is visibly damaged at all. *Thais* apparently does not have to insert its proboscis at all to get the oysters open for many show no discernible signs of shell damage under low power binoculars.

"Data on this point were taken on 226 oysters killed by *Thais* in the laboratory. The following table is a summary.

Shells bored at bill edge			Shells not bored		
	Seed	Adults		Seed	Adults
Numbers	88	61		52	25
Per cent ..	38·7	27		23·02	11·3
Total per cent ..	65·7			34·3	
Per cent seed bored	62·8		Per cent seed not bored		37·2
Per cent of adults bored		70·1	Per cent of adults not bored		29·9

[These experiments show that under laboratory conditions, active, normal *Thais* may fail to drill over 30 per cent of the animals devoured, while the remainder are only slightly attacked at the edge. Burkenroad (*op. cit.*) and St. Amant (*op. cit.*) noted that borings at the edge of the shell are difficult to see in the field and thus may lead workers to minimize the amount of destruction caused.]"

Additionally, it may be said that some of these oysters were put on a kymograph and under attack they stayed tightly closed for 18 hours. Then they opened only partially and briefly for apparently a few seconds. In an hour or two they opened again and closed, but then in a still shorter time they opened again and apparently struggled to close but could never do so and slowly succumbed so that the gape was complete. I have removed the conchs from the victims at this time and have found that the oysters were intact but dead, with only a small hole in the mantle, but they contained what seemed to be a foreign mucous with a little of the purplish dye which is secreted by the muricid snails. These observations correspond with the statements of Colton and Federighi. They also explain the statement of Louisiana oystermen that conchs "smother" oysters. That, of course, is impossible because oysters can close their shells and live anaerobically for as long as three weeks during the cool weather of winter. On the other hand, it is quite possible that *Thais* and other gastropods inject a poison or narcotic into the oysters which causes them to die and open their shells. The evidence is rather convincing in that oysters may be regularly killed and eaten by *Thais* in twenty-four hours of time with not the slightest disturbance or boring of the shell, not even of the scales of conchyolin at the shell edge. No one has isolated this poison or paralytic agent, but no one has tried to do so, so far as I know.

D. *Boring or drilling through the shell*

Almost everyone who has taken a stroll along the sea beach has seen the bored shells of bivalve molluscs lying in the flotsam of the strand. The untold numbers of these shells signify but do not measure the great depredations of gastropods upon the bivalves. The matter is particularly impressive when we remember that a great many molluscs are destroyed by gastropods without any drilling at all.

Menzel and Hopkins (1954) stated that for fifty years biologists who studied oysters on the Gulf coast failed to recognize the depredations of *Thais* because they were looking for neatly bored holes and very few were to be found.

Of the boring gastropods, some, such as *Urosalpinx* and *Polynices*, always seem to bore through the shells of their prey, but others bore only at times.

THE ARGUMENT CONCERNING RADULAR MOVEMENT

Cuvier (1817) followed by Lacaze-Duthiers in 1856, Geddes in 1879, Amaudrut in 1898 and Simroth in 1901 all stated that the radula was held immovable on the odontophore cartilages and acted passively as that organ rocked back and forth. This view is completely in error and the radula moves as a band-over-a-pulley as stated by Huxley (1853). For that reason, I believe it is worthwhile to quote at some length from my paper of 1936, which describes the situation about as succinctly as if it were repeated anew.

> " Most writers in describing the odontophoral apparatus in gastropods have not mentioned the issue, but there have been adherents of both theories. Lacaze-Duthiers[4] (1856), Geddes[5] (1879), Amaudrut[6] (1898) and Simroth[7] (1901) rejected Huxley's hypothesis for that of Cuvier, either by direct statement or by implication in their descriptions. Geddes studied under Huxley and took up the subject at the latter's instigation. He rejected the chainsaw idea and concurred with Cuvier. His objection to Huxley's theory was based principally on the close attachment of the radula to the radular sac by the radular membrane and his belief that the radula could not slide over the acute angle formed by the apex of the cartilages.
>
> " Wegman[8] (1884) in describing Haliotis stated that the radular membrane slides over the cartilages, which implies that the radula does also. Herrick[9] (1906) in describing the anatomy of the odontophore of *Busycon canaliculatus* sided with Huxley, and gave a very clear exposition of his conception of its mode of action. Dakin[10] (1912) working on *Buccinum* also followed Huxley. He stated that the radula could be made to slide over the cartilages in narcotized animals by pressing the proboscis between the thumb and forefinger. Both he and Herrick stated as further evidence for their belief, that radular movement could be felt when animals were induced to rasp the finger tip. The writer has repeated this experiment with *Melongena corona* and *Thais floridana*, but has found it impossible to tell by such means whether the radula slides or is passively borne by the cartilages.
>
> " Because of the internal position of the radula in the radular sac within the proboscis, its small size, and the fact that when in use the whole proboscis is often covered by the foot and

---

[4] *Ann. Sci. Nat.*, **6** : 225-281, 1856.

[5] *Trans. Zool. Soc. London*, **10**: 485-491, 1879.

[6] *Ann. Sci. Nat.*, **7**: 1-291, 1898.

[7] *Bronn's Klassen und Ordnungen das Tierreichs.*, Band 3. Leipzig, 1901.

[8] *Arch. Zool. Exper. et Gen.*, **2**: 289-378, 1884.

[9] *Amer. Nat.*, **40**: 707-737, 1906.

[10] *Liverpool Marine Biology Committee Memoirs.*, **20**: 1-115, 1912.

its open end is placed on the food, observation of the living animal in the natural state seems to be almost impossible. These obstacles are probably the reasons why such observations, which would have settled the question, have been few and relatively incomplete. Some workers have stated that they have observed living animals, but most of their conclusions appear to be drawn from the anatomy, and the writer has not found a complete description of radular movement based on direct observations of the odontophoral mechanism at work in the living animal.

"*Fasciolaria gigantea* of the Florida coast is an ideal animal for study and observations were made on it at the Indian Pass Laboratory of the United States Bureau of Fisheries. It is one of the largest gastropods in the world and has a radula 2 mm. wide. When stimulated by a bit of oyster meat it gives the usual food reaction of carnivorous gastropods which culminates in the extrusion of the proboscis. This has been described in detail by Copeland[11] for *Nassa obsoleta* and *Busycon canaliculatum.* If the food is withdrawn the odontophore may be seen through the proboscis opening, with the naked eye, to continue working in the following manner. The cartilages bearing the radula move forward and upward with a licking motion. At the same time the radula moves upward and over the cartilages like a chainsaw or belt over a pulley, with a motion so rapid that it gives the illusion of rapid rotation. When the odontophore reaches the end of the forward movement it begins to move downward and backward. At the same moment the radula reverses its direction, almost too speedily for detection, and slides downward and under the cartilages. As the forward movement of the cartilages is started again the radula repeats the movement first described. The whole process proceeds at an even rate so that the radula has the appearance of a rapidly spinning wheel being carried back and forth on a frame. As Herrick (*op. cit.*, p. 721) has pointed out the teeth are folded together as they pass back and forth under the cartilages and rasping can only be done during the upward stroke. The mouth is situated so that food can be drawn into it only by this movement and not by the downward one. In *Thais* the food may be seen to progress down the proboscis in peristaltic waves, which are apparently timed and initiated by the piston-like strokes of the odontophore.

"The objections of Geddes and others to the theory that the radula has motion independent of that of the cartilages, were based on anatomical studies and cannot hold in the face of observations to the contrary on living animals. He seemed to disregard the significant fact that the radula is a long, ribbon-like, jointed apparatus, borne on a very flexible membrane; the whole being eminently fitted for the band-over-pulley type of function. The plates bearing the teeth are loosely joined together so that the whole radula can bend back upon itself. This jointed structure allows the radula to move over the apex of the cartilages as described for *Fasciolaria.* The radula is not too closely attached to the radular sac, as Geddes stated, or too firmly attached to the cartilages for independent movement, as shown by the fact that in *Thais floridana* and *Thais* sp. the radula of an amputated proboscis can be made to move over the cartilaginous support while the latter is perfectly stationary. These animals are very similar in structure to *Buccinum*, one species upon which Geddes worked and arrived at the opposite conclusion."

The radula is pulled up as the odontophore rocks forward and three speeds are superimposed one on the other. As the radula passes over the outer end of the odontophoral cartilages the teeth are spread and are in the same condition as the rim of a wheel, the speed being greater there than anywhere inside the circle. Then the upward licking motion of the odontophore which carries food to the mouth adds a second motion to the first. But the greatest speed is the fast pulling radula up and over the odontophoral outer rim as it rocks forward. This is effected by long muscles of the running up the proboscis.

Later this same statement essentially was reiterated in *Nature* (Gunter, 1952) in support of Jensen's (1951) contention in the same journal that the radula was an effective drilling mechanism and operated without acid in boring through the egg cases of skates and gastropods.

---

[11] *Jl. Exp. Zool.*, 25: 177–227, 1918.

A final proof of this matter is the moving picture of a *Thais haemastoma* eating oyster meat between two panes of glass, which was made recently by the Louisiana Wild Life and Fisheries Commission. The minute details cannot be seen but the extensive pull of the radula back and forth is quite clear.

Nevertheless, possibly because of the names involved doubt seems to linger. The distinguished zoologist Hyman (1967) reviewed the literature partially and came to the only one of three conclusions available to her that could not be correct, namely that the radula is held still in some prosobranchs and that it moves in others. It is scarcely possible that two types of odontophoral apparatus or buccal mass and even probosces (when we consider the long muscles involved) are found in the prosobranch gastropods, which is what Hyman's statement implies.

THE QUESTION OF ACID OR ENZYME AIDS TO SHELL DRILLING

Over one hundred years ago Preyer (1866) stated that sulphuric acid secreted by the salivary glands of *Dolium galea* attacked the shells of molluscs and the calcareous parts of echinoderms. Bayliss (1927) suggested that aspartic acid produced by similar molluscs had a similar function. However, except for Schiemenz (1891) no one has been able to confirm acidity in the proboscis of gastropods. And many physiologists have tried. Dr. Warren S. Rehm, then of the Department of Physiology of the University of Louisville Medical School, came to this Laboratory some years seeking acid secreting marine organisms and worked with several large prosobranchs. His negative results were never reported.

Just recently Carriker, Van Zandt, and Charlton (1967) report detection by microelectrodes of acid within bored holes of oysters after the accessory boring organ of *Urosalpinx* was placed in the hole. It is quite possible that previous crude methods, the use of litmus papers, etc., as well as excised and non-secreting tissues account for non-detection of acid. However, the situation needs further elucidation.

REGENERATION OF THE PROBOSCIS

Pleuropocra gigantea and *Melongena corona* for instance seem to have tough probosces, which they wave about freely in the water and even in air. On the other hand other gastropods such as *Thais*, *Urosalpinx*, and *Polynices* seem never to expose their probosces under natural conditions. However, hungry *Thais* will slowly and timidly extrude its proboscis to an amazing length following a piece of oyster flesh down the side of an aquarium. The slightest touch causes the organ to snap back into the body as if it were a rubber band. Nevertheless, the proboscis can be cut off with a quick slash of a safety razor blade. We carried on such amputations many times with the aim of finding out if an animal with no proboscis would attempt to kill an oyster by poison. But we were amazed to see that the whole proboscis, as good as new and just as large, was regenerated in three weeks time, which is not much longer than the time between heavy meals for these creatures (Demoran and Gunter, 1956).

This is one of the most amazing regenerative feats known for a prosobranch proboscis is an extremely complicated organ. And yet the phenomenon fits in very well if examined in the light of natural history and evolution. Even an animal with a highly sensitive and fast retracting proboscis might be expected to get it caught occasionally between bivalve shells. I know of two instances where *Thais* was caught by oysters, one observed and one reported to me by another zoologist. In such situations it would be of great survival value to *Thais* if it could quickly grow another proboscis, and apparently this led to prosobranchs with astonishing regenerative ability, at least of the proboscis.

DISCUSSION

The Mollusca is a very diverse group of animals and yet a radula is present in each class of this phylum, except the Bivalvia. This organ and the cartilages that go with it, the odontophore, reaches its maximum development in the order Stenoglossa of the subclass Prosobranchia. Many of these snails bore holes in other molluscs with their radula. They leave evidence of their deeds, so to speak, and their prey is often other molluscs of commercial importance. For that reason the stenoglossate prosobranchs have been extensively studied in their drilling habits. As a result we are insidiously presented with the idea that the radula arose as a drilling mechanism. That view is quite incorrect, I believe, and it is much more likely that the radula began as a feeding mechanism.

In an aplacophoran, *Cyclomenia*, the radula is a large denticulated plate on each side of the foregut wall, which is regarded as the primitive condition by recent malacologists (Hyman, *op. cit.*). Other solenogastres show conditions almost as primitive.

An open tube such as the proboscis without the buccal mass is not a very good food gathering organ, although the minute opisthobranch, *Odostomia*, has only a tube with which it can take in only the fluids of other molluscs, and is epiparasitic upon them.

The mouth in all the radular organisms is within the proboscis tube and the odontophore lies under it. As the odontophore moves forward and ventrodorsally it carries food into the mouth. And so we may say the Mollusca developed this strange and efficient mechanism, the radula, instead of jaws as a food-gathering mechanism. This generality is not complete, however, for the genus *Conus* has worm-like jaws at the end of the proboscis, and it is well known that the Cephalopoda have developed jaws while retaining the radula.

Many molluscs developed the radula into vegetable eating organs or scrapers. Others used it as a weapon of attack, especially of the gastropods on bivalves or other gastropods without any attempt at boring. Even on land pulmonate predators attack the pulmonate vegetarians, and on the grounds of this Laboratory the vegetarians fight back valiantly so that a rasping sound is heard when the radulae meet as these little animals fight to the death.

In fact predation must have long preceded shell boring, although bored molluscs go back about 400 million years. Furthermore, predation by gastropods without drilling may still be the dominant method. Nevertheless, it is quite obvious that boring by gastropods is the present-day evolutionary end point of the use of the radula in predation. It permits the small snail, *Urosalpinx*, which is not much larger than a man's thumb to penetrate and eat an oyster as large as a man's hand.

Whether or not an acid or enzyme from an accessory boring organ is needed to help the efficient radula is still a matter of some dispute. Proponents of this theory stated some years ago that excised ABOs, as they call it, etched shell but no acid could be detected. Now that they have purported to have found acid they say the ABOs formerly tested were excised, dead, or moribund and not secreting (Carriker *et al.*, *op. cit.*).

In this respect it should be pointed out that plant eating, rock scraping snails erode this material at a measurable rate and they certainly do not need or use an ABO, for their effort is not extended towards eating the rock.

In any case I think it is clear that applied and theoretical molluscan biologists will find many things of value and interest in further elucidation of the radula mechanism and connected feeding habits, especially of the Prosobranchia.

LITERATURE CITED

BAYLISS, W. M. 1927. *Principles of General Physiology*. pp., xxvii+882, Longmans Green & Co., London.

CARRIKER, M. R., D. VAN ZANDT AND G. CHARLTON 1967. Gastropod *Urosalpinx*: pH of accessory boring organ while boring. *Science*, 158 (3803): 920–922.

Colton, H. S. 1908. How *Fulgur* and *Sycotypus* eat oysters, mussels and clams. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **60**: 3–10.

Cuvier, Georges 1817. *Memoire pour servir à l'histoire et à l'anatomie des mollusques*, Paris.

Demoran, W. J. and G. Gunter 1956. Ability of *Thais haemastoma* to regenerate its drilling mechanism. *Science*, **123**: 1126.

Geyer, Richard, A. 1955. The effect of the Gulf of Mexico and the Mississippi River on Hydrography at Redfish Bay and Blind Bay. *Publications of the Institute of Marine Science*, **4** (1): 158–168.

Grave, Caswell 1905. Investigations for the promotion of the oyster industry of North Carolina. *Report of the U.S. Commissioner of Fisheries*, **29**: 247–341.

Gunter, Gordon 1936. Radular movement in gastropods. *Journal of the Washington Academy of Sciences*, **26** (9): 361–365.

———. 1952. Radula movement and boring efficiency of gastropods. *Nature*, **169**: 630.

———. 1955. Mortality of oysters and abundance of certain associates as related to salinity. *Ecology*, **36** (4): 601–605.

———. 1961. Some relations of estuarine organisms to salinity. *Limnology and Oceanography*, **6** (2): 182–190.

Gunter, G. and R. W. Menzel 1957. The crown conch, *Melongena corona*, as a predator upon the Virginia oyster. *The Nautilus*, **70** (3): 84–87.

Huxley, T. H. 1853. On the morphology of the cephalous Mollusca as illustrated by the anatomy of certain Heteropoda and Pteropoda collected during the voyage of H.M.S. Rattlesnake 1846–5. *Philosophical Transactions of the Royal Society of London*, **143**: 29–65.

Hyman, Libbie H. 1967. *The Invertebrates*, Vol. VI. *Mollusca* I, pp. vii + 792, McGraw-Hill Book Co., New York, London.

Jensen, A. S. 1951 *a*. Do the Naticidae (Gastropoda: Prosobranchia) drill by chemical or by mechanical means? *Videnskabelige meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn*, **113**: 251–261.

Jensen, A. S. 1951 *b*. Do the Naticidae drill by mechanical or by chemical means? *Nature*, **167**: 901.

Menzel, R. W. and S. W. Hopkins 1954. Studies on oyster predators in Terrebonne Parish, Louisiana. *Texas A. & M. Research Foundation, Project Nine*, 145 pp. 18 figs. Multilithed, Bryan, Texas.

Moore, Donald R. 1956. Observations of predation on echinoderms by three species of Cassididae. *The Nautilus*, **69** (3): 73–76.

Nelson, Thurlow C. 1938. The feeding mechanism of the oyster. *Journal of Morphology*, **63** (1): 1–61.

Pearse, A. S. and G. Gunter 1957. *Salinity*. Chapter 7, pp. 129–157 in: *Treatise on Marine Ecology and Paleoecology*. *Ecology*, Vol. 1, pp. vii + 1296. *Memoir* 67, Geological Society of America.

Powell, E. H. Jr. and Gordon Gunter 1968. Observations on the stone crab, *Menippe mercenaria* in the vicinity of Port Aransas, Texas. *Gulf Research Reports*, **2** (3): (in press).

Preyer, W. 1866. Ueber das für Speichel gehaltene Sekret von *Dolium galea*. *Sitz. Ber. niederrhein. Ges. Natur. Heilkunde in Bonn.*, pp. 6–9.

Schiemenz, P. 1891. Wie borht Natica die Muscheln an? *Mitt. Zool. Stat. Neapel*, **10**: 153–169.

St. Amant, L. S. 1938. Studies on the biology of the Louisiana oyster drill *Thais floridana haysae* Clench. Unpublished master's thesis, Louisiana State University, pp. 116.

Wells, Harry W. 1958 *a*. Predation of pelecypods and gastropods by *Fasciolaria hunteria* (Perry). *Bulletin of Marine Science of the Gulf and Caribbean*, **8** (2): 152–166.

———. 1958 *b*. Feeding habits of *Murex fulvescens*. *Ecology*, **39** (3): 556–558.

STATOCYST FUNCTION IN *POMACEA PALUDOSA* (SAY)[1]

ANDREW McCLARY

Michigan State University, East Lansing, Michigan, U.S.A.

ABSTRACT

Populations of the Prosobranch snail *Pomacea paludosa* were maintained under controlled laboratory conditions, and used in a study of statocyst function. Three sets of snails were used in experiments. These were operated snails, from which both statocysts had been removed; sham-operated snails, in which the body wall was opened but statocysts left intact; and control snails. Experiments were conducted in cylindrical (inside diameter 28 cm.) and in rectangular aquaria. Previous experiments had indicated that snails deprived of statocysts can successfully travel upwards to the water's surface when in cylindrical aquaria. Three cues were considered of possible importance in directing this movement. These were overhead light, the downward pull of the shell, and the curvature of the aquarium wall. Experiments indicated that the apparent cue was the wall curvature. Operated snails deprived of overhead light and/or the weight of their shell could still move upwards in cylindrical aquaria, but were unable to do so in rectangular ones.

INTRODUCTION

EVER since the initial suggestion made by Delage (1887), attempts have been made to show experimentally that statocysts are vital to directional movement of molluscs. In opposition to this view, several early workers maintained that much directional movement among gastropods is mediated by passive cues associated with shell weight and musculature. The general literature on this controversy will not be given here as it has been summarized recently by Wilbur and Yonge (1966). Of the experimental work concerning the statocyst function of snails, the most impressive is that of Lever and Geuze (1965) who demonstrated that removal of statocysts from *Lymnaea stagnalis* resulted in complete loss of orientation when the animals were placed on 15° or 30° slopes in air. Recently McClary (1966) found that after statocyst removal the prosobranch *Pomacea paludosa* still appears able to travel directively to the surface when placed in cylindrical water-filled aquaria. To attempt to resolve the seeming contradiction between these results and those of Lever and Geuze, further experiments, which are here reported, were undertaken.

MATERIALS AND METHODS

Laboratory populations of snails were maintained under controlled conditions as described in earlier work (McClary, 1964).

Three groups of snails were used in these experiments. Operated snails had both of their stato cysts removed as previously described (McClary, 1966). These snails were allowed to recover for at least seven days before being used in experiments. Sham-operated snails had been incised on both sides of their body above the area where statocysts were located, so that effects of incision could be distinguished from effects of statocyst removal. These snails were also allowed to recover for at least seven days before use. Control snails comprised a third group.

Experiments were conducted in two types of aquaria. One was cylindrical, glass, and 30 cm. deep by 28 cm. inside diameter. It was filled with water to a level of 20 cm. The second type was

---

[1] This study was supported by Grant GB-3672 from the National Science Foundation.

rectangular, glass, and 30 cm. wide by 76 cm. long by 30 cm. deep. In use, it was filled with water to a level of 20 cm.

When experiments were carried out in these aquaria, the following variables were introduced:

1. In some experiments the aquaria were illuminated from an overhead light, in others from a lower light. In the latter case a translucent plastic was placed between the light and the aquarium floor so as to diffuse the entering rays.
2. In some experiments the shells of animals were left untouched, in others, a small plastic buoy was affixed to the shell apex so that the shell position was changed from a roughly vertical axis to one roughly horizontal (Fig. 1).
3. In some experiments involving the rectangular aquarium the inner glass walls were covered with a roughened plastic layer.

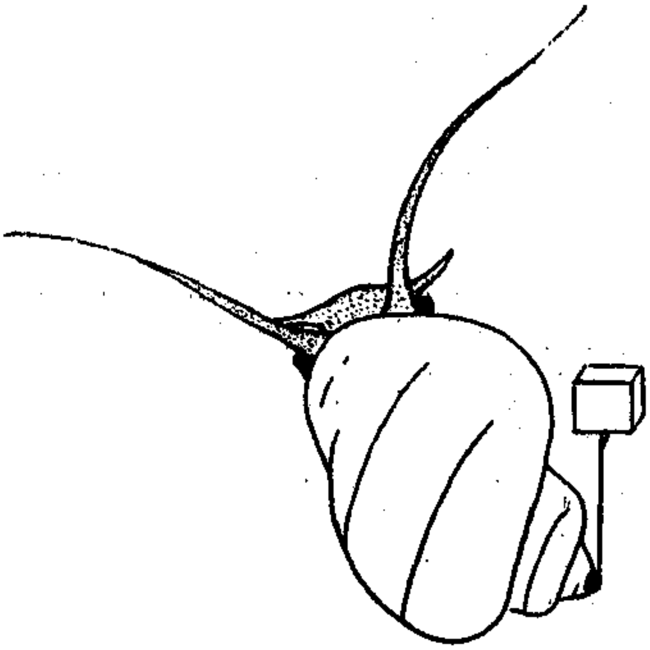


FIG. 1. Method of affixing buoy to snail apex. Thread was attached to shell using plastic rubber cement.

To test the snails' ability to surface in these aquaria they were first placed in perforated plastic containers in their home aquarium so that they were held from the water's surface overnight. In previous work it had been found that a snail thus restricted would seek the surface upon release. In any one experiment six snails of each group were simultaneously placed in an aquarium and observed. The subsequent movements of the snails were recorded on the aquarium wall by marking pencil and later copied onto paper.

EXPERIMENTS

The following experiments were designed:

I. *Experiments involving ability to surface*

A. In the cylindrical aquarium:

Expt. (1) Overhead light present, shell unaltered,

Expt. (2) Overhead light present, shell raised to horizontal axis by buoy.
Expt. (3) Lower light present, shell unaltered.
Expt. (4) Lower light present, shell raised to horizontal axis by buoy.

B. In the rectangular aquarium:

Expt. (5) Walls of glass, overhead light present, shell unaltered.
Expt. (6) Walls of plastic, overhead light present, shell unaltered.

In Experiments 3 and 6 sham-operated snails were not used. In Experiment 3 control snails were not used.

II. *Experiments involving body twisting*

In these experiments which were made on plastic walls in the rectangular aquarium, snails which were moving to the surface were diverted one or more times by applying a glass rod to their body so that both shell and foot were turned to face horizontally. Resultant behavior of the manipulated snail was then recorded. Twenty-four operated and 13 control snails were thus manipulated.

RESULTS

I. *Experiments involving ability to surface*

As shown in Table I snail groups in the cylindrical aquarium were normally successful in surfacing regardless of shell elevation or position of light (Experiments 1–4). In contrast to their performance in the cylindrical aquarium, operated snails in the rectangular glass-walled aquarium

TABLE I

Ability of Pomacea paludosa *to reach surface after statocyst removal*

Experiment	Group	Number of snails observed	Snails surfacing		Snails not surfacing	
			No.	%	No.	%
1	Operated ..	61	57	93·4	4	6·6
	Sham ..	52	51	98·1	1	1·9
	Control ..	57	56	98·0	1	2·0
2	Operated ..	43	40	93·0	3	7·0
	Sham ..	35	35	100·0	0	0·0
	Control ..	56	56	100·0	0	0·0
3	Operated ..	26	26	100·0	0	0·0
	Sham ..	..	..	..	..	..
	Control ..	..	..	..	..	..
4	Operated ..	53	50	94·3	3	5·7
	Sham ..	32	32	100·0	0	0·0
	Control ..	30	30	100·0	0	0·0
5	Operated ..	27	6	22·2	21	77·8
	Sham ..	22	21	95·4	1	4·6
	Control ..	34	34	100·0	0	0·0
6	Operated ..	16	9	56·3	7	43·7
	Sham ..	..	..	..	..	..
	Control ..	27	27	100·0	0	0·0

were typically not able to reach the surface (Experiment 5). In some cases operated snails turned and travelled downward. In others, they slipped or fell from the wall. The performance of operated snails travelling on plastic in this aquarium (Experiment 6) showed some improvement, but was still well below that in the cylindrical aquarium. Figure 2 shows typical tracks made by snails in the two aquaria.

Under all conditions, both in the cylindrical and rectangular aquaria, operated snails appeared to orient less efficiently in their climb to the surface than did the sham-operated or the control snails. This loss of efficiency was indicated by placing a $2\ \text{cm.}^2$ grid over each recorded track and counting the number of vertical lines each snail crossed during its travel upward. As shown in Figure 3 operated snails cross a larger number of vertical lines.

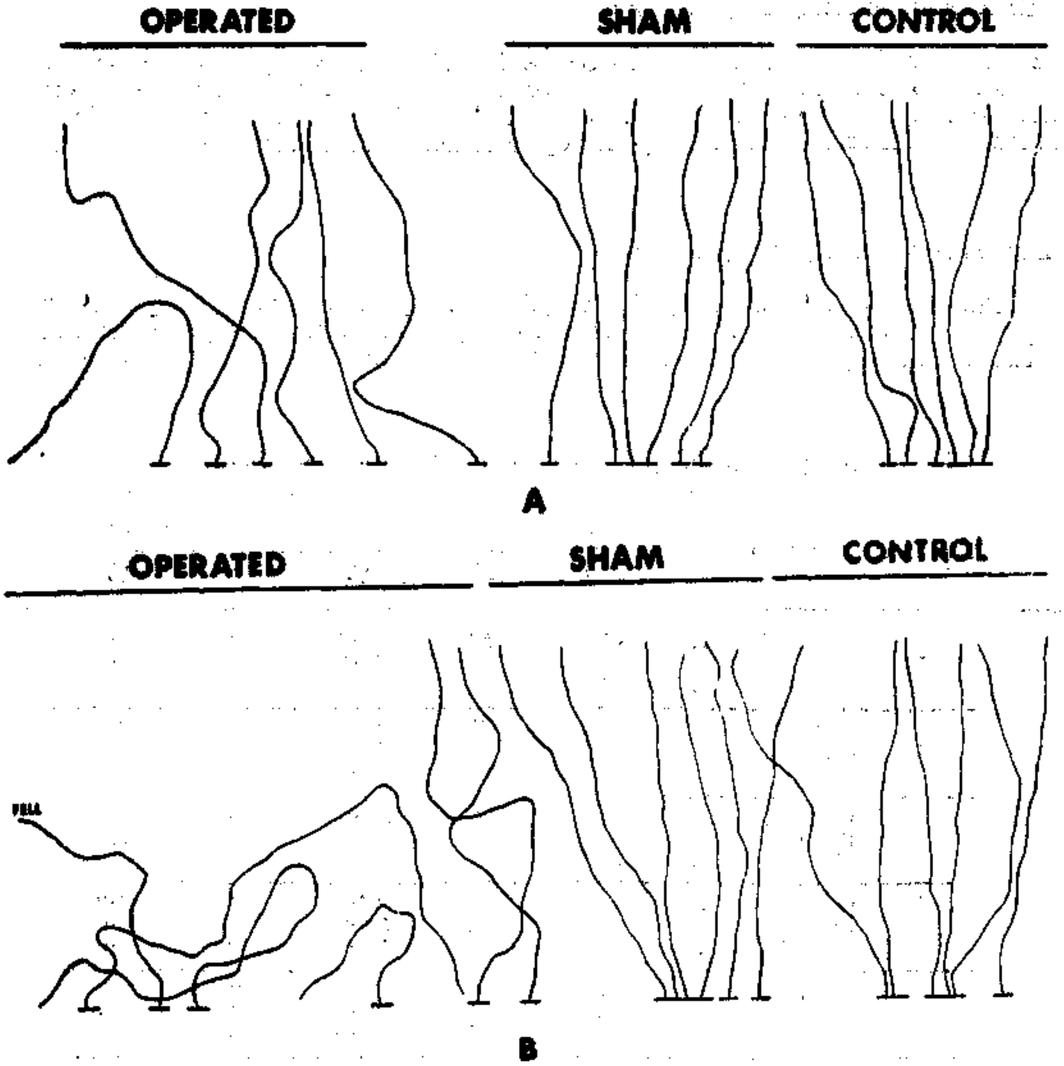


FIG. 2. Some typical tracks of snails in aquaria. A indicates tracks of snails in Experiment 1, in cylindrical aquarium. B indicates tracks of snails in Experiment 5, in rectangular aquarium. Note general disorientation of operated snails in B. Snails of this group typically either crawled back to starting level, or fell from wall.

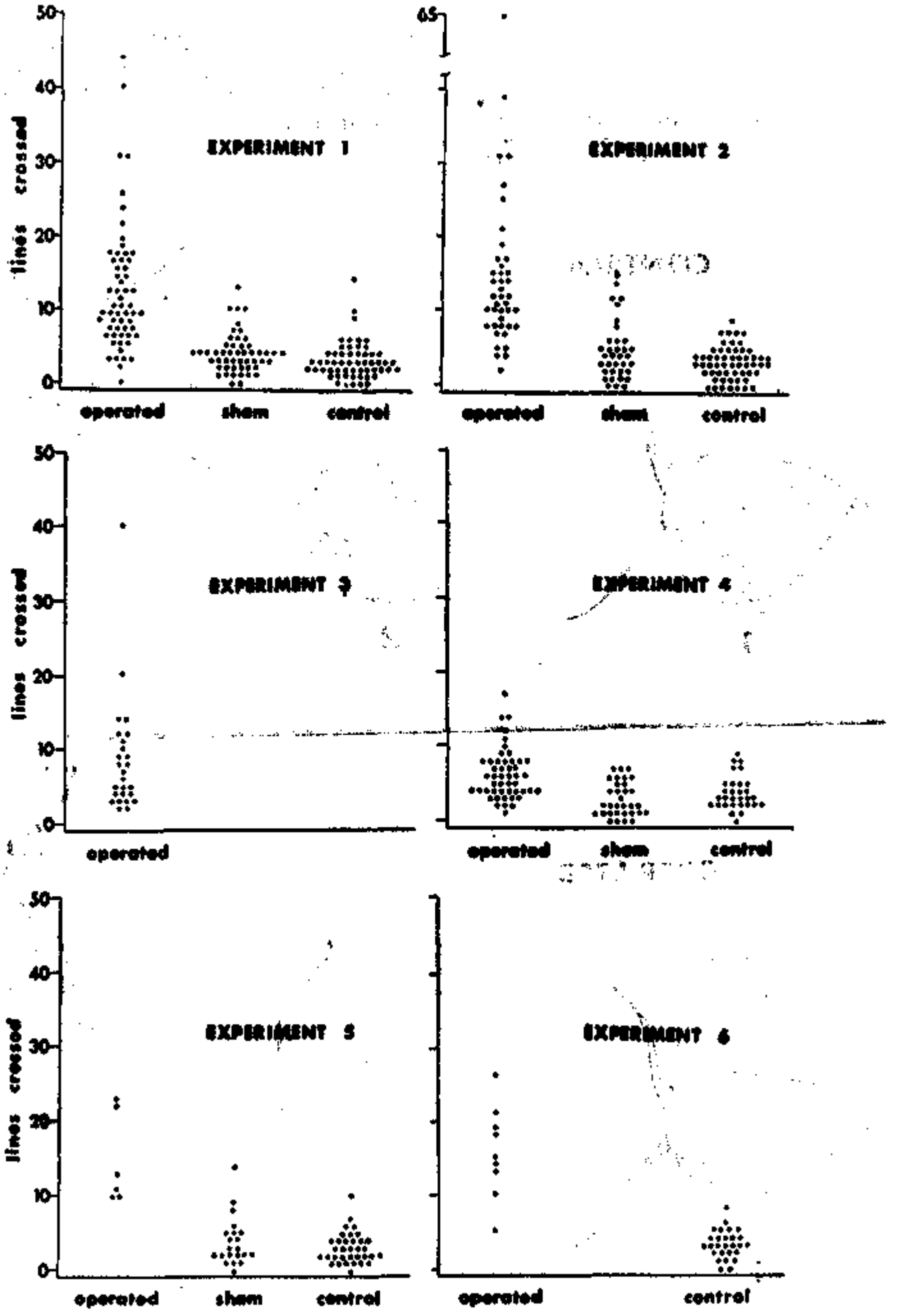


FIG. 3. Number of vertical lines crossed by snails. Each dot represents one snail. When groups in each experiment were compared by Mann-Whitney U-test, it was found that in all cases operated snails crossed significantly more vertical lines than did their controls. In no case was there a significant difference between sham groups and their controls.

II. *Experiments involving body twisting*

When the shell and body of a control animal were turned so that the animal faced horizontally, the usual reaction was for the animal to first turn its fore-foot and head upward followed by the body and shell. In contrast, when operated snails were similarly manipulated, the fore-foot and head remained facing horizontally and continued to face in this direction until the animal as a whole swung back into a vertical position (Fig. 4).

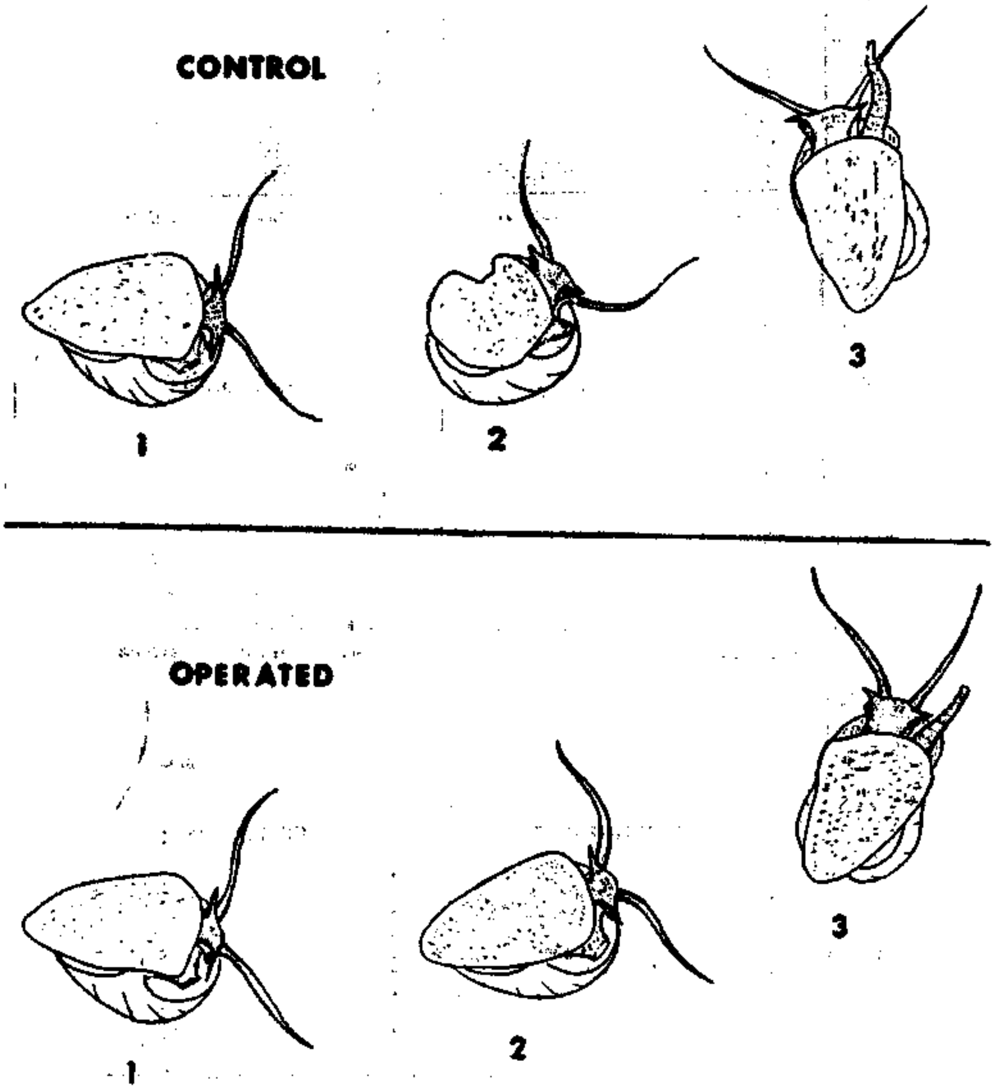


Fig. 4. Performance of control and operated snails after being turned to horizontal position. Control snails react by first turning head and fore-foot upward, followed by rest of body. Operated snails turn upward as a unit, the body as a whole apparently being pivoted by weight of shell. Snails in position 3 have siphons extended.

DISCUSSION

The difference in the performance of operated snails in cylindrical as compared to their performance in rectangular aquaria can presumably be interpreted in either of two ways. It is possible that in Experiments 1-4 the curvature of the cylinder was used by operated snails as a cue to direction of surface. This view is supported by the difference in performance between operated snails in the two aquaria. Another interpretation of the results is that the operated snails' loss of ability to reach the surface in the rectangular aquarium was not due to lack of a directional cue, but to the fact that operated snails cannot effectively hold their foot to a flat surface, but are able to do so against a slightly curved one. This view is supported by the improved performance of operated snails when on the rougher plastic wall in the rectangular aquarium (Experiment 6), and by the observation that many of the operated snails which failed to reach the surface in the rectangular aquarium seemed to slip, rather than actively travel, downward. This view is also supported by the fact that many operated snails tend to travel on vertical surfaces with their shell sagging away from the foot, a posture which would presumably make it difficult for the animal to retain effective contact with the surface. This behavior has been previously observed (McClary, 1966) and was again observed in the present study. If the latter view is correct, and the curve of the cylindrical aquarium provided not a cue to direction, but merely a more adequate surface to adhere to, some other cue for upward movement must be found. One possibility is that this cue is the weight of the pendant shell; that those experiments in which a snail's shell was raised by means of a buoy actually failed to remove this cue. This could be argued on the basis that as here designed, the buoy simply acted to pull shell and snail upwards. In future experiments this might be rectified by designing some way of removing the shell weight while at the same time applying an angular motion to the shell, rather than an upward one. The experiments in which the bodies of operated and control snails were turned to the horizontal tend to support the view that upward movement by an operated snail is actually mediated by shell, or perhaps by shell and body weight. After being turned horizontally, control snails twist their head and fore-foot back upward to seek the surface. Operated snails, in contrast, appeared to regain an upward position not by active turning of the head and fore-foot, but by a passive swinging downward of the posterior body parts.

The differences between the present work and that of Lever and Geuze seem best explained by a lack of directional cues available to the animals used in the latter study. Neither of the directional cues postulated here—a curved surface or the weight of a pendant shell and body—would be available to the animals studied by Lever and Geuze, for these snails were studied while travelling downward on a flat surface.

LITERATURE CITED

DELAGE, Y. 1887. Sur une fonction nouvelle des otocystes commes organes d'orientation locomotrice. *Arch. zool. exptl. et gen.*, 2 (5): 1-26.

LEVER, J. AND J. J. GEUZE 1965. Some effects of statocyst extirpations in *Lymnaea stagnalis*. *Malacologia*, 2: 275-280.

MCCLARY, A. 1964. Surface inspiration and ciliary feeding in *Pomacea paludosa*. *Ibid.*, 2: 87-104.

———. 1966. Statocyst function in *Pomacea paludosa*. *Ibid.*, 3: 419-431.

WILBUR, K. M. AND C. M. YONGE 1966. *Physiology of Mollusca*, Vol. 2. Academic Press, New York and London, pp. 645.