ANADARA (BIVALVIA) IN THE INDIAN AND PACIFIC WATERS OF AUSTRALIA*

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Abstract

• Anadara, widespread in the North Pacific during the Cainozoic, migrated to the Australian mainland much later. It is now widely distributed in the waters of the Indian Ocean (Western Australia) and the Pacific Ocean (Eastern Australia). During the Last Interglacial it extended as far south as Tasmania.

INTRODUCTION

AUSTRALIA is an island continent, and therefore many of its forms of marine life have migrated from elsewhere. The story is being slowly unravelled. Berthelina migrated in the Pliocene, Pecten s.s. in the Lower Pleistocene, and Anadara to southern Australia at least in the Upper Pleistocene. Anadara was widespread in the North Pacific Ocean for most of the Cainozoic, and at some time in the Upper Cainozoic migrated south. For example, Anadara is well known in the Tertiary marine faunas of California (Nicol, 1950) and Japan (Noda and Tada, 1968). After tens of millions of years in the North Pacific, this genus achieved a crossing of the Equator and colonized Australia and New Zealand.

It would appear that Anadara followed what Professor G. G. Simpson has called a 'sweepstakes route' to southern Australia because although the same or similar climatic conditions were repeated a number of times in the successive stages of the Pleistocene, it was not until the Upper Pleistocene that migration occurred. It is a fair inference from this history that the migration was not an easy one.

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UPPER PLEISTOCENE MIGRATION TO SOUTHERN AUSTRALIA

Anadara occurs in the Indian Ocean in Western Australia, and in the Pacific Ocean in north and east Australia. However, in the past it has been more widespread than it is at present, occurring also in the Southern Ocean in South Australia, and as far south as north Tasmania. Johnston (1878) reported the genus from Flinders Island in Bass Strait, where I am told (R. Kershaw, pers. comm.) it occurs in emerged marine shell beds; also in a bleached and worn state on present beaches. Tennison Woods said Anadara trapezia was plentiful at the mouth of the Tamar

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River. My enquiries suggest that the species is not now present in Tasmania, but the shells are plentiful from an extension there during the postglacial thermal maximum. No one has been able to find a living mollusc, or a shell retaining the periostracum. Muddy estuaries are the milieu of *Anadara trapezia*, and they are common between tidemarks. However, at the limit of their range they disappear from the intertidal zone or are scarce because the frost kills them.

The distribution of Anadara in Victoria has been studied in detail because it is here (as in the Albany area in the Indian Ocean, Kendrick and Wilson 1958) where the southerly distribution of the living mollusc ceases. In east Victoria it flourishes where the influence of the warm East Australia current is felt, but it quickly becomes relatively rare further west in Bass Strait. It is normal for this species to occur in very great numbers, so the decrease in populations is itself significant. Kendrick and Wilson (1958) and Macpherson (1966) have not taken this sufficiently into account. Anadara lives in Western Port Bay, east of Melbourne, but for a long time it was believed to be extinct in Port Phillip on which Melbourne stands. However, careful search of early record shows that it was present before industrial development affected the waters in Hobsons Bay. Until recently (W. P. Evans, pers. comm.) it was present below L.W.M. at Williamstown. Also a biological survey of Port Phillip (Black, 1971) showed it to be present, though not plentiful, in the sublittoral down to seven fathoms (1.8 m). Thus while Anadara trapezia is very common at Sydney between tidemarks (being called the Sydney Cockle), it is rarely seen at Melbourne. However, the converse was the case during the postglacial thermal maximum, for it was then present in gargantuan numbers and growing to a large size. From the postglacial beds at Appleton Dock at Melbourne, 2000 specimens were readily collected for biometrical study when the dock was being built. The age of the formation has been checked by radiocarbon dating (Gill, 1961, 1968). Measurement shows the shells grew larger then, in spite of Macpherson's statement (1966: 229) to the contrary.

Anadara AND PALAEOCLIMATES

Anadara is thus a warmer water mollusc whose changes in distribution have palaeoclimatic significance. Even the small change in mean temperature between the present and the postglacial thermal maximum was sufficient to make the difference between being at the thin end of its range now, but prolific of the order of 5000 years ago, in Port Phillip. It is thus a sensitive indicator of small changes in climate, and very useful for Quaternary studies. At Melbourne, in the Coode Island Silt of the Yarra delta, Anadara is only prolific in the top of the formation, rapidly cutting out with depth. It has not been found in deposits 8000 years old or older in Flandrian sediments. The genus is likewise present in the top of the lithologically similar Fishermens Bend Silt of Last Interglacial age, now compacted and oxidized.

Anadara trapezia was previously common in South Australia, but at present is apparently extinct there. In 1957 members of the Malacological Society of Australia tried to re-introduce it artificially there, but without success.

In the Indian Ocean waters of Western Australia there is a comparable history of change in distribution with change in climate. In the Perth region there are shell beds with *Anadara* of Last Interglacial age (Teichert, 1967). Postglacial beds also occur having this fossil. The species was for long believed to be absent in S.W. Australia, but was later found below the intertidal zone, i.e. instead of being present

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in vast numbers intertidally, it is at the thin end of its range. Within its normal range, *Anadara* is washed up on the shore in large numbers, and its occurrence is obvious.

Anadara AND PALAEOBCOLOGY

Anadara in Australia is a reliable indicator of estuarine conditions. Because it lives in quiet water conditions, it is not uncommonly found with both valves still together in position of growth. As it is a surface dweller it can be used for measuring precise levels of the sea in the past. All shells in place are definitely below the high water level of the time when they lived. Where such shell beds are now above H.W.L., they are excellent evidence for emergence. Their thick shells are good for radiocarbon dating. Conversely, where such beds now occur under the open sea, they can be accepted as evidence of submergence. At Seaspray on the Ninety Mile Beach in east Victoria, there is an open ocean sandy beach, a shoreline barrier, and landward of that are estuarine environments. Boring shows that there have been oscillations of sealevel. In tracing these changes, *Anadara* is a reliable indicator of the return of estuarine conditions.

In those places known to me where *Anadara* and mangroves co-exist, it is normal for *Anadara* to occupy the muddy flats on the seaward side of the mangroves. This fact can be used in reconstructing past ecologies. One advantage of Australian *Anadara* is that they occur in vast numbers. Consequently, reduction to small numbers is an indicator of marginal conditions. This can be applied to the past where in depth the genus becomes rare in a formation, or geographically where it comes to the limit of its range. Some authors have applied a simple presence/ absence antithesis, but more refined interpretations are possible with *Anadara*. Thin populations are significant.

Mud or muddy sand is the substrate to which this genus is adapted in Australia. Thus in a Quaternary estuarine sequence, on passing from sand (with its characteristic suite of molluscs) to muddy sand, *Anadara* appears. It is therefore out of character when it is collected from sandy formations, but the fact conveys information. Such shells are usually worn and few in number. They have been transported. However, they provide evidence of a mud or muddy sand environment in that area that has been eroded. The formation may still exist, or it may have been completely destroyed. Such data assist in reconstructing the former estuary.

Some workers have endeavoured to account ecologically for the absence of *Anadara* from Western Victoria where it occurred in the past, by suggesting that it does not live there now because of lack of suitable habitats. The estuaries of the Barwon, Hopkins, Moyne and other rivers had suitable muddy estuaries under natural conditions before the channels were cleared. Change of ecology brought about by change of sealevel no doubt had its effects, but in my opinion cannot account for all the facts.

TIME OF MIGRATION

Where the Indian Ocean meets the S.W. coast of Australia there is an extensive formation of aeolianite called the Coastal Linestone. At Rottnest Island near Perth, this rests on a fossil coral reef that was radiometrically dated as $100,000 \pm$.

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20,000 years old (Teichert, 1967). Immediately above the coral, and in the same formational series, is a shell bed with *Ninella torquata*. This is not the facies for *Anadara*, but Teichert correlates the Peppermint Grove coquina in the Swan River estuary (Teichert, 1950) which has *Anadara trapezia* (Fairbridge, 1954). These and other sites of Last Interglacial age have *Anadara*, but it has not been found in any earlier formation.

Similarly in S.E. Australia, where there are similar aeolianites, there is a formation extending for at least 30 miles along the coast of Western Victoria which is beyond the range of radiocarbon, and shells from which have given a radiometric age of about 100,000 years (Valentine, 1965). The town of Port Fairy stands on this formation, and so it has been called the Port Fairy Calcarenite. From there it has now been traced through to the city of Warrnambool, which stands on an embankment infilled with a series of Pleistocene dunes, each superposed on the next (Gill, 1967). Anadara has been found in the Port Fairy Calcarenite (Last Interglacial) and in the Pertobe Coquina (Mid-Holocene). Although there are two older formations in the series, no sign of Anadara has been found; however, good shelly horizons have not yet been found in them, so opportunities are limited.

On the east coast of Australia stands the city of Newcastle. In the early days of radiocarbon dating, the Hunter District Water Board there sent me some Anadara shells and oyster shells from 174-177 feet in their Bore 29A. The fossils came from an estuarine mud overlain by the Tomago Sands. The shells proved to be beyond the range of radiocarbon dating, and are believed to be Last Interglacial or thereabouts in age. There are tectonic complications in this area in that Phipps (1966) has described a recent seaward flexure of this coast.

Thus the oldest dated Anadara in southern Australia is Last Interglacial, and it remains to be established when this genus crossed the Equator and reached the Australian mainland.

TAXONOMY OF Anadara

The oldest known Anadara from the Last Interglacial strata must be the nearest in character to the original migrants for southern Australia at least. These are robust shells of the A. trapezia type with about 28 ribs. The young shells are much more regular in outline, suggesting that the trapezoid A. trapezia was derived from a more regular species. The early Anadara are occasionally nodulose along the ribs, or part of the shell has these structures. For example, the Anadara from the Newcastle area had the umbonal part of the shell nodulose. There is thus the potential for developing a shell with completely nodulose ribs. Looking at the known Australian Anadara of both past and present, one may generalize by saying that the southern part of the continent has smooth shells, while the northern part of the continent has nodulose shells. These are typified by the species trapezia and 'granosa' respectively.

A small thin arcid from the Oligocene has been referred to Anadara in Australia, but I do not accept this identification. In any case, it is quite a different type of shell. No succession can be traced from the Oligocene form to the Quaternary one. If it were Anadara, it would mean that the genus migrated twice to this continent. Fossil and recent Anadara can only be compared by their shells, so populations of A. trapezia from Brisbane (Moreton Bay, collected by Mr. F. S. Colliver), Sydney (Port Jackson, collected by Dr. R. W. T. Wilkins), and Appleton Dock, Melbourne (collected by the author), were studied by their shells. Variations were noted in outline (in the plane of valve contact and normal thereto), thickness of shell, ribs (number, cross-sections of ribs and interspaces, presence or absence of nodes on ribs, nodes as bars or cones, growth lines), teeth (straightness of tooth file, nature of teeth and their regularity), subumbonal area (angle formed by valves, nature of chevron, shape and regularity of units), and so on. However, there were definite limits of variations in a single population. Width (distance along hingeline) to length (longest radius of shell from end of hingeline to edge of flared part of valve) ratios were worked out for 20, 50, 100, 200, 300, 500, 900, 1000, 1100, 1200, 1500, 1600, 1700, 1800 and 2000 valves, but after 100 specimens there was no significant change in the graph. The number of ribs was found to be a fairly constant feature for right valves, left valves, and paired valves. The number varied mostly with the stage of maturity of the specimen. The mode for the Moreton Bay population was 27, that for Port Jackson 27.5, and that for Appleton Dock 28. These differences are not significant, as it is often doubtful whether the last little ridge should be regarded as a rib or not. The fossil from Newcastle had 28 ribs.

Of the features biometrically studied, the ribs were the most stable. The number of ribs of the various named species was therefore studied. A radiation pattern was sought in the variants.

Anadara RADIATION

Australia has a large number of species of *Anadara* (Iredale, 1939) which are limited thereto, and constitute a local radiation. Of interest to the present symposium is the disparity between the number of species recorded for the Indian Ocean coastline and those for the Pacific coastline.

Indian Ocean

Pacific Ocean

A. trapezia (Deshayes) 1830 A. thackwayi Iredale 1927 A. 'granosa' (Linné 1758) A. trapezia (Deshayes) 1830 A. thackwayi Iredale 1927 A. nicholsoni Iredale 1927 A. pilula A. crebricostata (Reeve) 1844 A. addita Iredale 1939 A. jurata Iredale 1939 A. nugax Iredale 1939 A. passa Iredale 1939 A. maculosa (Reeve) 1844 A. exulta Iredale 1939 A. suggesta Iredale 1939 A. 'granosa' (Linné) 1758

The explanation of the disparity is probably that Iredale (1939) described most of the Pacific species when studying the shells collected by the British Museum (Natural History) Great Barrier Reef Expedition 1928-9. The Anadara species are not strongly separated, some of them overlap, and some have (according to present records) disparate distribution. For example, A. thackwayi was described from

between Port Jackson and Port Hacking south of Sydney; it has also been recorded from the Dampier Archipelago in N.W. Australia, but such a bipolar distribution is unlikely, especially as the areas are in different climatic zones. One species (addita) was described on a solitary young valve.

It is not unusual for molluscs in the tropical zone to have more extensions of exoskeleton such as nodes and spines than those in the temperate zone. Anadara has forms with nodose ribs in the tropical zone, but there is a transition. Occasional nodose or partially nodose specimens are found in the temperate zone, and the subspecies A. trapezia posita described by Iredale from north of Moreton Bay but south of the Tropic of Capricorn has subnodulose ribs. Of the species listed for the Pacific coast, three occur south of the Tropic of Capricorn and have 21 to 28 ribs; the other nine species occur north of the Tropic of Capricorn and have 28 to 44 ribs. Thus while there is a tendency to greater rib number in the north, there is no sharp transition, and A. passa as far north as Cairns has the same rib number as trapezia in the south.

Possibly the numerous species described are not really species but subspecies or geographical races, or even (although less likely) a cline. This would be in keeping with the very recent radiation (for Southern Australia at least) during the past 120,000 years. The large number of forms separated with difficulty is characteristic of a genus in process of radiation. A quantitative study of the whole series is needed.

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