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SOME ASPECTS OF THE ZOOGEOGRAPHY OF NORTHWESTERN AUSTRALIAN ECHINODERMS (OTHER THAN HOLOTHURIANS)

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ABSTRACT

The long coastline of northwestern Australia, with a high diversity of habitats, and the broad continental shelf, provide abundant living space for a rich echinoderm fauna which is still incompletely known but there are now sufficient data to enable statements to be made, with some degree of confidence, about its composition and relationships.

The shelf edge atolls, offshore islands, and to a lesser extent the barrier reef which runs southwards from North West Cape, have an echinoderm fauna principally of widespread Indo-West Pacific species, characteristic of coral reefs in clear water. The coastal and shelf fauna on the other hand has a large component of endemic species. Its greatest affinity lies with the Indo-Malayan area, particularly Indonesia and the Philippines.

Forty-five species of echinoderms are here recorded from Western Australia for the first time.

The echinoderm fauna of tropical Australia has been described in several publications, notably those of H. L. Clark (1921; 1938; 1946) and A. M. Clark and Rowe (1971). H. L. Clark (1946) discussed the composition and origin of littoral and shelf echinoderms from both temperate and tropical waters of Australia, while Clark and Rowe included all records of northern Australian shallow-water forms (to 20 m), as far south as Shark Bay in the west and southern Queensland in the east.

There were, however, very few records or collections from the northwestern Australian shelf or offshore islands, available for inclusion in these publications.

The present paper summarizes some of the findings from a study of echinoderms of the North West Shelf and of some of the offshore and nearshore reefs and islands, based on collections in the Western Australian Museum, Perth and the Australian Museum, Sydney. The major part of the shelf material was collected by the authors and others during CSIRO cruises to investigate the demersal fishes of the North West Shelf by trawling from R/V COURAGEOUS (1978–1979) and R/V SOELA (1979–1982). This was supplemented by dredging, scuba diving, snorkelling and low tide collecting wherever possible.

Literature records included are from the German scientific expedition in SMS GAZELLE (1874–1876) the echinoderms from which were described by Studer (1880; 1882; 1884), Lampert (1889) and Clark (1909); British Navy collections made by H.M.S. PENGUIN from Holothuria Banks and Sahul Bank, reported by Bell (1893; 1894); Dr. Mjoberg's Swedish Scientific Expedition to North West Australia (1911–1913), the echinoderms from which were described by Ekman (1918), Mortensen (1918), Gislén (1919) and Döderlein (1926) and the major contribution to knowledge of the shallow water echinoderm fauna of northwestern Australia made by H. L. Clark (1938; 1946), who spent several months collecting echinoderms from shore and shallow water in the Northern Territory and northwestern Australia, principally around Broome.

Material accumulated by Clark during his two visits to Australia amounted to over 11,000 specimens, representing 422 species of 184 genera of echinoderms (H. L. Clark, 1938).

Thus Clark had a considerable data base on which to draw for his discussion of the composition and origin of the Australian echinoderm fauna (H. L. Clark, 1946). However, the coral reefs of the northwest, which may have given Clark a somewhat different picture of the fauna, were inaccessible at the time of his visits and few collections had been made from the deeper shelf waters.

More recently the distribution of Western Australian Asteroidea has been summarized by Marsh (1976) and taxonomic changes and descriptions of new species have resulted from studies of certain genera and species (Baker and Marsh, 1976; Baker, 1980; Rowe, 1976; 1977; Pope and Rowe, 1977; Rowe and Marsh, 1982; McNamara and Philip, 1980; McNamara, 1982a and b; Sukarno et Jangoux, 1977).

The Study Area

Geomorphology, Geological and Climatic History of Northwestern Australia

The northwestern coast of Australia lies within the tropics, between the latitudes of 13°46′S at Cape Londonderry in the north Kimberley and 21°47′S at North West Cape and spans nearly 15 degrees of longitude between 129°E and 114°10′E (Fig. 1).

The coastline is low and flat adjacent to the Eighty Mile Beach, low to moderately rugged with adjacent mainland islands, including the Dampier Archipelago, off the Pilbara coastline, while the Kimberley coast is steep and deeply dissected with numerous nearshore continental islands.

The Continental Shelf is very narrow off North West Cape, where there is an inner shelf (less than 110 m) only 6 nm wide with the 200-m line 24 nm offshore. Northeastwards the shelf broadens into a gently sloping western Rowley Shelf (named for the three atolls known as the Rowley Shoals rising from its outer edge at 400 m), and separated from the more northerly Sahul Shelf by the Leveque Rise, a morpho-tectonic boundary running northwest from Cape Leveque. The shelf is widest (220 nm) off Cape Jaubert, where the shelf edge break lies between 350 and 550 m. The 200-m contour is of no structural significance on either the Sahul or Rowley shelves, but there is a sinuous step at 55–60 fm (100–110 m) which may mark a low Pleistocene sea level (Fairbridge, 1953).

The Sahul Shelf (Molengraaff and Weber, 1919; Fairbridge, 1953) extends from Cape Leveque (16°20′S:123°E) seawards to 15°S:121°E and northeastwards to Melville Island (131°E), where it is separated from the Arafura Shelf by submarine canyons. The Sahul Shelf is widest (220 nm) off Cape Londonderry where the continental slope drops sharply to 2,000 m in the Timor Trough.

The inner part of the Sahul Shelf appears as a drowned landscape developed during arid cycles of erosion. It was a plateau, terrace and plain country in which the streams were fairly deeply incised, the down-cutting having been revived in stages to present a step-like cross section to the canyons, similar to the Kimberley landscape today. The terraced inner shelf comes to an end at the 100–110-m step after which there is a steady outward slope down to the continental edge, suggesting tectonic subsidence of the outer shelf (Fairbridge, 1953). Isolated coral reefs (Browse and Cartier Islands) rise from near the edge of the 100–110-m step, while Scott and Seringapatam atolls rise from about 500 m on the western edge of the shelf. Ashmore Reef, Sahul Bank and Troubadour Reef form an ill-defined barrier near the northern shelf edge.

In shallow water near the coast are large platform and fringing reefs (Lacepede Is, Adele Reef, Holothuria Banks), while off the Kimberley coast most of the continental islands are surrounded by fringing reefs.

Together, the Rowley and Sahul shelves, collectively known as the North West Shelf, make up an area of 600,000 km^2, overlain by the Indian Ocean and the Timor Sea, respectively.

Coral reefs are represented by the atolls, offshore and nearshore platform reefs of the North West Shelf, fringing reefs around mainland islands off the Kimberley and Pilbara coastlines and a part barrier, part fringing reef lying off the west coast of North West Cape, extending southwards for some 150 km. The Houtman Abrolhos (28°–29°S), coral islands lying off the midwest coast, provide a southern extension of habitat for the tropical marine fauna.

Reconstructions of continental positions from the Cretaceous commencement of the break-up of Gondwanaland 100 my BP (Windley, 1977; Knox 1980; Powell et al., 1981) show the northwestern coast of Australia bathed by the Tethys Ocean with currents flowing from east to west, north of Australia.

The northern edge of the Australian plate, including Timor, did not reach the present latitudes of the southern margin of Sundaland until about 15 my ago in the mid-Miocene (Powell et al., 1981).

During Pleistocene glaciations, much of the Sahul and Rowley shelves would have been exposed

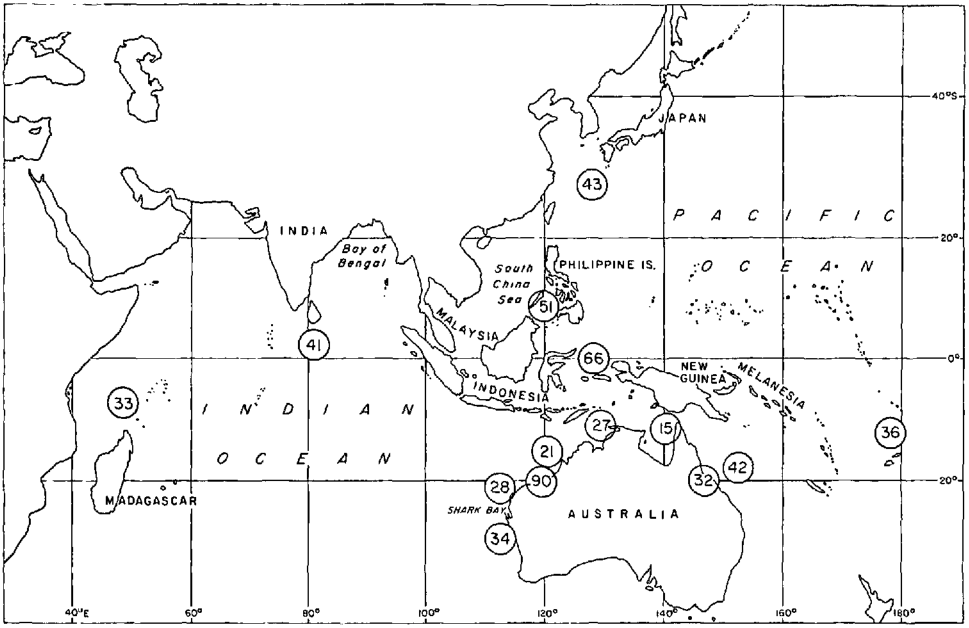

Figure 1. Northwestern Australia and the western Northern Territory showing localities mentioned in the text, and the extent of the Rowley and Sahul shelves.

and Australia connected to southern New Guinea by the exposed Arafura shelf. The extent of land and sea at 20,000, 17,000 to 14,000 and 8,000 years BP is illustrated by Nix and Kalma (1972).

At the height of the last glacial, 18,000 years BP, the sea surface winter isotherm of 18°C lay across North West Cape and the sea between the northwest coast and the island arc of Indonesia ranged from 18–26°C, well within the tolerance of tropical species (Shackleton, 1978). With the sea level at this time 85 m below its present level, the exposed Sunda shelf extended Asia southwards to include Borneo and Java which, with the Sunda and Arafura shelves exposed, left only a narrow connection between the Indian and Pacific Oceans along the Timor Trough and the edge of the Australian shelf, through the Molucca Sea and the Celebes Sea, south of the Philippines.

Torres Strait opened for the last time between 8,000 and 6,000 years BP (Jennings, 1972) when the sea level stabilized at its present level (Thom and Chappell, 1975; Chappell, 1982).

Oceanography

The tides are semidiurnal along the northwest coast varying from a spring tide range of 2.7 m at North West Cape to 11 m at Broome, decreasing eastwards to 7.9 m at Darwin (Anon, 1979); atmospheric pressure and weather may moderate or accentuate these ranges. The very large tidal range on the Kimberley coast causes strong tidal currents which mobilize fine sediment causing turbidity or milkiness of the waters for some distance offshore.

On the Pilbara coast the tidal range is less but still sufficient to cause strong currents and considerable turbidity during the spring tide cycle.

In contrast to these turbid inshore waters, the reefs on the west side of North West Cape and the North West Shelf edge atolls are bathed by clear oceanic water.

Some features of the hydrology of the water masses between Australia and Indonesia have been described by Wyrtki (1957; 1962) and Rochford (1962). Wyrtki (1957) found that during the southeast monsoon, from May to September, the South Equatorial Current of the Pacific Ocean flows north of New Guinea, and, in part through the Halmahera Sea to form the source of the monsoon current flowing westwards into the Java Sea and the Timor Current flowing south of Timor into the Indian Ocean. Since the inflow from the Pacific is less than the outflow, upwelling takes place in the Banda and Arafura Seas. During the northwest monsoon (November to March) the current direction is reversed in the Java Sea and the monsoon current flows partly into the Pacific via the Halmahera and

Molucca Seas and in part joins the Timor Current while considerable water masses submerge in the Banda and Arafura Seas.

The South Equatorial current in the Indian Ocean draws some water from the Timor Sea during the southern winter when winds are blowing strongly from the southeast between Australia and Indonesia (Wyrtki, 1973).

Water movements through Torres Strait, summarized by Jennings (1972), may be of significance for the distribution of marine organisms in northern Australia. High temperature, low salinity water of the Arafura Sea and Gulf of Carpentaria passes through Torres Strait into the Coral Sea under the influence of the northwest monsoon in the southern summer (December to March). From April to December, the stronger and more persistent southeast trades set a drift northwest and northwards in the Coral Sea with a branch of the Pacific South Equatorial current. Together they pile equatorial water against the shelf east of Torres Strait but not much can pass into the strait.

Thus there is some potential for a two-way passage of pelagic larvae through Torres Strait.

On the west coast of Western Australia the subtropical anticyclonic gyre brings cool water across the southern Indian Ocean by way of the west wind drift. However, there is little evidence of an eastern boundary current along the west coast of Australia (Wyrtki, 1973), which was observed to be influenced by a warm current by Saville-Kent (1897) who recorded a substantially tropical marine fauna, including reef building corals at the Houtman Abrolhos in contrast to the fauna of the mainland coast 80 km to the east where the water was several degrees cooler.

An autumn and winter southward flow of tropical low salinity water adjacent to Western Australia has been described and named the Leeuwin current (Cresswell and Golding, 1980). It is most clearly defined on the continental slope from 29°S and pivots at Cape Leeuwin to run eastward to the Great Australian Bight. Legeckis and Cresswell (1981) used infrared imagery from United States environmental satellites to describe the seasurface temperature fronts and eddies associated with the Leeuwin current.

Published data on sea temperatures on the North West Shelf are sparse but measurements made in the vicinity of Dampier over a 12-month period (Woodside, 1979) give some indication of the temperature regime. Near shore in the Dampier Archipelago, at a depth of 9 m (with bottom at 11 m) the temperature ranged from a minimum of 19°C in July–August to a maximum of 32°C in February with 34°C in shallow bays; in the outer waters of the archipelago, at a depth of 20 m (with bottom at 37 m) the range was from 22°C in August to 30°C in March, while 130 km offshore, at 20 m (with bottom at 127 m) the range was from 24°C in August to 30°C in March.

Results

Analysis of Some Elements of the Northwestern Australian Echinoderm Fauna

In the past, the lack of collections of echinoderms and corals from coral reefs in Western Australia has led to the understandable zoogeographical conclusion (Clark, 1946; Endean, 1957) that most Indo-West Pacific coral reef echinoderms did not occur in Western Australia and to the conclusion that northwestern Australia had an impoverished coral fauna (Stehli and Wells, 1971; Rosen, 1971). Wilson and Marsh (1979) showed that northwestern Australia has a far richer coral fauna than was previously believed and the present study indicates that there is a correspondingly diverse coral reef echinoderm fauna.

Table 1 lists the asteroids, ophiuroids and echinoids associated with coral reefs in northwestern Australia, with their distribution within Western Australia and elsewhere. A coral reef offers many habitats besides coral, e.g. sand flats, sea-grass beds and even lagoon mud, thus a few species have been included which might not be generally regarded as coral reef species.

Forty-five species are recorded from Western Australia for the first time (12 species of Asteroidea, 20 species of Ophiuroidea and 13 species of Echinoidea).

Of the 109 coral reef species recorded here, 17 (16%) have only been found on the offshore reefs and atolls, the remainder are found either on offshore and inshore coral reefs or only on inshore coral reefs.

The number of coral reef species drops from 84 (77%) on the northwest coast and inshore islands to 53 (49%) on the reefs west of North West Cape and 47 (43%) at the Houtman Abrolhos where there is a mingling of tropical and temperate species.

Table 1. Asteroids, ophiuroids and echinoids associated with coral reefs in northwestern Australia, with their further distribution

	Western Ind. O./ Red Sea	Indonesia/ Philippines	Abrolhos	N.W. Cape	N.W.A. Inshore	N.W.A. off-shore reefs	G.B.R.	West Pacific
ASTEROIDEA								
Astropectinidae								
Astropecten polyacanthus Müller & Troschel	CR	CR			M+		+	CR
Archasteridae								
Archaster angulatus Müller & Troschel	SJ	CR	+	(C)	(C)			
Oreasteridae								
**Choriaster granulatus* Lütken	CR	CR				+	+	CR
Culcita novaeguineae Müller & Troschel		CR			C	+	E	CR
C. schmideliana (Retzius)	CR			M+	M+			
Protoreaster lincki (de Blainville)	CR	CR		M+	M+			
P. nodulosus (Perrier)			M+	M+	C	+		
Pentaceraster gracilis (Lütken)	CR†	CR	+		C		C	
**P. multispinus* (von Martens)	CR†	CR			+	+		
**P. regulus* (Müller & Troschel)	CR†	CR			+	+	L	CR
Asteropseidae								
**Asteropsis carinifera* (Lamarck)	CR	CR				+	C	CR
Ophidiasteridae								
**Celerina heffernani* (Livingstone)		GJ				+		CR
**Dactylosaster cylindricus* (Lamarck)	CR	CR		+		+		CR
**Fromia eusticha* Fisher		F+				+		
F. indica/elegans Perrier/Clark	CR	CR	C+	+	+	+	C	CR
**F. milleporella* (Lamarck)	CR	CR				+	C	CR
F. monilis Perrier	+	CR	M+	+		+	+	CR
**F. pacifica* H. L. Clark		+	+		+			CR
Leiaster leachi (Gray)	CR	CR	M+		+		C	CR
Linckia guildingi Gray	CR	CR	M+		C	+	C	CR
L. laevigata (Linnaeus)	CR	CR		M+	M+	+	C	CR
L. multifora (Lamarck)	CR	CR	M+	M+	M+	+	+	CR
Nardoa galatheae (Lütken)		CR		M+	M+		(C)	CR
N. tuberculata Gray		CR			C	+	+	CR
Ophidiaster granifer (Lütken)	+	CR		M+	M+	+	C	CR
**O. hemprichi* Müller & Troschel	CR	CR				+	(E)	CR
O. robillardi/cribrarius de Loriol/Lütken	CR		M+	M+	+		+	CR

Table 1. Continued

	Western Ind. O./ Red Sea	Indonesia/ Philippines	Abrolhos	N.W. Cape	N.W.A. Inshore	N.W.A. off-shore reefs	G.B.R.	West Pacific
Asterinidae								
Asterina burtoni/cepheus Gray/M&T.	CR	CR	M+	+	+	+	C	CR
**Disasterina abnormalis* Perrier						+	(C)	CR
Echinasteridae								
Echinaster luzonicus (Gray)		CR		M+	M+	+	E	CR
Acanthasteridae								
Acanthaster planci (Linnaeus)	CR	CR		M+	M+		C	CR
Mithrodiidae								
**Mithrodia clavigera* (Lamarck)	CR	CR			+	+		CR
Total asteroids	22	28	11	15	23	22	21	26
OPHIUROIDEA								
Ophiomyxidae								
Ophiomyxa australis Lütken	CR†	CR	+	+		+	E	CR
Euryaldae								
Euryale aspera Lamarck	CR†	CR	B+		Bl+		C	
Gorgonocephalidae								
Astroboa granulatus (H. L. Clark)			B+		+		(C)B	B
Amphiuridae								
Amphioplus depressus (Ljungman)	CR†	CR	+	+	C+		G	CR
Amphipholis squamata (Delle Chiaje)	CR	CR	+	+	C+		C	CR
Amphiura brachyactis H. L. Clark			+		C+			
A. constricta Lyman			+		C+		G	C
A. leucaspis H. L. Clark				+	C+			
A. velox Koehler	CR	CR	+		C+			
**A. septemspinosa* H. L. Clark			+		+		C	
Ophiactidae								
Ophiactis acosmeta H. L. Clark			+		C+		E	
O. luteomaculata H. L. Clark			+		C+		C	
O. modesta Brock	CR	CR	+		C+			CR
O. savignyi (Müller & Troschel)	CR	CR	+	+	C+	+	E	CR

Table 1. Continued

	Western Ind. O./ Red Sea	Indonesia/ Philippines	Abrolhos	N.W. Cape	N.W.A. Inshore	N.W.A. off-shore reefs	G.B.R.	West Pacific
Ophiotrichidae								
Macrophiothrix belli (Döderlein)			+	+	C+		G	
M. longipeda (Lamarck)	CR	CR	+	+	Bl+	+	E	CR
Ophiothrix ciliaris (Lamarck)	CR	CR	+		C+		C	CR
O. trilineata Lütken	CR	CR			Bl+	+	C	CR
O. (*Keystonea*) *martensi* Lyman	CR	CR		+	Bl+		E	CR
**O.* (*Acanthophiothrix*) *purpurea* von Martens	CR	CR				+	G	CR
Ophiomaza cacaotica Lyman	CR	CR		+	Bl+		C	CR
Ophiothela danae Verrill	CR	CR	+	+	+	+	G	CR
Ophiocomidae								
**Ophiarthrum elegans* Peters	CR	CR			+	+	C	CR
**O. pictum* Müller & Troschel	CR	CR			+	+	C	CR
**Ophiocoma anaglyptica* Ely		+				+		CR
**O. brevipes* Peters	CR	CR		+		+	C	CR
O. dentata Müller & Troschel	CR	CR	(C)+	+	+		E	CR
**O. doederleini* de Loriol	S	+				+		D
**O. erinaceus* Müller & Troschel	CR	CR		+	+	+	E	CR
**O. pica* Müller & Troschel	CR	CR		+	+	+	C	CR
**O. pusilla* (Brock)	CR	CR	+	+		+	D	D
**O. scolopendrina* (Lamarck)	CR	CR				+	E	CR
Ophiocomella sexradia (Duncan)	CR	CR	+	+	C+		C	CR
**Ophiomastix annulosa* (Lamarck)	CR	CR				+	C	CR
O. caryophyllata Lütken	CR	D			D+		D	D
**O. mixta* Lütken		CR		+	+		C	CR
O. variabilis Koehler	CR	CR			(C)	+		CR
Ophionereididae								
Ophionereis dubia (Müller & Troschel)	CR	CR	+	+	Bl+		G	
**O. porrecta* Lyman	CR	CR		+	+	+	C	CR
Ophiodermatidae								
**Ophiarachna affinis* Lütken	S	CR				+		CR
**O. incrassata* (Lamarck)	CR	CR				+	C	CR
Ophiarachnella gorgonia (Müller & Troschel)	CR	CR	+	+	C+	+	C	CR
O. septemspinosa (Müller & Troschel)	CR	CR			+	+	C	

Table 1. Continued

	Western Ind. O./ Red Sea	Indonesia/ Philippines	Abrolhos	N.W. Cape	N.W.A. Inshore	N.W.A. off-shore reefs	G.B.R.	West Pacific
**Ophiochaeta hirsuta* Lütken	CR	CR			+	+		CR
Ophioconis cincta Brock		CR	+		C+		K	CR
**Ophiopeza spinosa* (Ljungman)	CG	CR		+		+	C	CR
Ophiopsammus yoldii (Lütken)	CR	CR			Bl+		G	
Ophiuridae								
Dictenophiura stellata (Studer)	CR	CR	+	+	C+			
**Ophiolepis cincta* Müller & Troschel	CR	CR				+	C	CR
**O. superba* H. L. Clark	CR	CR			+	+	C	CR
Ophioplocus imbricatus (Müller & Troschel)	CR	CR	C+	+	C+	+	C	CR
Ophiura kinbergi (Ljungman)	CR	CR	+	+	C+		E	CR
Total ophiuroids	41	44	26	24	40	27	42	40
ECHINOIDEA								
Cidaridae								
**Eucidaris metularia* (Lamarck)	CR	CR			+	+	+	CR
Diadematidae								
Diadema savignyi Michelin	CR	CR	C+	+	C+	+	C	CR
D. setosum (Leske)	CR	CR	C+	+	C+		C	CR
**Echinothrix calamaris* (Pallas)	CR	CR	+	+	+	+	C	CR
**E. diadema* (Linnaeus)	CR	CR		+	+	+	C	CR
Stomechinidae								
**Stomopneustes variolaris* (Lamarck)	CR	CR		+			C	CR
Temnopleuridae								
Mespilia globulus (Linnaeus)	CR	CR			C+	+	G	CR
Temnopleurus alexandri (Bell)		CR	C+		C+	+	G	
Toxopneustidae								
Nudechinus scotiopremnus H. L. Clark	CR		+	+	C+			
**Pseudoboletia maculata* Troschel	CR	CR				+		
**Toxopneustes pileolus* (Lamarck)	CR	CR			+	+		CR
Tripneustes gratilla (Linnaeus)	CR	CR	C+	+	+	+	C	CR

Table 1. Continued

	Western Ind. O./ Red Sea	Indonesia/ Philippines	Abrolhos	N.W. Cape	N.W.A. Inshore	N.W.A. off-shore reefs	G.B.R.	West Pacific
Parasaleniidae								
Parasalenia gratiosa A. Agassiz	CR	CR			C+	+	C	CR
Echinometridae								
Echinometra mathaei (de Blainville)	CR	CR	C+	+	+	+	C	CR
**Echinostrephus molaris* (de Blainville)	CR	CR		+	+	+	C	CR
Heterocentrotus mammillatus (Linnaeus)	CR	CR			C?	+	C	CR
Echinoneidae								
**Echinoneus cyclostomus* Leske	CR	CR		+	+	+	C	CR
Clypeasteridae								
**Clypeaster fervens* Koehler	CR	CR	+		+			
**C. reticulatus* (Linnaeus)	CR	CR	+		+			CR
Laganidae								
Peronella orbicularis (Leske)	CR	CR		+	C+	+	G	
Echinolampadidae								
Echinolampas ovata (Leske)	CR	CR		+	C+	+		
Brissidae								
**Brissus latecarinatus* (Leske)	CR	CR		+		+	E	CR
**Metalia dicrana* H. L. Clark	S	CR				+		CR
**M. spatagus* (Linnaeus)	CR	CR			+	+	C	CR
Loveniidae								
Breynia desorii Gray			(C)	+	(C)+	+		
Total echinoids	23	23	10	14	21	20	17	18
Total asteroids, ophiuroids, echinoids	86	95	47	53	84	69	80	84
109 = 100%	79%	87%	43%	49%	77%	63%	73%	77%

Key to symbols: B = Baker, 1980; Bl = Bell, 1894; C = H. L. Clark, 1921, 1938, 1946; CR = Clark and Rowe, 1971 (which gives earlier references); CR† = indicates not west of India and Ceylon; D = Devaney, 1970, 1978; E = Endean, 1957; F = Fisher, 1919; G = Gibbs, Clark and Clark, 1976; GJ = Guille et Jangoux, 1978; K = Kingston, 1980; L = Livingstone, 1932; M = Marsh, 1976; S = Sloan, Clark and Taylor, 1979; SJ = Sukarno et Jangoux, 1977.
( ) indicates species recorded under another name; + = WAM collection; * = new record for Western Australia.

Wilson and Marsh (1979) observed that of the 138 species of echinoderms recorded from the Abrolhos 73% were tropical, 15% temperate and 9% endemic to the west coast of Western Australia.

The northwestern Australian coral reefs are populated by widespread Indo-West Pacific echinoderm species augmented by a small group shared only with Indonesia and the Philippines.

Endean (1957) noted that "the bulk of the reef species which occur outside Australia do not occur in Australian waters west of Torres Strait." His table of reef and mainland species listed 67 reef species of asteroids, ophiuroids and echinoids of which 51 (76%) were not known at that time to occur west of Torres Strait and 16 species (24%) which were recorded west of Torres Strait. When present day Western Australian distribution records are added to the same list of species, the figures present a different picture, with 25 of the species (37%) not recorded west of Torres Strait and 42 (63%) now recorded west of Torres Strait, principally in northwestern Australia.

These data seriously undermine the concept of a separate zoogeographical province for the Great Barrier Reef fauna (Whitley, 1932; Endean, 1957; Knox, 1963; 1980) at least as it applies to echinoderms. It is evident that the majority of the reef species have a wide Indo-West Pacific distribution, including northeastern and northwestern Australia.

Table 2 and Figure 2 show the distribution of 376 species of echinoderms (excluding holothurians) recorded from northwestern Australia, including the coral reef species discussed in the previous section.

No records of crinoids on the Queensland coast west of Cape York could be found from the literature, hence the question mark in that column of the table. The crinoid fauna of the offshore reefs of northwestern Australia is unexpectedly impoverished, but has not yet been fully documented.

The data on which this table is based are taken principally from a study of echinoderms of the North West Shelf (Marsh and Marshall, in preparation).

As may be expected (Clark, 1946), the data show the close relationship of the northwestern Australian fauna with that of Indonesia. Taking the 376 species found in northwestern Australia as 100%, 250 or 66% are shared with Indonesia, while 159 species (42%) are shared with the Great Barrier Reef, 134 (36%) with the west Pacific and 123 (33%) with the western Indian Ocean. Within Western Australia the diversity of habitats found on the northwest coastline and among the island archipelagoes and coral reefs, together with the extremely wide, gently sloping continental shelf, existing since the Cretaceous at least, must account for the rich and diverse echinoderm fauna with 90% of the species recorded from northwest Australia. The off-shore reefs, in contrast, are limited in both area and habitat diversity, as are the reefs off North West Cape. Predictably, the number of tropical species decreases southwards on the west coast shelf and shore.

There are 49 species (13%), made up of three species of crinoids, 19 asteroids, 14 ophiuroids and 13 echinoids, which are at present believed to be endemic to northwestern Australia and the western part of the Northern Territory. However, these figures are subject to correction in the light of future taxonomic and distributional studies. Previously published figures for endemic asteroids (Marsh, 1976) have since been reduced by the synonymy of *Archaster laevis* with *A. angulatus* (Sukarno et Jangoux, 1977) and of *Nepanthia veriabilis* and *N. magnispina* with *N. belcheri* (Rowe and Marsh, 1982), the latter distributed through South East Asia, northeastern and northwestern Australia.

In northwestern Australia coral communities are found from the turbid inshore waters to clear water atolls far offshore. Reef habitats, with one suite of echino-

Table 2. The numbers and percentages of echinoderms (other than holothurians) recorded from north Western Australia and their distribution (Data from Western Australia Museum collections and published records)

Species Recorded from Northwestern Australia	W. Ind. Ocean	India Ceylon	Indo-nesia	Philip-pines	China Japan	W. Coast & Shelf W.A.	W. Coast W.A. Coral Reefs	N.W.A. Shelf & Inshore Islands	N.W.A. Offshore Reefs	N.T.	Qld W. of C. York	Qld E. of C. York	GBR	West Pac.
Crinoids—61 spp.	6	21	47	36	27	24	20	55	10	12	?	22	31	20
Asteroids—110 spp.	30	41	66	52	39	40	23	99	22	31	28	28	35	35
Ophiuroids—136 spp.	51	51	88	66	56	41	40	122	27	38	16	38	67	52
Echinoids—69 spp.	36	40	49	39	40	24	21	62	20	21	13	33	26	27
376	123	153	250	193	162	129	104	338	79	102	57	121	159	134
100%	33%	41%	66%	51%	43%	34%	28%	90%	21%	27%	15%	32%	42%	36%

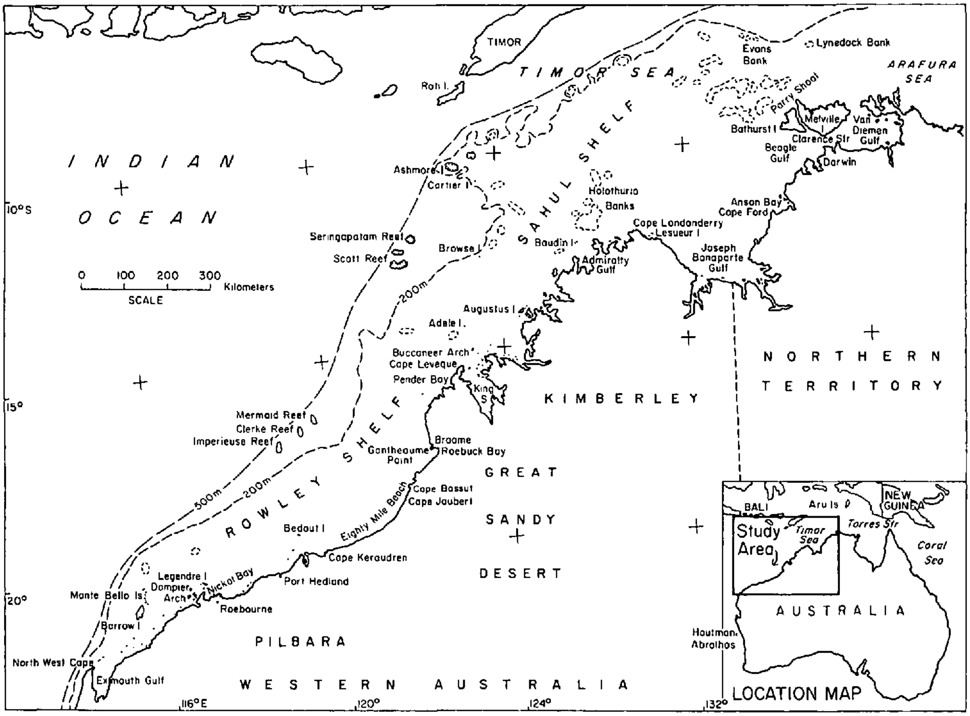

Figure 2. The Indo-West Pacific with the percentage of northwestern Australian echinoderms shared with other areas, from Table 2. (The Pacific and Indian Ocean figures refer to the general area, not the precise locality where the figures are placed.)

derms, may be found juxtaposed with sandflats, mudflats or rocky shores on which other suites of species occur, as they are around the island archipelagoes of Indonesia. The groups of species may thus overlap geographically, but not ecologically, making it impossible to separate a mainland from a reef fauna in either area.

A distribution pattern similar in paired (possibly sibling) species of several genera of asteroids and echinoids has emerged and is illustrated by the following examples:

Archaster typicus is found from the Andaman Islands through Malaysia, Indonesia, the Philippines and New Guinea to Samoa and in the Northern Territory and North Queensland. From the Kimberley coast to the south coast of Western Australia it is replaced by *A. angulatus* Müller and Troschel which is also found in the Philippines, Ryukyus and East Africa (Sukarno et Jangoux, 1977).

Protoreaster nodosus has an almost identical distribution to *A. typicus* but extends into the Pacific only as far as New Caledonia (Yamaguchi, 1977). In Northern Australia it is found in the Northern Territory and North Queensland but is replaced westwards by *P. nodulosus,* found along the northwest coast and as far south as the Houtman Abrolhos.

Unlike the *Nepanthia* species which proved to be synonymous across northern Australia, the two *Archaster* and *Protoreaster* species are clearly distinguished.

Comparing the coral reef asteroid fauna of Guam and Palau, Yamaguchi (1977) found the species composition to be rather different in the two areas and interpreted this as a difference between continental species and widely distributed species. He found that two continental species (*Archaster typicus* and *Protoreaster nodosus*) and two widely distributed species (*Culcita novaeguineae* and *Acanthaster planci*) had similar larval morphology and rate of development but the larvae of the continental species exhibited positive geotaxis, while those of the widely distributed species showed negative geotaxis during most of their pelagic larval life span.

If this proves to be a general characteristic of the larvae of continental species, it may be one factor in restricting the distribution of these species to the core area of Indonesia, the Philippines and southern Japan with extensions eastwards to New Caledonia and in some cases Fiji.

Culcita species show a somewhat different pattern: *C. novaeguineae*, a widespread Indo-West Pacific species, is found from the Andaman Islands to Eastern Polynesia (Yamaguchi, 1977). In northwestern Australia *C. novaeguineae* occurs on the offshore reefs and islands while *C. schmideliana* is found on the nearshore reefs and extends across the Indian Ocean to East Africa (Clark and Rowe, 1971).

Among echinoids *Arachnoides placenta* (Linnaeus) found from the Andaman Islands to Samoa and from Darwin to North Queensland, is replaced in the northwest by *A. tenuis* H. L. Clark, found from the Kimberley to Exmouth Gulf. *Breynia desorii* occurs in northwestern Australia, and *B. australasiae* on the east coast with a third species, *B. neanika* McNamara in the Northern Territory and northeast Queensland (McNamara, 1982b).

In these examples the dividing line between pairs of species occurs not at Torres Strait but between Darwin and the North Kimberley. However, many species occur throughout Northern Australia, wherever habitats are suitable, although much remains to be learned of the detailed distribution of species in Northern Territory waters.

North West Cape marks the end of the range of many of the predominantly continental species since there is an abrupt change of habitat from the sheltered, somewhat turbid waters of Exmouth Gulf to the high energy, oceanic waters and coral reefs on the western side of the Cape.

Discussion and Conclusions

The larval development of coral reef echinoderms has been studied by Mortensen (1921; 1931; 1937; 1938), Komatsu (1973), Henderson and Lucas (1971), Yamaguchi (1973; 1975; 1977) and discussed by Thorson (1961) and Devaney (1973).

Thorson (1946) found that 33% of the species for which the duration of larval life is known, have 10–20 days of pelagic existence, while 26% have a larval life of 21–30 days, 7% have less than 9 days and 13% have up to 50 days. Curiously, *Astropecten polyacanthus*, one of the most widespread species, has one of the shortest larval lives, only 3 to 4 days from fertilization to metamorphosis (Mortensen, 1937).

Since the minimum distance between the Indonesian island of Roti and Ashmore reef on the Sahul Shelf is only 140 km, and the currents favorable, the length of larval life is not considered to be a limited factor in determining the distribution of widespread Indo-West Pacific species on the North West Shelf. The periodic opening and closing of Torres Strait has probably had little effect on the distribution, in northwestern Australia, of Indo-West Pacific species which have had a continuous distribution from the Pacific to the Indian Ocean through the coral reefs of the Philippines and Indonesia, aided by seasonal current reversal.

The shelf edge and platform reefs of the Sahul Shelf, and the offshore atolls and shoals of the Rowley Shelf provide stepping stones for Indo-West Pacific species to reach the reefs off North West Cape, while the Leeuwin current brings many of these to the Abrolhos, where the high diversity of habitats may explain the presence of tropical species which occur off the northwest coast but have not been found on reefs at North West Cape. While populations of some tropical echinoderms at the Abrolhos may be sexually self-sustaining, others may depend on larval recruitment via the Leeuwin current for their maintenance, and some such as *Ophidiaster robillardi* and *Linckia multifora* may be maintained partially by asexual reproduction.

At the time of maximum glacio-eustatic lowering of sea level, below −120 m, between 17,000–14,000 years BP, the continental margin would have lain along the edge of the Sahul Shelf so that the area now covered by the Timor and Arafura seas and the Gulf of Carpentaria would have been dry land (Nix and Kalma, 1972). The Sahul and Arafura shelves have thus been colonized by a marine fauna only since the marine transgression which commenced about 8,000 years BP (Jennings, 1972).

The Rowley Shelf in contrast, was only partially exposed and the existing fauna could have migrated seawards during the sea level regression and recolonized the inner shelf as the transgression occurred. Winter sea temperatures during the last glaciation (18,000 years BP) were above 18°C on the Rowley Shelf (Shackleton, 1978) so that the tropical fauna would not have been markedly affected by the glaciation and its connection with Indonesia would have been maintained along the edge of what is now the Sahul Shelf.

The continuous oceanic exposure of northwestern Australia, at least since the Cretaceous, may have allowed relict species to survive as part of the endemic fauna but it is not yet clear which species fall into this category.

The configuration of the continental shelves provides a continuous present-day pathway for the spread of shelf organisms between northern Australia, the Aru Islands and New Guinea but deep water separating the area from the rest of the Indonesian archipelago may be a barrier to some species with geotactic larvae.

The dividing line between pairs of allopatric species occupying the same niche, one found through South-East Asia and northeastern Australia, the other occurring only in Western Australia, does not appear to coincide with any present or past barrier, and this pattern of speciation merits further investigation.

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