WITH THE COMPLIMENTS OF THE HEAD ZOOLOGY

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By R. Endean

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By R. Endean*

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Summary

Analysis of Queensland's shallow-water echinoderm fauna reveals that approximately 44 per cent. of the 267 species recorded are confined to Queensland mainland waters and approximately 35 per cent. to Barrier Reef waters; the remainder are common to both environments.

Marked faunistic attenuation with increasing latitude is exhibited by echinoderms occurring on the mainland north of lat. 25° S. and also by those found on the Great Barrier Reef. In both cases there are few substitutions. South of lat. 25° S. Peronian species occur, but an apparently isolated population of tropical species is found in the Moreton Bay–Caloundra area.

Queensland mainland echinoderms have strong affinities with those of the East Indies. The principal exchange route utilized by mainland species common to both areas seems to be via Torres Strait and the Arafura Sea. The Coral Sea appears to present a barrier to the spread of mainland species to the West Pacific area.

On the other hand Barrier Reef echinoderms have strong ties with those of the latter region. Gene flow between populations of species common to the Barrier Reef and the West Pacific area probably occurs by way of the Coral Sea as a result of the transport of the pelagic larval stages of West Pacific populations by the Pacific south equatorial current. A dearth of coral structures immediately to the west of Torres Strait seems to have prevented the spread of Barrier Reef species to northern Australian waters. However, a few reef echinoderms appear to have entered north-western Australian waters from the East Indies, probably by way of atolls and reef platforms found on the Sahul and Rowley Shelfs.

The echinoderm fauna of north-western Australia contains a large number of endemic species but has marked affinities with those of East Indian and Queensland mainland waters.

The origin of the echinoderm fauna of tropical Australia is discussed in the light of palaeogeographic and zoogeographic findings. It is concluded that the present fauna of the area is derived predominantly from recent East Indian and West Pacific stocks. Also it is postulated that barriers between echinoderm populations present in tropical Australian waters were set up during the Pleistocene falls of sea-level and that this has resulted in the formation of closely allied sympatric and allopatric species.

Available evidence indicates that the Solanderian Province should be restricted to the Great Barrier Reef area and, since Torres Strait does not present a barrier to the dispersal of echinoderms typically found in habitats in which terrigenous sediments predominate, the fauna of Queensland mainland waters and that of the Dampierian Province are grouped together tentatively in a single Tropical Australian Province.

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I. Introduction

Thanks to the work of H. L. Clark, the specific composition and general distribution of Australia's echinoderms are now reasonably well known. He has shown (Clark 1946) that there is a predominance of tropical species which he believed had their origins in regions to the north of Australia. In 1921 he put forward much evidence in support of his contention that the present echinoderm fauna of the Queensland coast has resulted from the mixing of immigrant species from the Pacific Ocean with East Indian species which have entered Queensland waters via Torres Strait.

However, Endean (1953) noted that the echinoderm fauna of Port Curtis (a mainland locality) differed markedly from that of Heron I. and Lady Musgrave I.—coral cays near the southern tip of the Barrier Reef. Later (Endean 1956), it was noted that the bulk of species occurring on coral structures along the Great Barrier Reef were rarely found on the shores of the Queensland mainland, whilst species common in mainland waters seemed to be restricted to muddy, sandy, stony, or gritty habitats. This suggests that Great Barrier Reef and mainland echinoderms may represent two distinct stocks which have not intermingled to any great extent.

Clark (1946) agreed with Hedley on the limits of the Australian marine faunistic provinces. Hedley (1904, 1926) had recognized four faunistic provinces on the Australian coast. On the eastern coast Hedley delineated the "Solanderian Province" as the area extending from Torres Strait to Wide Bay (about 26° S.) and the "Peronian Province" as the region from Wide Bay to eastern Victoria. The region from Bass Strait west and north to Geraldton in Western Australia he termed the "Adelaidean Province" (later changed to Flindersian by Cotton (1930)), and the remaining sector of the Australian coast—the region from Geraldton to Cape York —the "Dampierian Province".

Subsequently Whitley (1932) proposed that the term "Solanderian" be restricted to the fauna of the Great Barrier Reef and that the name "Banksian" be given to the fauna of the Queensland coast proper. Clark (1946) either ignored or overlooked Whitley's proposal, for he stated (p. 467) that "the Solanderian province is essentially the Great Barrier Reef area, extending from the Murray Is. in the north to Lady Elliott Island in the south, but it includes as well, very naturally, the coastal fauna of Queensland from Cape York southward".

However, Endean, Kenny, and Stephenson (1956) considered that the junction between the Solanderian and Peronian Provinces should be re-located at about lat. 25° S., and in a later paper (Endean, Stephenson, and Kenny 1956) put forward evidence which, to some extent, supported Whitley's proposal.

If Clark's work on Australian echinoderms be used as a basis, recent information obtained on the distribution of Queensland species (Endean 1953, 1956) sheds new light on the biogeography of these species and on the delineation of Queensland's faunistic provinces.

II. The Queensland Echinoderm Fauna

Table 1 includes all well-authenticated species (excluding crinoids) that have been recorded from waters of less than 20 fm off the Queensland coast. New species

can still be expected from Queensland but there is no reason to believe that the discovery of these will alter radically the conclusions reached in this paper. Owing to the author's unfamiliarity with the Crinoidea this class is excluded from the present discussion.

Species occurring only on reefs of the Great Barrier Reef or on coral islands off the coast are designated "reef" species, whilst species found elsewhere in Queensland waters are regarded as "mainland" species. It will be noted that some species occur in both reef and mainland waters.

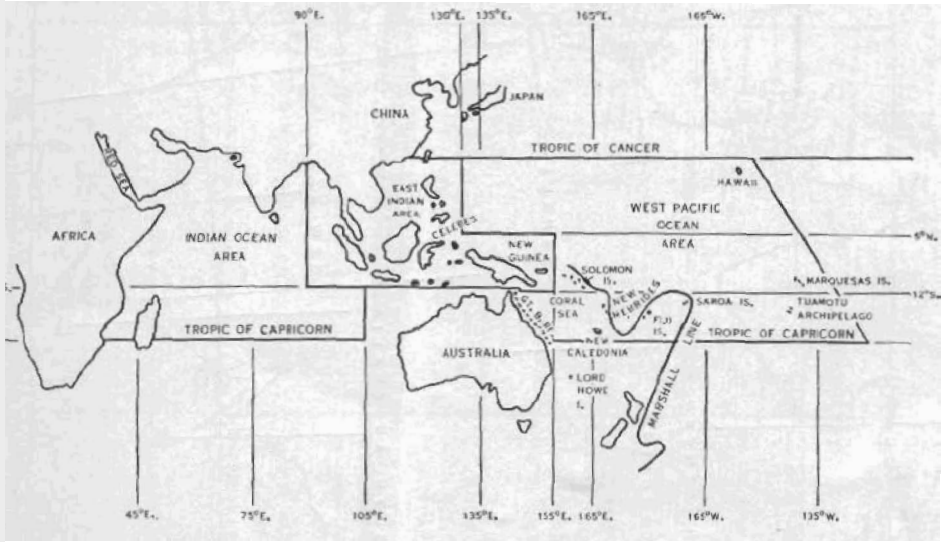

Fig. 1.—The Indo-West Pacific region, showing biogeographical areas mentioned in the text.

Owing to a lack of ecological data uncertainty has arisen regarding the designation of many species recorded from continental islands off the coast. Since the intertidal fauna of these islands has been shown to be closely allied to that of the mainland (Endean, Stephenson, and Kenny 1956) such species are regarded as mainland species.

For the purposes of this paper the geographical limits of the East Indies are based on those fixed by Clark (1946). The tropical region to the east of the East Indies–Australian area, stretching as far as Hawaii, the Marquesas Is., and the Tuamotu Archipelago, is here referred to as the West Pacific Ocean area, whilst the region to the west of the East Indies–Australian area as far as the east coast of Africa and the Red Sea is here termed the Indian Ocean area. The boundaries of these geographical areas are shown on Figure 1, and localities within Australia on Figure 2.

One species, *Clypeaster australasiae* (Gray), is recorded by Clark (1946) from Brisbane Water, Queensland. It is believed that the record should be Brisbane Water, N.S.W., as there is no locality of that name to be found in Queensland.

III. Existence of "Mainland" and "Reef" Elements in Fauna

Analysis of the species list in Table 1, which comprises 267 echinoderm species belonging to 128 genera, reveals that 112 have not been recorded from the Great

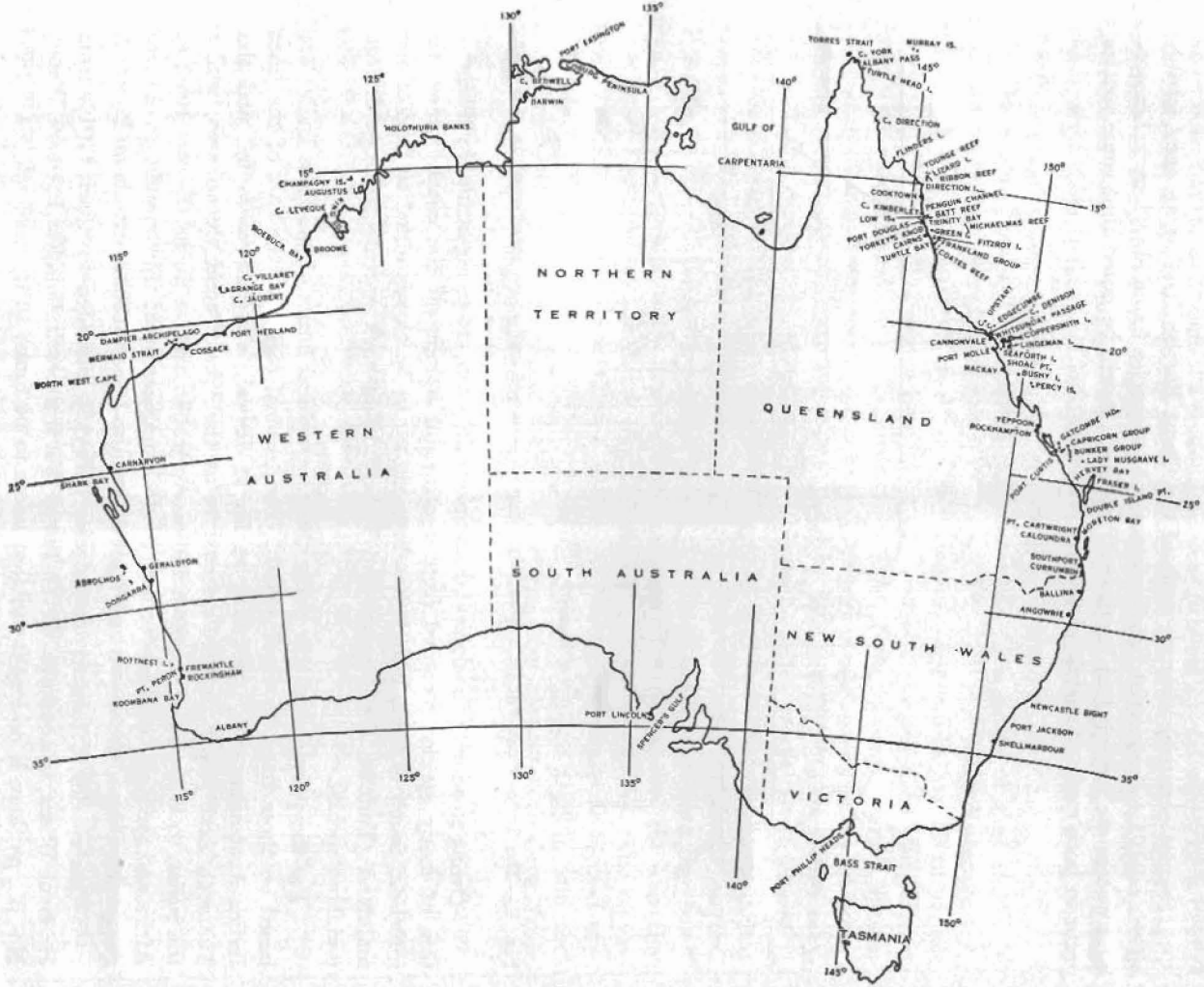

Fig. 2.—Australia, showing localities where echinoderm species mentioned in the text have been recorded.

TABLE 1

THE DISTRIBUTION OF LITTORAL ECHINODERMS FOUND IN QUEENSLAND WATERS

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA					
LUIDIIDAE					
**Luidia australiae* Doderlein	Moreton Bay S. to Vic. and around southern shores of Australia to Fremantle, W.A.				
**Luidia forficifera* Sladen	Torres Strait S. to Newcastle Bight, N.S.W.		×	×	
ASTROPECTINIDAE					
**Astropecten granulatus* Muller & Troschel	Torres Strait S. to Hervey Bay and W. around northern half of the continent to Fremantle, W.A.				
Astropecten monacanthus Sladen	Gulf of Carpentaria W. to Broome, W.A.		×	×	
**Astropecten polyacanthus* Muller & Troschel	Torres Strait S. to Port Jackson, N.S.W.		×	×	×
**Astropecten vappa* Muller & Troschel	Probably right around Australia				
ARCHASTERIDAE					
**Archaster typicus* Muller & Troschel	Torres Strait S. to Lindeman I. and W. to Coburg Pensinsula, N.T.	Low Isles		×	×
GONIASTERIDAE					
Mediaster praestans Livingstone		Barrier Reef near Cairns			
**Goniodiscaster coppingeri* (Bell)	Torres Strait S. to Port Curtis and W. to Cape Bedwell, N.T.				
**Goniodiscaster integer* Livingstone	Lindeman I.; Port Curtis; Moreton Bay				
Goniodiscaster pleyadella (Lamarck)	Torres Strait			×	

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA (*Continued*)					
Pseudogoniodiscaster wardi Livingstone	Port Curtis				
Tosia queenslandensis Livingstone		Low Isles; Capricorn Group			
Iconaster longimanus (Mobius)	Torres Strait S. to Percy Isles and W. to Broome, W.A.			×	
**Stellaster incei* Gray	Torres Strait S. to Moreton Bay and W. around tropical Australia to Lagrange Bay, W.A.		×	×	
Stellaster princeps Sladen	Torres Strait W. around northern Australia to Port Hedland, W.A.				
**Anthenea acanthodes* Clark	Port Curtis				
**Anthenea acuta* (Perrier)	Fraser I. S. to Tasmania				
**Anthenea aspera* Doderlein	Port Curtis				
**Anthenea crassa* Clark	Port Curtis				
Anthenea mertoni Koehler	Gulf of Carpentaria W. around shores of N.T.			×	
OREASTERIDAE					
**Protoreaster nodosus* (L.)	Torres Strait S. to Mackay**	Murray Is. S. to Low Isles	×	×	×
**Pentaceraster australis* (Lutken)	Lizard I. S. to Moreton Bay				
Pentaceraster gracilis (Lutken)	Torres Strait to SE. of Lady Musgrave I. and W. around tropical Australia to Lacépède Is., W.A.			×	
**Culcita novaeguineae* Muller & Troschel		Murray Is. S. to Capricorn Group; Augustus I., W.A.	×	×	×
ASTEROPIDAE					
**Asterope carinifera* (Lamarck)	Fitzroy I.	Murray Is. S. to Low Isles	×	×	×
**Petricia vernicina* (Lamarck)	Caloundra S. and W. to Spencer's Gulf, S.A.				

* In collection of Zoology Department, University of Queensland. **Unpublished record.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA (*Continued*)					
METRODIRIDAE					
**Metrodira subulata* Gray	Torres Strait S. to Moreton Bay and W. to Carnarvon, W.A.		×	×	
OPHIDIASTERIDAE					
Fromia elegans Clark		Murray Is. S. to Coates Reef; Abrolhos, W.A.			
**Fromia milleporella* (Lamarck)		Murray Is. S. to Bunker Group	×	×	×
Nardoa mollis de Loriol		Murray Is.	×	×	
**Nardoa novaecaledoniae* (Perrier)		Murray Is. S. to Bunker Group		×	×
**Nardoa pauciforis* (von Martens)		Murray Is. S. to Bunker Group		×	×
**Nardoa rosea* Clark		Murray Is. S. to Capricorn Group			
**Neoferdina ocellata* (Clark)		Murray Is. S. to Capricorn Group			×
**Linckia guildingii* Gray		Younge and Ribbon Reefs S. to Bunker Group; Broome, W.A.	×	×	×
**Linckia laevigata* (L.)		Murray Is. S. to Bunker Group	×	×	×
Bunaster uniserialis Clark		Murray Is.			
Leiaster speciosus von Martens		Murray Is.		×	
Ophidiaster armatus Koehler	Lindeman I.			×	
**Ophidiaster confertus* Clark	Fraser I. S. to Shellharbour, N.S.W.	Capricorn Group			
**Ophidiaster granifer* Lutken		Murray Is. S. to Bunker Group		×	×
Ophidiaster lioderma Clark		Murray Is.			
Ophidiaster propinquus Livingstone		Ribbon Reef			
Ophidiaster squameus Fisher		Murray Is.		×	×
**Ophidiaster watsoni* Livingstone	Bushy I., off Mackay	Capricorn Group			

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TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA (*Continued*)					
Hacelia helicosticha (Sladen)	Torres Strait W. to Holothuria Bank, W.A.				
Tamaria fusca Gray	Off Direction I.			×	
Tamaria megaloplax (Bell)	Torres Strait W. to Broome, W.A.	Snake Reef	×	×	
ASTERINIDAE					
Asterina anomala Clark		Murray Is.; Cape Leveque, W.A.			×
**Asterina burtonii* Gray		Murray Is. S. to Bunker Group; Roebuck Bay, Shark Bay, and the Abrolhos, W.A.	×	×	×
**Asterina nuda* Clark	Caloundra	Murray Is.			
**Patiriella calcar* (Lamarck)	Currumbin S. to Tas. and W. to Spencer's Gulf, S.A.				
**Patiriella exigua* (Lamarck)	Torres Strait S. to Tas. and W. to Spencer's Gulf, S.A.	Murray Is. S. to Low Isles	×	×	×
Disasterina abnormalis Perrier		Murray Is. S. to Michaelmas Cay, off Cairns			×
**Disasterina leptalacantha*(Clark)		Capricorn Group			
Disasterina praesignis Livingstone	Port Curtis				
**Nepanthia belcheri* (Perrier)	Yeppoon S. to Port Jackson, N.S.W.				
**Nepanthia brevis* (Perrier)	Torres Strait S. to Port Curtis and W. to Darwin, N.T.				
Tegulaster emburyi Livingstone		Capricorn Group			
**Anseropoda rosacea* (Lamarck)	Fraser I.; Broome and Port Hedland, W.A.	Capricorn Group	×	×	
ECHINASTERIDAE					
Echinaster acanthodes Clark	Off Fraser I.				
**Echinaster luzonicus* (Gray)	Torres Strait S. to Fraser I.	Murray Is. S. to Bunker Group		×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA (*Continued*)					
ACANTHASTERIDAE					
Acanthaster planci (L.)		Murray Is. S. to Low Isles	×	×	×
VALVASTERIDAE					
Valvaster spinifera Clark		Murray Is.			
PTERASTERIDAE					
**Retaster insignis* Sladen	Torres Strait S. to Moreton Bay and W. around northern Australia to Shark Bay, W.A.			×	
OPHIUROIDEA					
OPHIOMYXIDAE					
**Ophiomyxa australis* Lutken	Off Lizard I. S. to Tas. and W. around southern Australia to between Geraldton and Fremantle, W.A.	Low Isles S. to Bunker Group	×	×	×
TRICHASTERIDAE					
**Euryale aspera* Lamarck	Torres Strait S. to Double I. Point and W. around tropical Australia to Cape Villaret, W.A.			×	
Astrobrachion adhaerens (Studer)	Port Molle; Whitsunday Passage; off "north-western Australia"				
GORGONOCEPHALIDAE					
Astrocladus granulatus Clark	Lindeman I.				
Astrochalcis tuberculosus Koehler	Albany Passage			×	
OPHIACANTHIDAE					
Ophiacantha discoidea Lyman		Murray Is.		×	
Ophiacantha gracilis (Studer)		Murray Is.; "north of Dampier Archipelago", W.A.			
Ophiacantha tenuispina Clark	Off Gatcombe Head, Port Curtis				

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
AMPHIURIDAE					
Amphiura bidentata Clark	Port Curtis; Broome, W.A.				
Amphiura constricta Lyman	Probably right around Australia				
Amphiura diacritica Clark	Black I., Whitsunday Passage				
Amphiura microsoma Clark		Murray Is.; Broome and Rottnest I., W.A.			
Amphiura septemspinosa Clark		Murray Is.; Cape Bedwell, N.T.			
Ophiocentrus dilatatus (Koehler)		Murray Is.; Darwin		×	
Ophionephthys octacantha Clark	Torres Strait; Broome, W.A.				
**Amphipholis squamata* (Delle Chiaje)	Probably right around Australia	Probably right along the Barrier Reef	×	×	×
Amphiodia ochroleuca (Brock)	Probably right around Australia			×	
Amphioplus depressus (Ljungman)	Torres Strait W. around tropical Australia to Point Peron, W.A.		×	×	×
Amphioplus parviclypeus Clark	Torres Strait				
Ophiactis acosmeta Clark	Port Curtis; Broome, W.A., W. and S. to Rockingham, W.A.				
Ophiactis delicata Clark		Murray Is.			
Ophiactis hemiteles Clark		Murray Is.			
Ophiactis luteomaculata Clark		Murray Is.; off Ballina, N.S.W.; Broome, W.A.			
Ophiactis modesta Brock	Torres Strait W. to Broome, W.A.		×	×	×
**Ophiactis savignyi* (Muller & Troschel)	Torres Strait S. to Port Jackson, N.S.W., and W. around tropical Australia to Fremantle, W.A.	Murray Is. S. to Bunker Group	×	×	×
OPHIOTRICHIDAE					
**Ophiothrix acestra* Clark	Port Curtis S. to Shellharbour, N.S.W.	Low Isles			
**Ophiothrix caespitosa* Lyman	Caloundra S. around southern Australia and N. to Shark Bay, W.A.				

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TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
**Ophiothrix exigua* Lyman	Torres Strait S. to Port Curtis and W. to Broome, W.A.			×	×
Ophiothrix stelligera Lyman	Torres Strait W. around tropical Australia to Koombana Bay, W.A.	Murray Is.	×	×	×
Amphiophiothrix demessa (Lyman)		Murray Is.	×	×	×
**Macrophiothrix longipeda* (Lamarck)	Torres Strait S. to Moreton Bay and W. around northern Australia to Broome, W.A.	Murray Is. S. to Capricorn Group	×	×	×
Macrophiothrix megapoma Clark	Cape York S. to Penguin Channel				
Macrophiothrix rhabdota (Clark)		Murray Is.		×	
Macrophiothrix rugosa Clark		Murray Is.			
**Placophiothrix lineocaerulea* (Clark)	Moreton Bay; Broome, W.A.				
Placophiothrix melanosticta (Grube)	Torres Strait W. around northern Australia to Port Hedland, W.A.			×	
**Placophiothrix spongicola* (Stimpson)	Currumbin S. around southern coasts of Australia to Dongarra and the Abrolhos, W.A.				
Placophiothrix striolata (Grube)	Torres Strait S. to Lindeman I.			×	
Placophiothrix trilineata (Lutken)		Murray Is. S. to Bott Reef, near Cairns		×	×
Placophiothrix virgata (Lyman)		Murray Is.		×	×
**Ophiothela hadra* Clark	Torres Strait S. to Ballina, N.S.W., and W. around tropical Australia to Albany, W.A.	Murray Is.			
Ophiotrichoides irregularis Clark	Port Curtis				

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
Ophiotrichoides liodisca (Clark)		Murray Is.		×	
**Ophiotrichoides martensi* (Lyman) *australis* (Clark)	Torres Strait S. to Port Curtis and W. around tropical Australia to Cossack, W.A.	Murray Is.			
**Ophiotrichoides nereidina* (Lamarck)	Lizard I. S. to Fraser I.	Murray Is. S. to Capricorn Group		×	
Ophiotrichoides propinqua (Lyman)		Murray Is.	×	×	×
Ophiomaza cacaotica Lyman	Torres Strait S. to Port Curtis and W. around tropical Australia to Broome, W.A.	Murray Is.	×	×	×
Ophiomaza cataphracta (Brock)	Cape York				
Ophiomaza obscura (Ljungman)		Murray Is.; "north-west Australia"	×	×	×
Ophiogymna lineata Clark	W. of Low Isles				
OPHIOCHITONIDAE					
Ophionereis lineata Clark	Lindeman I.				
Ophionereis porrecta Lyman		Murray Is.	×	×	×
**Ophionereis semoni* (Doderlein)	Torres Strait S. to Lindeman I. and W. around northern Australia to Broome, W.A.	Low Isles		×	
Ophionereis tigris Clark		Capricorn Group			
OPHIOCOMIDAE					
**Ophiocoma brevipes* Peters	Green I.	Murray Is. S. to Bunker Group	×	×	×
**Ophiocoma erinaceus* Muller & Troschel		Murray Is. S. to Capricorn Group	×	×	×
**Ophiocoma insularia* Lyman *variegata* Smith		Murray Is. S. to Capricorn Group; Abrolhos, W.A.			

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
Ophiocoma parva Clark		Murray Is.; Port Essington, N.T.; Cape Leveque and Rottnest I. W.A.			
**Ophiocoma pica* Muller & Troschel		Murray Is. S. to Low Isles	×	×	×
Ophiocoma schoenleinii Muller & Troschel	Lindeman I.; Frankland Group	Murray Is.		×	×
**Ophiocoma scolopendrina* (Lamarck)		Murray Is. S. to Bunker Group	×	×	×
Ophiomastix annulosa (Lamarck)		Murray Is. S. to Ellison Reef		×	
**Ophiomastix asperula* Lutken		Murray Is. S. to Low Isles		×	×
Ophiomastix bispinosa Clark	Lizard I.				×
Ophiomastix caryophyllata Lutken		Murray Is.		×	×
Ophiomastix corallicola Clark		Murray Is.			
Ophiomastix flaccida Lyman		Murray Is.		×	
Ophiomastix janualis Lyman		Murray Is.		×	
**Ophiomastix mixta* Lutken	Frankland Group	Murray Is. S. to Low Isles		×	×
**Ophiarthrum elegans* Peters	Torres Strait S. to Lindeman I. and W. around northern Australia to Augustus I., W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Ophiarthrum pictum* (Muller & Troschel)	Lindeman I.	Murray Is. S. to Low Isles		×	×
OPHIODERMATIDAE					
**Ophiarachna incrassata* (Lamarck)		Murray Is. S. to Capricorn Group	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE I (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
Ophiarachna megacantha Clark	Lindeman I.				
Ophiopezella spinosa (Ljungman)	Torres Strait	Murray Is.		×	×
Ophiochasma stellatum (Ljungman)	Torres Strait S. to Lindeman I.; Broome, W.A.			×	
**Ophiarachnella gorgonia* (Muller & Troschel)	Torres Strait S. to Cairns and W. around tropical Australia to Port Hedland, W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Ophiarachnella infernalis* (Muller & Troschel)	Torres Strait S. to Port Molle and W. around northern Australia to Broome, W.A.	Murray Is. S. to Low Isles		×	
**Ophiarachnella septemspinosa* (Muller & Troschel)		Murray Is. S. to Bunker Group; Augustus I., W.A.	×	×	×
Cryptopelta granulifera Clark	Off Lizard I.		×		
OPHIOLEPIDIDAE					
Ophiura kinbergi Ljungman		Murray Is.; Port Jackson, N.S.W., S. to Bass Strait and W. to Spencer's Gulf, S.A.; Broome, W.A.	×	×	×
Ophioteichus multispinum Clark	Lindeman I.				
Ophiolepis cincta Muller & Troschel	Torres Strait	Murray Is.	×	×	×
Ophiolepis nodosa Duncan	Frankland Group			×	
**Ophiolepis superba* Clark	Torres Strait S. to Port Douglas and W. to Darwin, N.T.	Murray Is. S. to Capricorn Group	×	×	×
**Ophioplocus imbricatus* (Muller & Troschel)		Murray Is. S. to Capricorn Group; Darwin, N.T.; Broome, Shark Bay, and the Abrolhos, W.A.	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA					
CIDARIDAE					
Phyllacanthus imperialis (Lamarck)	Torres Strait	Murray Is.	×	×	×
**Phyllacanthus parvispinus* Tenison Woods	Point Cartwright S. to Tas.				
Prionocidaris australis (Ramsay)	Fraser I. S. to Bass Strait				
Prionocidaris bispinosa (Lamarck)	Torres Strait S. to Port Denison and W. around northern Australia to Shark Bay and the Abrolhos, W.A.		×	×	
Prionocidaris verticillata (Lamarck)		Low Isles	×	×	×
CENTRECHINIDAE					
**Diadema setosum* (Leske)	Torres Strait S. to Moreton Bay; Augustus I. and the Abrolhos, W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Diadema savignyi* Michelin		Murray Is. S. to Capricorn Group; Abrolhos, W.A.	×	×	×
**Echinothrix calamaris* (Pallas)		Murray Is. S. to Capricorn Group	×	×	×
**Echinothrix diadema* (L.)		Murray Is. S. to Capricorn Group	×	×	×
Astropyga radiata (Leske)	Torres Strait, Double I. Point		×	×	×
ECHINOTHURIIDAE					
Asthenosoma intermedium Clark	Seaforth I., near Mackay				
STOMOPNEUSTIDAE					
**Stomopneustes variolaris* (Lamarck)	Trinity Bay to Port Denison	Murray Is. S. to Low Isles	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA (*Continued*)					
TEMNOPLEURIDAE					
**Temnopleurus alexandri* (Bell)	Torres Strait S. to Port Jackson and W. to Broome, W.A.			×	
**Temnopleurus toreumaticus* (Leske)	From 15° S. on Qld. coast to Moreton Bay; Gulf of Carpentaria		×	×	×
Salmacis belli Doderlein	Torres Strait S. to Lindeman I. and W. to Holothuria Bank, W.A.			×	
**Salmacis sphaeroides* (L.)	Torres Strait S. to Port Jackson, N.S.W., and W. to Broome, W.A.	Low Isles		×	
Temnotrema bothryoides (Agassiz & Desor)	Torres Strait W. around tropical Australia to King Sound, W.A.			×	
Temnotrema siamense (Mortensen)	Torres Strait; Holothuria Bank, W.A.	Murray Is.	×	×	
Mespilia globulus (L.)	Trinity Bay; Augustus and Champagny Is., W.A.			×	×
ECHINIDAE					
Cyrtechinus verruculatus (Lutken)	Green I.		×	×	×
**Nudechinus darnleyensis* (Tenison Woods)	Torres Strait S. to Moreton Bay and W. around tropical Australia to Cape Jaubert, W.A.				
Nudechinus multicolor (Yoshiwara)		Low Isles, Three Isles		×	
**Tripneustes gratilla* (L.)	Moreton Bay S. to Port Jackson, N.S.W.; Shark Bay and the Abrolhos, W.A.	Murray Is. S. to Capricorn Group	×	×	×
Gymnechinus epistichus Clark	Torres Strait S. to Port Denison			×	

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA (*Continued*)					
STRONGYLOCENTROTIDAE					
**Echinostrephus molaris* (de Blainville)		Murray Is. S. to Low Isles	×	×	×
**Echinostrephus aciculatus* Agassiz		Capricorn Group		×	×
**Heliocidaris erythrogramma* (Valenciennes)	Caloundra S. around southern shores of Australia to Shark Bay and the Abrolhos, W.A.				
**Heliocidaris tuberculata* (Lamarck)	Caloundra** S. to Port Jackson, N.S.W.				
ECHINOMETRIDAE					
Parasalenia gratiosa Agassiz	Green I.; Augustus and Champagny Is., W.A.	Murray Is.	×	×	×
**Echinometra mathaei* (de Blainville)	Torres Strait S. to Moreton Bay; Shark Bay, the Abrolhos, and Rottnest I., W.A.	Murray Is. S. to Bunker Group	×	×	×
**Heterocentrotus mammillatus* (L.)		Murray Is. S. to Capricorn Group; "north-west Australia"	×	×	×
CLYPEASTRIDAE					
**Clypeaster telurus* Clark	Torres Strait S. to Southport and W. around tropical Australia to Fremantle, W.A.				
**Arachnoides placenta* (L.)	Torres Strait S. to Moreton Bay and W. around northern Australia to Augustus and Champagny Is., W.A.			×	×
LAGANIDAE					
**Laganum depressum* Agassiz	Torres Strait	Low Isles S. to Capricorn Group	×	×	×
Peronella lesueuri (Agassiz)	Torres Strait S. to Port Molle and W. around tropical Australia to Fremantle, W.A.			×	

* In collection of Zoology Department, University of Queensland. **Unpublished record.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA (*Continued*)					
Peronella orbicularis (Leske)	Torres Strait S. to Cape Upstart and W. around tropical Australia to Shark Bay, W.A.			×	
Peronella peronii (Agassiz)	"Southern Queensland" S. to Tas.				
FIBULARIIDAE					
Fibularia volva Agassiz & Desor	Torres Strait W. to Cape Jaubert, W.A.		×	×	×
SCUTELLIDAE					
Echinodiscus tenuissimus (Agassiz & Desor)	Torres Strait			×	×
ECHINONEIDAE					
**Echinoneus cyclostomus* Leske		Murray Is. S. to the Capricorn Group	×	×	×
HEMIASTERIDAE					
Schizaster lacunosus (L.)	Torres Strait; Turtle I.		×	×	
**Moira lethe* Mortensen	Probably right around Australia				
SPATANGIDAE					
Metalia spatagus (L.)	Torres Strait	Low Isles	×	×	×
Metalia sternalis (Lamarck)		Low Isles; Port Essington, N.T.	×	×	×
**Rhynobrissus hemiasteroides* Agassiz	Shoal Point S. to Moreton Bay; Broome, W.A.				×
**Brissus latecarinatus* (Leske)	Torres Strait; Port Jackson, N.S.W.; Port Essington, N.T.; Port Lincoln, S.A.	Murray Is. S. to Capricorn Group	×	×	×
**Maretia planulata* (Lamarck)	Cooktown S. to Port Jackson, N.S.W.	Low Isles	×	×	×
**Breynia australasiae* (Leach)	Torres Strait S. to Port Jackson, N.S.W., and W. around tropical Australia to Fremantle and the Abrolhos, W.A.				
Lovenia elongata (Gray)	Lindeman I.; Broome, W.A.		×	×	

* In collection of Zoology Department, University of Queensland.

Lovenia elongata (Gray)	Fremantle and the Abrolhos, W.A. Lindeman I.; Broome, W.A.		×	×	

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA (*Continued*)					
Echinocardium cordatum (Pennant)	Flinders I.; Port Jackson, N.S.W.; Tas.		×	×	×
HOLOTHURIOIDEA					
CUCUMARIIDAE					
Cucumaria semperi Bell	Torres Strait S. to Port Denison and W. around northern Australia to Broome, W.A.			×	
Pentacta australis (Ludwig)	Probably right around Australia				
**Pentacta cucumis* (Semper)	Torres Strait S. to Coppersmith I.			×	
Pentacta minuta (Ludwig)	Off Low Isles, Port Denison; Albany, W.A.				
**Pentacta quadrangularis* (Troschel)	Lizard I. S. to Moreton Bay; Broome, W.A., W. and S. to Albany, W.A.			×	
**Pentacta tuberculosa* (Quoy & Gaimard)	Torres Strait S. to Port Jackson, N.S.W., and W. around tropical Australia to Shark Bay, W.A.			×	
**Pseudocolochirus axiologus* (Clark)	Mackay; Augustus I. W. to Cape Jaubert, W.A.				
**Acolochirus challengeri* (Theel)	Torres Strait S. to Moreton Bay			×	
Pentathyone mirabilis (Ludwig)	Torres Strait S. to Port Curtis and W. around tropical Australia to Shark Bay, W.A.				
**Thyone buccalis* Stimpson	Torres Strait S. to Port Jackson, N.S.W., and W. around tropical Australia to Shark Bay, W.A.		×	×	
**Thyone papuensis* Theel	Torres Strait S. to Moreton Bay and W. around tropical Australia to Mermaid Strait, W.A.				

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
HOLOTHURIOIDEA (*Continued*)					
Actinocucumis difficilis Bell	Torres Strait W. to Broome, W.A.				
Actinocucumis typicus Ludwig	Torres Strait S. to Port Denison and W. around tropical Australia to Shark Bay, W.A.				
**Discucumaria africana* (Semper)	Torres Strait S. to Caloundra and W. to "north-western Australia"	Murray Is. S. to Bunker Group	×	×	
Pseudocucumis aciculus (Semper)		Murray Is.	×	×	×
**Mensamaria intercedens* (Lampert)	Torres Strait S. to Moreton Bay and W. around tropical Australia to King Sound, W.A.			×	
Phyllophorus proteus Bell	Torres Strait S. to Port Molle and W. to Broome, W.A.				
Phyllophorus trapezus Clark	Off Cape Kimberley	Low Isles			
**Urodemas schmeltzii* (Ludwig)	Torres Strait S. to Moreton Bay and W. around northern Australia to Cape Jaubert, W.A.				
STICHOPODIDAE					
**Stichopus chloronotus* Brandt	Torres Strait	Murray Is. S. to Bunker Group	×	×	×
**Stichopus horrens* Selenka	Torres Strait S. to Moreton Bay	Murray Is. S. to Low Isles		×	×
**Stichopus variegatus* Semper	Torres Strait; Broome, W.A., W. and S. to "south-western Australia"	Murray Is. S. to Bunker Group	×	×	×
Thelenota ananas (Jaeger)		Murray Is.		×	×
HOLOTHURIIDAE					
**Labidodemas semperianum* Selenka		Murray Is. S. to Capricorn Group	×	×	×
Holothuria albiventer Semper	Off Direction I.; Carnarvon, W.A.		×		
**Holothuria arenicola* Semper	Port Denison S. to Moreton Bay	Murray Is. S. to Bunker Group	×	×	×

* In collection of Zoology Department, University of Queensland.

	Off Direction I.; Carnarvon, W.A.		×		
**Holothuria arenicola* Semper	Port Denison S. to Moreton Bay	Murray Is. S. to Bunker Group	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
HOLOTHURIOIDEA (*Continued*)					
**Holothuria argus* (Jaeger)	Cooktown	Murray Is. S. to Bunker Group	×	×	×
**Holothuria atra* Jaeger	Caloundra; Augustus I., W.A.	Murray Is. S. to Bunker Group	×	×	×
Holothuria axiologa Clark		Murray Is.			
**Holothuria coluber* Semper	Torres Strait	Murray Is. S. to Low Isles		×	
**Holothuria difficilis* Semper	Caloundra; "West Australia"	Murray Is. S. to Capricorn Group	×	×	
**Holothuria edulis* Lesson		Murray Is. S. to Capricorn Group	×	×	×
**Holothuria erinaceus* Semper	Shoal Point, Cape Edgecumbe	Low Isles		×	×
**Holothuria fuscocinerea* Jaeger	Torres Strait S. to Port Denison	Murray Is. S. to Low Isles	×	×	×
**Holothuria fusco-olivacea* Fisher		Low Isles			×
**Holothuria impatiens* (Forskål)	Torres Strait S. to Caloundra and W. around tropical Australia to Shark Bay, W.A.	Murray Is. S. to Bunker Group	×	×	×
Holothuria inhabilis Selenka		Murray Is.		×	×
**Holothuria leucospilota* (Brandt)	Torres Strait S. to Angowrie, N.S.W., and W. around tropical Australia to Shark Bay, W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Holothuria marmorata* (Jaeger)		Murray Is. S. to Capricorn Group; Broome, W.A.	×	×	×
**Holothuria martensii* Semper	Torres Strait S. to Cannonvale	Murray Is.	×	×	
**Holothuria modesta* Ludwig	Torres Strait S. to Port Curtis and W. around northern Australia to Cape Jaubert, W.A.		×	×	×
**Holothuria moebii* Ludwig	Mackay; Yorkey's Knob		×	×	×
**Holothuria monacaria* Lesson	Torres Strait W. to Cape Leveque, W.A.	Murray Is. S. to Capricorn Group	×	×	×
Holothuria notabilis Ludwig	Port Denison	Low Isles		×	
**Holothuria ocellata* (Jaeger)	Torres Strait to Moreton Bay			×	
**Holothuria paradoxa* Selenka		Low Isles			×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
HOLOTHURIOIDEA (*Continued*)					
**Holothuria pardalis* Selenka	Torres Strait S. to Moreton Bay and W. around northern Australia to Broome, W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Holothuria pervicax* Selenka		Murray Is. S. to Bunker Group; Shark Bay, W.A.	×	×	×
Holothuria remollescens Lampert		Murray Is.	×		
Holothuria rigida (Selenka)	Turtle Bay, Green I.	Murray Is.	×	×	×
Holothuria rugosa Ludwig		Murray Is.		×	×
**Holothuria scabra* Jaeger	Torres Strait S. to Moreton Bay	Low Isles S. to Capricorn Group	×	×	×
**Holothuria verrucosa* Selenka		Murray Is. S. to Low Isles	×	×	×
Actinopyga echinites (Jaeger)	Torres Strait S. to Port Denison and W. around tropical Australia to Shark Bay, W.A.		×	×	×
Actinopyga lecanora (Jaeger)	Torres Strait W. to Broome, W.A.	Murray Is.	×	×	×
**Actinopyga mauritiana* (Quoy & Gaimard)		Murray Is. S. to Bunker Group	×	×	×
**Actinopyga miliaris* (Quoy & Gaimard)	Torres Strait; "Western Australia"	Murray Is. S. to Low Isles	×	×	×
MOLPADIIDAE					
**Paracaudina australis* (Semper)	Rockhampton, Mackay; various localities in S.A.				
SYNAPTIDAE					
Euapta godeffroyi (Semper)	Torres Strait	Murray Is.	×	×	×
Opheodesoma grisea (Semper)	Torres Strait S. to Port Denison	Murray Is.	×	×	
**Polyplectana kefersteinii* (Selenka)		Murray Is. S. to Low Isles	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
HOLOTHURIOIDEA (*Continued*)					
**Synapta maculata* (Chamisso & Eysenhardt)		Murray Is. S. to Low Isles	×	×	×
Chondrocloea nigra (Semper)		Murray Is.		×	
**Chondrocloea recta* (Semper)	Torres Strait S. to Moreton Bay and W. around tropical Australia to Shark Bay, W.A.	Low Isles	×	×	×
CHIRIDOTIDAE					
**Chiridota rigida* Semper	Moreton Bay	Murray Is. S. to Capricorn Group		×	
**Polycheira rufescens* (Brandt)	Cape York S. to Port Denison	Low Isles	×	×	×

* In collection of Zoology Department, University of Queensland.

Barrier Reef or from localities where corals are a dominant element in the fauna. Indeed these 112 echinoderms appear to be restricted to mainland coastal waters and to the waters around the continental islands.

An additional 6 species (*Archaster typicus*, *Ophiothrix acestra*, *Ophionereis semoni*, *Salmacis sphaeroides*, *Maretia planulata*, and *Polycheira rufescens*) are very common in mainland waters, and in Queensland have been recorded from only one coral-dominated locality—Low Isles. As Low Isles is relatively close to the mainland (about 7 miles distant) and since the species listed occur there on the sand flat or amongst rubble, these species can be regarded as species which have strayed into the coral environment (see Endean 1956).

Thus 118 or approximately 44 per cent. of the total number of echinoderm species found in Queensland waters are essentially mainland species.

Of the total Queensland species 85 appear to be confined to coral-dominated areas. An additional 9 (*Asterope carinifera*, *Ophiocoma brevipes*, *Ophiomastix mixta*, *Ophiarthrum pictum*, *Stichopus chloronotus*, *Holothuria argus*, *Holothuria atra*, *Holothuria difficilis*, and *Chiridota rigida*) have each been recorded from only a single mainland locality but are very common in Barrier Reef waters. Thus 94 or approximately 35 per cent. of Queensland echinoderms are essentially reef species.

There remain 55 species, or 21 per cent. of the total, which occur both in coral-dominated and in mainland waters. Some species are not well known, and eventually may be found to belong to one or other of the preceding categories. However, the majority appear to be just as common in Barrier Reef waters as in mainland coastal waters.

IV. Faunistic Attenuation with Increasing Latitude

(*a*) *Species Found in Mainland Waters North of Lat. 25° S.*

Figure 3 illustrates the attenuation with increasing latitude of tropical echinoderms occurring in eastern Queensland mainland waters. (Species which range right around Australia have been excluded.)

The majority of species considered range from Torres Strait southward for various distances but some endemic species have been found only in restricted regions along the coast. Also some species found on the east coast of Queensland have not been recorded from the Torres Strait region although they occur in extra-Australian regions further north or on the Australian mainland coast to the west. It is a reasonable assumption that such species occur in Torres Strait but have been overlooked. They are:

Amphiura bidentata, *Anseropoda rosacea*, *Astrobrachion adhaerens*, *Cryptopelta granulifera*, *Cyrtechinus verruculatus*, *Echinocardium cordatum*, *Holothuria albiventer*, *H. arenicola*, *H. erinaceus*, *H. moebii*, *H. notabilis*, *H. rigida*, *Lovenia elongata*, *Maretia planulata*, *Mespilia globulus*, *Ophiactis acosmeta*, *Ophiocoma schoenleinii*, *Ophiolepis nodosa*, *Ophiomyxa australis*, *Ophionereis nereidina*, *Parasalenia gratiosa*, *Pentacta quadrangularis*, *Placophiothrix lineocaerulea*, *Pseudocolochirus axiologus*, *Rhynobrissus hemiasteroides*, *Stomopneustes variolaris*, *Tamaria fusca*, *Temnopleurus toreumaticus*.

Of the 19 asteroids recorded from, or (*Anseropoda rosacea, Tamaria fusca*) believed to occur in, Torres Strait (Fig. 3*a*), 4 have not been found to the south. All but 1 of the remainder occur to at least lat. 20° S., 10 still further to the biogeographical boundary at about lat. 25° S., and 3 into New South Wales waters. There are 5 asteroids endemic to the Port Curtis region and 1 to the Lindeman I. area, and 1 has been taken only from the vicinity of Lizard I. In addition *Pentaceraster australis* appears to be confined to the area between Lizard I. and Moreton Bay, *Goniodiscaster integer* to that between Lindeman I. and Moreton Bay, and

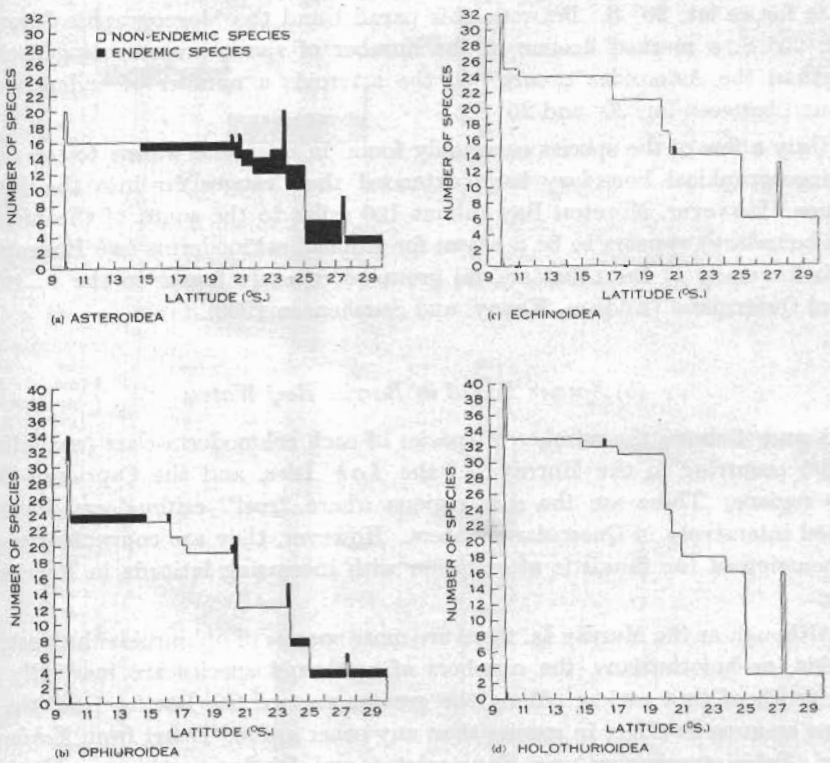

Fig. 3.—Distribution of mainland echinoderm species with latitude.

Nepanthia belcheri to the region between Yeppoon and Port Jackson, N.S.W. The last-named may be a southern species.

Of the ophiuroids, 34 species probably occur in Torres Strait (Fig. 3*b*); 24 of these have extended their ranges to the south. At lat. 20° S. 19 are represented but at the biogeographical boundary at lat. 25° S. only 7 occur. Several ophiuroids seem to be endemic to certain restricted localities along the coast. *Ophiothrix acestra* ranges from Port Curtis to Port Jackson, N.S.W., and is possibly a Peronian species which has extended its range to the north of the biogeographical boundary.

Of the 32 echinoids which have been recorded from or thought to occur in Torres Strait, 7 have not been recorded to the south, 19 extend southwards along

the Queensland coast, and the remaining 6 range south along the New South Wales coast (Fig. 3*c*). Only 1 species, *Asthenosoma intermedium*, seems to be endemic to mainland waters.

Holothurians are well represented in Queensland mainland waters (Fig. 3*d*). A total of 40 species probably occur in the Torres Strait region, 31 of these range as far south as lat. 20° S., and 16 occur in Moreton Bay. Only 3 species, however, range into New South Wales waters.

In general it would appear that the majority of echinoderm species occurring in eastern Queensland mainland waters range from Torres Strait southwards at least as far as lat. 20° S. Between this parallel and the biogeographical boundary at lat. 25° S. a marked decline in the number of species representing each class other than the Asteroidea occurs. Of the asteroids a number of endemic species are found between lat. 20° and 25° S.

Only a few of the species commonly found in mainland waters to the north of the biogeographical boundary have extended their ranges far into the Peronian Province. However, Moreton Bay (about 100 miles to the south of the biogeographical boundary) appears to be a haven for tropical echinoderms (see Endean 1953) as it is for many of the other animal groups commonly found on the coastline of tropical Queensland (Endean, Kenny, and Stephenson 1956).

(*b*) *Species Found in Barrier Reef Waters*

Figure 4 shows the number of species of each echinoderm class (excluding the crinoids) occurring in the Murray Is., the Low Isles, and the Capricorn–Bunker Group regions. These are the sole regions where "reef" echinoderms have been collected intensively in Queensland waters. However, they are conveniently placed for discussion of the faunistic attenuation with increasing latitude in Barrier Reef waters.

Although at the Murray Is. there are more species of ophiuroids than asteroids, echinoids, or holothurians, the numbers of ophiuroid species are markedly fewer to the south of that region. Along the greater part of the Barrier Reef the holothurians seem to be richer in species than any other group. Apart from *Echinometra mathaei*, *Echinostrephus molaris*, *E. aciculatus*, and *Diadema setosum*, echinoids are not well represented in Barrier Reef waters.

Of the 25 asteroids found at the Murray Is. (Fig. 4*a*) 11 range along the entire length of the Barrier Reef and 6 to the vicinity of Low Isles, whilst 8 (4 of which seem to be endemic) do not appear to range south. *Nardoa rosea* seems to be endemic to the Barrier Reef area. *Asterina nuda* has been recorded only from the Murray Is. and Caloundra. As Caloundra is south of the Barrier Reef area, this species is considered to range along the whole length of the Great Barrier Reef. *Tosia queenslandensis* has been recorded only from Low Isles and the Capricorn Group. *Disasterina leptalacantha* and *Tegulaster emburyi* appear to be confined to the Capricorn Group. *Ophidiaster watsoni* has been recorded only from the Capricorn Group and from Lindeman I.; and although *Anseropoda rosacea* has been recorded only from Fraser I. and the Capricorn Group, it occurs in waters to the north of Australia and presumably

extends right along the Queensland coast north of lat. 25° S.; but whether as a reef or a mainland species or as one common to both environments is not known. It has been omitted from Figure 4*a*.

Of interest is the occurrence of the Peronian asteroid *Ophidiaster confertus* at the Capricorn Group, since this appears to be the only instance of a Peronian species extending its range into Barrier Reef waters.

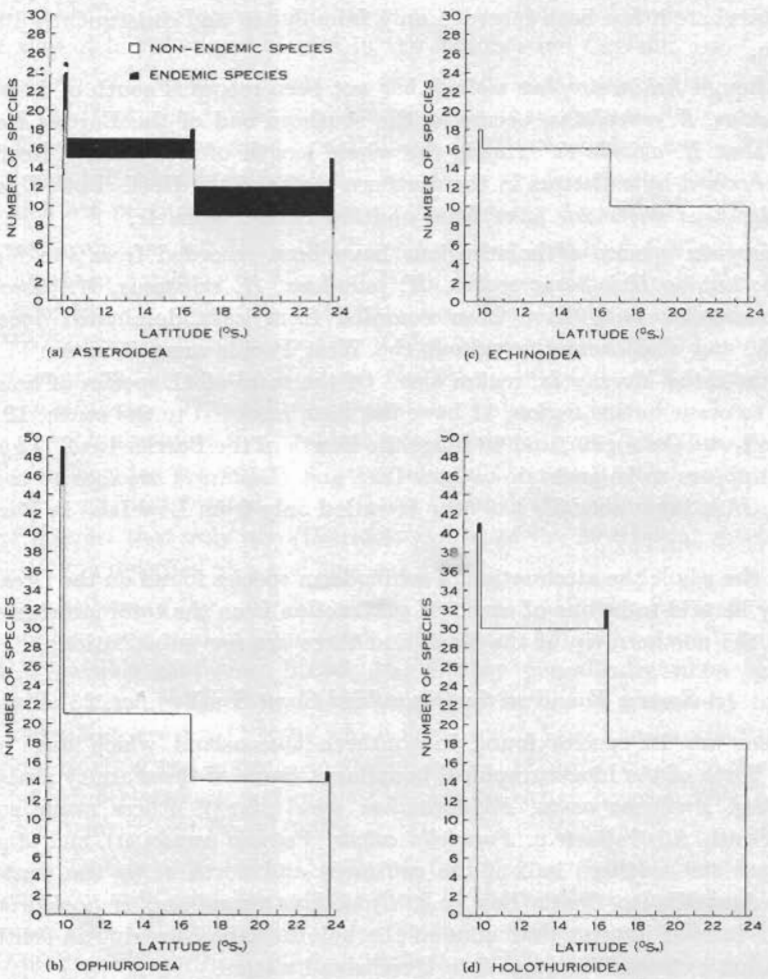

Fig. 4.—Distribution of reef echinoderm species with latitude.

Attenuation with increasing latitude is particularly marked in the ophiuroids (Fig. 4*b*). Of the 49 species of ophiuroids occurring at the Murray Is. (it is assumed that *Ophiomyxa australis* occurs there) only 14 appear to range the length of the Barrier Reef. Seven range south to the vicinity of Low Isles and 18 (4 of which are endemic) have not been recorded south of the Murray Is. *Ophionereis tigris* appears to be endemic to the Capricorn Group.

Eighteen echinoids are believed to occur at the Murray Is. (Fig. 4*c*). (*Prionocidaris verticillata, Laganum depressum*, and *Metalia sternalis* are assumed to occur in the Murray Is. region since they occur south of that region, in Barrier Reef waters, and also occur to the north.) Of these 18 species, 2 are not found south of the Murray Is., 6 range as far south as the Low Isles region, and 10 range the length of the Barrier Reef.

Nudechinus multicolor has been recorded in Australian waters only from Low Isles. Elsewhere it has been recorded only from Japan and consequently its range is uncertain.

Although *Echinostrephus molaris* has not been recorded south of Low Isles, an allied species, *E. aciculatus*, occurs at the southern end of the Barrier Reef. It is possible that *E. aciculatus* extends the whole length of the Barrier Reef but has been overlooked by collectors in the northern sector of the Reef. Both *E. aciculatus* and *Nudechinus multicolor* have been omitted from Figure 4*c*.

Thirty-six species of holothurians have been recorded from the Murray Is. (Fig. 4*d*); but as *Holothuria scabra, H. paradoxa, H. erinaceus, H. fusco-olivacea*, and *Chondrocloea recta* have been recorded from coral-dominated localities to the south, and also occur throughout the West Pacific area, it is considered that they occur in the Murray Is. region also. Of the total of 41 species of holothurians believed to occur in this region, 11 have not been recorded to the south, 12 range as far as the Low Isles region, and 18 range the length of the Barrier Reef. *Phyllophorus trapezus* appears to be endemic to Low Isles and *Holothuria axiologa* to the Murray Is., while *Holothuria notabilis* has been recorded only from Low Isles in Barrier Reef waters.

On the whole the attenuation of echinoderm species found on the Great Barrier Reef may be said to be one of constant subtraction from the total number of species found at the northern tip of the Reef, and there are few substitutions.

(*c*) *Species Found on the Queensland Coast South of Lat.* 25° *S.*

There are 12 species found in southern Queensland which have not been recorded north of the biogeographical boundary. Some of these are typical Peronian species (e.g. *Anthenea acuta, Phyllacanthus parvispinus*), others range south and west to South Australia (e.g. *Patiriella calcar, Petricia vernicina*), and others occur right round the southern half of the continent and north along the west coast of Western Australia to Shark Bay (e.g. *Ophiothrix caespitosa, Heliocidaris erythrogramma*). It is of interest that none of the holothurians occurring in south-eastern Australia has extended its range into Queensland waters.

As mentioned earlier, a few tropical echinoderms found commonly at mainland localities range south well into the Peronian Province. Most of these, however, occur only in Moreton Bay. Thus of the 35 species recorded from Moreton Bay, 6 are tropical species which occur as far south as Port Jackson, N.S.W., whilst 24 are tropical species which have not been found elsewhere in the Peronian Province. Of the remainder, 2 probably occur right round Australia, 2 are probably southern species which have extended their ranges to the north of the biogeographical boundary, and 1 is apparently a southern species.

As southern species predominate in oceanic waters encircling Moreton Bay it would appear that a set of ecological factors operates within Moreton Bay which favours tropical species and excludes most southern species. The average summer temperature of the water over the shallow flats is presumably a critical factor (see Endean, Kenny, and Stephenson 1956).

The Moreton Bay population appears to be an isolated one and might be expected to exhibit some degree of incipient speciation. However, this is not the case, presumably because gene interchange with northern echinoderm populations occurs by way of larval stages carried in the Notonectian Current.

This warm current is a branch of the Pacific south equatorial current and impinges on the Queensland coast near Fraser I. It then veers to the south, passing down the New South Wales coast (see Halligan 1921). According to the "Australia Pilot", Volume III (British Admiralty 1950), there are frequently eddies from this current which set northward in inshore waters notably near Moreton Bay.

The occurrence of *Asterina nuda*, *Holothuria atra*, and *H. difficilis* at Caloundra (near the northern entrance to Moreton Bay), but not elsewhere in the Peronian Province, is of interest. These species have been found only in reef waters to the north of the biogeographical boundary. Other species found at Caloundra which are also common on the Barrier Reef are *Holothuria leucospilota*, *H. impatiens*, and *Discucumaria africana*. These three species also have not been found in Moreton Bay. It is possible therefore that tropical species occurring at Caloundra prefer fully saline, fully oxygenated sea-water. Fluctuations in the salinity and oxygen tension of the water must be tolerated by northern echinoderms found in Moreton Bay; and it is of interest that only one (*Chiridota rigida*) of the 29 tropical species found in Moreton Bay is recorded as a reef species.

As the numbers of the northern species found at Caloundra fluctuate considerably from year to year, and in some years some species appear to have been entirely absent, it is possible that they invade the locality periodically when conditions are favourable. Presumably their larval stages are carried to Caloundra by eddies from the warm Notonectian Current which flows south from the Capricorn–Bunker Group region, skirting the eastern Australian coast. Likewise many of the tropical echinoderms found elsewhere in Peronian waters appear to be periodic invaders as was noted by Bennett and Pope (1953).

Thus in Queensland waters south of the biogeographical boundary, both northern and southern species occur but most of the northern species are confined to the Moreton Bay–Caloundra area. A few northern species range well into Peronian waters. However, no southern species (with the possible exceptions of *Nepanthia belcheri* and *Ophiothrix acestra*, mentioned earlier) has invaded mainland waters north of lat. 25° S., and only one southern species (*Ophidiaster confertus*) occurs also in reef waters.

(*d*) *Species Found at Lord Howe Island*

Of the 48 non-endemic echinoderm species found at Lord Howe I. (lat. 31° 33′ S., long. 159° 5′ E.) 41 have now been recorded from Queensland waters; 36 of these occur in southern Queensland.

It has been postulated that the Notonectian Current was responsible for bringing the larval stages of these species to the island (Endean 1953). In this respect it is significant that most of the common species at Lord Howe I. are common in southern Queensland but are not found on the nearby New South Wales coast. Indeed only two (*Coscinasterias calamaria* (Gray) and *Ophiactis resiliens* Lyman) of these common species are common in New South Wales waters and not yet recorded from southern Queensland.

V. Zoogeographical Affinities of Tropical Australian Echinoderm Fauna

(*a*) *Queensland Fauna*

(i) *Mainland Species.*—A group of 12 species occurring in southern Queensland but not extending their range north of the biogeographical boundary at about lat. 25° S. is omitted from subsequent discussion. These species are Peronian or Peronian and Flindersian with the centres of their distributions to the south. Such species have made a negligible contribution to the fauna north of lat. 25° S.

The range of *Paracaudina australis* is not known with certainty and it too is excluded. Species endemic to the Queensland mainland and species occurring north of lat. 25° S. which are endemic to eastern Australian waters (21 in all), together with 5 species which probably range right around Australia, are also omitted.

The following is an analysis of the occurrence of the 79 remaining species.

Occurrence	Recorded on Australian Coast West of Torres Strait	Not Recorded on Australian Coast West of Torres Strait
Endemic to tropical Australia	21	—
East Indies	25	13
West Pacific	1	1
East Indies and West Pacific	10	8
Total	57	22

It can be seen that the bulk of the 79 species listed have been recorded in Australian waters to the west of Torres Strait. Of the 22 species not recorded west of Torres Strait 21 occur in the East Indies and only 8 of these also occur in the West Pacific Ocean. It is probable therefore that the majority of these 21 species will be found between the Aru Is. and Torres Strait when the echinoderm fauna of that region becomes better known.

Also it will be noted that the bulk of the non-endemic species listed occur in the East Indies. Moreover the nearest relatives of most of the 21 species endemic to tropical Australia (and also of those endemic to Queensland mainland waters) occur commonly in the East Indies (e.g. species belonging to the genera *Astropecten*, *Goniodiscaster*, *Nepanthia*, *Placophiothrix*, *Salmacis*, and *Pentacta*).

Since relatively few of the species listed occur in waters to the east of New Guinea, it would appear that Torres Strait is the principal exchange route used by mainland echinoderms common to Queensland and northern Australia and by those common to Queensland and the East Indies.

It is possible that exchange of mainland species common to Queensland and the East Indies could occur via the northern and eastern shores of New Guinea. However, deep water is found immediately offshore along the northern coast of New Guinea and as both the Mamberamo and Sepik Rivers pour out continually large volumes of fresh water into this area it would seem that there exists a barrier to the spread of littoral echinoderms generally in northern New Guinea waters.

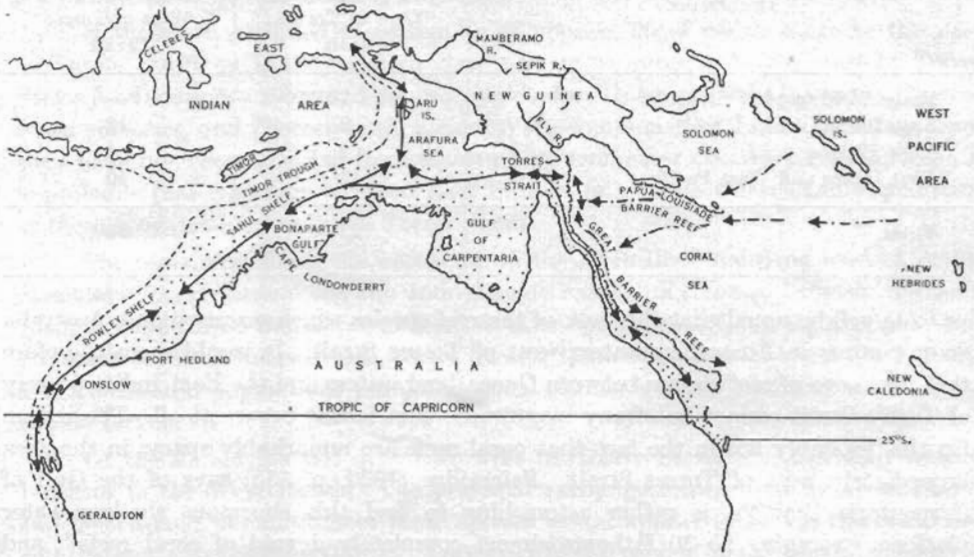

Fig. 5.—Exchange routes used by echinoderm species in tropical Australia. The Tropical Australian Province is stippled.

——➤ Routes used by mainland species.

—·—➤ Routes used by reef species.

Also in south-eastern New Guinea there appears to be a dearth of suitable habitats for mainland echinoderms. Indeed the Papua-Louisiade Barrier Reef and numerous fringing reefs along the south-eastern coastline probably constitute an additional barrier to the movements of mainland species.

On the other hand there is a shallow-water communication between Torres Strait and the East Indies via the west coast of New Guinea and the Aru Is. (see Fig. 5) which could be utilized by the majority of mainland echinoderms.

The spread of Queensland mainland species to the West Pacific area is probably prevented by the fact that Queensland is separated by the deep waters of the Coral Sea from the Solomons, the New Hebrides, and other West Pacific localities. In this connexion it should be noted that echinoderms which are strictly littoral have a limited bathymetrical range and Clark (1921) maintains that they rarely extend into water deeper than 30 fm.

It is possible that species possessing prolonged larval stages could cross deep water as a result of larval transit by currents. However, currents in the Coral Sea area move towards the Queensland coast, not away from it.

(ii) *Reef Species.*—Of the total Queensland echinoderm fauna 94 or 35 per cent. are regarded as reef species, and 15 of these are endemic to eastern Australian waters.

The following is an analysis of the occurrence of the remaining 79 species.

Occurrence	Recorded on Australian Coast West of Torres Strait	Not Recorded on Australian Coast West of Torres Strait
Endemic to tropical Australia	7	—
East Indies	2	12
West Pacific	1	4
East Indies and West Pacific	13	40
Total	23	56

It will be noted that the bulk of the reef species which occur outside Australia do not occur in Australian waters west of Torres Strait. It would seem therefore that exchange of reef species between Queensland waters and the East Indies by way of Torres Strait cannot be of any magnitude, if in fact it occurs at all. The reason for this probably lies in the fact that coral reefs are remarkably sparse in the area immediately west of Torres Strait. Fairbridge (1950, p. 335) says of the Gulf of Carpentaria that "it is rather astonishing to find this enormous shallow water platform averaging 25–30 fathoms almost completely devoid of coral reefs", and (p. 375) that "in the Gulf of Carpentaria . . . much muddy sediment is carried down by the larger rivers of tropical Queensland. This mud and other concomitant factors have largely inhibited coral growth here".

Likewise in southern New Guinea large quantities of fresh water and silt are poured out from coastal rivers such as the Fly River, and coral growth in the region is thereby inhibited. Apparently then there is an ecological barrier to the spread of reef forms to the west of Torres Strait.

Accordingly specific exchange of Queensland and Indo–West Pacific echinoderms must occur chiefly by way of eastern New Guinea and the Coral Sea.

It is doubtful whether adult littoral echinoderms can spread along the northern New Guinea coast as noted earlier. Also there do not appear to be any records of the occurrence of coral structures in this region. Consequently it would seem that reef echinoderms are not well represented in the region if indeed they occur at all. On the other hand reef echinoderms could occur on the Papua-Louisiade Barrier Reef in the waters of south-eastern New Guinea.

Since New Guinea and the Great Barrier Reef are both separated by deep water from localities in the West Pacific area, it would seem that there can be no

exchange of Queensland and Indo–West Pacific species via the Coral Sea route. However, the pelagic young of the West Pacific species could use this route, since in the Coral Sea area a branch of the Pacific south equatorial current, which has passed between the Solomon Is. and the New Hebrides, impinges on the Great Barrier Reef (for seasonal current charts see Endean, Kenny, and Stephenson 1956). It is noteworthy that there can be no movement of Queensland species in the reverse direction, and that gene flow between West Pacific and Queensland populations of various species is unidirectional.

(iii) *Species Occurring in both Reef and Mainland Waters.*—Of the 55 species found both in Barrier Reef and in mainland waters 2 are endemic to tropical Australia, 3 are endemic to Queensland, 1 is a southern form, and 1 occurs right round Australia.

If these are excluded there remain 48 species, 25 of which range to the west of Torres Strait on the Australian coast. Of those ranging to the west of Torres Strait 5 (*Anseropoda rosacea, Tamaria megaloplax, Ophiarachnella infernalis, Temnotrema siamense,* and *Discucumaria africana*) are common East Indian species. Since they have not been recorded from eastern New Guinea or the West Pacific Ocean it is probable that exchange between East Indian and eastern Queensland populations of these species occurs only via Torres Strait.

The remaining 20 species occurring on the Australian mainland west of Torres Strait are found throughout the Indo–Pacific region. Exchange between northern Australian and East Indian populations of these species with Queensland populations no doubt occurs principally via Torres Strait. Gene exchange between West Pacific and Queensland populations probably occurs also as a result of transit of the Coral Sea by larvae.

Of the 23 species not occurring west of Torres Strait in Australian waters, 18 occur in the West Pacific. The principal exchange routes used by West Pacific and Queensland populations of these species would appear to be via the Coral Sea and the east coast of New Guinea. Transport of the pelagic larval stages by currents would again be involved here. The 5 remaining species occur in the East Indies but not in the West Pacific, and will probably be found between Torres Strait and the Aru Is.

(*b*) *Northern Australian Fauna*

If the echinoderm fauna of the region between the Gulf of Carpentaria and Geraldton is examined, using as a principal source of information Clark's (1946) monograph, it will be found that 222 well-authenticated species (belonging to 110 genera) of shallow-water echinoderms (excluding crinoids) occur in this region. Six of these occur right round Australia and are excluded from subsequent discussion.

Of the remaining 216 species, 86 are apparently endemic to the region—particularly to the coastline near Broome—and an additional 30 are endemic to Australia. Of the remainder, 98 occur in the East Indies but only 44 of these occur also in the West Pacific. Two occur elsewhere only in the latter area. Most of the endemic species belong to genera which are common in the East Indies (e.g. *Anthenea, Astropecten, Goniodiscaster, Archaster, Protoreaster, Nepanthia, Macrophiothrix, Ophiactis, Salmacis, Nudechinus, Pentacta, Thyone*).

It would appear therefore that the echinoderm fauna of tropical Australia west of Torres Strait has stronger affinities with the fauna of the East Indies than with that of any other outside geographical area.

Also, the tropical Australian fauna of the region west of Torres Strait is closely allied to that of Queensland waters. Of the 216 tropical Australian species recorded from the region west of Torres Strait, 107 occur in eastern Queensland waters, comprising 57 mainland species, 23 reef species, and 27 common to both environments. Whilst some of these species do not occur west of Darwin the great majority range west to north-western Australia and many as far as the Shark Bay region on the west coast of Western Australia.

The East Indies are separated from north-western Australia by the Timor Trough, which is over 1000 fm deep (see Fig. 5). This must provide a barrier to the direct exchange of littoral echinoderms between the East Indies and north-western Australia as it has for long in the case of terrestrial animals (Wallace 1869; Mayr 1944*a*). There is the possibility that the pelagic larval stages of some echinoderms could cross this barrier, but in the Timor Trough area the currents move to the west (see Royal Netherlands Meteorological Institute 1949). The only shallow-water communication between Australia and the East Indian region is along the west coast of New Guinea past the Aru Is., and this must be the principal exchange route utilized by mainland species common to the East Indies and tropical Australia. Some echinoderms, either because their bathymetrical range is very restricted or because they are adapted to ecological conditions peculiar to the region they inhabit, appear not able to traverse this shallow-water route. Consequently a number of endemic species occur in northern Australian waters.

There is the further difficulty that several reef species occur in north-western Australia. In this connexion it should be noted that on the coastline of north-western Australia there are regions where rocks and terrigenous sediments predominate and others where corals are commonly found. Fringing reefs are common between Cape Londonderry and Lagrange Bay, between Port Hedland and Onslow, and in the Abrolhos further to the west (Fairbridge 1950). It is in such regions that reef species occur.

It has already been noted that there is a dearth of coral structures immediately to the west of Torres Strait and that it is unlikely that reef species can pass in either direction through this region.

Of possible significance with respect to the exchange of reef species between the waters of north-western Australia and those of the East Indies is the occurrence of a series of reef platforms and atolls along the margins of the Sahul Shelf and the Rowley Shelf (Teichert and Fairbridge 1948; Fairbridge 1950). Also near-shore reef platforms are of common occurrence in the region. These atolls and reef platforms could provide stepping stones for exchange of reef species found in the East Indies and north-western Australia.

It is significant in view of the above that only one reef species common to Queensland and north-western Australia has not been recorded from the East Indies.

VI. The Apparent Origin of the Fauna of Tropical Australia

There is evidence that during the Palaeozoic and Mesozoic Eras the Australian continent extended much further north and east than it does to-day. Abendanon (1919) postulated a Palaeozoic continent stretching from Tasmania to the Celebes, and Fairbridge (1953) has summarized palaeogeographic and zoogeographic data which indicate that much of northern Australia and its continental shelf "formerly extended far to the north-west, including the northern Molluccas, in Mesozoic times and possibly reaching to the Celebes in the late Palaeozoic" (p. 29).

During the Mesozoic too, the available evidence suggests that the Australian continent extended out into the Pacific Ocean well beyond its present limits—possibly as far as the Marshall Line (see Fig. 5)—although there were apparently occasional transgressions by the sea during this and the preceding era (see Benson 1923, 1924; Bryan 1944).

Fairbridge (1953) noted that during the Permian and Triassic periods the geosynclinal evolution of the Timor-Banda arc caused the sea to encroach on the old continent. Benson (1923, 1924) postulated that this geosyncline extended during the Trias around New Guinea to New Caledonia and New Zealand, thereby disrupting the old continent.

Mayr (1944*a*), on zoogeographical grounds, followed Kuenen (1935) in believing that there were continental connexions between the East Indies and Australia until the early Eocene, but that from the Eocene to the early Pleistocene there was complete separation of these two regions. Thus by the beginning of the Tertiary the relation of the Australian land-mass to the seas around it was probably much as at present, and Indo-Pacific echinoderms were given the opportunity to invade what appears to have been a virgin region in northern and north-eastern Australia.

Clark (1921) postulated that when, as a result of the depression of land areas to the east of New Guinea, what is now the Coral Sea became linked with the Pacific Ocean (see Hedley 1909) an influx into Queensland waters of Pacific echinoderms already present on the north-eastern shores of the old continent occurred. This influx he believed gave rise to a major part of the Queensland fauna, "not only of the Murray Is. and Barrier Reef, but of the coast of tropical Queensland as well" (Clark 1921, p. 209).

Clark also maintained that when the Indian Ocean and the Coral Sea became united by the formation of Torres Strait, a migration of East Indian echinoderms present in northern Australian waters occurred. Many of the migrating species passed eastward and southward "to mingle on the Queensland coast with the species of the Pacific Influx" (Clark 1921, p. 212). Thus according to Clark the present-day echinoderm fauna of the eastern Australian coast is a result of the mixing of the Pacific influx with the Torres Strait migrants. Of these two introductions he believed that the former was the more important.

Unfortunately there is a lack of Tertiary sediments from Queensland waters, as would be expected, and palaeontology can therefore throw no light on early migrations to this region. Apparently, however, many of the invading echinoderms extended their ranges to south-eastern Australia. Barraclough Fell (1953, p. 254)

noted that the "Australian and New Zealand Tertiary echinoderm faunas show marked similarities throughout those portions of the stratigraphical record represented by comparable deposits on either side of the Tasman Sea", and that these faunas had a common origin in the Indo-Pacific.

Clark (1921) believed that the early echinoderm migrants were the ancestors of the present echinoderm fauna of the Queensland coast. However, these early species could not have been the immediate ancestors of the present ones. Despite the paucity of endemic genera in this region today, such genera originated in mid-Tertiary times in or near Australasia, and there is evidence that a northward migration occurred as pointed out by Barraclough Fell (1953). This author also noted that in the late Miocene a great extinction of the old echinoderm fauna occurred. Other marine groups suffered a similar fate (Fleming 1949). Both authors attribute this occurrence to a cooling climate. Subsequently in the Pliocene, a new Indo-Pacific stock entered eastern Australian waters.

Thus the available evidence indicates that the present Queensland echinoderm fauna is derived from a recent Indo-Pacific stock.

As noted earlier, zoogeographical evidence indicates that from the Eocene to the Pleistocene there were no land barriers to the migration of marine organisms round tropical Australia. This poses two problems:

(*a*) Since no barriers were present, there would be little likelihood of populations becoming isolated for a sufficient length of time for mutations to accumulate and so give rise to the region's present-day endemic species.

(*b*) There are over twice as many endemic species in the tropical waters of Australia west of Torres Strait as in eastern Queensland waters, and yet northern Australian waters are in direct contact with an outside geographical area and have been, apparently, since the Eocene. Clark (1921) accounts for the large number of endemic forms in north-western Australian waters by postulating (p. 209) that whilst "New Guinea and Australia were still united as one land mass, a bay of the Indian Ocean lay to the north-west of what is now Torres Strait", and that "the echinoderms occupying the southeastern shores of this bay or sea formed the first echinoderm fauna of Australia". This fauna, Clark believed, still forms a large part of the fauna of northern Australia west of Torres Strait.

However, if, as zoogeographical and geological evidence indicates, Australia was separated from the East Indian region as early as the Eocene period then it is apparent that these early species could not have been the immediate ancestors of the region's present-day species. As mentioned earlier, a number of genera have appeared in the Australasian region since the Eocene, many of these having reached Australia via the East Indian region, and some having originated in Australasia and migrated northwards. Moreover there is the question of the age of species to be considered. Ekman (1953) postulates that the average age of species belonging to the crinoids, decapod crustaceans, and sea urchins is at most 4 to 6 million years. He also notes (p. 29) that a period of a million years was "sufficient for a fairly large number of animal species to undergo changes of a magnitude which differentiated them as new species".

Accordingly it is necessary to examine the recent (Quaternary) history of tropical Australia if light is to be thrown on the present-day specific composition of the echinoderms in the area. A study of probable conditions in the area during the Pleistocene ice ages is especially useful.

During the Pleistocene, eustatic lowerings of sea-level occurred with a minimum fall of 50 fm (Daly 1934; Zeuner 1945; Fairbridge 1950). This was more than sufficient to link New Guinea to Australia. (Fairbridge (1953) states that an emergence of less than 10 fm would provide a bridge from New Guinea to Australia.) Thus a major biogeographical barrier to the dispersal of echinoderms around tropical Australia was set up. Moreover it is probable that the climate on the two sides of this barrier differed. Thus Mayr (1944*b*) and Gentilli (1949) state that possibly north-western Australia had an arid climate during this period, whilst Stanley (1928) maintained that it was only in the warmer northern half (north of lat. 17° S.) of the present Barrier Reef area that coral reefs could be expected during the Pleistocene.

The closure of Torres Strait would separate echinoderm stocks on either side. Populations of mainland species on opposite sides of this barrier could then diverge genetically, provided of course there was no direct contact between these populations via northern New Guinea. There is no evidence that such contact existed. On the contrary it is likely that barriers to the movement of marine species round north-western New Guinea were set up in the East Indies during the Pleistocene falls in sea-level.

It would be expected that, if the above hypothesis is substantially correct, mainland species would evolve east of Torres Strait which would have marked affinities with the East Indian or northern Australian species from which they were derived.

Of the Sahul Shelf area of north-western Australia Fairbridge (1953) remarks that "for long periods during the Pleistocene, the great transverse 'rises' recognised in the regional bathymetry of the Sahul Shelf would have been emergent promontories . . . Most of the depressions on the other hand with their broad shallow bays would seem to favour the development of extensive mangrove swamps, whilst the Bonaparte depression may have been reduced to a swampy lake whenever the sea-level was more than 30-40 fathoms below the present".

Thus in the Sahul Shelf area numerous echinoderm populations could have been isolated—a prerequisite for speciation—and possibly this accounts in large measure for the numerous endemic species found there today.

Subsequently, with the final retreat of the Pleistocene ice caps and the final rise in sea-level that attended this, Torres Strait was reopened, barriers to migration around northern and north-western Australia and probably in the East Indian area to the north were broken down. Echinoderms could once more spread around tropical Australia, extending their ranges southwards as the climate warmed. Some appear to have done so but others seem restricted to short regions of the coastline.

Many species originating in East Indian waters during the Pleistocene could then extend their ranges into Australian waters, and vice versa. Others, possibly because they were adapted to specialized habitats or because their bathymetrical ranges

were restricted, did not spread between the two geographical areas; or, if they did spread initially, populations in the two areas were isolated subsequently by the deepening waters of the post-glacial period. Amongst these would be found many of the species endemic to tropical Australian waters.

Thus in tropical Australia today there should be closely allied species some of which are sympatric (because subsequent to the breakdown of isolating barriers their ranges have overlapped) and others allopatric.

SYMPATRIC SPECIES

Astropecten monacanthus, A. granulatus, A. pulcherrimus Clark
Stellaster incei, S. princeps
Anthenea australiae Doderlein, *A. conjungens* Doderlein
Pentaceraster gracilis, P. australis
Tamaria megaloplax, T. tumescens (Koehler)
Nepanthia variabilis Clark, *N. tenuis* Clark
Nepanthia brevis, N. belcheri
Amphioplus depressus, A. didymus Clark, *A. stenaspis* Clark
Ophionephthys octacantha, O. decacantha Clark, *O. tenuis* Clark
Amphiura microsoma, A. stictacantha Clark, *A. phrixa* Clark, *A. velox* Koehler, *A. bidentata*
Ophiarachnella gorgonia, O. rugosa Clark
Ophiotrichoides martensi australis, O. smaragdina (Studer)
Ophiactis modesta, O. fuscolineata Clark
Salmacis sphaeroides, S. belli
Nudechinus darnleyensis, N. scotiopremnus Clark
Actinocucumis typicus, A. difficilis, A. longipedes Clark
Thyone papuensis, T. micra Clark, *T. buccalis, T. minuta* Clark
Phyllophorus trapezus, P. parvipedes Clark

ALLOPATRIC SPECIES

Archaster typicus, A. laevis Clark
Goniodiscaster pleyadella, G. integer
Anthenea mertoni, A. acanthoides
Protoreaster nodosus, P. nodulosus (Perrier)
Echinaster luzonicus, E. superbus Clark
Phyllacanthus imperialis, P. irregularis Mortensen
Temnotrema bothryoides, T. elegans Mortensen

It may be found that the few characters which distinguish *Goniodiscaster pleyadella* and *G. integer* form parallel clines, and *G. integer* may be merely a variant of *G. pleyadella* which inhabits slightly cooler waters. However, the pairs of allopatric species listed seem generally to inhabit comparable environments. This is also true of most of the pairs or groups of sympatric species mentioned, and it seems a reasonable conclusion that many of them have arisen from geographical isolates which initially diverged genetically during the Pleistocene lowerings of sea-level.

It would be expected that during the Pleistocene ice ages reef species would retreat northwards. Because of the great depth of water between the Barrier Reef and the West Pacific area it is unlikely that populations of species at present common to both areas would have been isolated. As the climate warmed in the post-glacial era reefs would appear in the southern half of the Great Barrier Reef area and gradually reef echinoderms could have extended their ranges southwards.

VII. Limits of Tropical Marine Provinces

It has been shown that the Queensland mainland and Barrier Reef echinoderm faunas are in the main distinct entities, and that the mainland fauna has strong affinities with that of the East Indies whilst the Barrier Reef fauna has strong ties with that of the West Pacific area.

It would seem logical therefore to follow Whitley (1932) in restricting the Solanderian Province to the Great Barrier Reef area. However, Whitley's proposal that the area inhabited by the fauna of the Queensland mainland inside reef waters north of the Peronian Province be regarded as a separate province, the "Banksian", requires modification. Firstly, the echinoderm fauna of the continental islands must be grouped with the mainland fauna proper (see also Endean, Stephenson, and Kenny 1956). Secondly, it is extremely doubtful whether Torres Strait can be regarded as a natural geographical barrier preventing "Banksian" echinoderms from ranging into the Dampierian Province and vice versa.

Of the 118 mainland echinoderm species found in Queensland waters 12 do not occur north of lat. 25° S. If these be excluded, together with 21 species which are endemic either to Torres Strait or to regions of the coast south of that locality, 1 species (*Paracaudina australis*) whose range is uncertain, and 2 species not found east of the Gulf of Carpentaria, there remain 82 species.

Of these 11 have not been recorded south of Torres Strait but range to the west of that locality on the northern Australian coast or are considered to occur between the East Indies and Torres Strait. Another 7 species range south of Torres Strait in Queensland mainland waters but have not been recorded to the west of Torres Strait in northern Australian waters and possibly do not occur between that locality and the East Indies.

However, to 64 of the 82 species considered, Torres Strait does not seem to present a barrier to migration in either direction. Moreover, echinoderms have not been as intensively collected between Direction I. and Torres Strait, nor in the Gulf of Carpentaria, as in the Torres Strait region. It is probable that some of the echinoderms to which Torres Strait appears to be a barrier have actually extended their ranges through this region.

Thus to Queensland mainland echinoderms generally Torres Strait does not present a major biogeographical barrier. Indeed, there is no evidence that any natural biogeographical boundary exists between Hedley's Dampierian Province and Whitley's Banksian Province. This apparent lack of any major barrier between the faunas of the two provinces indicates that they may be considered a single faunistic unit. Neither Hedley (1904, 1926) nor Clark (1946) separated the Barrier Reef fauna from the Queensland mainland fauna. Very few Barrier Reef species have extended their range through Torres Strait, and presumably this is the basic reason why these authors placed the boundary between the Dampierian and Solanderian Provinces at Torres Strait.

On the other hand, one of the basic requirements for the fauna of a geographical area to be classed as an entity distinct from those of adjoining areas is that it should possess endemic forms. The more endemic species it possesses the more distinct it

is from other areas. A high degree of endemism characterizes the echinoderm fauna of north-western Australia, but it remains to be seen whether this is more apparent than real. A number of species previously thought to be endemic to north-western Australia have been found in Queensland in recent years.

Another mode of delimiting faunistic provinces is based on changes in the degree of dominance exhibited by members of a group of species found along a strip of coast. Stephenson (1948, p. 213) remarks that in some cases "the mixture is so obvious and covers such a long strip of coast that the area which it occupies is recognizably distinct from neighbouring areas, even if it has few or any endemic forms". In such cases the fauna of adjacent faunistic provinces would overlap considerably and the line of demarcation between these provinces would not be sharply defined.

For many of the echinoderms and other marine invertebrates of northern Australia, the full extent of individual ranges of species and the degree of dominance possessed by each species are not known.

It is possible that, if the recent histories of the marine fauna of north-western Australia and that of Queensland have differed, as postulated in Section VI, a line of demarcation between the Dampierian and Banksian Provinces can be drawn in the waters of northern Australia. The apparent high degree of endemism exhibited by echinoderms in north-western Australia strengthens this possibility. However, the question of existence of a faunistic boundary in northern Australian waters awaits resolution by future research. For the present the known distribution of Australia's tropical echinoderms (excluding those belonging to the Solanderian fauna) indicates that they belong to a single Tropical Australian Province.

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