# PART II

# THE RELATIONSHIPS OF THE AUSTRALIAN ECHINODERM FAUNA

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Though it is not to be supposed that our knowledge of the echinoderms of Australia is nearly complete, there is justification for assuming that our further knowledge of the group will not greatly alter conclusions which may now be drawn regarding the origin and relationships of that fauna. Though there are still long stretches of coast, notably between Torres Strait and Darwin, between Darwin and Cape Leveque, around the northwestern corner of the continent, and in the Great Australian Bight, which will prove happy hunting grounds for the marine zoologist, there is no reason to believe that the novelties to be found will be extraordinary.

## The Recent Echinoderms of Australia

Disregarding, for the present, the extinct echinoderms, the first step is obviously to study the composition of the Australian fauna with reference to the four sides of the continent, for the most superficial observation shows striking differences between the echinoderms of the eastern and western coasts and between the northern and southern. It is true that A. H. Clark in his important discussion of the Australian crinoid fauna (1911) considered the fauna of the tropical and subtropical coasts of the continent from Shark Bay on the western coast to Sydney on the east to be a "North Australian Subregion" of the "General Indo-Pacific-Japanese Region," and believed that the remaining coast of the continent "must be subordinated as a daughter division." No doubt this conservative view concerning the Australian marine fauna is largely due to the small number of species involved in Clark's discussion—only 46. Some fifteen years later, Charles Hedley, the well known conchologist of Sydney, published his conclusions based on his knowledge of Australia's marine Mollusca, numbering thousands of species (see "The Australian encyclopedia," vol. 2, 1926, article on Zoogeography). Hedley recognized four "provinces" on the continental coast: the Dampierian on the north, extending from the Abrolhos Islands and Geraldton on the west to Cape York at the northeastern corner of the continent; the Solanderian, extending southward from Cape York to Wide Bay, Queensland, at about 26° S.; the Peronian, from Wide Bay to eastern Victoria in Bass Strait; and the Adelaidean, from Bass Strait westward and northward to Geraldton. Tasmania, except the Bass Strait coast, is designated as Mangean. Objection has been made to his term Adelaidean because that adjective was previously used in a different sense, so

Flindersian has been substituted by Cotton and others for the fauna of the southern continental coasts.

The study of the echinoderm fauna as a whole seems to confirm this suggested grouping and warrants belief that although the proposed areas are not sharply defined but tend to merge where they meet, they are rather well marked by characteristic groups of species. Whether they should be designated as regions or subregions or provinces matters little save for consistency in comparing them with corresponding areas in other parts of the world. If the Australian fauna warrants treating the area as a distinct region, each of Hedley's provinces would be a "subregion," but since some zoogeographers consider Australia a subregion of a larger area including much of the western Pacific, Hedley's choice of the term "province" is to be preferred. For a clear understanding of the echinoderm fauna of the continent it is necessary to consider each of these zoological provinces by itself. It should again be emphasized that species occurring only at great depths (over 500 fathoms or 900 meters) are not considered.

### *The Dampierian Province*

As the fauna of the Dampierian province includes more species than any of the others (290) and is the only one in direct contact with an outside zoological area, it will be desirable to examine it first. The other three provinces are separated by very deep water from any other zoological area. The western limit of the Dampierian province is for the present somewhat arbitrarily set at Geraldton and the neighboring group of islands known as Houtman's Abrolhos, but several characteristic genera and species extend as far south as Rottnest Island and the vicinity of Fremantle. The fauna of Shark Bay, however, is very imperfectly known, and the vicinity of Northwest Cape has not been explored at all for echinoderms. Moreover, the very extensive coastal area west of Darwin as far as Cape Leveque has seen little collecting, and that eastward from Darwin to Cape York is also well-nigh a *terra incognita*. Nevertheless our present knowledge warrants treating this extensive coast line between Cape York and Geraldton as a unit, concerning which the following facts are pertinent: Of the 290 species, only 69 have been taken in the Darwin region, including the Coburg Peninsula; 45 of these occur also in the northern Queensland fauna, but only 3 are found on the coast of New South Wales. These are the ubiquitous *Amphipholis squamata* and *Ophiactis savignyi* and the circumcontinental *Amphiura constricta*. On the other hand, of the 69 species at Darwin, 50 have been taken farther west but only 9 extend their range to the western coast below Geraldton. Of these, 3 are the widespread brittle stars just mentioned as occurring in New South Wales, 2 others are common East Indian ophiurans, 2 more are Australian brittle stars of



wide but as yet ill defined range, and 2 are flat laganids of the genus *Peronella*, which have been found in the East Indies as far north as the Philippines and southern Japan. It is evident, therefore, that although the Dampierian province is worthy of recognition, it merges markedly with the Solanderian on the eastern coast and the Flindersian on the west without very sharp lines of separation. It is characterized well by the following species, which have not been taken east of Cape York or south of Houtman's Abrolhos:

Comanthina belli
Petasometra, 2 species
Stellaster princeps
Gymnanthenea globigera
Asterina coronata fascicularis
Amphioplus depressus
Amphioplus didymus
Ophiactis fuscolineata
Ophiactis modesta
Macrophiothrix scotia
Macrophiothrix belli
Placophiothrix melanosticta
Placophiothrix plana
Lissophiothrix delicata
Ophiotrichoides smaragdina
Ophiurodon cinctum
Phyllacanthus longispinus
Protankyra verrilli

This small group is supplemented by the following species which are essentially of the Dampierian province, but whose range has not yet extended, so far as we know, east of Cape Londonderry. It is of course possible, one might almost say probable, that careful collecting between Darwin and the Port George Mission would reveal many of these western species, of which the following are representative:

Zygometra comata
Monilimetra, 4 species
Astropecten monacanthus
Goniodiscaster australiae
Goniodiscaster acanthodes
Pseudoreaster obtusangulus
Anthenea conjungens
Protoreaster nodulosus
Asterina lutea
Echinaster varicolor
Amphiura phrixa
Placophiothrix lineocaerulea
Ophiocnemis marmorata
Ophionereis stigma
Ophiarachnella rugosa
Cryptopelta callista
Dictenophiura stellata
Arachnoides tenuis
Peronella tuberculata
Echinodiscus auritus

The Dampierian province is thus seen to have a very characteristic fauna of more than 40 species of echinoderms which are not known from the more southern coasts. Their relation to the East Indian fauna will be considered farther on, but it may be mentioned at this point that of the 290 species here regarded as Dampierian, 147, almost exactly half, are endemic in Australia.

### *The Solanderian Province*

The Solanderian province is essentially the Great Barrier Reef area, extending from the Murray Islands in the north to Lady Elliot Island in the south,

but it includes as well, very naturally, the coastal fauna of Queensland from Cape York southward. Just how far south we should place the southern limit is debatable, but as Hedley selects Wide Bay, it is proper to accept his judgment and adopt that locality. It should, however, be mentioned that a few Solanderian species extend their range to the vicinity of Port Jackson and to Lord Howe Island. The majority of the 208 species here regarded as Solanderian are found in the East Indies, only 87 being endemic in Australia. Characteristic echinoderms of this province are the following, chosen because they do not extend their range on the Australian coast west of Cape York or south of Wide Bay:

Goniodiscaster integer
Ogmaster capella
Asterope carinifera
Nardoa pauciforis
Linckia laevigata
Ophidiaster granifer
Ophiotrichoides nereidina
Ophiocoma schoenleinii
Ophiarthrum pictum
Ophiarachna incrassata
Astropyga radiata
Stomopneustes variolaris
Temnopleurus toreumaticus
Salmacis belli
Salmacis dussumieri
Lytechinus verruculatus
Pentacta cucumis
Phyllophorus trapezus
Stichopus chloronotus
Holothuria argus
Holothuria edulis
Holothuria arenicola
Opheodesoma grisea
Synapta maculata
Polycheira rufescens

*The Peronian Province*

The Peronian province is the area between Wide Bay, Queensland, and Hobart, Tasmania, with a bit of the eastern end of the Victorian coast. There is nothing about the echinoderms of Tasmania that warrants the recognition of a Mangean province, distinct from the Peronian and Flindersian, except for a very few species which also occur in New Zealand. If the origin of Bass Strait is quite recent, as is generally accepted, the Tasmanian fauna is just what might be expected at the southeast corner of the continent well below tropical influences. Whether Lord Howe Island should be included in the Solanderian or Peronian province is perhaps more debatable, but on the whole the evidence seems to favor its inclusion in the Solanderian province, as nearly half its echinoderms occur on the Barrier Reef and 10 more are endemic. Only about a dozen are really Peronian, and half a dozen are wide-ranging species not peculiar to any province. All together only 107 species of echinoderms are characteristic of the Peronian province, but of these 82 per cent are endemic in Australia. The others are found also in New Zealand or the East Indies, but are in general species of whose distribution we still lack adequate knowledge. The following species are typical of the Peronian province and give a characteristic facies to the fauna of Port Jackson:

Austrometra thetidis
Ptilometra australis
Anthenea acuta
Asterina inopinata
Patiriella calcar
Paranepanthia praetermissa
Uniophora granifera
Ophiacantha heterotyla
Amphiura multiremula
Amphiura dolia
Ophiocentrus pilosus
Macrophiothrix lampra
Ophiomisidium flabellum
Haplophiura gymnopora
Dictenophiura ctenophora
Phyllacanthus parvispinus
Centrostephanus rodgersii
Holopneustes pycnotilus
Urodemas perspicillum
Taeniogyrus australianus
Scoliorhapis théelii



*The Flindersian Province*

Extending as it does from Hobart, Tasmania, and the eastern end of Bass Strait to Geraldton, Western Australia, and Houtman's Abrolhos, the Flindersian province is of about the same extent as the Dampierian but does not include nearly so rugged or varied a coast line. As in the case of the northern province, there is an extensive area between the eastern and western ends concerning the fauna of which we are still comparatively ignorant. Little indeed is known of the echinoderms of the coast between Port Lincoln, South Australia, and Albany, Western Australia, and although much of it is apparently a sandy waste, there is a considerable area east of Albany that should harbor a fairly rich marine fauna. The echinoderm fauna of the Flindersian province is much smaller than that of the Dampierian, but very much more distinctive. The number of species now known from this southern province is only 166, but of these nearly 89 per cent are endemic in Australia. Most of these have not yet been taken on all the coasts of the Flindersian province, but they may fairly be looked for anywhere along the coast between Port Phillip and Fremantle.

In December 1942, an important paper on the "Echinodermata of the Flindersian Region, Southern Australia," by Bernard C. Cotton and Frank K. Godfrey, appeared (see bibliography). This list includes 164 species, and the present report includes 166. There is a striking discrepancy, however, as regards the echini, and an equally striking but reversed difference in the tabulation of the holothurians. Cotton and Godfrey include 43 echini, whereas the present report counts only 33 species as Flindersian. This apparent discrepancy is due to these authors' recognition and tabulation of several varieties which do not seem to me valid, and to the fact that I treat as Peronian, Dampierian, or Solanderian a number of species which they have included as

Flindersian. There are, however, 4 species which seem to me unquestionably Flindersian that are omitted by them. As these differences are purely a matter of opinion, they do not in the least lessen the value of their report. As regards the holothurians, the list of 17 species given by Cotton and Godfrey is obviously a compilation, apparently based chiefly on Joshua's work, but it overlooks several of the species which he listed in 1914 and others reported in recent years by other writers. It is not strange, therefore, that the list is incomplete.

The 166 species of echinoderms which characterize the Flindersian province may be grouped in three divisions. First are those which are strictly Flindersian, being found on the coasts of Victoria, South Australia, and Western Australia, but not having been taken as yet east of Bass Strait or north of Geraldton. The following species are typical of this group:

Comatulella brachiolata
Ptilometra macronema
Anthaster valvulatus
Austrofromia polypora
Paranepanthia grandis
Echinaster arcystatus
Phyllacanthus irregularis
Temnopleurus michaelseni
Microcyphus, 3 species
Amblypneustes, 3 species
Holopneustes, 2 species
Protenaster australis
Lipotrapeza vestiens
Holothuria hartmeyeri
Paracaudina tetrapora
Trochodota roebucki

Some 60 species have been found as yet only at the eastern end of the province, on the South Australian coasts, while more than 50 others are known as yet only at the western end and have not been found east of Albany. There are, however, a dozen or more Flindersian species which extend their range eastward into the Peronian province, most of them occurring also in Western Australia. These may well be listed here:

Cenolia trichoptera
Luidia australiae
Astropecten vappa (extends into the Solanderian province)
Pentagonaster dübeni
Tosia australis
Patiriella gunnii
Placophiothrix spongicola
Ophionereis schayeri
Ophiocoma canaliculata
Ophiocoma pulchra
Ophiarachnella ramsayi
Goniocidaris tubaria
Heliocidaris erythrogramma

There are 7 species found still farther to the east in New Zealand waters. Probably these are best considered New Zealand species which have extended their range westward. They are:

Allostichaster polyplax
Ophiactis resiliens
Lipotrapeza dearmatus
Mensamaria bicolumnata
Mensamaria thomsoni
Stichopus mollis
Chiridota gigas



Finally, there are a dozen species with a still wider range, and most of these are no more Flindersian than Peronian or Dampierian. These are:

*Psilaster acuminatus*, a deep-water species, taken off New Zealand, southern Australia, and South Africa.

*Henricia hyadesi*, a South American species; the Henricias from the Great Australian Bight, now listed as *hyadesi*, are almost certainly not that species, but material and data are too scanty to make proper treatment possible.

*Coscinasterias calamaria* ranges from Natal and Mauritius on the west to Lord Howe Island and New Zealand on the east.

*Ophiomyxa australis* is also known from Mauritius and Lord Howe Island. It extends its range northward into the East Indies, but is replaced in New Zealand by an endemic species.

*Amphiura constricta* occurs on all the coasts of Australia and at Lord Howe Island.

*Ophiozonella elevata*, *Ophiomusium simplex*, and *Taeniogyrus cidaridis* are Japanese species reported from Australia, but adequate material for validating these identifications is lacking.

*Fibularia craniolaris* and *Holothuria cinerascens* are East Indian species of ill defined range and equally ill defined specificity.

*Echinocardium cordatum* is nearly cosmopolitan in its distribution, occurring in the northern hemisphere as well as in South Africa, Australia, and New Zealand.

*Leptosynapta dolabrifera* is found not only in the Flindersian province, but in the Peronian and the western part of the Dampierian also. It occurs at Lord Howe Island, but not in New Zealand.

The above analysis of the existing Australian echinoderm fauna brings out the interesting fact that the farther one goes from the Torres Strait region, either south and then west or west and then south, the more endemic and characteristic the fauna becomes, until at the southwestern corner of the continent, between Fremantle and Albany, we have a group of echinoderms of which practically none of the species and very few of the genera occur in the East Indian region. The origin of this fauna is possibly bound up with the geological history of Australia and its past relationships with other land areas, but it is justifiable to point out that this further study of Australian echinoderms confirms the conclusions reached (H. L. Clark, 1921, p. 212) from a critical study of the echinoderms of Torres Strait. It can scarcely be questioned that the Solanderian fauna of Queensland is quite closely related to that of the area northeast of it and is distinctly less endemic (only 42 per cent) than that of any of the other Australian provinces. Further discussion of this interesting matter may, however, be better postponed until the extinct fauna of the Australian continent is considered and the existing faunas of the land masses lying west, north, and east of the continent are critically compared with that of Australia.

## The Extinct Echinoderms of Australia

The inclusion of the extinct echinoderms in this report is not for the purpose of discussing the geological relations of various areas and strata, but solely for the purpose of ascertaining whether they throw any light on the origin or movements of the present-day fauna. The fact that so large a number are from very old rocks and that very few are closely allied to species now living is disconcerting. It makes any use of the data concerning them in discussing the Recent forms hazardous if not futile, and seriously invalidates any conclusions one might hope to draw. Nevertheless it is desirable to formulate such conclusions as we can concerning them, and this can best be done by considering each class by itself.

### *Crinoidea*

Few of the fossil crinoids found in Australia have as yet been collected in sufficient quantity (not to mention quality of preservation) to enable us really to know them adequately from the zoologist's point of view.

In the Silurian rocks of New South Wales and Victoria 4 species are known to occur, but none of them are nearly related to any Recent forms. Some 10 or a dozen more are recorded from Carboniferous or Permocarboniferous rocks, from Queensland to Tasmania but chiefly in New South Wales. Their relationship to any of the Recent species is remote and uncertain. From the Cretaceous rocks of Western Australia have come fragments of individuals of 2 genera (*Marsupites* and *Uintacrinus*) which are widely distributed in the northern hemisphere. They have no near relatives among living crinoids. In the Cretaceous rocks of Queensland, New South Wales, and South Australia, abundant remains occur of a large stalked crinoid which for the present is referred to *Isocrinus*. It is obviously related to the Recent species of *Metacrinus* still living in moderately deep water off the northwestern and southeastern coasts of Australia, but until it is more fully described and figured, it can hardly be considered as in any sense ancestral to them. Obviously, then, our fragmentary knowledge of the extinct crinoids of Australia throws practically no light on the past history of the continent or on the origin and relationships of the present crinoid fauna.

### *Asteroidea*

From the zoologist's point of view the extinct sea stars of Australia are as exasperatingly imperfect and unsatisfactory as the crinoids. Though 17 species have been described and figured to such an extent that it is possible to include them in this report, in some sort of natural relation to the living species, they really throw no light on either the geological or the morphological history



of Australia's sea-star fauna of today. Nearly all are from the Silurian rocks of Victoria, only 3 having been found in the Permocarboniferous rocks of New South Wales. About two-thirds of the species are regarded as Phanerozonia, the remainder being placed in the Spinulosa, but very little of the material is adequate for the basing of positive conclusions. On the whole, the Australian fossil sea stars are of no use to the zoologist who is striving to throw light on either the phylogeny or the geographical distribution of the Asterozoa. As horizon indicators for the geologist they may perhaps be of more service.

### *Ophiuroidea*

The extinct ophiurans of Australia are of little more use to us than the sea stars in an effort to find connecting links between the extinct fauna and that of the present day. Fourteen fossil species are described with reasonable care, and one of these can even be referred to a Recent family. But they are in no sense really connecting links between the far distant paleozoic and the present. The one species referable to a Recent family is from the Mesozoic rocks of Queensland and is referred to the heterogeneous group *Ophiacantha*, but the material is too inadequate to warrant attempting to find in it a connecting link. The remaining fossils are referred to 10 genera in half a dozen or more families (all extinct), but the material is too scanty to justify any positive conclusions as to their relation either to Asterozoa or to one another.

### *Echinoidea*

The number of fossil echini now known from Australia (56) considerably exceeds the number of extinct species of the other four classes combined. Moreover, they are for the most part from far more recent strata, and their relationship to existing species is much more obvious. Only 3 occur in rocks older than the Tertiary, 1 having lived in the Paleozoic and 2 in the Mesozoic. The Paleozoic species (*Archaeocidaris selwyni*) is very old phylogenetically as well as geologically. Extinct since Carboniferous days, it is apparently in no sense ancestral to any part of the present-day Australian fauna. The 2 Mesozoic species have been found on opposite sides of the continent—one, a cidaroid (*Cidaris comptoni*), in Western Australia; the other, a spatangoid (*Micraster sweeti*), in Queensland. The former is very possibly in some sense ancestral to *Stylocidaris* (see p. 281). The latter is too incompletely known to warrant any assertions as to its descendants, but it might possibly have been in the line from which *Brissus* or *Brissopsis* has come.

The 53 Tertiary species are all from the southeastern coastal region of the continent, and it is quite conceivable that some of them are ancestral to some

of the species now living on those coasts. That *Eupatagus valenciennesi* and *Protenaster australis*, for instance, are derived from some of the related Tertiary spatangoids is quite possible, but in the light of our actual knowledge the steps are not yet visible. When the amount and condition of the material enables us to work out the development of such forms, the relation of the Recent to the Tertiary species may be ascertained with a greater or lesser degree of probability. Meanwhile it must be admitted that our knowledge of the extinct forms and of the developmental growth changes of the Recent species is inadequate.

### *Holothurioidea*

No fossils that could reasonably be regarded as the remains of holothurians have yet been found in the rock record of Australia save for the wheel-like spicule found by T. S. Hall in the Bird Rock zone, Spring Creek, Victoria. This spicule is about double the size of the "wheels" occurring in the body wall of the chiridotids now living on the coast of Victoria. But of course we cannot be sure that the species characterized by such spicules is actually extinct, for it may still be living under conditions which make it inaccessible to a collector. Clearly paleontology throws no light on the history of Australian holothurians.

## The Echinoderms of Lands Surrounding Australia[1]

### *Kerguelen*

The nearest land to Australia on the southwest is the desolate island of Kerguelen. Although large, well covered with vegetation, and with many more or less good harbors, it is uninhabited by man. It has been visited and to a great extent explored and mapped by scientific expeditions, and its fauna is fairly well known. The "Challenger" spent about three weeks there and took many echinoderms. Subsequent visitors have taken additional forms, and 70 species are now listed from Kerguelen. No other land mass of importance lies so far south between the Greenwich meridian and 80° E., but Stewart Island, New Zealand, is only about 2° nearer the equator. Directly south of Australia lies only the Antarctic Ocean, the echinoderm fauna of which is now fairly well known. It is, however, entirely lacking in forms characteristic of Australia; for example, of the more than 50 genera of sea stars listed by Fisher (1940) as Antarctic, only 4 occur in Australia, and those are all found in the northern hemisphere also. Obviously the Antarctic echinoderms have played little or no part in the development of the Australian fauna.

This is equally true of the echinoderms of Kerguelen. Only 1 of them has

[1] Species occurring only at great depths (500 fathoms or 900 meters or more) are not considered.



ever been reported from Australia, and that is almost certainly wrongly identified. Joshua and Creed (1915) record a single specimen of a *Cucumaria* from Encounter Bay, South Australia, as *C. squamata* Ludwig, itself known from only a single small specimen collected at Betsy Cove, Kerguelen. Without more material or at least without actual comparison of specimens, we cannot admit this Kerguelen holothurian to the Australian fauna (see p. 389). *Promachocrinus*, the characteristic crinoid of Kerguelen, is not known from Australia. Six genera of sea stars occur in Australia and also in Kerguelen, but 5 of these are well-nigh cosmopolitan, and the Australian member of the sixth (*Smilasterias*) is of very dubious status. The situation is virtually the same as regards the ophiurans, and none of the Kerguelen genera of echini occur in Australia. It is proper, therefore, to say that there is nothing in common between the echinoderms of Australia and those of Kerguelen.

### *Mauritius*

Far to the north of Kerguelen and somewhat to the west lies the island of Mauritius. With its neighbors, Rodriguez and Réunion, it makes up the next nearest land mass to Australia, on the west, south of 10° S. The echinoderm fauna of Mauritius is remarkably well known, thanks principally to the industry of M. V. Robillard as a collector and of P. de Loriol as the zoologist who not only provided the stimulus for the work, but carefully described the material collected. There have been also a few other collectors and students to whom marine zoologists are indebted for our present knowledge of the echinoderm fauna of the island. This fauna consists of rather more than 150 species; some of these are perhaps invalid, but no doubt others are as yet unrecognized. Comparison of this fauna with that of Australia reveals the following noteworthy facts. From Mauritius, 7 species of crinoid are known, each representing a different genus. All these genera occur in Australian seas, but in every case the Mauritian species is different from the Australian. Moreover, each of the Mauritian crinoids belongs to a genus which is fundamentally East Indian, ranging from the Red Sea along the southern coast of Asia to southern Japan on the north and to the Tonga Islands on the southeast. Most of the Mauritian species occur in Madagascar and several are found on the African coast either southwestward toward Natal or northwestward to the Red Sea.

The Asteroidea are better represented in Mauritius, at least 35 species, in 23 genera, being reported from the island. Of these a dozen occur also in Australia, and their occurrence in Mauritius is therefore of importance. But 9 of the 12 are widespread in the Indo-Pacific region and may properly be considered East Indian species. Of the other 3, *Linckia guildingii* is practically tropico-

*politan, and its occurrence in Mauritius is not surprising. More puzzling is the case of Leiaster leachii,* which occurs at Lord Howe Island as well as at Mauritius. It is highly probable that this species occurs throughout the East Indian *region,* but it is very secretive in its habits and few specimens have been collected. Lastly we have the remarkable case of *Coscinasterias calamaria,* which occurs on the South African coast, at Mauritius, all along the southern coast of Australia, at Lord Howe Island, and in New Zealand. Whether this range through 150 degrees of longitude involves 1, 2, or more species cannot be determined without far more comparable specimens than are yet available, but it matters little so far as the remarkable distribution is concerned, for it can scarcely be doubted that this is all a single stock with a common origin. A simple, but quite unprovable, explanation is that these sea stars have traveled on foul ship bottoms in the cool waters of the south temperate seas from New Zealand to Australia, Lord Howe Island, and Tasmania, and thence to South Africa. From here the introduction to Mauritius is equally imaginable. The warmer seas of the equatorial regions have prevented any extension of range to the north of latitude 20° S. If this be nonsense, make the most of it!

The ophiurans of Mauritius are not so numerous as might be expected, but this is probably due to M. Robillard's not having hunted for and collected the small, easily overlooked forms such as *Amphiura* and its allies. Only 38 species are as yet listed from Mauritius, whereas 51 are known from the little island of Mer at the northern end of the Great Barrier Reef. Mortensen (1924) lists only 41 species from New Zealand, so Mauritius is not far behind that much larger area. It is a very striking fact that not a single species of ophiuran is common to New Zealand and Mauritius. Of the 38 ophiurans found at Mauritius, 17 occur in Australia, but one of these is the tropicopolitan *Ophiactis savignyi,* and its occurrence has no significance. Of the others, all occur in the East Indian region save one, the rare and little-known *Cryptopelta granulifera,* once taken at the Low Isles, Queensland, and once at Mauritius, with a close congener in the Philippines. Of only one other is any discussion necessary. That one is *Ophiomyxa australis.* It occurs at Lord Howe Island and throughout the Flindersian region of Australia, like *Coscinasterias calamaria,* but unlike that sea star, it is found along the eastern coast of Australia, in the East Indies, and even as far north as southern Japan. Hence its occurrence at Mauritius, though unexpected, does not require any extraordinary explanation. The occurrence in Lord Howe Island, Tasmania, and the coastal waters of the southern side of Australia would seem to be the perplexing feature of its distribution. Apparently it does not occur on the western coast of the continent. None of the other ophiurans of Mauritius occur in the Flindersian province of Australia, at least at its western end.



More species of echini than of ophiurans are known from Mauritius; in Australia there are only 134 Recent echini to 223 ophiurans; in Mauritius there are 39 echini to 38 ophiurans. The explanation, however, is probably to be found in the fact that M. Robillard, being a paid but untrained collector, naturally found the echini a more noticeable, interesting, and easily preserved group. It seems likely that his collection of echini is more completely representative of the Mauritian fauna than is the collection of ophiurans. Of the 39 species of sea urchins now known from the island, 23 are found also in Australia, but 14 are characteristic of the Solanderian province, 8 of the Dampierian, and 1 (*Echinoneus cyclostomus*) is tropicopolitan. All 23 are found more or less commonly in the East Indian region. It is a striking fact that none of the echini of Mauritius occur in the Flindersian province of Australia, with the possible exception of stragglers from the Dampierian province which occur at Houtman's Abrolhos and even at Rottnest. But a very characteristic Flindersian genus, *Microcyphus,* is represented at Mauritius by a species (*maculatus*) which is not found in Australia. It is, however, found at the Andaman Islands and in southern Japan and is reported from Samoa. Hence the occurrence in Mauritius is a tie with the East Indian region rather than with Australia.

The holothurians of Mauritius are apparently pretty completely known, as 34 species are already recorded. Of these 22 occur in Australia, 14 being Dampierian species and 8 Solanderian. All are widespread Indo-Pacific species, and their occurrence in Mauritius is quite natural. There is no indication whatever that the Mauritius holothurians are allied to those of Australia, and particularly Western Australia, any more than to those of the East Indies.

It is evident from this survey of the echinoderms of Mauritius that the littoral fauna of that island is of East Indian origin. The peculiar distribution of *Coscinasterias calamaria* and *Ophiomyxa australis* must be explained in some other way than by an assumption of former land connection between Mauritius and Australia.

### *Southeastern Africa: Mozambique to Cape Town*

During the past twenty years the marine fauna of the South African coast, especially east from Cape Town, has received much attention, and the echinoderms may be considered fairly well known. No fewer than 235 species are recorded with more or less detail, and it is therefore possible to compare this fauna profitably with that of Australia, particularly with the Flindersian element of the southwestern part of the continent.

The crinoid fauna of South Africa is relatively depauperate, containing only half a dozen species each representing a different genus. Two of these genera, *Cenolia* and *Tropiometra,* occur in Australia, but the other 4 are East Indian

groups having widely different ranges, yet not entering the Australian fauna. *Tropiometra* is represented in the Australian tropics (Dampierian province) by a large species nearly related to one from Japan, whereas the South African species is a small form with an extraordinary range, from the western part of the East Indian region, around South Africa, northwestward to the southern West Indies. The South African *Cenolia*, on the other hand, finds its nearest relatives in the Flindersian province of Australia and in New Zealand, a striking reminder of *Coscinasterias calamaria*. The habits of these little comatulids are such as to make their distribution on foul ship bottoms very easy, and it is reasonable to suppose that *Cenolia*, like *Coscinasterias*, has reached South Africa in this way. It should be noted, of course, that the African *Cenolia* is a different species from the Australian, and that the latter is not known from west of King George Sound.

The sea stars of South Africa are a large and interesting group of 75 Recent species and 1 fossil form. The latter is called "*Archaster pattersoni*," but it is certainly not congeneric with the Recent species now included in *Archaster*, and even more certainly it is not nearly allied to any of the extinct Australian sea stars. It has no significance, then, in the matter of the relation between the South African and Australian faunas. The 75 Recent species represent 45 genera, of which 20 are found in Australian waters, but of the 75 species only 6 are common to the two areas. Of these, 3 are wide-ranging Indo-Pacific species whose occurrence in South Africa is merely the extreme southwesterly extension of their range. Of the other 3, one is *Coscinasterias calamaria*, whose occurrence is, as already suggested, probably due to transference from Australia on foul ship bottoms. Another is *Disasterina leptalacantha*, which is too rare and little known to carry much weight, but whose distribution is quite likely East Indian like that of *Patiriella exigua*, a near relative. The third is *Psilaster acuminatus*, first taken off New Zealand and New South Wales, subsequently found in Bass Strait and the Great Australian Bight, and lastly recorded several times off South Africa. That its occurrence there could be by transference on ship bottoms is so highly improbable that we must account for it in some other way. The genus is virtually world-wide in distribution, with representatives in all seas, including both Arctic and Antarctic oceans. It also occurs at all depths from very shallow water (in the Antarctic Ocean) to over 1800 fms. Since great depths are apparently not barriers to the spread of *Psilaster*, the distribution of *P. acuminatus* in South Africa, southern Australia, and New Zealand is possibly not beyond comprehension, but it is certainly of unusual interest.

Of the other 14 genera of sea stars common to Australia and South Africa, 4 are widely distributed Indo-Pacific groups, and 5 others are even more widely distributed, being tropicopolitan or having representatives in temperate seas of the northern hemisphere. Of the others, the South African species have notable



peculiarities that justify skepticism as to their generic position. Thus, the South African *Tosia* is very different from any of the Australian species and can hardly be congeneric. The *Anthenoides* is almost certainly not congeneric with the much smaller Australian sea star doubtfully referred to this West Indian genus. The *Austrofromia* is quite different from the Australian species; specimens of the two are rare and have never been compared. The *Hacelia* is very near the West Indian genotype and not very similar to the Australian species. As for *Parasterina*, comparison of Mortensen's figure of his South African species (1933, pl. 12, figs. 9, 10) and my figure of the Western Australian species (1938, pl. 21, fig. 5) certainly justifies great doubt whether the two are really congeneric. Satisfactory material is still too scanty to permit the necessary direct comparison, but the supposed resemblances do not outweigh the obvious differences. Clearly, then, none of the cases of genera recorded from both Australian and South African seas give any justification for a belief in their common origin save by the gradual diversification of widely distributed ancestral stocks.

The brittle stars of South Africa are little more numerous than the sea stars, only 79 species being known. These represent 40 genera, of which 23 occur in Australian seas, but 16 of these are more or less tropicopolitan and 4 others are East Indian. The remaining 3 have been found as yet only on Australian or South African coasts, but in no case is the South African species identical with the Australian. Indeed, of the 79 South African brittle stars only 7 are recorded from Australia, and all these are widely distributed tropicopolitan or East Indian species. *Astroconus* has a representative in South Africa, but it is so different from the Australian species of that genus that Mortensen, the describer, hesitated about calling it congeneric with them. The Australian *Cryptopelta* is conspicuously different from the African species, and occurs only in the Dampierian province. The same is true of the Australian *Dictenophiura*. The South African *Ophiomyxa* is supposed to be identical with that of southern South America, and is not closely allied to the Australian species. It must therefore be admitted that the ophiurans of southwestern Australia have very little in common with those of South Africa.

The South African echinoid fauna as now known contains 45 Recent and only 1 fossil species. The single extinct form is *Cidaris pustulifera*, which is probably related to one of the Recent cidarids now living on the South African coast, but more material is necessary to establish its real position. The 45 species of echini now living on the coast represent 37 genera, no genus having more than 2 species. Of these genera, 24 occur in Australia, but of the 45 species, only 16 are known from that continent. Of the 16 species, 14 are well known East Indian forms whose occurrence in the South African region is only the extreme southwestern extension of their tropical range. One is the

almost cosmopolitan *Echinocardium cordatum*. The sixteenth is the remarkable *Dermechinus horridus*, first found by the "Challenger" in 175 fms. off the southern end of South America, but later discovered in somewhat greater depths off the southeastern coast of South Africa and in similar depths off the southeastern corner of Australia. Whether we consider that the collected material represents a single species, or 3 closely related but probably distinguishable forms, does not alter the remarkable nature of the distribution of this urchin. It may, however, be pointed out that the genus *Echinus*, even if rather strictly defined, is well-nigh world-wide in its range and may have spread southward along several widely separated lines. On the other hand, the occurrence of *horridus* as at present known could be used as an argument in support of the former approximation of the three southern continents. What is more probable (in keeping with the distribution of several New Zealand echinoderms), it may indicate the former existence of an Antarctic land mass, or at least a shallow-water area, connecting South America, New Zealand, Tasmania, and South Africa. The apparent absence of *horridus*, however, from both New Zealand and Kerguelen throws doubt on this. It is curious that there is no other echinoderm known with a distribution like that of *horridus*.

The holothurian fauna of South Africa seems to be rather depauperate, as only 28 species are known and these represent but 10 genera, all but 1 of which are more or less cosmopolitan or at least tropicopolitan. The monotypic *Discucumaria* is widespread in the East Indian region. None of the genera are in any way distinctive of South Africa. Of the 28 species, 12 occur on the Australian coast, but all are more or less common, widely distributed East Indian forms and give no indication of any connection between South Africa and Australia other than by way of the East Indies.

This comparison, then, of the Australian and South African echinoderm faunas brings out very clearly the lack of any evidence in that conspicuous group of littoral marine animals to justify belief in any former closer relation between the two continents. The four suggestive cases (the comatulid *Cenolia*, the sea stars *Coscinasterias* and *Psilaster*, and the sea urchin *Dermechinus horridus*) all involve either New Zealand or South America as much as they do South Africa, and might be construed as evidence for a Gondwana-land connection such as is demanded according to the Wegener hypothesis.

### *East Africa: the Zanzibar Region, from 14° 30′ S. to 10° N., with Madagascar and the Seychelles*

There is reason to believe that our knowledge of the Recent echinoderms of the East African area is still very incomplete, but thanks to the activities of French geologists and paleontologists our knowledge of the *fossil* echini is very considerable. Few or no fossils of the other classes of echinoderms have been described, and the Recent species are neither numerous nor remarkable.



Of crinoids, only 16 species are listed, representing 13 genera. The genus *Heterometra*, of which 2 species occur in Australia, is represented by 4 species, but none of them are known from the island continent. Of the other dozen genera, 10 are found in Australia, but only 3 of the African species occur there, and these are well known, widespread East Indian forms. All the African genera are extensively distributed in the Indo-Pacific region or at least in its western half. There is therefore no indication of any close relation with Australia.

The 36 species of sea star now known from the Zanzibar region represent 24 genera, all but 5 of which are more or less common in tropical Australia. A dozen of the species are also found in the Dampierian or the Solanderian province of that continent, but these are all widely distributed East Indian forms whose range has stretched southward along the eastern coasts of both Africa and Australia. There is nothing, apparently, in the sea-star fauna of East Africa that is suggestive of Australia except through an East Indian connection.

The ophiuran fauna of the Zanzibar and Madagascar area includes some 57 species of 36 genera. Twenty-two of the genera occur in Australia and 17 of the species. But all these genera and species occur in the East Indies and are characteristic of that fauna. Hence there is no evidence that the ophiurans of the East African coast have any relation to those of Australia except by way of the East Indies.

The echini of the East African region must be treated under two heads, the living Recent fauna and the extinct fossil forms. The activity of French paleontologists in Madagascar has thrown a flood of light on the fossil echini, revealing an extraordinarily rich fauna, and a comparison of this with the much smaller extinct group in Australia will naturally be interesting. But first, consideration may better be given to the Recent fauna, which includes 46 species of 38 genera. It is surprising to find that it is notably different from that of Mauritius, only a short distance farther east. Of the 32 genera found at Mauritius, 11 have not been found in the Zanzibar-Madagascar area, and of the 38 genera in the latter region, 21 have not been found at Mauritius. No doubt this striking difference is in part due to incomplete collecting, but it is possible that local conditions markedly alter the character of the fauna. Comparison of the Zanzibar-Madagascar fauna with that of the Australian region shows that 29 of the 46 species are found on the coasts of that continent; 17 are Solanderian, 9 Dampierian, and 1 Flindersian; the *Echinoneus* is tropicopolitan and the *Echinocardium* is even more widespread. The remaining 17 are all either East

Indian species or endemic species of East Indian genera. There is no evidence of a distinctive Australian element.

Comparison of the fossil echini of the Zanzibar-Madagascar region with that of the similar fauna in Australia is somewhat difficult, as the Madagascan group is so much larger. It includes more than 175 species of at least 120 genera, whereas in Australia only 56 species of 40 genera are as yet known. Only 12 of the 40 are found in the Madagascan fauna, and these nearly all belong to large, ill defined groups such as *Cidaris* and its allies, *Salenidia*, *Clypeaster*, *Nucleolites*, *Echinolampas*, *Linthia*, and *Schizaster*. Naturally none of the species of the two regions can be considered identical. On the whole, the impression given by comparison of the two faunas is one of surprising dissimilarity. There is not the least indication that they were ever in any way associated or even remotely connected.

The East African holothurians are a small group of 32 species of 14 genera. Of the genera, all but 1 (*Patinapta*) occur in Australia. Of the 32 species, 24 occur in Australia. This would seem like a remarkable similarity in the makeup of the faunas were it not that the same genera and most of the species also occur throughout the East Indian region, so that the natural explanation of the similarity between the East African and the Australian faunas is that each is a southern or southwestern extension of the East Indian fauna. All the Australian species concerned are found in the Dampierian region or on the eastern coast, evidently incomers from the East Indies. The holothurians of the western coast are not so much like those of East Africa as are those of the northern and northeastern coasts.

### *Arabian Area, including Red Sea, Gulf of Aden, and Persian Gulf*

The northwestern part of the East Indian area has a relatively small echinoderm fauna, especially as contrasted with that of the central and eastern parts. It includes about 170 Recent species, not many more than are found at the small island of Mauritius and much fewer than are found on the coast of southeastern Africa. As in the case of the Zanzibar-Madagascar area, the fossil echini are very numerous, at least 110 species in 80 genera having been recorded from Egypt, Persia, and Baluchistan.

The crinoid fauna of the Arabian area includes 17 species of 12 genera. All the genera, save 2, occur in the Australian seas, but only 3 of the species, all well known East Indian forms, are known from the island continent. All the genera, save the recently described, endemic, monotypic *Repometra*, are well known East Indian groups, but a dozen of the species are apparently endemic in the Arabian region, indicating a long period of relative isolation.

The sea-star fauna of the region includes 36 species of 20 genera. All but



5 of the genera occur in Australia, but only 7 of the species. The missing genera, like the 15 that are present, are widespread East Indian groups, or more or less endemic in the western Indian Ocean. Of the 7 Australian species, 3 occur in the Dampierian province and 4 in the Solanderian. All are widespread in the East Indian region. There is then no indication of any connection between the Arabian and Australian areas except by way of the East Indies.

The ophiurans of the Arabian region are neither numerous nor notable. Forty-two species of 21 genera are recorded; all but 4 of the genera but only 7 of the species are also Australian. Just as in the case of the sea stars, the fauna is essentially East Indian though 1 of the 4 non-Australian genera is endemic in the Arabian area. All the 7 Australian species (2 Dampierian and 5 Solanderian) are East Indian, yet of the 35 non-Australian species only 10 are East Indian, some 25 being more or less endemic in the Arabian area. All this accords well with the situation among the crinoids.

The Recent sea-urchin fauna of the Arabian area is not rich, but the fossil forms are numerous and varied. Thirty-six Recent species, grouped in 28 genera, are now found in the region. Of the 28 genera, all are East Indian and all but *Acanthocidaris* and *Toxopneustes* are Australian. Of the 36 species, however, 8 are not East Indian, 15 not Australian. One very interesting case is that of the species *Nudechinus scotiopremnus*, which is found in the Red Sea and also on the northwestern coast of Australia, but which has not yet been found in the East Indies. The genus is, however, known from the Amirante Islands in the western Indian Ocean, from northeastern Australia, and from the Sulu Archipelago, Philippine Islands, so it is quite possible that *scotiopremnus* will ultimately be found in the East Indies.[1] The other 7 species which have not yet been taken in the East Indies are more or less endemic in the Arabian area or at least in the western Indian Ocean. They are in no sense connecting links with Australia.

The fossil echini of the Arabian area are in general surprisingly different from those of Madagascar. Of the 80 genera, 46 have not yet been found south of the equator in Africa. But they are much more unlike those of Australia, with which they have nothing in common save for 8 or 10 large, ill defined genera of cidaroids and spatangoids widely distributed in the Mesozoic. One looks in vain for any evidence that the Mesozoic Australian echinoid fauna had any geographical association with that of the Arabian area.

The holothurians of the northwestern corner of the Indian Ocean and its associated gulfs comprise some 38 species in a dozen genera, all of which (except 1 or 2 concerning whose validity there may be question) occur in

[1] The similar case of *Nudechinus gravieri* is vitiated by the inadequacy of the material and the very great doubt whether the Australian specimens really are *gravieri*.

Australia and throughout the East Indies. Of the 38 species, however, about 16 appear to be endemic; the remainder are East Indian and apparently most of them extend their range into the Dampierian or the Solanderian province of Australia. The high percentage of endemic species confirms what was suggested by the crinoids and ophiurans, that the Arabian region has been more or less isolated for a long period.

### *Ceylon*

The echinoderm fauna of Ceylon being fairly well known and the island being somewhat nearer to northwestern Australia than is Mauritius, it is interesting to note the characteristic features of the fauna. The statements made in 1915, however (H. L. Clark, 1915, p. 92), regarding the incompleteness of our knowledge are still true, and the deductions made here will very likely be considerably modified at some future day. Some 193 species of echinoderms are now included in the Ceylon list, nearly one-third more than have yet been reported from Mauritius.

At least 25 species of crinoids are recorded from Ceylon, whereas only 7 have been taken at Mauritius. The latter represent 7 genera, all but 1 of which occur in Ceylon, but of the 7 Mauritian species only *Comanthus parvicirra* and *Oligometra serripinna* are in the Ceylon list. Both of these are widespread East Indian species, and the *Comanthus* is notoriously variable. When we compare the Ceylon list with the Australian, we are struck with the similarities, for all the Ceylon genera, except *Mastigometra*, occur in Australia, and even when the species are different, as is true in several genera, the similarities are more striking than the differences. There can scarcely be any question that the two faunas have had a common origin.

Turning now to the sea stars, we find 35 species in Mauritius as against 41 in Ceylon. Twenty genera occur in Ceylon and 23 in Mauritius; 16 are common to the two. Comparing species, we find but 15 in common, indicating that the two faunas have long been completely isolated from each other. Comparison of the sea stars of Mauritius with those of Australia revealed a dozen species in common. In the case of Ceylon, we find 18. In other words, 33 per cent of Mauritian sea stars are Australian, and 44 per cent of those in Ceylon.

In the case of the brittle stars, there are 38 species in Mauritius and 37 in Ceylon. Of the 22 genera occurring in Ceylon, 9 have not been found in Mauritius; of the 21 found in Mauritius, 8 have yet to be taken in Ceylon. As for the species, we find only 15 of the Ceylon species at Mauritius, and of course 14 of the Mauritius species at Ceylon. These differences in the faunas of the two islands are interesting but are no doubt due in part to incomplete collecting. Comparison of the ophiurans of Mauritius with those of Australia



revealed 17 species in common. In the case of Ceylon we find 21. That is, 45 per cent of Mauritian ophiurans are Australian and 56 per cent of Ceylonese species.

In the case of the echini, there are 39 species in Mauritius and 38 in Ceylon. Of the 28 genera occurring in Ceylon, 23 are found in Mauritius; of the 32 found in Mauritius, 9 have yet to be taken in Ceylon. As for the species, we find 25 of the Ceylon species at Mauritius, and of course 13 of the Mauritius species at Ceylon. Though these differences may be due in part to incomplete collecting, this is less likely to be the case than with the brittle stars, as echini are less easily overlooked. Of the echini now known from Mauritius, 23 occur also in Australia; of the Ceylonese echini, 25. That is, 59 per cent of Mauritian sea urchins are Australian, and 66 per cent of those found at Ceylon.

Turning now to the holothurians, we find no fewer than 51 species recorded from Ceylon as contrasted with only 28 from Mauritius. This is obviously due in part to the fact that Robillard and de Loriol made no effort to include the holothurians in their collecting and study of Mauritian echinoderms. Of the 15 genera listed from Ceylon, only 8 have been reported from Mauritius; 2 genera, *Psolus* and *Discucumaria*, reported from Mauritius, are not yet recorded from Ceylon. So far as species are concerned, only 10 of the species listed from Ceylon are reported as yet from Mauritius, but comparison with Australia shows 26 species in common. Of Mauritian holothurians only 12 are Australian. That is to say, 43 per cent of the Mauritian holothurians and practically 50 per cent of those in Ceylon also occur in Australia.

It seems evident, then, that the Ceylon echinoderm fauna is not less than 10 per cent more Australian than is that of Mauritius, a fact no doubt to be explained in part by the location of Ceylon so much nearer to the island continent (about a thousand miles). But the more probable reason is that Ceylon is so much nearer than Mauritius to the East Indian islands, the hotbed of echinoderms, if not of all marine life.

### *The East Indian Area*

The boundaries of this great and interesting tropical region are necessarily artificial. For practical purposes in the present connection, it includes the sea and its islands between 90° and 155° E., with arbitrary and irregular southern and northern limits. Obviously the southern limit must coincide with the northern limit arbitrarily fixed herein for the Australian region (9° 30′ S.) as far as 145° E., where it drops to 12° S. for the next 10°. The eastern boundary then follows longitude 155° between the Bismarck Archipelago and the Solomon Islands to 5° N., where it turns west to 130° E., then north to 20° N., on which parallel it runs westward to 90° E., then straight

south to 9° 30′ N. The western boundary thus excludes most of the Bay of Bengal but includes the Andaman Islands. The northern boundary includes the Philippines and the coasts of Indo-China and the Malay Peninsula. Though these boundaries are admittedly arbitrary and artificial, the area contained is a natural marine province. Obviously its boundaries have nothing to do with the lines which delimit the areas occupied by the land vertebrates of the region. The echinoderm fauna of this interesting area is extremely rich, and thanks to the "Siboga" and "Albatross" collections and those made by Sluiter, Mortensen, and other zoologists, it is remarkably well known. More than 1300 Recent species, in about 400 genera, are already recorded from the East Indies—more than one-fourth of all the echinoderms at present known. There are in addition scores of fossil species, nearly all echini, recorded in about 60 genera, of which three-fourths are long since extinct. Comparison of this rich fauna with that of the Australian region is most interesting and informative.

The crinoids of the East Indies are surprisingly numerous, more species being known than in any of the other classes, except the ophiurans. There are a number of fossil forms, imperfectly known, but as these have no near relation to either the Recent species or the extinct Australian crinoids, it is not necessary or desirable to include them in this discussion. The Recent crinoids number 245 species of 75 genera. Of these genera, 35 occur in Australia, and the remaining 7 Australian genera are endemic, all but 1 being confined to the Peronian or the Flindersian province. Of the 83 species of Recent Australian crinoids, 33 are endemic. The remaining 50 all occur in the East Indies and are obviously members of that fauna. The single tropical endemic Australian genus is the curious *Monilimetra* of the Broome region, with 4 species apparently differentiated in that area. Its nearest relatives, so far as we may guess at them, occur in the northern East Indies. Clearly the relationship between the East Indian crinoids and those of Australia is very close. The facts justify the conclusion that the Australian crinoid fauna is the southern extension of that of the East Indies.

The East Indian Asteroidea are numerous and diversified to a marked degree, 231 species grouped in 83 genera—not quite 3 species to a genus. The Australian Asteroidea form a group more nearly comparable with them in size and diversity than was the case with the crinoids. In Australia, there are 189 species of sea stars in 73 genera, about 2.5 species to a genus. Apparently this indicates more active speciation in the more southern group, associated with its greater isolation. Of the 73 Australian genera, 30 are lacking from the East Indian list, and of these 18 are endemic; 9 of the latter are in the Flindersian region and 2 are Peronian. Three genera are so widely dispersed that they are found in the northern and western hemispheres as well as in



the southern and eastern. The remaining 9 genera which are not endemic occur in New Caledonia, New Zealand, Kerguelen, Mauritius, and South Africa. In several of these cases, however, material is scanty and our knowledge of the genus is very incomplete. Of the 189 Recent species of Asteroidea occurring in Australia, 139 are endemic. The remaining 50 are all East Indian species, except half a dozen of whose distribution we know very little or which occur in New Zealand as well as in southern Australia. There can be little doubt, therefore, that the Australian asteroid fauna is an extension southward of that of the East Indies, which has become diversified and distinctive as a result of its isolation in a cooler or otherwise different environment.

The brittle stars of the East Indies are a very large group, containing nearly as many species as the crinoids and sea stars together. There are 458 species of 110 genera, and the comparison with the large Australian group is interesting and instructive, though the latter contains only about half as many species. There are 70 genera of Australian ophiurans; of these, 54 may fairly be called East Indian, and 13 are endemic. The remaining 3 are *Asteroporpa*, which occurs in the West Indies, in Japan, and in New Zealand; *Ophiocomina*, which is known as yet only from South Australia and from European seas and the northwestern Atlantic (a perfectly inexplicable distribution); and *Ophioprium*, a West Indian genus. A comparison of the Australian and East Indian species shows that of the 223 Australian forms 133 are endemic, and 85 are East Indian. The remaining 5 are 2 New Zealand species of *Ophiactis*, an *Ophiocoma*, an *Ophiomastix* (known as yet only from the far distant Paumotu Islands), and *Cryptopelta granulifera* from Mauritius. These last 3 will almost surely prove to be East Indian forms. Obviously the relationship of the Australian ophiurans to the East Indian fauna is so close that there can be no doubt of their common origin or of the southern group's being derived from the larger tropical one.

The East Indian echini are a large and diversified group of 166 Recent species, representing 85 genera. There is also a large group of extinct species of 46 additional genera. Fossil species of 13 of the Recent genera have also been found. Not all these fossil forms are from the East Indian area as defined for the Recent species; many are from mainland areas outside the limits given above. A comparison of these extinct forms, however, brings out the interesting fact that 26 of the genera occur in Australia, 17 as extinct, 9 as still living genera. It is probable that when the extinct faunas of Australia and of the East Indies are more fully known and proper consideration can be given to the geological horizons, and their correlation in the two regions, the resemblance between the two faunas will be striking. Meantime a comparison of the Recent genera and species shows that 9 of the East Indian genera and 56 of the species

occur in Australia, and that 9 genera and 69 species are endemic there. The 10 remaining species occur in South Africa, New Zealand, the Pacific Islands, or Japan. In most of these cases it is probable the species occurs also in the western part of the East Indian area but has not yet been collected there. The extraordinary case of *Dermechinus horridus* has been discussed in connection with South Africa (see p. 480). On the whole, the relation between the Australian echini and those of the East Indies is about as close as in the case of the sea stars.

Coming now to the holothurians, we find a rich East Indian fauna of over 200 species, in some 40 or more genera. No fossil holothurian remains have yet been reported. When we compare the East Indian and Australian faunas, we realize that the latter has been more critically studied and hence the number of genera in proportion to the number of species is considerably greater in the Australian area—about 4 species to a genus, whereas in the East Indies there are 5 species to a genus. Moreover, thanks to the work of the "Siboga," 7 genera of deep-water holothurians are known from the East Indies which have not yet been collected in Australia, owing to the very small amount of dredging that has been done on the continental slope. Making due allowance for these facts, we find that the genera of East Indian and Australian holothurians are otherwise almost identical. The two small apodous genera *Anapta* and *Labidoplax* have not yet been found in Australia. Looked at in reverse, it may be said that all Australian genera occur in the East Indies except the small apodous genus *Trochodota* and perhaps some of the recent segregates from the genera *Cucumaria, Thyone,* and *Phyllophorus*. Examination of the lists of species found in the two areas reveals the following facts: Eighty-two of the holothurians found in Australia are endemic. Of the remaining 76, 67 are East Indian, the other 9 being New Zealand or Pacific species. Of these 9, several are of dubious validity and uncertain relationships. There can be no doubt, then, that the Australian holothurians are, like the other echinoderms, almost certainly of East Indian origin.

### *The Southwestern Pacific*

Our knowledge of the echinoderm fauna of the southwestern Pacific is fragmentary and incomplete. No thoroughgoing, adequate collecting or studying of the marine fauna of even the well known island groups has ever been carried on. There is, however, some material in various museums which has enabled us to gain a little knowledge of the echinoderms of this interesting and important region. Most of this material has come from Fiji, Samoa, or Tonga. About 150 species have been listed at various times in scattered



publications from this southwestern Pacific area, and it is of interest to study this list in comparison with the East Indian and Australian faunas.

Only about a dozen crinoids are reported from the southwestern Pacific area. As carefully reidentified and correctly named by A. H. Clark (1936), there are apparently 13 comatulids in the list, with several additional species found in depths below 500 fms. All the genera and 10 of the species occur in Australia, but all the genera and *all the species*, barring possible varietal differences, are East Indian. Apparently the crinoids of the southwestern Pacific are a development parallel to the Australian group from a common East Indian center.

Only 23 species of sea stars have been reported from Fiji, Tonga, and Samoa, but they represent 17 genera. Only 12 of the genera and 12 of the species occur in Australia, but 16 of the genera and 18 of the species are East Indian. The other species are little-known sea stars whose status and distribution are yet to be made clear. There seems to be little doubt that the sea stars of the southwestern Pacific have diverged from the East Indian group rather less than the Australian asteroids, but this divergence has led to obvious differences between the faunas of the two regions.

Of brittle stars only 40-odd species of 27 genera are recorded from Fiji, Tonga, and Samoa, and these are probably not more than half the forms occurring in that area. Comparison with Australia shows only 6 genera and a dozen species not known in that region. This indicates a much closer resemblance between the brittle stars of the southwestern Pacific and those of Australia than we find in the sea-star population. But this difference is probably due at least in part to a very incomplete knowledge of the brittle stars of the southwestern Pacific; for 4 of the genera and 10 species are not East Indian, so far as we yet know, and this is an abnormal proportion as compared with the other classes.

Only 32 species of echini are listed from the southwestern Pacific, but this is a much larger proportion of the actual echinoid population than we have found among the sea stars or ophiurans. The 32 species represent 22 genera, one of which is the remarkable endemic *Zenocentrotus* of Tonga, which includes 2 species. Aside from this case, 1 genus and 6 species do not occur in Australia, but every genus and all but 2 species are East Indian. As *Zenocentrotus* is apparently a local specialization of *Echinometra*, it is obvious that the East Indian fauna is the source of the echinoid fauna of the southwestern Pacific.

The holothurian fauna of the Fiji-Tonga area is almost completely East Indian, for of the 34 species so far listed, all but 1 occur in the East Indies. That one is the deep-water synaptid *Protankyra challengeri*, which was taken in comparatively shallow water at Fiji but in the East Indies has been collected only at great depths. The absence of 4 species of *Holothuria*, as well as of

*Protankyra*, from the Australian fauna distinguishes it from the southwestern Pacific group, in addition to the fact that it includes more than a hundred species not known in that area.

The result of this survey of the echinoderm fauna of the southwestern Pacific, so far as it is at present known, leaves little doubt that it has been derived from the East Indies and that any resemblance it may have to the Australian fauna is quite secondary.

## *The New Zealand Area*

Thanks to Mortensen (1921, 1924, 1925), our knowledge of the echinoderm fauna of New Zealand is definite and reliable and probably reasonably complete, except for the Kermadec Islands and the northwestern part of the North Island. A comparison of it with that of Australia is of particular interest.

Only 3 species of crinoids have been found in New Zealand, and these are all endemic forms occurring on the west coast of the south island and off North Cape and the Three Kings Islands. They are closely related to species of the southern coast of Australia and somewhat less closely to a South African species and to one from Hawaii.

Of sea stars, some 30 species (and 1 variety) are recognized by Mortensen, of which all but 4 are endemic. They represent 22 genera, of which 6 have a world-wide distribution and 6 are Australian. The remainder are of southern relationships or are endemic. Ten of the genera are East Indian or at least are represented in that fauna, and a dozen are Australian in the same way. There can be no doubt of the striking fact that the New Zealand sea stars have but little in common with those of Australia and even less with those of the East Indies.

More than 40 species of ophiurans occur in New Zealand, and of these, all but 4 or 5 are apparently endemic. Of the 22 genera, only 1 is strictly endemic; 1 occurs also on the coast of California, 1 occurs in Australia and the West Indies, 14 others occur in Australia, and 18 occur in the East Indies. The ophiuran fauna is thus somewhat more closely allied to the East Indian than to the Australian. There are apparently only 1 or 2 ophiurans that suggest a southern relationship.

The sea-urchin fauna of New Zealand is small, only 20 species being represented, but these are distributed in 17 genera. One is based on so young a specimen it may well be ignored in the present connection, and another, *Holopneustes*, is too doubtfully a New Zealand urchin to be useful in this connection. The remarkable habit of *Holopneustes* of living wrapped in the fronds of *Ecklonia* and *Cystophora* (and possibly other algae) would naturally lead to its wide distribution wherever uprooted algae were driven by winds



and currents. As only 2 specimens of *Holopneustes* are known from New Zealand, and both are dead, bare tests washed up on the beach, it seems to me beyond doubt that this sea urchin does not live in New Zealand waters and cannot properly be regarded as a member of that fauna. There are then only 18 species of 15 genera to be considered here. Of these, 14 of the species are endemic and the other 4 occur in Australia, 2 of them also in the East Indies or Japan, and 1 in the Kermadec Islands. Of the genera, 2 are endemic: *Ogmocidaris*, closely related to the southern *Austrocidaris*, and *Evechinus*, possibly related to the East Indian *Echinus armatus*. Four are more or less world-wide in distribution. Of the remaining 9, 8 occur in Australia (4 of these in the East Indies also), and 1 is evidently a southern form. The relationships of such a fauna are difficult to determine. How to account for such genera as *Brissopsis*, *Spatangus*, and *Echinocardium* is beyond me.

The holothurian fauna of New Zealand has been fairly well studied, and Mortensen's list of 28 species and 2 varieties is probably nearly complete. A striking feature is the almost complete absence of species of *Holothuria* and the very large number of Cucumarias. Fourteen genera are represented, of which 11 occur in Australia. The other 3 are endemic, and 2 of them show a distinctly southern relationship. One genus, *Trochodota*, occurs in Australia but not in the East Indies. The other genera are, however, East Indian. Of the species, 6 occur in the Flindersian province of southern Australia. The rest are apparently endemic, but 9 are obviously subantarctic in their relationship.

This hasty summary of the echinoderm fauna of New Zealand reveals strikingly how different it is from that of Australia, and even more from that of the East Indies. Mortensen has very fully discussed (1925) this remarkable fauna and made the surprising suggestion that the similarities between the echinoderms of New Zealand and those of Australia indicate a "former closer connection" between the two areas and are "easily explained through the Continental drift theory of Wegener according to which New Zealand was originally directly connected with Australia, forming the eastern border of the great Australian continental block from which it was then separated through Australia drifting away from it." The resemblances between the two faunas are too few and trivial and the differences too numerous and striking to warrant any such conclusion. The absence from New Zealand of numerous characteristic Australian genera such as *Comatula*, *Comanthus*, *Philometra*, *Compsometra*, *Tosia*, *Stellaster*, *Anthenea*, *Petricia*, *Uniophora*, *Astroconus*, *Ophiocrossota*, *Phyllacanthus*, *Salmacis*, *Temnopleurus*, *Microcyphus*, *Amblypneustes*, *Breynia*, *Urodemas*, *Actinopyga*, and *Taeniogyrus*, not to mention numerous East Indian genera common in Australia, precludes any idea that

New Zealand has derived any considerable part of its echinoderms from the island continent. On the other hand, the notable proportion of its echinoderms derived from a southern source suggests a subantarctic or south temperate area with which New Zealand and possibly Tasmania and southeastern Australia were associated. Since the origin of the New Zealand fauna is no concern of the present work, all that needs to be emphasized here is that its echinoderms have very little significance as regards the composition and origin of the Australian fauna. The suggestion that Lord Howe Island is to be associated with New Zealand rather than Australia is strongly contradicted by its echinoderm fauna. Of its 39 genera and 59 species, 1 genus and 10 species are endemic, 21 genera but only 4 species occur in New Zealand, and 36 genera and 46 species occur on the Australian coast. All the 4 species and 20 of the 21 genera occurring in New Zealand also occur in Australia.

## The Apparent Origin of Australia's Echinoderm Fauna

Having now surveyed the echinoderm fauna of each of the adjoining areas, we are in a position to consider fairly the origin of Australia's and the probable routes it has followed in finding its present homes. The most conspicuous fact that stands out as we look over the preceding data is the predominance of tropical forms and influence. The Dampierian and Solanderian provinces include more than 500 of the 787 species recorded from the continent, almost two-thirds indeed, and many of the Flindersian and Peronian species belong to genera which are for the most part tropical. It has already been mentioned (p. 471) that the greatest preponderance of tropical forms is to be noted in the Torres Strait region, where the Dampierian and Solanderian provinces meet. In that region more than half the echinoderms are definitely tropical forms, but as we pass westward toward Cape Londonderry and still farther to Northwest Cape, the percentage of endemic species increases, and the same change occurs as we pass southward toward Cape Howe and Bass Strait. In the Peronian province 82 per cent of the echinoderms are endemic, and in the Flindersian province practically nine-tenths. It can scarcely be questioned, then, that the echinoderm fauna of Australia has come from the north and apparently from the East Indian region, particularly from its southeastern part, where New Guinea overlaps Queensland, and from its extreme southern point at Timor and across the Sahul Banks. As was shown in my Torres Strait report (1921), the Queensland fauna is clearly derived from the depression of land areas east of New Guinea which led to the connection of the Coral Sea with the western Pacific and the East Indian region. The Dampierian fauna, on the other hand, came from farther west and was probably already well extended down the western coast of the continent when the formation of Torres Strait



made a mingling of the two faunas possible. Apparently, however, there has never been a very extensive mingling, and the Solanderian fauna is still quite distinguishable from the Dampierian and is less differentiated from the original stock. This explains also why the echinoderm fauna of the southwestern corner of the continent shows the highest percentage of endemic forms. It is the youngest and hence the most specialized echinoderm stock to be found in Australia. This Flindersian fauna is naturally continuous to the north with the Dampierian, and on the southern coast it has extended to the east until it has met and mingled with the Peronian, which is the most specialized part of the echinoderm stream that flowed down the Queensland coast.

Comparison of the Australian fauna with that of southern and eastern Africa, Madagascar, and Mauritius gives practically no evidence of any common origin or close relationship, save for the few species already discussed and concerning which further discussion will be found on page 494. Comparisons between the echinoderm faunas of the Arabian and Ceylon areas and the Australian emphasize the connections through the East Indian fauna, and comparison of the latter with the Australian shows a very striking relationship. This similarity between the Australian and neighboring faunas reaches its climax in the East Indies and leaves little room for doubt as to the origin of the Australian fauna. Comparison with the still imperfectly known fauna of the southwestern Pacific indicates a less close relationship than the East Indian fauna itself shows, but this is possibly due in part to our greater ignorance of the island faunas.

Coming now to New Zealand, we are struck by the conspicuous differences between its fauna and that of Australia, but equally striking are the similarities shown, though they are much fewer. The fact that over 80 per cent of the New Zealand species are endemic indicates a long-isolated fauna. Only about 20 of the species are known to occur in Australia, and many of these are found in the East Indies or even more widely distributed (*Echinocardium cordatum*, *Laganum depressum*, *Placophiothrix aristulata*, etc.), but a few are local (*Araeosoma thetidis*, *Heliocidaris tuberculata*, etc.). Among these species common to New Zealand and Australia, a number call for special comment, as indicators of a possible relationship between the two faunas which deserves careful consideration.

Among crinoids, we find the genus *Cenolia* with small closely allied species in New Zealand, Tasmania, Lord Howe Island, the southern coasts of Australia, and South Africa. Among sea stars, *Coscinasterias calamaria* has the same distribution, with Mauritius as an additional locality. The much smaller *Allostichaster polyplax* occurs in New Zealand, Tasmania, and southern Australia, with an allied species in southern South America, but the

genus is not known in South Africa. The sea star *Psilaster acuminatus* occurs in moderately deep water off New Zealand, Australia, and South Africa, but the genus is widely distributed in deep water and hence is of doubtful value in determining former land connections. *Nectria*, characteristic of the Flindersian coasts of Australia, has an endemic species in New Zealand but is not known elsewhere. Of brittle stars, *Ophiomyxa australis* is characteristic of the Flindersian region of Australia, but it (or very closely allied species) has a wide range in the East Indian region, in Mauritius, South Africa, New Zealand, Fiji, Japan, and southern South America. The genus is an old one with 17 species or more, ranging throughout the tropics, down to depths of over 300 fms. Specific lines are not well drawn or easy to make out, but there can be little question that the southern forms are very closely allied. The Australian *Ophiactis resiliens* is a Flindersian species which also occurs in New Zealand and at Lord Howe Island. Allied species occur in many parts of the world. Their secretive habits would facilitate transportation by artificial means, such as floating seaweed or foul ship bottoms.

Among echini, we have two interesting cases showing possibilities as land-connection indicators, one of which, that of *Dermechinus horridus*, has already been discussed (see p. 480). It is difficult to account for its occurrence in South African, South American, and southeastern Australian seas except by some sort of land connection. Its absence from New Zealand is interesting but proves nothing. The genus *Pseudechinus* has developed 4 species in New Zealand and 2 in southern Australia, a fact which is at least suggestive of former shallow-water connection. Among the holothurians we find 4 cases of New Zealand species occurring on the southern coasts of Australia: *Stichopus mollis, Mensamaria thomsoni, Lipotrapeza dearmatus*, and *Chiridota gigas*. With the possible exception of *Stichopus mollis*, none of these species is sufficiently well known to make a firm basis for any argument about distribution.

As we review this summary of similarities between the echinoderms of New Zealand and those of Australia and South Africa, we are forced to the conclusion that in most cases they can be accounted for by transportation on ship bottoms or floating masses of seaweed or other flotsam. Such forms as *Psilaster* and *Dermechinus* can hardly have reached their present locations in this way, and the assumption that a shore-line connection once existed between the southern land masses is an easy explanation. But if such a connection ever really existed, it is hard to see why there is not more evidence of it. Much greater similarities ought to exist between the faunas of South America, South Africa, Australia, and New Zealand than we have found. Only a desperate desire to validate the Wegener hypothesis can find in the echinoderm fauna of Australia any evidence that it is at all closely allied to that of South Africa



or even of New Zealand. The evidence is overwhelming that the Australian echinoderms have come southward from the East Indian area,[1] either around the eastern end of New Guinea or across the Timor Sea. Any similarities to the South African fauna are due to the fact that the latter fauna has come in large part from the northeast and hence traces back to the same East Indian source as Australia's. So, too, the similarities between the New Zealand and Australian faunas are due to a common source in the East Indian fauna which passed around the southeastern end of New Guinea into the Coral Sea, one line following the western shore of that sea down the Queensland coast, the other following the eastern shore to New Caledonia (of which we know almost nothing) and New Zealand. That an antarctic land mass, some sort of Gondwana-land, may have existed in the remote past seems possible, but it has played only a trivial part in the formation and development of the Australian echinoderm fauna.

[1] In 1911, Austin H. Clark wrote (1911*c*, p. 132), "The crinoids of Australia have come from the north, from the great East Indian Archipelago"—a statement amply confirmed by the present study.