

The distribution of the recent crinoids on the coasts of Australia.

By

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The distribution of the species of recent crinoids on the coasts of Australia offers an interesting problem in the study of zoogeography.

While it may be suggested that as yet our records are not sufficiently numerous to warrant drawing any sweeping conclusions, still they are numerous enough to warrant presentation in such form as to indicate the differences in the faunal conditions on the southern, eastern and western coasts, and to serve thereby as a stimulus for future intensive work.

Two faunal units are represented in Australia, (1) the East Indian, or Malayan, and (2) the Australian, the latter being subdivided into (a) a Tropical and (b) a southern section.

The distribution of the species included in each of these is as follows:

East Indian Species.

	West	East	Difference
Comasteridae			
Comatella stelligera	—	33° 50'	—
Comatella maculata	—	20° 00'	—
Capillaster sentosa	29° 00'+	—	—
Capillaster multiradiata	25° 30'	14° 10'	11° 20'
Comatula solaris	13° 35'	24° 00'	10° 25'
Comatula pectinata	14° 08'	33° 50'	19° 42'
Comaster typica	20° 17'	21° 40'	1° 23'
Comantheria briareus	31° 55'	19° 55'	12° 00'
Comantheria alternans	—	20° 30'	—
Comantherina schlegelii	—	21° 40'	—

	West	East	Difference
Comasteridae			
<i>Comanthus bennetti</i>	—	19° 55'	—
<i>Comanthus samoana</i>	28° 30'	—	—
<i>Comanthus annulata</i>	31° 55'	20° 00'	11° 55'
<i>Comanthus parvicirra</i>	32° 00'	27° 10'	4° 50'
Himerometridae			
<i>Craspedometra acuticirra</i>	—	33° 50'	—
<i>Amphimetra crenulata</i>	14° 08'	24° 00'	9° 52'
<i>Amphimetra milberti</i>	—	20° 30'	—
<i>Amphimetra discoidea</i>	31° 55'	20° 30'	11° 25'
Stephanometridae			
<i>Stephanometra monacantha</i>	—	10° 37'	—
Mariametridae			
<i>Dichrometra articulata</i>	—	20° 30'	—
<i>Dichrometra gyges</i>	31° 55'	20° 30'	11° 25'
Colobometridae			
<i>Colobometra perspinosa</i>	—	33° 50'	—
Thalassometridae			
<i>Stiremetra arachnoides</i>	—	19° 55'	—

A critical examination of the foregoing data gives the following results.

Of the 14 East Indian species of Comasteridae occurring in Australia 5 are known from one coast only; of the remaining 7, 4 extend further southward on the west than on the east (*Capillaster multiradiata*, 11°20'; *Comantheria briareus*, 12°00'; *Comanthus annulata*, 11°55'; and *Comanthus parvicirra*, 4°50'), and 3 extend further southward on the east than on the west (*Comatula solaris*, 10°25'; *Comatula pectinata*, 19°42'; and *Comaster typica*, 1°23').

The 4 species which extend further southward on the west than on the east vary in the excess of their southerly extension on the west from 12°00' to 4°50', the average being 10°01'.

The 3 species which extend further southward on the east than on the west vary in the excess of their southerly extension on the east from 19°42' to 1°23', the average being 10°30'.

These 7 species therefore show an excess of southerly extension on the east of 0°29'.

Of the 3 East Indian species of Himerometridae only 1 is known from both coasts; this extends further southward ($9^{\circ}52'$) on the east than on the west (*Amphimetra crenulata*).

Of the 2 East Indian species of Mariametridae 1 is known from both coasts; this extends further southward on the west ($11^{\circ}25'$) than on the east (*Dichrometra gyges*).

Taking all of the 22 East Indian crinoids which occur on the Australian coasts we find 9 known from both sides; of these 5 extend further southward on the west than on the east, the average excess of their southerly extension on the west being $10^{\circ}43'$; and 4 extend further southward on the east than on the west, the average excess of their southerly extension on the east being $10^{\circ}11'$.

These 9 species collectively show an excess of southerly extent on the west coast of $0^{\circ}46'$.

Approaching the same problem in another way, we find that the average southern limit of distribution for all East Indian species known from the west coast of Australia (regardless of whether they are known from the east coast or not) is $25^{\circ}05'$ (11 records): while the average southern limit of distribution for all East Indian species known from the east coast (regardless of whether they are known from the west coast or not) is $22^{\circ}54'$ (21 records).

This gives an excess of southerly extent on the west coast of $2^{\circ}11'$.

Australian Tropical Species.

	West	East	Difference
Comasteridae			
<i>Comatula rotalaria</i>	$13^{\circ} 35'$	$20^{\circ} 30'$	$6^{\circ} 55'$
<i>Comatula etheridgei</i>	$14^{\circ} 08'$	—	—
<i>Comatula purpurea</i>	$31^{\circ} 55'$	$14^{\circ} 10'$	—
<i>Comaster belli</i>	$28^{\circ} 30'$	$10^{\circ} 37'$	—
Zygometridae			
<i>Zygometra microdiscus</i>	$26^{\circ} 00'$	$20^{\circ} 30'$	$5^{\circ} 30'$
<i>Zygometra elegans</i>	$31^{\circ} 55'$	$24^{\circ} 00'$	$7^{\circ} 55'$
<i>Zygometra punctata</i>	$13^{\circ} 35'$	$24^{\circ} 00'$	$10^{\circ} 25'$
Himerometridae			
<i>Amphimetra nematodon</i>	—	$20^{\circ} 30'$	—
<i>Amphimetra discoidea</i>	$31^{\circ} 55'$	$20^{\circ} 30'$	$11^{\circ} 25'$
Colobometridae			
<i>Petasometra helianthoides</i>	$26^{\circ} 00'$	—	—
<i>Cenometra cornuta</i>	$15^{\circ} 30'$	—	—

	West	East	Difference
Colobometridae			
<i>Decametra studeri</i>	25° 30'	—	—
<i>Oligometrides adeonae</i>	14° 08'	24° 00'	9° 52'
<i>Oligometrides thetidis</i>	—	34° 25'	—
<i>Oligometra carpenteri</i>	14° 08'	24° 00'	9° 52'
Tropiometridae			
<i>Tropiometra afra</i>	29° 00' †	20° 00'	9° 00' †
Calometridae			
<i>Neometra gorgonia</i>	29° 00' †	—	—
<i>Neometra conamiuis</i>	29° 00' †	—	—

This table brings out the followings facts.

Of the 4 Australian tropical species of Comasteridae 3 are known from both coasts; af these 2 extend further southward on the west than on the east (*Comatula purpurea*, 17° 45'; and *Comaster belli*, 17° 53'), while 1 extends further southward on the east (6° 55') than on the west (*Comatula rotalaria*).

The average excess of the southerly extent of the 2 species the range of which is greater on the west than on the east is 17° 49' while the excess of the southerly extent of the single species the range of which is greater on the east than on the west is 6° 55'; therefore these species of Comasteridae show a total average excess of southerly distribution on the west coast of 10° 54'.

All of the 3 Australian tropical species of Zygometridae are known from both coasts; 2 extend further southward on the west than on the east (*Zygometa microdiscus*, 5° 30'; and *Z. elegans*, 7° 55'), and 1 extends further southward on the east than on the west (*Zygometa punctata*, 10° 25').

The average excess of the southerly extend of the 2 species the range of which is greater on the west than on the east is 6° 42', while the excess of the southerly extent of the species the range of which is greater on the east than on the west is 10° 25'; therefore these species of Zygometridae show a total average excess of southerly distribution on the east coast of 3° 43'.

Of the 2 Australian tropical species of Himerometridae 1 is known from both coasts (*Amphimetra discoidea*); its southerly extension on the west coast exceeds that on the east coast by 11° 25'.

Of the 6 Australian tropical species of Colobometridae 2 are known from both coasts (*Oligometrides adeonae* and *Oligometra carpenteri*); with both of these the southerly extension on the east exceeds that on the west by $9^{\circ} 52'$.

The 1 species of Tropiometridae definitely known from Australia ranges $9^{\circ} +$ further south on the west coast than on the east coast.

Considering all of the 18 Australian tropical species together we find 10 known from both sides of the continent; of these 6 extend further southward on the west than on the east, the average excess of their southerly extension on the west being $11^{\circ} 14'$; and 4 extend further southward on the east than on the west, the average excess of their southerly extension on the east being $9^{\circ} 06'$.

These 10 species collectively show an excess of southerly extent on the west of $2^{\circ} 08'$.

The average southern limit of distribution for all Australian tropical species known from the west coast is $23^{\circ} 22'$ (16 records); while the average southern limit of distribution for all Australian tropical species known from the east coast is $21^{\circ} 26'$ (12 records).

This gives an excess of southerly extent on the west coast of $1^{\circ} 56'$.

Taking all the tropical species, both East Indian and Australian tropical, together, we find that 11 extend further southward on the west than on the east, while 8 extend further southward on the east than on the west; excess of southerly distribution on the west is $2^{\circ} 54'$.

Of all tropical species 27 are known from the west coast and 33 from the east coast; by comparing the average southerly extension of each of these groups we find that the excess of southerly extent on the west is $2^{\circ} 03'$.

South Australian Species.

	West	East	Difference
Comasteridae			
<i>Comatulella brachiolata</i>	$30^{\circ} 55'$	—	—
<i>Comanthus trichoptera</i>	$33^{\circ} 15'$	$32^{\circ} 37'$	$0^{\circ} 38'$
Thalassometridae			
<i>Ptilometra macronema</i>	$25^{\circ} 30'$	—	—
<i>Ptilometra mülleri</i>	—	$32^{\circ} 37'$	—

	West	East	Difference
Antedonidae			
<i>Compsometra incommoda</i>	33° 15'	—	—
<i>Compsometra lovéni</i>	20° 30'	14° 10'	6° 20'

One of the south Australian species of Comasteridae does not occur east of Port Phillip, and therefore does not reach the east coast at all; the other (*Comanthus trichoptera*) ranges 0° 38' further northward on the east than on the west.

The genus *Ptilometra* is confined to Australia, where one species occurs on the west coast and as far east as Port Phillip (*Pt. macronema*) and the other is found only on the east coast (*Pt. mülleri*); of these two species the western has by far the greater range, and extends 7° 07' further northward than the eastern.

Of the two species of *Compsometra* one does not occur further eastward than Port Phillip (*C. incomoda*); the other extends 6° 20' further northward on the east than on the west (*C. lovéni*).

Of all the south Australian species the average excess of northerly extent of those which reach further northward on the west than on the east is 7° 07', while the average excess of northerly extent of those which reach further northward on the east than on the west is 3° 29'; the excess of northerly distribution on the west coast is 3° 38'.

The average northern limit of the five south Australian species which occur on the west coast is 28° 53', while the average northern limit of the three which occur on the east coast is 26° 28'; this gives an excess of northerly range on the east of 2° 25'.

But there are good reasons for believing that *Compsometra lovéni* should, in the present state of our knowledge, be omitted in a discussion of this kind. It is very small and very likely to be overlooked; it probably, like many of the other species in the same subfamily (Antedoninae), swims more or less readily; and, being very closely related to certain tropical species, it may well be that it is merely a tropical species of wide adaptability which has succeeded in establishing itself all around the Australian coasts.

Leaving this form out of consideration we find that the average excess of the two types which inhabit both coasts of Australia is 6° 29' in favour of a northerly limit on the west coast; while the

average northern limit of the south Australian species on the west coast is $30^{\circ} 58'$ that on the east coast being $32^{\circ} 37'$, showing that the south Australian species extend $1^{\circ} 39'$ further up the west than up the east coast.

Briefly stated the faunal conditions about Australia are as follows.

On the west coast the East Indian species extend southward to $32^{\circ} 00'$ (1 species) and $31^{\circ} 55'$ (3 species), and the tropical Australian forms extend southward to $31^{\circ} 55'$ (3 species).

On the east coast the East Indian species extend somewhat further to the southward, reaching $33^{\circ} 50'$ (4 species), but the tropical Australian do not come so far, reaching only $24^{\circ} 00'$ (4 species).

On the west coast the average southern limit of the East Indian species is $25^{\circ} 05'$, and of the Australian tropical species $23^{\circ} 32'$.

On the east coast the average southern limit of the East Indian species is $22^{\circ} 54'$ and of the Australian tropical species $21^{\circ} 26'$.

Thus on the west coast the East Indian forms extend $1^{\circ} 43'$ further southward as a whole than the tropical Australian, on the east coast exceeding the latter by $1^{\circ} 28'$.

On the west coast the average northern limit of south Australian types is $28^{\circ} 53'$, while on the east coast it is $26^{\circ} 28'$; thus on the west coast the northern average limit of south Australian types is $3^{\circ} 48'$ south of the southern average limit of East Indian types and $5^{\circ} 21'$ south of the southern average limit of tropical Australian types; while on the east coast the northern average limit of south Australian types is $3^{\circ} 34'$ south of the southern average limit of East Indian types and $5^{\circ} 02'$ south of the southern average limit of tropical Australian types.

On the west coast the southern limit of the East Indian types is $32^{\circ} 00'$ and of the tropical Australian types $31^{\circ} 55'$, while the northern limit of the south Australian types (excluding *Compsometra lovéni*) is $25^{\circ} 30'$; thus the East Indian and the south Australian species occur together over $6^{\circ} 30'$ of latitude, and the tropical Australian and south Australian species occur together over $6^{\circ} 25'$ of latitude.

On the east coast the southern limit of the East Indian types is $33^{\circ} 50'$ and of the Australian tropical types $24^{\circ} 00'$, while the northern limit of the south Australian types (excluding *Compsometra lovéni*) is $32^{\circ} 37'$; thus the East Indian and the south Australian species occur together over $1^{\circ} 13'$ of latitude, but the

tropical Australian species are separated by $8^{\circ} 37'$ of latitude from the south Australian species.

The points of chief interest are:—

1. On the west coast the tropical Australian species extend $7^{\circ} 55'$ further south than on the east coast.

On the east coast the East Indian species extend $1^{\circ} 50'$ further south than on the west coast.

2. The average southern limit of East Indian species on the west coast is $1^{\circ} 43'$ south of the average southern limit of the tropical Australian species.

The average southern limit of East Indian species on the east coast is $1^{\circ} 28'$ south of the average southern limit of the tropical Australian species.

3. On the west coast the East Indian species extend $0^{\circ} 05'$ further south than the tropical Australian.

On the east coast the East Indian species extend $9^{\circ} 50'$ further south than the tropical Australian.

4. On the west coast the northern average limit of South Australian types is $3^{\circ} 48'$ south of the southern average limit of East Indian and $5^{\circ} 21'$ south of the southern average limit of tropical Australian species.

On the east coast the northern average limit of South Australian types is $3^{\circ} 34'$ south of the southern average limit of East Indian, and $5^{\circ} 02'$ south of the southern average limit of tropical Australian species.

5. On the west coast south Australian and East Indian species occur together over $6^{\circ} 30'$ of latitude, and south Australian and tropical Australian species occur together over $6^{\circ} 25'$ of latitude.

On the east coast south Australian and East Indian species occur together over $1^{\circ} 13'$ of latitude; but the northern limit of the south Australian types is separated from the southern limit of the tropical Australian species by $8^{\circ} 37'$ of latitude.

6. The portion of the south coast of Australia west of Port Phillip belongs faunally with the southwestern coast; the portion east of Port Phillip with the southeastern coast.

7. The fauna of the Aru Islands and of the southern coast of New Guinea, and of the shores of the Arafura Sea, so far as we

know it, is composed of tropical Australian types, to the exclusion of East Indian species; the Ki Islands, however, support an East Indian fauna resembling most closely that of southern Japan.

A Comparison between the Fauna of the East and West Coasts of Australia, in Tabular Form.

	West	East
Number of East Indian Species	10	20
Number of Australian Tropical Species	16	12
Number of South Australian Species	5	3
Total Number of Exclusively Australian Species	21	15
Excess of the maximum southerly extent of the East Indian fauna on the East as compared with the west	—	1° 50'
Excess of the average southerly extent of the East Indian fauna on the West as compared with the East	2° 11'	—
Excess of the maximum southerly extent of the Tropical Australian fauna on the West	7° 55'	—
Excess of the average do.	2° 06'	—
Excess of the maximum southern limit of the East Indian over the Tropical Australian fauna	0° 05'	9° 50'
Excess of the average do.	1° 43'	1° 28'
Distance between the northern average limit of South Australian types and the southern average limit of East Indian	3° 48'	3° 34'
Distance between the northern average limit of South Australian types and the southern average limit of Tropical Australian	5° 21'	5° 02'
Distance wherein South Australian and East Indian types occur together	6° 30'	1° 13'
Distance wherein South Australian and Tropical Australian types occur together	6° 25'	do not overlap
Distance separating extreme limits of South Australian and Tropical Australian types	the two overlap	8° 37'

Before discussing the facts brought out in the preceding pages it is necessary to mention in as few words as possible the characteristics of the two faunal groups represented in Australia.

The so-called Australian fauna, which is entirely composed of tropical types, includes about 50% of the crinoids known from the Australian coasts. It is a true faunal unit, the range of all of the component species collectively being restricted within a definite and circumscribed region embracing the coasts of Australia (and Tasmania), the Aru Islands and New Guinea, beyond which region none

of the species extend. It is divisible into two faunal units, one tropical with its area of maximum intensity in the north, including 70% of the species, the other southern with its area of maximum intensity in the south, including 30% of the species. The component species of the latter are characterized by a certain appearance of compactness arising from the shortness of the individual ossicles of the cirri, arms and pinnules; they are all more closely related to species occurring in the tropical Australian region than to species of any other area, though one of them superficially most resembles the corresponding form from South Africa.

The present Australian fauna appears to be the last remnant of what was once a fauna of very wide distribution, which, through the inability of its component species to adjust themselves to the new conditions constantly arising through geological and other changes, everywhere else has become either so profoundly altered that it has almost entirely lost its original characteristics, or has been entirely supplanted by a faunal unit of later origin.

The East Indian fauna as here considered is a very heterogeneous aggregation of rather more than one hundred species scarcely any two of which have the same range, the most widely spread occurring from east Africa to Japan, while many are known only from the Philippine Islands. Between Formosa and Celebes and the Sunda Islands only this fauna occurs, and from this area of maximum intensity it extends itself in every direction in the form of more or less attenuated branches which are superposed upon the faunas of other regions.

This fauna appears to be a residual fauna composed of derivatives from types occurring in each of the surrounding faunal regions, which themselves are localized derivatives from types forming part of the ancient generally distributed fauna of which the present Australian fauna, though greatly impoverished and greatly changed, is the most perfect relict. The East Indian fauna appears to be composed of vigorous and adaptable types which worked their way into the East Indian region as that region was slowly submerged and later, after a period of incubation, as it were, in the waters of the Malay Archipelago, gradually spread outward encroaching upon the surrounding faunas. In other words it appears to be a new and very young faunal complex composed of newly arisen types derived through a process of rejuvenation from preexisting types

which, aided by a continuation of the same geological changes which gave it birth, is overspreading and gradually submerging the older fixed and unadaptable types in all of the surrounding faunal units. Each of these surrounding faunal units is a localized and greatly attenuated remnant of what was once the general fauna of the entire region, and all of them are now disappearing before the encroachment of a new faunal complex which is better fitted to meet the present conditions. Of these faunal units the Australian has undergone the least change, for its species today make up about 50% of all the species known from the Australian region.

One of the striking features of the component species of the East Indian fauna is the retention by the adults of characters occurring only in the young of the corresponding species in other faunal units, such as the development of spinous or granular ornamentation or of keels on the earlier brachials, and great irregularity in the number of the arms. This would indicate that the East Indian fauna was a new and vigorous fauna composed of new and vigorous species, a collection of vigorous immigrants from many different sources just in the process of welding themselves into a powerful faunal entity.

One of the characteristics of the East Indian fauna which differentiates it from all the other faunas is that the species show a regular decrease in frequency from the littoral and sublittoral zones downward; this probably means that the East Indian fauna is as yet so young that it has not had time to assume all the attributes of a true fauna. If we take all of the crinoids occurring in the Caribbean Sea and plot their bathymetric ranges upon a chart we find that at certain depths a greater number of species is found than at the immediately adjacent depths; furthermore these nodes upon the curve of bathymetric distribution are regularly placed. If we take 50 fathoms as our unit (a) we find that these nodes are developed at a , $2a$, 2^2a , 2^3a , 2^4a and 2^5a . In the localities in the Indian and Pacific Oceans where we have sufficient data we find the same thing to be true, but the node $2a$ is omitted, probably on account of the much less bathymetric range of the individual species as compared with Caribbean types.

Taking up the details of the distribution of crinoids in Australia we find that as a whole species are about equally divided between Australian and East Indian, but the proportions between them are

not the same on the two coasts. The west coast possesses only 50% of the East Indian species occurring on the east coast, while on the other hand it supports about 25% Australian species. Thus while on the west coast about 66% of the endemic species are Australian and 33% East Indian, on the east coast conditions are approximately reversed, for here we find about 40% of the species Australian and about 60% East Indian.

While the East Indian species are 50% fewer in number on the west coast and their maximum southerly extension is $1^{\circ} 50'$ less than on the east, the difference between their average and their maximum southern limit is only $6^{\circ} 55'$ as compared with $10^{\circ} 56'$ for the east coast.

The maximum southerly extension of the tropical Australian species on the west coast, where in numbers they exceed those of the east coast by about 25%, is $7^{\circ} 55'$ more than on the east coast; but the average southerly extension is only $2^{\circ} 06'$ greater; while the difference between the average and the maximum southerly extension on the west coast is $8^{\circ} 23'$, it is only $2^{\circ} 34'$ on the east, the conditions on the two coasts being therefore just the reverse of what we found them in the case of the East Indian species.

On the west coast the average southern limit of the East Indian species is $3^{\circ} 48'$ north of the average northern limit of South Australian species, while on the east coast the difference is only $3^{\circ} 34'$; on the west coast the South Australian and the East Indian species occur together over $6^{\circ} 30'$, but on the east over only $1^{\circ} 13'$.

On the west coast the average northern limit of the South Australian species is $5^{\circ} 21'$ south of the average southern limit of the tropical Australian forms, this difference on the east coast being $5^{\circ} 02'$; on the west coast the South Australian and the tropical Australian species occur together through $6^{\circ} 25'$, but on the east they are separated by a gap of $8^{\circ} 37'$.

In short the native Australian (including the South Australian) species are more numerous, though less regularly and evenly distributed, on the west than on the east coast; while the East Indian species are much more numerous, but less regularly and evenly distributed on the east than on the west. On the east the faunal division into a tropical fauna (including both Australian and East Indian elements) and a southern fauna is much better marked

than on the west where the southern fauna extensively overlaps both the elements of the tropical fauna.

The supplanting of the native Australian fauna by intrusive East Indian species has progressed further on the east than on the west because of the much greater accessibility of the east coast to East Indian forms which form the dominant portion of the crinoid population of the islands north, east and southeast of New Guinea, but which form a very much smaller proportion of the species which inhabit the Sunda Islands, the Moluccas and Celebes, this region being the home of a distinctive faunal unit corresponding to the Australian faunal unit, but most nearly resembling the faunal complex occurring of southern Japan.
