Zoogeography of the southern African echinoderm fauna

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Pertinent features of the oceanography of southern Africa are reviewed and an analysis of the echinoderm fauna in relation to the genera] biogeographic regions and local faunistic provinces is given. The last such analysis appeared in 1923, based on fewer species (216) and long before Stephenson's comprehensive analysis of the distribution of the southern African marine biota. Over 400 species of echinoderms are currently known from southern African waters, south of the tropic of Capricorn. These comprise 17 crinoids, 99 asteroids, 124 ophiuroids, 59 echinoids and 108 holothuroids. The endemic component is the richest, accounting for at least 47% of the fauna, with the Indo-Pacific component, including those species restricted to the Indian Ocean, or specifically to the West Indian Ocean, making up 37% of the fauna. The remaining species are either cosmopolitan (3%), tropicopolitan (1%), or shared with the Atlantic (6%) or Southern Oceans (2%), or are 'Other Foreign' species (4%). The distribution pattern along the coast supports the division of the southern African marine region into three faunistic provinces – tropical, subtropical and temperate. The echinoderm fauna appears to have had mostly an Indo-Pacific origin but evidence indicates that, once it became well established and isolated, there was a secondary development of an active evolutionary centre.

Pertinente kenmerke van die oseanografie van Suider-Afrika word oorsigtelik behandel en 'n analise word gegee van die Echinodermata-fauna in terme van die algemene biogeografiese streke en plaaslike faunistiese provinsies. Die laaste soortgelyke analise, gebaseer op 'n kleiner aantal spesies (216) het in 1923 verskyn, lank voor Stephenson se omvattende analise van die verspreiding van die Suider-Afrikaanse marine biota. Meer as 400 spesies van Echinodermata is tans bekend uit Suider-Afrikaanse waters, suid van die Steenbokskeerkring. Dit sluit in 17 Crinoidea, 99 Asteroidea, 124 Ophiuroidea, 59 Echinoidea en 108 Holothuroidea. Die endemiese komponent is die rykste, en sluit ten minste 47% van die fauna in, terwyl die Indo-Pasifiese komponent, insluitende daardie spesies wat beperk is tot die Indiese Oseaan, 37% van die fauna behels. Die oorblywende spesies is òf kosmopolities (3%), òf tropikopolitaan (1%), of word gedeel met die Atlantiese (6%) of Suidelike oseane (2%), of is 'ander vreemde' soorte (4%). Die verspreidingspatroon langs die kus ondersteun die onderverdeling van die Suider-Afrikaanse mariene streek in drie faunistiese provinsies, naamlik, tropies, subtropies en gematig. Die Echinodermata-fauna het blykbaar 'n hoofsaaklik Indo-Pasifiese oorsprong gehad maar aanduidings bestaan dat, nadat die fauna goed gevestig en geisoleer is, daar nietemin 'n sekondêre ontwikkeling van 'n aktiewe evolusionêre sentrum plaasgevind het.

Introduction

The southern African subcontinent, lying south of 23½°S latitude forms a small landmass, narrowing gradually southwards. Since it is the meeting place of two of the world's greatest oceans, it has received faunal invasions from both sides, producing a highly complex fauna, with numerous endemic species.

Its coastline of over 4000 km is very exposed with no large offshore islands to break the force of ocean swells. Nevertheless the subcontinent offers a variety of marine habitats: from coral reefs to rocky shores, sandy beaches to mudflats, mangrove swamps to kelp beds, shallow estuaries to ocean depths in excess of 5000 m, narrow shelves to wide shelves and shoals, gentle slopes to steep slopes, canyons to ridges and submarine mountains. There are, in addition, tropical, subtropical, warm and cold temperate waters as determined by the latitude of a particular region and the prevailing ocean currents. Hence it is not surprising that over 400 species of echinoderms have so far been recorded from this region and this is by no means the full extent of our knowledge of this group.

Marine geology and bottom topography

It is well established that southern Africa was once part of the supercontinent of Gondwanaland, some 225 mya. The Indian Ocean was formed on its eastern side some 180 mya by the drifting away of Australia, Antarctica and India while the Atlantic Ocean was formed on its western side some 100 mya by the drifting away of the South American continent. Shillington (1986) pointed out that the stress caused by the separation of the Falkland Plateau from the eastern side resulted in a shallow (150 m) and narrow shelf (*c.* 12,5 km at Port St. Johns), sloping steeply from its edge to the abyssal plain at 4000 m. This steep slope, in combination with numerous gullies, canyons, ridges, submarine mountains etc., makes dredgings on the east coast very difficult, if not impossible in places. Further, Flemming (in Heydorn 1978) describes southward migrating marine dunes on the east coast, some up to 8 m high, in water depths greater than 50 m. Such massive sediment transport, according to Heydorn (1978) forms a powerful physical barrier to most benthic organisms. Even the outer shelf with its relict algal nodules and shell fragments is said to support only sparse populations of sedentary organisms and hence is unsuitable for the mostly mobile, benthic echinoderms. Thus it is not surprising that only about a third of the echinoderms recorded from the east coast have been taken from waters between 50–1000 m depth.

South and west of Knysna, however, is a submerged plain, the Agulhas Bank, with a gentle slope (1:1000) and fairly deep (190–250 m) and wide (*c.* 300 km) continent shelf, the widest anywhere on the subcontinent.

The west coast of southern Africa is characterized by sand dunes, with occasional rocky outcrops. North of 32°S latitude the coastline is regular and, except for Walvis Bay and Luderitz, devoid of significant embayments. However, south of this latitude, the coastline becomes irregular with several capes and bays, making the south-west Cape topographically different from the remainder of the area (Shannon 1985). Shillington (1986) states that the west coast resulted perhaps from tension faulting. It may be due to this that its bathymetry is so variable. According to Shannon (1985) the continental shelf is narrowest (20 km) in southern Angola (not truly part of the southern African region here considered), but widest (180 km) off the Orange River. Generally, the western shelf is much wider than the eastern shelf and gently sloping. Green mud, just offshore from Walvis Bay, at 50–150 m is said to reflect sterile areas owing to the abundance of hydrogen sulphide and lack of oxygen (Kilburn & Rippey 1982).

Currents and other environmental factors

Brown & Jarman (1978) emphasize two environmental factors of paramount importance in determining the distribution of marine organisms: the degree of separation of the continental landmasses and the temperature of the water. In the southern hemisphere the continents are widely separated, resulting in limited migration of species between them. The species thus shared between the landmasses must have been transported passively by flotsam, etc. or have migrated during shallower times. Thus each such continent has many endemic species, e.g. *c.* 47% of the echinoderms occurring in southern Africa are endemic to this region. A high proportion of endemic species has also been reported for other groups by various workers (Day 1967; Griffiths 1974; Millard 1978; Kilburn & Rippey 1982; Williams 1986; Gosliner 1987). (See Table 3).

Many workers, from Setchell (1917) to Stephenson (1944) and others, have shown that the coastal temperatures have had a great deal of influence on the distribution of the southern African marine biota. These temperatures are a direct result of the latitude of a particular region and of ocean currents. The origin and effects of the major currents washing our shores are complex but well understood and have received tremendous attention from numerous oceanographers. The southbound warm Agulhas current washing the eastern shores produces mean maximum surface water temperatures of between 22–28°C between Port St. Johns and Inhaca Island, while the cold surface water temperatures of between 8–16°C on the west coast are largely a result of the combination of the northbound cold Benguela current and the frequent upwellings owing to the effects of the southerly winds. It is interesting to note that while upwelling on the west coast might lower the summer temperatures of the surface waters to 8–10°C, downwelling in winter, owing to northerly winds, may increase the surface water temperatures to 15–16°C (Shillington 1986). Both Agulhas and Benguela currents interact in the extreme south-west of the Cape Province. Further, between Cape Peninsula and Cape Agulhas there is some injection of cold water derived from the West Wind Drift (Dietrich 1935; Clowes 1950). The mixing of water masses and the degree of upwelling are both variable and seasonal. Hence in the extreme southwest region of the Cape Province, especially in and around False Bay, there are extreme temperature fluctuations with new species perhaps continuously evolving to adapt to these specialized conditions. Mass mortalities often result amongst those species which cannot adapt to these temperature fluctuations. Hence it is not surprising that about 10% of all the echinoderms so far reported from the temperate region of southern Africa are endemic to False Bay where, according to Day (1970), high summer temperatures of up to 23°C have been reported. While this figure might just be a reflection of the frequency of collections, at least some species may exist which will be found not to extend their range out of False Bay.

On the east coast, owing to the shearing action of the southbound Agulhas current, clockwise eddies are generated, occasionally giving rise to north-setting counter currents. While the origin of the latter is debatable and subjected to speculations (Mallory 1961; Bang & Pearse, in Heydorn 1978) there is little doubt that they are responsible for transporting warm temperate species northwards along the east coast, especially those with drifting, planktonic larvae. The complexities of the southern African ocean currents become apparent when local distributions of the various marine groups are analysed.

Review of biogeography

The biogeographical history of southern Africa has recently been well reviewed by Brown & Jarman (1978) and there is no need to go into any detail here. Stephenson's comprehensive analyses of the southern African intertidal fauna, summarized in 1944 and 1948, and his division of the marine region into the tropical east coast, warm temperate south coast and cold temperate west coast provinces, has been widely used. While several workers like Hedgpeth (1957), Day (1959) and Knox (1960) supported Stephenson in his division of the temperate region into warm and cold faunistic provinces, Ekman (1967) and subsequently Briggs (1974) considered the west coast fauna also as warm temperate like that of the south coast. In support of Stephenson, Brown & Jarman (1978) state that while there are many common elements between the west and south coasts, the algae of the west coast show clear affinities with those of the subantarctic region.

Day (1967), in his distributional analysis of the southern African polychaetes, states that whereas the intertidal species show two definite temperate elements, the shelf species do not. He, therefore, recognizes a single temperate province for the Cape and South West African fauna which, according to him, is only weakly differentiated into two components. On this basis he recognizes four faunistic provinces: a tropical Mozambique–Madagascar province on the east coast reaching Delagoa Bay; a Natal subtropical province south of this point to Bashee River, south of Port St Johns; a temperate Cape–South West African province dominated by endemics, reaching Walvis Bay; and a tropical Angolan province north of this point. This last province, however, is not truly part of the southern African region here defined. Day's viewpoint has received support from Griffiths (1974) who analysed the gammaridean and caprellid amphipods, Millard (1978) the hydroids, Williams (1986) the octocorals and Gosliner (1987) the opisthobranch gastropods. In fact Gosliner categorically states that 'well defined boundaries, previously described for southern African biogeographical provinces, are blurred when opisthobranch molluscs are considered'.

According to Brown & Jarman, such findings are not surprising since, while the surface water temperatures vary considerably between both coasts, the water temperatures below 30 m from Port Elizabeth to Luderitz are fairly uniform throughout the year, varying within the narrow range of 12–14°C.

Because of the differences of opinion among Stephenson, Ekman, Briggs and Day as to the best way of dividing the southern African marine region into faunistic provinces, Clark & Courtman-Stock (1976), in analysing the distribution of the southern African echinoderms (excluding the holothuroids), divide the southern African marine region into nine areas arbitrarily demarcated by points along the coast, and treat each area separately. However, their three Luderitz Bay to Cape Town areas correspond roughly to Stephenson's West Coast or Ekman's Namaqua province; their four False Bay to Port Elizabeth areas to Stephenson's South Coast and Brigg's Agulhas province; while their Durban and Lorenzo Marques (Maputo) areas respectively correspond to Day's Natal and Mozambique-Madagascar provinces.

In the present analysis of the zoogeography of the southern African echinoderms, heavy reliance is of necessity placed upon Clark & Courtman-Stock's analysis, which serves as an authoritative guide, and on Clark's (1977) additions to the fauna, while that of the holothuroids has recently been worked out by the writer in a yet largely unpublished work (Thandar 1984).

Distribution in relation to general biogeographic regions

This aspect of the distribution of the southern African echinoderms has been considered by H.L. Clark (1923), Mortenson (1933) and Clark & Courtman-Stock (1976). However, many new taxa have been discovered since H.L. Clark's analysis, Mortenson's account included only the ophiuroids and asteroids, while that of Clark & Courtman-Stock, is treated in a short paragraph in the introduction and excludes the holothuroids.

Approximately 407 species of echinoderms are known to occur in southern Africa, south of the tropic of Capricorn (23½°S). These include 17 crinoids, 99 asteroids, 124 ophiuroids, 59 echinoids and 108 holothuroids. Of these approximately 263 are shelf forms, occurring in waters less than 200 m deep.

Omitted from the latter group are several species whose depth records are not known, those recorded from single specimens or those whose identities are not yet certain.

The 407 species are here grouped into seven faunistic components on the basis of their distribution beyond the limits of southern Africa and each component is treated separately. Table 1 lists the faunistic components and their relative composition in each of the five echinoderm classes. The histogram in Figure 1 compares these components with those represented by only the shelf forms.

The cosmopolitan component is poorly represented and comprises only about 3% of the total fauna (Figure 1) with most of the species belonging to the two largest classes, the Ophiuroidea and Holothuroidea (Table 1). The latter includes only deep-sea species. Because of their lecithotrophic larvae with more or less direct development, there are no cosmopolitan crinoids. Since echinoderms are remarkably stenothermic there are only a few shallow water cosmopolitan forms. Thus, if only the shelf species are considered, the cosmopolitan component drops to under 1%. A figure of 12% was recorded by Day (1967) for the polychaetes and 11,2%

Table 1 Faunistic components and their relative composition in each of the five extant echinoderm classes (all species)

	Crinoids		Asteroids		Ophiuroids		Echinoids		Holothuroids		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Cosmopolitan	0	0	1	1,0	5	4,0	1	1,7	5	4,6	12	2,9
Tropicopolitan	0	0	1	1,0	1	0,8	0	0	2	1,8	4	1,0
Indo-Pacific	7	41,2	21	21,2	47	37,9	31	52,5	45	41,2	151	37,1
Atlantic	1	5,9	10	10,1	8	6,5	3	5,1	4	3,7	26	6,4
Southern	0	0	5	5,1	0	0	0	0	3	2,8	8	2,0
Other Foreign	1	5,9	4	4,0	6	4,8	1	1,7	4	3,7	16	3,9
Endemic	8	47,0	57	57,6	57	46,0	23	39,0	45	41,2	190	46,7
Total	17	100	99	100	124	100	59	100	108	100	407	100

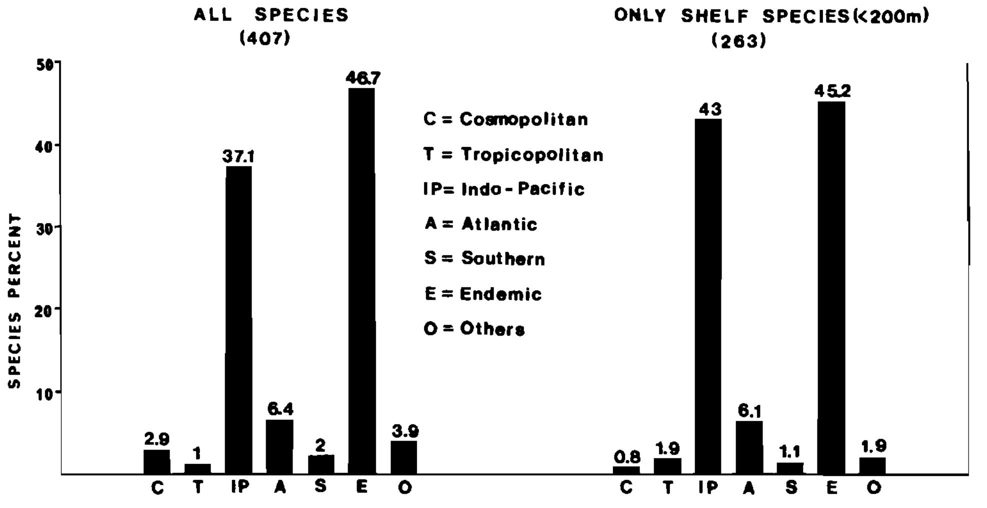

Figure 1 Southern African echinoderm faunistic components and their relative compositions.

for the hydroids by Millard (1978). It must, however, be borne in mind that since the polychaetes and hydroids are among the more adaptable groups with planktonic larvae, they are notorious for their wide distribution. For the other groups whose distributions have been well worked out, the figures range from 1,7% for the opisthobranch molluscs to 7% for the gammaridean and caprellid amphipods (see Table 3).

The tropicopolitan component is here taken to include those species which are common in the tropics of the Indian, Pacific and at least the West Atlantic oceans, but which may extend into the subtropical waters of both hemispheres. This component is even weaker than the cosmopolitan and, like it, does not form a significant component of the southern African echinoderms, representing only 1% of the total fauna. If only shelf species are considered this component rises slightly to about 2% (Figure 1). The polychaetes (Day 1967) and amphipods (Griffiths 1974) show a greater proportion of tropicopolitan species (13% and 10% respectively), while the figure for both the ophisthobranch molluscs (Gosliner 1987) and hydroids (Millard 1978) is about 8% (Table 3). Since the tropicopolitan component amongst the echinoderms is clearly Indo-Pacific in its origin and main distribution, it can just as well be included with the Indo-Pacific component considered below.

The Indo-Pacific component forms the second largest component and is here taken to include those species which are either distributed in the whole or parts of the Indo-West Pacific region, or extend as far as the tropical–subtropical East Pacific region. Thus species restricted to the West Indian Ocean are also included. This component represents roughly 37% of the total fauna with the proportion of the various classes ranging from about 21% for the asteroids, 41% for the crinoids and the holothuroids, to about 53% for the echinoids (Table 1). If only shelf forms are considered this component rises to about 43% (Figure 1). Low figures of 15% and 22% are recorded respectively for the more adaptable polychaetes and hydroids, but about 50% for the very mobile fishes. For the other groups the figures range from 10% for the amphipods to about 20% for non-opisthobranch molluscs to over 48% for the opisthobranch molluscs (Table 3). The wider distribution of the opisthobranchs can be attributed to their indirect development. In fact, Gosliner (1987) states that of the 200 southern African opisthobranch species only one is known with direct development. A high proportion of Indo-Pacific species amongst the echinoderms and octocorals can also be attributed to the indirect development of most species. Since the Indo-Pacific component is one of the largest and is maintained by continuous recruitment from the north and north-east, it is from this component one must expect regular additions to our fauna.

The Atlantic component is here taken to include species distributed in the whole or part of the tropical–temperate Atlantic Ocean. Like the cosmopolitan and tropicopolitan components it is also weak, representing only 6,4% of the total fauna. If only shelf species are considered it drops slightly to 6,1% (Figure 1). The component is highest for the asteroids (*c.* 10%) and lowest for the holothuroids (3,7%). Figures of 13% are recorded for the shelf polychaetes and amphipods, while those of the other groups range from about 3% for the octocorals and hydroids to 8,5% for the opisthobranch molluscs. The latter figure would have been higher if Gosliner (1987) included the area north of Lambert's Bay. A relatively high figure for the polychaetes and amphipods is perhaps due to the fact that Day (1967) included several species from Angola and Griffiths (1974) some from northern Namibia, both of which are not truly part of the southern African region.

The Southern component is here taken to include species from the Southern Ocean Islands and parts of the subantarctic region, but excludes those from southern Australia and New Zealand, which are included with

'Other Foreign' species. This component is also weak and makes up roughly 2% of the total fauna but with the species restricted to the asteroids and holothuroids. If only the shelf species are considered this component drops to 1,1%. A figure of 8% is recorded for the amphipods, but for the other groups it varies from 0% for the opisthobranch gastropods to 4% for the shelf polychaetes.

The endemic component is the richest and makes up roughly 47% of the total fauna. If only shelf forms are considered this component drops slightly to about 45% (Figure 1). However, if all shelf forms are taken into account, including those based on single specimens and those whose depth records are unknown, but which are most certainly shallow water forms, this component rises to 50%. The endemic component is highest for the asteroids (*c.* 58%) and lowest for the echinoids (*c.* 39%) (Table 1). Proportions for the other marine groups range from 13% for the fishes (Smith & Heemstra 1986) to approximately 89% for the cumacean crustaceans (Day 1978) and 73% for the non-opisthobranch molluscs (Kilburn & Rippey 1982). The latter group must be viewed against the background that most of the prosobranchs, which make up the bulk of the non-opisthobranch molluscs, undergo direct development and are hence not widely distributed. According to Gosliner (1987), species with direct development are far less widely distributed than those with planktotrophic larvae. Hence correlation between length of larval life and levels of endemism is said to be very strong in molluscs and this is perhaps true for most marine groups. Further, Kilburn & Rippey's analysis did not include species from Mozambique where a significant number of Indo-Pacific species occur. If the latter were included, they would have most certainly lowered the proportion of endemic species.

The high proportion of endemics among the echinoderms (47%) perhaps can also be explained on the basis of the absence of planktonic larvae in many species. In fact, Pawson (1970) states that dendrochirote holothuroids develop directly without a pelagic larval stage. Hence we notice that the level of endemism is high amongst this group when compared with the aspidochirote holothuroids. Kensley (1983) has also shown that decapod crustaceans show less endemism in southern Africa than amphipods and isopods, since most have pelagic larvae, while the latter two groups brood their young. Polychaetes also have a low level of endemism (36%) because a large number of species have pelagic larvae and are hence widely distributed. The low level of endemism amongst the fishes (13%) is perhaps attributable to their highly mobile habits.

The remaining species are all grouped here into *'Other Foreign'* species whose distribution extends beyond the limits of southern Africa, but cannot be assigned to any of the above components, probably owing to our imperfect knowledge of their distribution or to erroneous identifications. This complement of species represents roughly 4% of the total fauna but drops to about 2% when only shelf forms are considered.

Distribution in relation to faunistic provinces

Since abyssal species are often widely distributed owing to the more or less uniform bottom temperatures, only the 263 shelf forms are here considered for this analysis. The distribution of these species in relation to faunistic provinces is shown in Table 2 and Figure 2.

As would be expected, the shelf echinoderm fauna of Mozambique, south of the tropic of Capricorn, comprise mostly tropical Indo-West Pacific species, with a sprinkling of endemics in the region of Delagoa Bay (26°S). The approximately 124 species occurring here comprise *c.* 76% tropical Indo-Pacific and circumtropical species, with 19,4% local and southern African endemics. The rest of the species are made up of the Atlantic (2 spp.), Cosmopolitan (1 sp.) and 'Other Foreign' components. There are no endemic representatives amongst the crinoids, asteroids and echinoids. The high concentration of tropical species in this region of Mozambique is not surprising, since the mean maximum surface water temperature here is about 28°C, similar to that further north. This distribution pattern supports Day's (1967) Mozambique–Madagascar tropical province and Clark & Courtman-Stock's (1976) Lorenzo

Table 2 Echinoderm faunistic components and their relative composition in each of the four faunistic provinces (only shelf species)

	East coast Tropical		East coast Subtropical		South coast Temperate		West coast Temperate		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%
Cosmopolitan	1	0,8	1	0,8	2	1,6	2	2,6	2	0,8
Tropicopolitan	5	4,0	3	2,4	1	0,8	1	1,3	5	1,9
Indo-Pacific	89	71,8	60	48,0	19	15,5	6	7,9	113	43,0
Atlantic	2	1,6	6	4,8	11	8,9	14	18,4	16	6,1
Southern	0	0	1	0,8	3	2,4	3	4,0	3	1,1
Other Foreign	3	2,4	3	2,4	1	0,8	1	1,3	5	1,9
Endemic	24	19,4	51	40,8	86	70,0	49	64,5	119	45,2
Total	124	100	125	100	123	100	76	100	263	100

Table 3 Per cent geographical components of some well known southern African marine groups (all figures rounded off to facilitate comparison)

	Hydroids (Millard 1978)	Octocorals (Williams 1986)	Polychaete annelids (Day 1967)	Opisthobranch molluscs (Gosliner 1987)	Other molluscs (Kilburn & Rippey 1982)	Amphipods (Griffiths 1974)	Echinoderms (this paper)	Fishes (Smith & Heemstra 1986)
Cosmopolitan	11	4	12	2	–	7	3	33
Tropicopolitan	8	–	13	8	–	10	1	–
Indo-Pacific	23	36	15	48	20	10	37	50
Atlantic	3	3	13	9	6	13	6	3–4
Southern	4 }	3	4	0	1–2	8	2	1
Other Foreign	19 }		7	1	1	6	4	–
Endemic	33	55	36	33	73	46	47	13

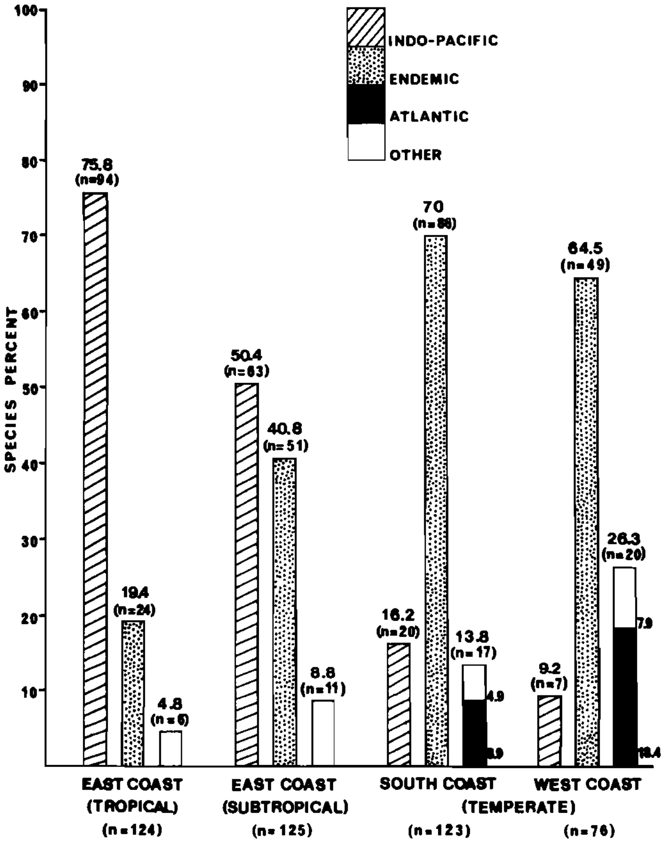

Figure 2 Distribution of southern African echinoderms in relation to each recognized faunistic province.

Marques (Maputo) area.

Beyond the Natal-Mozambique border (*c.* 27°S) to about the region of Port St Johns in northern Transkei (*c.* 32°S), the Indo-Pacific–tropicopolitan component drops sharply to 50,4% (i.e. 63 out of a total of 125 species), while the endemic component rises, also sharply, to 40,8% (51 spp.). This change is most certainly a reflection of cooling waters with mean maximum surface water temperatures of between 24–26°C, cooler than those further north. This area is hence characterized by a subtropical fauna and corresponds with Day's Natal province and Clark & Courtman-Stock's Durban area. There must be a transitional zone between Delagoa Bay and Kosi Bay on the Natal–Mozambique border, but this area has been poorly investigated.

South of Port St Johns and then westward to Cape Point, which is considered an artificial boundary between warm and cold temperate waters by several workers (Stephenson 1944; Ekman 1967; Briggs 1974), the Indo-Pacific component drops drastically to 16,3% while the endemic component increases to 70%. The latter figure represents 86 out of the total of 123 shelf species.

This drastic change is again a reflection of cooling waters, since it is in the region of Port St Johns that the Agulhas current begins to move away from the coast, with the northbound cooler 'counter current' flowing close inshore. As far as intertidal holothuroids are concerned there is 100% endemicity of the fauna west of East London and then northwards into Namibia.

On the west coast from Cape Point to Luderitz in southern Namibia, the number of species decreases to 76 because of colder surface waters. In this region both the Indo-Pacific and endemic components drop slightly to 9,2% and 64,5% respectively, while the Atlantic component, as one would expect, increases from 8,9% on the south coast to 18,4%. Thus there are some changes in the region of the Cape Peninsula but these are not as well marked as those in the region of Port St Johns. In fact, of the total number of shelf species occurring in the temperate region of southern Africa, between East London and Luderitz, as many as 50,8% are common to both coasts.

Of the 76 shelf species occurring on the west coast, only five (*c.* 6,6%) are endemic to the area. Since Briggs (1974) suggests a figure of 10% for an area to be considered a province, the west coast of southern Africa does not satisfy this requirement. In fact H.L. Clark (1946), Ekman (1967) and others, who have sought to justify Australian provinces using the distribution of echinoderms, have considered values in excess of 20%.

The Cape–Namibian region must therefore be considered a single temperate province with a high concentration of endemics but with a substantial decrease in the number of species northwards to Luderitz and beyond. The northern boundary of this temperate province cannot yet be fixed since the fauna of most of Namibia is not well known. Thus the distribution of the shelf echinoderms of the temperate region of southern Africa supports Day's (1967) Cape–South West African province and Millard's (1978) Agulhas–Namaqua region. Stephenson's separate south and west coast provinces are not supported.

Origin of the southern African echinoderm fauna

It is clear that the southern African Indo-Pacific echinoderms, including the tropicopolitan species, have moved in from the north and north-east under the influence of the Mozambique–Agulhas current and perhaps also the East Madagascar current. In fact, recent work summarized by Bang & Pearse (in Heydorn 1978) shows that the latter current forms a major component of the Agulhas current, whereas the Mozambique current is of less importance than has originally been supposed and may not at times even be confluent with it. Whatever the case, these currents aid the migration of tropical Indianic and Indo-West Pacific species down the coast, but since the Agulhas current cools as it progresses, the limit attained by each species is defined by the increasing coldness of the water. Since tropical echinoderm species are remarkably stenothermic, truly Indo-Pacific littoral species rarely occur south of Port St Johns.

As far as the origin of the endemic echinoderms is concerned, this remains problematical, as it is with most of our endemic fauna. The central Indo-Pacific region of the Indo-Malayan archipelago has been the nursery for the development of most of the families and hence it is probable that the ancestors of the southern African endemics must have come from that region. According to Smith (1977), the southern African endemic fishes may represent cold water tolerants of former Indo-Pacific species, survivors from earlier colonizations which became isolated by profound physical and climatic changes on southern African shores. This may be true for all our endemic fauna. The fact that most east coast endemic echinoderms are clearly related to some Indo-Pacific species and that, apart from the deep sea, cosmopolitan and endemic genera, most of the remaining genera are shared with other parts of the Indo-Pacific region, strongly support an Indo-Pacific origin of the endemics. The rifting of the Gondwanaland landmass and the subsequent redistribution of land and sea around South Africa might have played some role in this isolation, but the lack of any significant relationship of the shelf fauna with that of southern Australia, New Zealand, Antarctica and South America, and the absence of any relic species once common to the supercontinent, does not require us to invoke the continental drift theory to explain the distribution of the echinoderms. Some endemic genera found on the west coast are clearly Atlantic in origin and may represent descendents of species which were probably transported here during colder times and have survived on the relatively stable slope in the absence of effective competition.

Hence the nature of the fauna indicates that southern Africa, like the southern continents, has been a region of secondary colonization, built up initially by migration of taxa, rather than a region of primary development. However, once the fauna became well established and isolated, there was a later development of an active evolutionary centre as evidenced by the richness of the endemic species (*c.* 47%), the restriction of many species to the West Indian Ocean (*c.* 13%) or the East Atlantic (*c.* 5%) and some evidence of speciation by ecological or geographic isolation (*c.* 7%). A somewhat similar view was expressed by Millard (1978) for the hydroids and more recently by Thandar (1984, 1987) for the holothuroids and is perhaps true for all southern African shelf fauna.

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