Six new species of *Asterodiscides* A. M. Clark
(Echinodermata, Asteroidea),
with a discussion of the origin
and distribution of the Asterodiscididae
and other 'amphi-Pacific' echinoderms

by F. W. E. ROWE

Abstract. — Six new species are described in the genus *Asterodiscides* A. M. Clark : three from Madagascar and three from the tropical coasts of Australia. Sixteen nominal species are now included in the genus. Two major groups of species can be separated on the basis of possession of three or four superomarginal plates on each side of the arms. Within each of these groups of species, smaller subgroups of the most closely related species can be recognised. The biogeographic distribution of the genera and species is discussed. Despite the absence of asterodiscid fossils, it is concluded that the family arose probably in the early Tertiary. It is considered likely that the family arose in the central-west Pacific and became pan-Tethyan in distribution. Subsequent vicarient events are evoked as a primary cause of present-day generic and specific distributions. 'Amphi-Pacific' distributions of tropical echinoderms are discussed, with the conclusion that taxa occurring in the tropical east Pacific represent relic Tethyan distributions. The origin of the family Asterodiscididae remains obscure.

Résumé. — Six nouvelles espèces du genre *Asterodiscides* A. M. Clark sont décrites, trois provenant de Madagascar, les trois autres des côtes tropicales de l'Australie. Le genre comprend maintenant seize espèces que l'on peut séparer en deux groupes en fonction du nombre, trois ou quatre, de plaques branchiales supéromarginales. A l'intérieur de chacun de ces deux groupes d'espèces, des sous-groupes d'espèces très voisines peuvent encore être reconnus. La distribution géographique du genre et des espèces est discutée. Malgré l'absence de fossiles, l'hypothèse de l'apparition de la famille des Asterodiscididae au début du Tertiaire, dans le Pacifique central-ouest, est formulée. Cette famille a eu ensuite une large distribution dans la Téthys. Des phénomènes postérieurs de vicariance sont sans doute la principale raison de la distribution actuelle du genre et des espèces. Les distributions des échinodermes tropicaux dans le Pacifique sont discutées ; les taxons présents dans l'est-Pacifique tropical sont considérés comme des vestiges de la Téthys. L'origine de la famille des Asterodiscididae reste obscure.

F. W. E. ROWE, *The Australian Museum, 6-8 College Street, Sydney, N.S.W., 2000, Australia.*

INTRODUCTION

The family Asterodiscididae was described by ROWE (1977) to accommodate three genera, *Asterodiscides* A. M. Clark, 1974 (nom. nov. for *Asterodiscus* Gray, 1847, preoccupied), *Paulia* Gray, 1840, and *Amphiaster* Verrill, 1871. *Paulia* and *Amphiaster* were con-

sidered to be monotypic (though *P. galapagensis* and *Pauliella enigma* Ludwig, cannot be synonymous with *P. horrida* Gray, as DÖDERLEIN (1936) and ROWE (1977) have suggested D. BLAKE, pers. comm, see p. 553). These two genera occur in relatively shallow water (0-30 m) and are restricted in distribution to the eastern tropical Pacific. On the other hand, the nine species and two subspecies included in *Asterodiscides* by ROWE in 1977 extend into deeper water (0-?792 m, usually 30-100 m). The genus is widespread in the Indo-west Pacific region including temperate southern Australia and northern New Zealand but is notably absent from the waters of Indonesia, Malaysia, Papua New Guinea and, with the exception of its recent collection from New Caledonia (JANGOUX, 1984), the islands of the central-west Pacific.

During an overseas study tour, including a visit to the Muséum national d'Histoire naturelle in Paris in 1981, I was invited to examine material of *Asterodiscides* collected from the vicinity of Madagascar. It became apparent not only that three new species were represented in the collection but also that new material of *A. elegans belli* Rowe could be recognised and recorded from Madagascar for the first time. Through the courtesy of Dr. A. GUILLE, this material was returned to the Australian Museum for formal description. While this was being undertaken further material of *Asterodiscides*, which had been collected along the coast of western Australia since 1977, was forwarded to me by Mrs. L. M. MARSH (Western Australian Museum) and three specimens collected from the vicinity of Townsville, Queensland, were sent by Mr. A. BIRTLES (James Cook University, Queensland). Most recently Dr. JANGOUX (Université Libre de Bruxelles) forwarded to me the specimen collected from New Caledonia which he identified as *A. helonotus* (Jangoux, 1984). It was apparent from this material that two new species from western Australia (one of these also occurring in New Caledonia) and a third from Queensland were represented.

In this paper, therefore, six new species are described for the genus *Asterodiscides*, and *A. elegans belli* is raised to specific rank. A tabular key to the species of *Asterodiscides* is presented together with a map illustrating their distribution. A discussion is given of the origin of the genus and its distribution. The distributions of other tropical 'amphi-Pacific' echinoderm genera and species are also discussed.

The following abbreviations are used for Institutions in which material is held :

AM = Australian Museum, Sydney, Australia.
MNHN = Muséum national d'Histoire naturelle, Paris, France.
PMBC = Phuket Marine Biological Centre, Phuket, Thailand.
QM = Queensland Museum, Brisbane, Australia.
WAM = Western Australian Museum, Perth, Australia.

Family ASTERODISCIDIDAE Rowe, 1977

KEY TO THE SPECIES OF *Asterodiscides* A. M. Clark, 1974

1. Shape of body :
   P — pentagonal, R/r = 1.1 — 1.5 ;
   S — stellate, R/r = 1.5 — > 2.0.
2. Number of superomarginal plates.

3. Whether proximal superomarginals can be discerned from adjacent plates in large specimens :
   D — discernable ;
   N — not discernable.

4. Shape of distalmost superomarginal plates :
   L — elongate : vd > hd ;
   O — ovate : v ≃ hd ;
   S — squarish to oblong.

5. Relative size of distalmost superomarginal to proximal superomarginal plates :
   e — about equal ;
   l — much larger.

6. Convexity of distalmost superomarginal plates :
   F — flat ;
   M — moderately convex ;
   C — very convex.

7. Number of inferomarginal plates underlying the distalmost superomarginal plates :
   f — less than 6 ;
   m — more than 6.

8. Whether inferomarginal plates can be discerned from adjacent plates in large specimens :
   D — discernable ;
   N — not discernable.

9. Shape of abactinal tubercles :
   p — conical and/or very pointed ;
   s — subspherical ;
   l — inverted cones ;
   c — cylindrical.

9a. Horizontal diameter (mm) abactinal granules (*helonotus/soelae* only) :
   S = 1.1/3.0, juv/adult (*helonotus*) ;
   I = 1.5/3.6, juv/adult (*soelae*).

10. Horizontal outline of abactinal tubercles :
   R — rounded ;
   A — angular.

11. Basal ring of granules associated with tubercles :
   + — present ;
   — — absent.

12. Interstitial granules :
   p — present ;
   a — absent.

13. Actinal tuberculation :
   F — less than 10 subequal granules per actinal plate ;
   M — more than 10 subequal granules per actinal plate ;
   R — single (rarely 2-3) prominent, subspherical tubercle dominating the actinal plate ;
   S — single, prominent, spatulate tubercle dominating the actinal plate.

14. Number of furrow spines per adambulacral plate.

15. Number of series of subambulacral spines.

16. Number of subambulacral spines per adambulacral plate in first series :
   1 — one spine on each adambulacral plate ;
   2 — two spines on each adambulacral plate.

17. Number of subambulacral spines per adambulacral plate in second series :
    1 — one spine on each adambulacral plate ;
    2 — two spines on each adambulacral plate.

18. Number of additional subambulacral spines per adambulacral plate (parentheses signify occasionally present).

19. Distribution :
    A — Philippines (—? Nth China) ; B — Western — north eastern Indian Ocean ; C — Western Australia and New Caledonia ; D — Queensland, Australia ; E — Madagascar, Indian Ocean ; F — Philippines — Japan ; G — Southern Australia — Kermadec Is — northern New Zealand ; H — Arabian Sea ; I — Hawaii ; J — Queensland — Norfolk and Kermadec Islands and Japan ; K — Western Indian Ocean.

20. Depth range (m).

	1	2	3	4	5	6	7	8	9	9a	10	11	12	13	14	15	16	17	18	19	20
elegans (Gray)	P	3	n	O	1	F	f	D	p/s		R	+	a	M	4-5	2(3)	2	1/2	(1)	A	18-120
belli Rowe	P	?3	n	O	1	F/M	f	D	p/s		R	+	a	R	3-4(5)	2(3-4)	2	1	(1)	B	20-250
macroplax Rowe	P	3	n	O	1	F	f	D	p		R	+	p	R	4-5	2(3)	1	1	(1)	C	7-83
multispinus Rowe	P	?3	n	L	1	F	f	D	p/s		R	+	p	R	4(3-5)	3-4(6)	1	1	3-4	D	23-275
cherbonnieri Rowe	S	3	d	O	1	C	f	D	s		R	−	a	F	5	2	2	2	2	E	50-120
crosnieri Rowe	S	3	d	O	1	M	f	D	s		R	+	p	M	7	2	1/2	1	—	E	150
pinguiculus Rowe	S	?3	n	L	1	M	f	N	p/s		R	+	p	R	3-5	2(3)	1	1/2	(1)	C	23-27
fourmanoiri Rowe	S	4	n	L	1	M	f	D/N	s		R	+	p	R	5(6)	2	1	1	—	E	55-115
helonotus (Fisher)	S	4	n	S	1	F	m	D	i	S	R	+	p	S	3(4)	1-2	1	(1)	—	F	18-81
soelae Rowe	S	4	d/n	S	1	F	m	D	i	I	A/R	+	p	S(R)	3(4)	1(2)	1	(1)	—	C	33-80
tessellatus Rowe	S	4	d	S	1	F	m	D	i		A	+	a	S	3	2	1	1	—	K	99
truncatus (Coleman)	S	4	d	O	1	C	f	D	c		R	−	a	R	3-4(5)	1	1	—	—	G	14-792
lacrimulus Rowe	S	4	d	L	1	F	f	D	p		R	+	p	F/M	5	2	2	1	—	H	75-175
tuberculosus (Fisher)	S	4	d	L	1	M	f	D	p/s		R	+	p	R	5-6	2	2	1	—	I	59-396
grayi Rowe	S	4	d	L	1	M	f	D	p/s		R	+	p	F	5-7	2	2	1	—	J	71-108
culcitulus Rowe	P	4	d	O	e	F	f	D	s		R	+	p	M	5-7	2	2	1	—	C	31-180

Asterodiscides belli Rowe

(Fig. 1 ; pl. I, A-C)

Asterodiscus elegans ; BELL, 1909 : 19 (part) ; MACNAE and KALK, 1969 : 129 ; JAMES, 1969 : 52 ; CLARK and ROWE, 1971 : 34, 40, 53 (part) ; (non *A. elegans* Gray, 1847).

Asterodiscides elegans ; CLARK, 1974 : 435 ; CLARK and COURTMAN-STOCK, 1976 : 67.

Asterodiscides elegans belli Rowe, 1977 : 199, fig. 3A-D.

MATERIAL : Amirante Is, western Indian Ocean, 46 m ; 1 paratype, Stanley GARDINER Expedition (AM, J9734). Madras, India ; 1 specimen, E. THURSTON (AM, J9735). Laem Pan Wa, west coast Thailand, 20-30, coarse sand, gravel and mud, 19.x.1978 ; 1 specimen, N. ANUWAT and T. PITTIWONG (PMBC, E68). Passe nord Tulear, south-western Madagascar, 200-250 m ; 1 specimen, R. PLANTE (1969) (MNHN, ECAS 876). South-west of Ile Mitsio, northern Madagascar, 30 m, sand ; 1 specimen, A. CROSNIER (1960) (MNHN, ECAS 611). Ile Mitsio, northern Madagascar, 60 m, sand ; 1 specimen, A. CROSNIER (MNHN, ECAS 607).
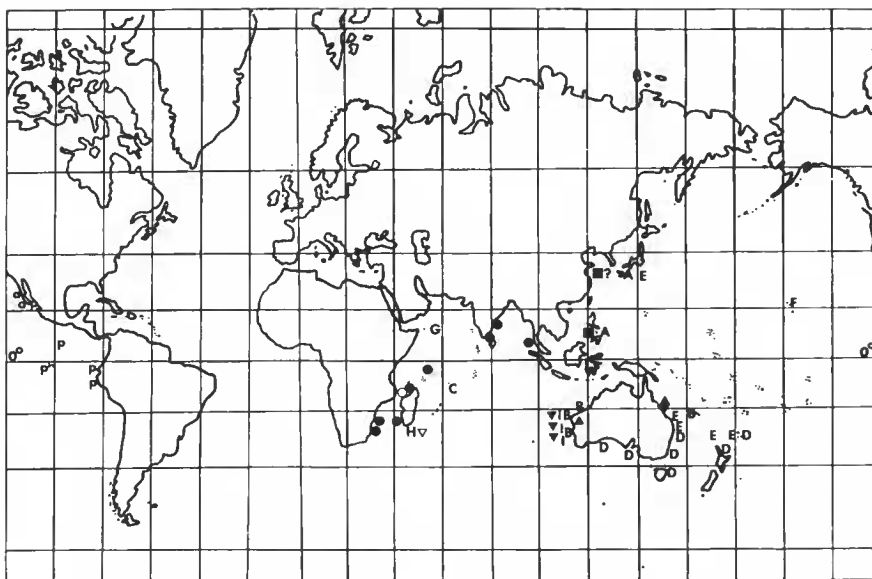
Fig. 1. — Distribution of family Asterodiscididae : *Asterodiscides helonotus* (A) ; *A. soelae* (B) ; *A. tessellatus* (C) ; *A. truncatus* (D) ; *A. grayi* (E) ; *A. tuberculosus* (F) ; *A. lacrimulus* (G) ; *A. fourmanoiri* (H) ; *A. culcitulus* (I) ; *A. belli* (•) ; *A. elegans* (■) ; *A. macroplax* (▼) ; *A. multispinus* (♦) ; *A. pinguiculus* (▲) ; *A. cherbonnieri* (▽) ; *A. crosnieri* (o) ; *Paulia horrida* (p) ; *Amphiaster insignis* (a).

DIAGNOSIS : Body more or less pentagonal, R/r = 1.1-1.4 ; abactinal tuberculation crowded, larger tubercles with basal ring of granules, interstitial granules present ; 3 superomarginal plates, distalmost tear-shaped, slightly convex, just contiguous above terminal plate, vd/hd = 1.76-1.96 ; proximal superomarginals (? 2) not discernable even after denuding arm ; 3-4, rarely 5 furrow spines, subambulacral spines in 2 series each adambulacral plate with a single inner and single outer spine (rarely a 3rd outer spine present on some plates) ; actinal plates with a single prominent, dome-shaped tubercle, rarely 2-3, and if so either near the interradial margin or adjacent to the adambulacral plates ; pedicellariae common.

REMARKS

All specimens from Madagascar and the specimen from the west coast of Thailand (an extension of range) compare very closely with the original description (ROWE, 1977). They have been directly compared with one of the paratype specimens from Amirante Is (AM, J9734) and a second specimen (AM, J9735) from Madras held in the Australian Museum. Following the examination of this material I believe that *belli* can be clearly distinguished from the closely related species *elegans, macroplax* and *multispinus* by a combination of body shape, and size of the distalmost superomarginal plates, actinal tuberculation, adambulacral armature, and geographic distribution. This close relationship would also indicate that only two proximal superomarginal plates are likely to occur in *belli*. However, this can only be confirmed when juvenile specimens, in which these plates are still

clearly discernable, are recovered. The relationship between *belli, macroplax* and *multispinus* appears to be closer than between any of them and *elegans*.

A. *belli* is herein recognised as a species distinct from *A. elegans*.

Asterodiscides macroplax n. sp.
(Fig. 1 ; pl. II, D-F ; pl. III, A-D)

A. pinguiculus Rowe, 1977 : 204 (part).

MATERIAL : West side Goss Passage, south of Long 1s, Wallabi Group, Houtman Abrolhos, western Australia, 33-36 m, sand and rubble ; 3 specimens, L. MARSH and S. SLACK-SMITH, 17.iv.1978 (1 paratype, AM, J16334 ; holotype, WAM, 186-78 ; 1 specimen, WAM, 187-78). Goss Passage, off Long 1s, Wallabi Group, Houtman Abrolhos, western Australia, 35 m, sand and rubble ; 1 specimen (paratype), S. SLACK-SMITH, 16.iv.1978 (AM, J16336). NW Rosemary 1s, Dampier Archipelago (20°04′ S : 166°06′ E), NW Australia, 63-62 m ; 1 specimen (paratype), S. SLACK-SMITH and L. MARSH, 5.xii.1979 (CSIRO, RV 'Soela') (AM, J14069). North of Malus 1s, Dampier Archipelago (19°45′ S : 116°38′ E-19°44′ S : 116°40′ E), NW Australia, 57-60 m, sponges, brittle-stars, crinoids abundant ; 1 specimen (paratype), S. SLACK-SMITH and L. MARSH, 4.xii.1979) (CSIRO, RV 'Soela') (AM, J14111). East side Goss Passage, Wallabi Group, Houtman Abrolhos, western Australia, 30-36 m, sand ; 1 specimen (paratype), C. BRYCE, 6.iv.1978 (WAM, 188-78). Hommock Id, Zeewyck Channel, Houtman Abrolhos, western Australia, 36-40 m ; 1 specimen (paratype), D. HEALD, 10-22.xi.1980 (WAM, 48-81). ENE Monte Bello 1s (20°17′ S : 116°01′ E-20°18′ S : 166°00′ E), NW Australia, 60 m ; 1 specimen (paratype), S. SLACK-SMITH and L. MARSH, 2.xii.1979 (CSIRO, RV 'Soela') (WAM, 405-80). NE Monte Bello 1s (19°55′ S : 116°00′ E-19°54′ S : 116°02′ E), NW Australia, 78-76 m, many large sponges ; 2 specimens (paratypes), S. SLACK-SMITH and L. MARSH, 3.xii.1979 (CSIRO, RV 'Soela') (WAM, 59-80). NW Australia (20°21′ S : 115°52′ E-20°21′ S : 115°54′ E) ; 2 specimens, B. HUTCHINSON, 11.v.1978 (CSIRO, RV 'Courageous') (WAM, 299-79). Goss Passage, Wallabi Group, Houtman Abrolhos, western Australia ; 1 specimen, B. R. WILSON, 6.iv.1978 (WAM, 831-78). North of Enderby 1s, Dampier Archipelago (19°50′ S : 116°28′ E-19°52′ S : 116°27′ E), NW Australia, 67-70 m ; 1 specimen, S. SLACK-SMITH and L. MARSH, 4.xii.1979 (CSIRO, RV 'Soela'). (WAM, 355-80) NE Monte Bello Is (20°20′ S : 115°38′ E-20°19′ S : 115°39′ E), NW Australia, 52 m ; 1 specimen, S. SLACK-SMITH and L. MARSH, 5.xii.1980 (CSIRO, RV 'Soela') (AM, J14083). NW Dampier, NW Australia, 55-83 m ; 1 specimen, C. OSTLE (WAM, 147-79). 56 miles NNW Dampier, NW Australia ; 1 specimen, C. OSTLE, vi.1978 (WAM 822-78). North of Enderby 1s, Dampier Archipelago (19°49′ S : 116°30′ E-19°51′ S : 116°29′ E), NW Australia, 65 m, with large sponges and few bryozoa ; 1 specimen, L. MARSH and S. SLACK-SMITH, 4.xii.1979 (CSIRO, RV 'Soela') (WAM, 407-80). 38 n miles NNE Port Walcott (19°59′ S : 117°24′ E-19°59′ S : 117°22′ E), NW Australia, 50 m, silty sand and large sponges ; 1 specimen, L. MARSH, 16.iv.1982 (CSIRO, RV 'Soela') (WAM 447-82). 48 miles NW of Port Hedland (19°45.2′ S : 117°58.1′ E-19°45.6′ S : 117°56.6′ E), NW Australia, 50-54 m, shelley-sand ; 1 specimen, L. MARSH and M. BEZANT, 6.x.1982 (CSIRO, 'Soela') (WAM, 1134-82). 57 n miles NW of Port Hedland. (19°34.2′ S : 117°57.4′ E-19°32.7′ S : 117°58.0′ E), NW Australia, 60-65 m, snad shell, rubble ; 1 specimen, L. MARSH and M. BEZANT, 5.x.1982 (CSIRO, RV 'Soela') (WAM, 1132-82). 64 n miles NW of Port Hedland (19°30.4′ S : 117°49.9′ E-19°30.3′ S : 117°46.2′ E), NW Australia, 62 m, sand ; 1 specimen, L. MARSH and M. BEZANT, 5.x.1982 (CSIRO, RV 'Soela') (WAM, 1133-82). 40 n miles NW Rosemary 1s, Dampier Archipelago (19°55′ S : 116°12.1′ E-19°55′ S : 116°10.8′ E), NW Australia, 66-67 m, shell, sand ; 1 specimen, J. MARSHALL, 15.viii.1982 (CSIRO, RV 'Soela') (WAM, 1128-82). 30 n miles NNW Rosemary 1s, Dampier Archipelago (20°01.2′ S : 116°21.1′ E-20°02.4′ S : 116°19.6′ E), NW Australia, 54 m, shell-sand ; 1 specimen, L. MARSH and M. BEZANT, 29.ix.1982 (CSIRO, RV 'Soela') (WAM 1129-82). NE Monte Bello 1s. (19°54′ S : 116°02′ E-19°55′ S : 116°00′ E), NW Australia, 76-

78 m ; 1 specimen, S. Slack-Smith and L. Marsh, 3.xii.1979 (CSIRO, RV 'Soela'). Exmouth Gulf, western Australia, 7-20 m ; 1 specimen (formerly identified as *A. pinguiculus* Rowe), J. Pennon, 'Flinders' (WAM, 361-76).

Diagnosis : Body pentagonal, sub-stellate in juvenile stage, R/r = 1.28 — 1.66 ; abactinal tuberculation spaced or crowded, larger tubercles with basal ring of granules or basal ring absent ; interstitial granules present ; 3 superomarginal plates, distalmost elongate, tear shaped, vd/hd = 1.7-2.7 ; 2 proximal superomarginals discernable in juveniles, not so in adults (R > 40 mm) ; 4-5 furrow spines, subambulacral spines in 2 series, each adambulacral plate with a single inner and single outer spine (rarely a 3rd outer spine present on some plates) ; actinal plates usually with single prominent tubercle, rarely 2-3 and if so adjacent to adambulacral plates ; pedicellariae usually present.

Description

The holotype is more or less pentagonal, R = 70 mm, r = 54 mm, R/r = 1.3. The abactinal tubercles are spaced, of three sizes and conical to bluntly pointed. The largest tubercles measure vd = 2.4 mm, hd = 1.9 mm. A basal ring of granules around the tubercles is absent but interstitial granules are scattered between the tubercles. The cushion-shaped madreporite occurs about 1/3r distance from the anus.

The proximal superomarginal plates are not discernable even after denuding the arm but the distalmost plates are elongate, tear-shaped, vd = 8 mm, hd = 4 mm, vd/hd = 2. These plates are flat, surrounded by a peripheral ring of small granules and each bears a pointed tubercle at its abactinal apex. The pair of plates on each arm are separated abactinally, either side of the terminal plate, by a single abactinal plate.

There are twelve inferomarginal plates. The proximal five plates can be distinguished amongst the general tuberculation since these plates are larger than adjacent plates. Each bears an enlarged tubercle on the abactinal edge with 3-7 subequal, but smaller, tubercles on the rest of the plate and a ring of small, prismatic granules on the periphery.

Actinal plates usually bear one, but up to four enlarged tubercles, of which one is prominent. A ring of inequal, prismatic granules occurs on the periphery of each plate. There are no interstitial granules between them. However, the prominent tubercles are well spaced, one from the other, not crowded and touching (as is the case in *A. belli*). The row of actinal plates adjacent to the furrow appears prominent because each plate bears a compact group of 3-4 tubercles which are more elongate than those on the rest of the actinal surface.

There are c. 42 adambulacral plates, each bearing 4 furrow spines. The proximalmost spine is smaller than the other three, which are longest and of similar size to each other. There are usually 2 subambulacral spines forming a double series along the arm. The periphery of each plate bears prismatic granules. On the abradial edge of some plates one of these granules (usually the central one of 3) may become spiniform, so that the plate appears to have 3 subambulacral spines.

The oral plates bear 8 furrow spines and 5-6 actinal spines.

Pedicellariae occur sparsely on the actinal and abactinal surfaces.

There are nine paratypes which range in size from R = 24 mm, r = 14.5 mm, R/r = 1.65 (AM, J14111) to R = 81 mm, r = 58.5 mm, R/r = 1.4 (WAM, 188-78). In the two smallest paratypes (R = 24 mm (AM, J14111) ; R = 31 mm (WAM, 59-80 (part)) the two

proximalmost superomarginals are discernable. At R = 37.5 mm (WAM, 59-80 (part)) these plates are barely discernable after denuding the arm. In these specimens the distalmost superomarginals have a vd/hd ratio 1.7-1.86. In the smallest specimen only 9 inferomarginal plates are present and the actinal plates can be clearly distinguished in chevrons of plates. The chevrons are formed from 5 rows of plates in each interradial area. In the largest paratype the granulation towards the tip of the arm becomes finer and rounded and there is a distinct difference between the size of actinal and abactinal granulation at the actino-abactinal margin of the animal. The vd/hd ratio of the distalmost superomarginal plates of the larger paratypes increases to 2-2.2. In all other respects the paratypes conform with the description of the holotype.

A further 15 specimens are referred to this species ranging in size from R = 30 mm, r = 19.1 mm, R/r = 1.6 (WAM, 407-80) to R = 78.5 mm, r = 57, R/r = 1.4 (WAM, 831-78) (see table).

The life colour noted for the holotype (WAM, 186-78) is dark red.

The species is named for its elongate distalmost superomarginal plates.

REMARKS

This species is clearly closely related to *A. elegans, A. belli* and *A. multispinus* but can be distinguished quite readily by the shape and size of the distalmost superomarginal plate. In addition the single enlarged tubercle on each actinal plate separates the species from *elegans*, while the number of subambulacral spines separates the species from *multispinus*.

Perhaps the most interesting comparison can be made with the sympatric *A. pinguiculus*. This latter species is based on a single, sub-stellate specimen from off Bernier Id, at the entrance of Shark Bay, western Australia. ROWE (1977) related *A. pinguiculus* to *A. lacrimulus, A. grayi* and *A. tuberculosus*. However, particularly in the form of the abactinal and actinal tuberculation and arrangement of subambulacral spines, this species appears to bear a very close relationship with *A. macroplax*. This is apparent from reidentification now, as *macroplax*, of a second specimen named *pinguiculus* by ROWE in 1977, from Exmouth Gulf, to the north of Shark Bay. Two features stand the holotype of *pinguiculus* apart from *macroplax* in my opinion. *A. pinguiculus* is larger than any know specimen of *macroplax* but is still sub-stellate (R/r = 1.6). In *macroplax* only juvenile forms are sub-stellate (R/r = 1.6) the animal becoming more pentagonal as it grows. Secondly, the size and shape of the distalmost superomarginal plate in *pinguiculus* differs from that of the largest know specimen of *macroplax* (see table 1). In fact the vd/hd ratio of the distalmost superomarginal in *pinguiculus* is similar to that of only the most juvenile *macroplax* (vd/hd = 1.7). Neither can it be ascertained the number of proximal superomarginal or any of the proximal inferomarginal plates in *pinguiculus*, so that until juvenile specimens are collected from the vicinity of Bernier Id, the relationships of that species are difficult to determine. Interestingly, MCNAMARA (1982), in discussing the distribution of the irregular echinoid *Breynia desori* Gray along the coast of western Australia, described adult specimens from Shark Bay as exhibiting paedomorphic characters. Normal populations also occur in Shark Bay. MCNAMARA was unable to explain this phenomenon. That *A. pinguiculus* from Bernier Id, at the entrance of Shark Bay, shows characters which may be interpreted as similar to those found in juvenile forms of *macroplax*, which is at localities on either side of Shark Bay, but so far not from the name locality as *A. pinguiculus*, might

TABLE 1. — Size range of specimens and distalmost superomarginal plates of *A. belli, A. macroplax, A. multispinus, A. pinguiculus* and *A. elegans*, examined in this paper.

REG. No.	SPECIMEN (mm)			SUPEROMARGINAL (mm)			LOCALITY
	R	r	R/r	vd	hd	vd/hd	
A. belli Rowe							
NMNH, ECAS 876	60.0	50.0	1.2	8.8	5.0	1.76	Indian Ocean : Madagascar
AM, J9734 (paratype)	65.0	60.0	1.1	8.2	4.2	1.95	Amirante Ids.
NMNH, ECAS 607 and 611	73.0	60.0	1.2	9.6	5.0	1.96	Madagascar
PMBC, E68	81.5	68.3	1.2	11.8	6.0	1.96	Laem Pan Wa, W coast Thailand
AM, J9735	82.0	72.0	1.1	9.6	5.0	1.96	Madras, India
A. macroplax n. sp.							
AM, J14111	24.0	14.5	1.6	3.9	2.3	1.70	Western Australia : Dampier Archipelago
WAM, 407-80	30.0	19.1	1.6	4.2	2.5	1.70	» »
WAM, 59-80 (paratype)	31.0	20.0	1.5	4.7	2.8	1.70	Monte Bello Ids
WAM, 1133-82	33.5	21.6	1.5	5.5	3.0	1.80	Port Hedland
WAM, 59-80 (paratype)	37.5	23.0	1.6	5.6	3.0	1.86	Monte Bello Ids
WAM, 822-78	39.0	30.0	1.3	6.1	3.2	1.90	Dampier Archipelago
WAM, 147-79	43.0	28.2	1.5	4.8	2.4	2.00	» »
WAM, 1132-82	44.0	31.0	1.4	6.4	2.9	2.20	Port Hedland
AM, J14083	46.0	31.0	1.4	6.4	2.5	2.60	Monte Bello Ids
WAM, 1128-82	48.6	33.8	1.4	6.8	2.6	2.60	Dampier Archipelago
WAM, 405-80 (paratype)	55.0	38.0	1.4	8.4	4.0	2.10	Monte Bello Ids
WAM, 1129-82	55.0	40.0	1.3	9.0	4.2	2.10	Dampier Archipelago
WAM, 355-80	60.0	43.0	1.4	8.0	4.0	2.00	» »
WAM, 299-79	60.0	43.5	1.4	6.9	3.1	2.20	NW Australia (20° S)
WAM, 361-76 (formerly *A. pinguiculus*)	62.0	42.0	1.5	8.2	4.0	2.05	Exmouth Gulf
WAM, 1134-82	63.0	48.5	1.3	7.5	3.3	2.27	Port Hedland
Wam, 299-79	63.0	50.0	1.2	6.7	3.2	2.1	NW Australia (20° S)
WAM, 447-82	64.0	46.0	1.4	7.4	3.0	2.50	Port Walcott
AM, J16336 (paratype)	64.0	47.0	1.3	6.8	3.2	2.10	Houtman Abrolhos
AM, J14069 (paratype)	65.0	43.0	1.5	8.2	4.0	2.05	Dampier Archipelago
WAM, 187-78	67.0	48.0	1.4	7.4	3.5	2.10	Houtman Abrolhos
AM, J16334 (paratype)	70.0	54.0	1.3	8.0	4.0	2.00	» »
WAM, 48-81 (paratype)	72.0	50.0	1.4	6.8	2.5	2.70	» »
WAM, 186-78 (holotype)	74.0	55.0	1.3	10.0	5.0	2.00	» »
WAM, 831-78	78.5	57.0	1.4	9.0	4.6	1.90	» »
WAM, 188-78 (paratype)	81.0	58.5	1.4	8.2	3.7	2.20	» »
A. pinguiculus Rowe							
WAM, 1079-74 (holotype)	92.5	58.5	1.6	12.0	7.0	1.7	Western Australia : Shark Bay
A. multispinus n. sp.							
AM, J16862 (paratype)	74.0	55.0	1.3	10.8	5.2	2.07	NE Australia : Townsville, Queensland
QM, GL2181 (holotype)	97.0	75.0	1.3	12.0	6.1	1.97	» »
AM, J16861 (paratype)	96.0	73.0	1.3	12.1	6.3	1.92	» »

Reg. No.	Specimen (mm)			Superomarginal (mm)			Locality
	R	r	R/r	vd	hd	vd/hd	

A. elegans (Gray)

BM, 1847.6.18.4	24.0	16.0	1.5			c.1.3-1.4	? North China
BM, 1845.3.5.353 (holotype)	36.0	24.0	1.5	5.5	3.5	1.57	? Locality
USNM, 40544	36.0	24.0	1.5	c7.0	5.5	1.27	Philippine Ids
BM, 1843.3.10.9	43.0	32.0	1.3			1.40	? North China
BM, 1849.1.31.4	62.0	47.0	1.3	8.0v	5.0	1.60	? China
BM, 1849.1.31.3	64.0	49.0	1.3	8.0	5.0	1.60	? North China
BM, 1890.5.7.501	90.0	67.0	1.3	9.25	5.20	1.77	Philippines

suggest an analogy. However there is insufficient evidence in the single specimen of *pinguiculus* to support that analogy so that the status of each of the species, *pinguiculus* and *macroplax*, is maintained.

Asterodiscides multispinus n. sp.
(Fig. 1 ; pl. III, E, F)

MATERIAL : 23 n miles NNE Townsville (18°55' S : 146°56' E), Queensland, 25.5 m, sand and mud ; 1 specimen (holotype) A. BIRTLES, 25.vi. 1977 (QM GL2181). 16 n miles NNE Townsville (19°00' S : 146°55' E), Queensland, 23 m, sand and mud ; 1 specimen (paratype), A. BIRTLES, 31.vii.1982 (AM J1686). 22 n miles NE Townsville (18°59' S : 147°05' E), Queensland, 27.5 m, sand and mud ; 1 specimen (paratype), A. BIRTLES, 1.viii.1974 (AM, J16862).

DIAGNOSIS : Body more or less pentagonal, R/r = 1.3 ; abactinal tuberculation and granulation as *A. macroplax* ; proximal superomarginal plates (2) not discernable even after denuding arm, distalmost superomarginals, flat, tear shaped, vd/hd = 1.9-2.0 ; 4 (3-5) furrow spines, 3-4, up to 6 subambulacral spines across the width of the adambulacral plate ; actinal plates with single, rarely 2-3, prominent tubercles ; pedicellariae not common.

DESCRIPTION

The holotype is more or less pentagonal, R = 97 mm, r = 75 mm, R/r = 1.3. The abactinal tubercles are spaced on the disc, of three sizes and bluntly pointed. Towards the arm tip the tubercles become subspherical and crowded. The largest tubercles measure vd = 2.4 mm, hd = 2.2 mm and are surrounded basally by a ring of small granules. The basal ring of granules is absent from the smaller tubercles. A few interstitial granules occur between the tubercles. There is a sharp change in size between the abactinal tubercles and the adjacent actinal tubercles at the actinal/abactinal edge of the arms and disc. The madreporite occurs about 1/3r distance from the anus.

The proximal superomarginal plates are not discernable even after denuding the arm. The distalmost superomarginals are flat, tear-shaped, vd = 12, hd = 61 mm,

vd/hd = 1.96. Each plate is surrounded by a ring of small granules and each pair is just in contact above the terminal plate. At one arm tip one superomarginal is fragmented into two smaller plates, each surrounded by its own ring of granules. This appears to be the result of damage repair.

There are 13 inferomarginal plates of which the proximal plates can be discerned after denuding the arm. A group of 7-10 plates occurs between the actinal edge of the supero-marginals and the inferomarginal line. Each plate bears a conical tubercle, surrounded at its base by a ring of small granules.

The actinal plates bear 1 or 2 (rarely 3) large conical tubercles (vd = 2.44 mm × hd = 2, vd/hd = 1.2) which become spiniform close to the proximal oral angle (vd = 3 mm × hd = 1.5, vd/hd = 2). Each plate has a peripheral ring of subquadrate granules. Prismatic interstitial granules occur between the tubercles.

There are about 50 adambulacral plates, each bearing 3-5 (usually 4) furrow spines. The proximalmost spine is the smallest. There are usually 3 often 4 but up to 6 subambulacral spines which occur across the wide adambulacral plate. This number occurs as far out as the 22nd-25th plate, thereafter 2 subambulacral spines occur on each plate. The spines are of similar size though the outermost has the tendency to be the largest. Prismatic granules occur around the periphery of the plates.

The oral plates bear 9 furrow spines and 5-7 large actinal spines.

Pedicellariae are absent abactinally, occurring sparsely actinally.

There are two paratypes which show little difference from the holotype. The larger paratype (AM, J16861) measures (R = 96 mm, r = 73 mm, R/r = 1.3). Pedicellariae occur sparsely on the abactinal surface and the distalmost superomarginals are variously irregular due probably to damage. The smaller paratype (AM, J16862) measures R = 74 mm, r = 55 mm, R/r = 1.35. The multiple subambulacral spines extend further along the arm, to about the 30th plate.

The colour in life is described for paratype AM, J16861. The abactinal background colour was cream with tubercles dark red. The tube-feet were orange (A. Birtles, pers. comm.).

The species is named for the unusually high number of subambulacral spines.

Remarks

This species is clearly closely related to *A. belli, A. macroplax, A. elegans* and *A. pinguiculus*. This very close relationship indicates that, like *macroplax* and *elegans*, only two proximal superomarginal plates would be present and obvious in juvenile specimens. *A. multispinus* differs from *A. pinguiculus* most markedly by its body shape, the shape of the distalmost superomarginal plates and the high number of subambulacral spines in *multispinus*. The shape of the distalmost superomarginal, the single (or at most 3) tubercles on the actinal plates and the number of subambulacral spines separate *multispinus* from *elegans*. *A. belli* and *A. macroplax* appear to be the most closely related to *multispinus*. The number of subambulacral spines of *multispinus* is the most striking difference but the closely packed actinal tubercles and coarser abactinal tuberculation additionally separate *belli*, and the size and shape of the distalmost superomarginal plates *macroplax* from the Queensland species *multispinus*.

Asterodiscides cherbonnieri n. sp.
(Fig. 1 ; pl. I, D-F)

MATERIAL : Off southeast coast, Madagascar (26°08' S : 45°42' E), 110-120 m ; 3 specimens, R. PLANTE, 1969 (holotype, MNHN, ECAS 2033 (part), paratype, MNHN, ECAS 2033 (part), paratype AM, J16422). Off southeast coast, Madagascar (25°45' S : 44°34' E), 50 m, fond d'algues et de blocs coralligènes ; 1 specimen (paratype), R. PLANTE, 1969 (MNHN, ECAS 883).

DIAGNOSIS : Body stellate, R/r = 1.5 ; abactinal tuberculation crowded, tubercles dome-shaped, lacking basal ring of small granules, interstitial granules absent ; 3 superomarginal plates, distalmost largest, markedly convex, bearing a few scattered granules, each pair of distalmost superomarginals contiguous above the terminal plate, proximal two superomarginals easily discernable amongst general tuberculation ; 5 furrow spines, subambulacral spines in two series, each adambulacral plate bearing an inner and an outer pair of spines ; actinal plates with up to 18 subequal granules ; pedicellariae common.

DESCRIPTION

The holotype is stellate, R = 63 mm, r = 41 mm, R/r = 1.54. The arms are wide basally (Br = 43 mm) tapering to a rounded tip. The ambulacral furrow is recurved at the arm tip so that it is just visible in dorsal aspect. The abactinal tubercles are dome-shaped, crowded, without recognisable order and in 3 sizes. The largest tubercles measure hd = 1.5 mm. There is no basal ring of granules associated with the tubercles, or any interstitial granules between the tubercles. The madreporite is circular and occurs interradially about 1/4r from the anus.

There are 3 superomarginal plates on each side of the arms. The distalmost are markedly convex, horizontally ovate (vd = 8.5 mm, hd = 10 mm, vd/hd = 0.85) and broadly contiguous above the terminal plate. Each superomarginal plate is surrounded by a ring of small granules and up to a dozen spaced granules occur on the surface of each plate. The two proximal superomarginal plates can be discerned without denuding the arms. They are slightly convex and more or less ovate (vd = 4 mm, hd = 3 mm, vd/hd = .1.3), bearing 20-25 granules of which the central 6-8 are larger than those towards the perifery of the plates. A pedicellaria occurs on the abactinal edge of each of the proximal superomarginal plates.

There are 11 inferomarginal plates of which 5-6 underly the distalmost superomarginal. The proximal plates can be discerned from amongst the actinal granulation. Similar to the proximal superomarginals, these plates are ovate, very slightly convex and covered, with the exception of a small, raised bare patch close to the actinal edge, by 50-60 small, subequal granules. The granules towards the abactinal edge of the plate become slightly larger. The proximal five plates increase in size (vd = 4.5-5.8 mm, hd = 3-4 mm) and are separated from each other by 3-4 small plates. The sixth plate measures vd = 5.2 mm, hd = 4 mm and is contiguous with the fifth. The seventh (vd = 3.8 mm, hd = 2.8 mm) and subsequent plates to the arm tip are contiguous and reduce rapidly in size. A pedicellaria is present on the actinal edge of some of the inferomarginal plates. The supero- and inferomarginal series of plates are separated, at least proximally, by about 5 rows of intermarginal plates.

The actinal plates bear 1-5 (usually 2-3) central granules, surrounded by 8-11 subequal, subquadrate granules. A ring, usually discontinuous, of very small granules occurs around the periphery of the plates. There are no prominent granules on the plates and the plates do not show any order of arrangement.

The adambulacral plates, about 50, bear 4 or 5 furrow spines. The proximalmost spine is often less than half the length of the other four which are very similar to each other in shape and size. The subambulacral spines are in two series. The first or inner series comprises two obliquely aligned, more or less similar, cylindrical spines on each of the first 25-27 plates, after which the proximal one of the two becomes smaller and insignificant. The second, or outer, series also comprises two obliquely aligned spines. These are shorter than the spines of the inner row and are sub-equal. The proximal one of the two is the smaller, rather pointed and peg-like whereas the distal one is flattened, spatulate. Distally along the arm the proximal spine of this pair becomes insignificant. The proximal and distal edges of the adambulacral plates bear several prismatic granules.

The oral plates bear 6 furrow spines and 3-5 large actinal spines.

Pedicellariae are present actinally and abactinally as well as being associated with some of the marginal plates.

The paratypes agree in all essential details with the holotype. They vary slightly in size. Paratype MNHN, ECAS 883 measure R = 67 mm, r = 42 mm, R/r = 1.6 and R = 64 mm, r = 41 mm, R/r = 1.56 respectively. Paratype AM, J16422 measures R = 71 mm, r = 47.5 mm, R/r = 1.5.

The species is named for Dr. G. CHERBONNIER who has recently retired from the Muséum national d'Histoire naturelle in Paris and who has contributed so much to our knowledge of the taxonomy of echinoderms.

REMARKS

Like *A. elegans, macroplax* and *A. crosnieri*, this species is known to possess only 3 superomarginal plates. As with *crosnieri*, but unlike *elegans* and *macroplax*, the identity of the proximal two superomarginals is retained in large, adult specimens. This forms, together with the stellate body, large convex distal superomarginals, actinal granulation and arrangement of the subambulacral spines, clear differences from *elegans* and *macroplax* and their nearest relatives *pinguiculus, multispinus* and *belli*. The finer abactinal tuberculation, actinal granulation and shape of the superomarginal plates are all distinctive characters which clearly separate *cherbonnieri* from *crosnieri*.

Asterodiscides crosnieri n. sp.

(Fig. 1 ; pl. II, A-C)

MATERIAL : Off northwest coast, Madagascar (15°21' S : 46°12.5' E), 150 m ; 1 specimen (holotype), A. CROSNIER, 1972 (MNHN, ECAS 1244).

DIAGNOSIS : Body stellate, R/r = c.2.0 ; abactinal tuberculation coarse, without order, tubercles with basal ring of granules, interstitial granules scattered between tubercles ; 3 superomarginal plates,

distalmost largest, ovate vd/hd = 1.4, each pair contiguous above the terminal plate, proximal 2 superomarginals discernable amongst general tuberculation ; 7 furrow spines, subambulacral spines in two series, each adambulacral plate bearing a single, occasionally a pair of, inner and a single outer spine ; actinal plates with up to 10 subequal granules ; pedicellariae common.

DESCRIPTION

The holotype is somewhat distorted but is stellate, R = 112 mm, r = 55 mm, R/r = 2. The arms appear to be wide basally (Br = c.63 mm) and taper to a relatively pointed tip. The ambulacral furrow is not recurved at the arm tip or visible in abactinal aspect in this dried specimen. The abactinal tubercles are dome-shaped, crowded, without recognisable order and in about 3 sizes. The largest tubercles measure hd = 3.3 mm. A ring of granules occurs around the base of the tubercles and interstitial granules are scattered between. The ovate madreporite occurs interradially about 1/3r from the anus.

There are 3 superomarginal plates on each side of the arms. The distalmost is slightly convex, ovate (vd = 7 mm, hd = 5 mm, vd/hd = 1.4) and narrowly contiguous above the terminal plate. A pedicellaria occurs on the proximal edge of the plate. Each plate is surrounded by a ring of small granules. The two proximal superomarginal plates are irregular in shape and convex (vd = 4 mm, hd = 3 mm). Each bears a peripheral ring of small, inequal granules and on the actinal half of the plate are 3-4 tubercles. A slender pedicellaria (occasionally 2) sits in a deep crescentic depression on the abactinal edge of the plate. Between the tubercles and the pedicellaria the plate is usually produced into a bare, abactinally directed cone-like convexity. The distinctive shape and tuberculation of these plates allow easy recognition amongst the adjacent tuberculation.

There are 13 inferomarginal plates of which 4 underlie the distalmost superomarginal plate. The more proximal plates can be discerned from amongst the actinal tuberculation because of their shape and tuberculation. The plates are irregularly circular and convex. The first two measure 3.1 mm diameter, thereafter the more distal plates rapidly become smaller. Each of the first 10 plates is armed similarly to the proximal superomarginals. Each bears a peripheral ring of small but inequal granules. Three or four enlarged tubercles occur on the abactinal edge and a pedicellaria occurs in a deep crescentic depression on the actinal edge of the plate. The area between the tubercles and pedicellaria is produced into a bare, actinally directed cone. The superomarginal and inferomarginal series are separated, proximally, by 3-4 rows of small plates.

The actinal plates are irregular in shape and convexity. They bear up to 10 large, subequal granules none of which becomes prominent. A peripheral ring of small, inequal granules occurs on the periphery of the plates. Interstitial granules occur between the tubercles.

The adambulacral plates (c. 57) bear 6-7 furrow spines for about 1/2 R, the number reducing to 5 and 4 towards the arm tip. The furrow spines are very similar in size and shape except that the proximalmost is slightly shorter than the others. The subambulacral spines are in two series. The inner series usually comprises a single, broadly flattened, truncate spine on each plate but may comprise two spines which may be more or less equal in size or the proximal or distal spine of the pair may be smaller than its partner. Distally the spine is single and becomes slender. The outer series comprises a single, broad spine, flattened on its inner side but rounded on the outer edge. It is shorter than the inner

spines on the proximal plates but on the distal 1/4 R these spines form the more prominent series.

The oral plates bear 10 furrow spines, 7 large actinal spines and 7-8 small prismatic granules.

Pedicellariae are common abactinally and actinally as well as being associated with the marginal plates.

The species is named for Dr. A. CROSNIER who collected the specimen.

REMARKS

This species appears to be most closely related to *A. cherbonnieri* from which differences have already been outlined (p. 543). The discussion relating *cherbonnieri* to other species in the genus *Asterodiscides* equally applies to *crosnieri* so that no further comment is required here. However additionally *crosnieri* does have some similar features shared with *A. lacrimulus* Rowe, known from off Sokotra (western Arabian Sea), particularly in the form of the proximal marginal plates. The much coarser tuberculation and most particularly the possession of only two proximal superomarginal plates in *crosnieri* (there are 3 in *lacrimulus*) readily separate the two species.

Asterodiscides fourmanoiri n. sp.
(Fig. 1 ; pl. V, E ; VI, A-E)

MATERIAL : Sainte-Lucie, southeast coast, Madagascar, 55 m, shell and sand : 3 specimens, A. CROSNIER and P. FOURMANOIR, 1958 (holotype, MNHN, ECAS 875, 2 paratypes MNHN, ECAS 877 and 879). Southeast coast, Madagascar (25°13.1′ S : 47°17.8′ E), 105-115 m ; 2 specimens, A. CROSNIER, 1973 (2 paratypes MNHN, ECAS 1245, AM, J16423). Madagascar (no other data) ; 1 specimen, PETIT, 1926 (paratype, MNHN, ECAS 878).

DIAGNOSIS : Body stellate, R/r 1.6-2.0. Abactinal tuberculation fine, without regular order except in juvenile specimens in which larger tubercles form rows along the length of the arms, most tubercles with basal ring of granules, interstitial granules present between tubercles ; 4 superomarginal plates, proximal 3 discernable in juvenile (R = 40 mm) ; distalmost superomarginals slightly convex, more or less circular in juvenile, ovate in larger specimens (R = 73-85 mm), contiguous above terminal plate ; 4 (rarely 5) furrow spines, subambulacral spines in 2 series, each adambulacral plate bearing a single inner and single outer spine ; actinal plates dominated by a single, large, subspherical tubercle ; pedicellariae common on larger specimens, absent on the juvenile.

DESCRIPTION

The holotype is stellate, R = 85 mm, r = 45 mm, R/r = 1.9. The arms are wide basally (Br = 46 mm), and taper to a rounded tip. The ambulacral furrow is recurved and can just be seen abactinal aspect. The abactinal tubercles are subspherical, crowded on the arms but more spaced towards the centre of the disc. They are in 3 sizes and do not form any recognisable order. The largest tubercles measure up to hd = 2.1 mm. A ring of small granules surrounds the base of the larger tubercles. Interstitial granules occur between the tubercles. The madreporite is more or less circular and occurs interradially about 1/2 r from the anus.

Only the distalmost superomarginal plates are discernable. Each is moderately convex,

ovate (vd = 9.6 mm, hd = 7 mm, vd/hd = 1.37). Each pair is narrowly contiguous above the terminal plate. Each superomarginal has a peripheral ring of small granules.

There are about 13 inferomarginal plates of which the distalmost 5-6 underly the distal superomarginal plate. The proximal inferomarginals are only barely discernable, after denuding the arm of tubercles, because they are a little larger than the adjacent plates (diameter 1.8 mm). Each bears a dome-shaped tubercle which becomes conical on plates towards the arm tip. There are also 2-3 smaller prismatic tuberculiform granules on the actinal edge of each plate. A ring of small granules occurs, irregularly, around the periphery of the plates.

The actinal plates bear a peripheral ring of inequal, prismatic granules and a single dome-shaped to conical tubercle. Often one or two prismatic granules may be judged to be large enough to be termed tubercles.

There are about 57 adambulacral plates each of which bears 4 (rarely 5) furrow spines for almost the whole length of the arm, reducing to 3 then 2 distally. The spines are subequal, the proximalmost being the shortest and most slender and the distalmost being the thickest. The subambulacral spines are in 2 series. Each adambulacral plate bears a single inner and single outer thick, somewhat laterally flattened spine. Distally the inner spine becomes slender and tapering. The periphery of the plate bears inequal, prismatic granules, the granule on the proximal-abradial edge often becoming large and spiniform. A pedicellaria occurs on the proximal edge of a few plates, sitting between the two subambulacral spines.

The oral plate bears 8 furrow spines and 4 actinal spines.

Pedicellariae occur on the actinal plates.

Paratype MNHN, ECAS 877 measures R = 76 mm, r = 42 mm, R/r = 1.8. On several proximal adambulacral plates the prismatic granules on the proximal-abradial edge become a spine, almost as large as or larger than the subambulacral spines. Thus on a number of adjacent plates a third series of spines is evident. Paratype MNHN ECAS 879 is a similar size to ECAS 877. One distal superomarginal plate has been lost and the area is covered by small granules. Both paratypes MNHN, ECAS 1245 and AM, J16423 measure R = 73, r = 45, R/r = 1.6. With the exception of the points outlined all these paratypes are closely similar to the holotype.

A sixth paratype (MNHN, ECAS 878) measures R = 40 mm, r = 20 mm, R/r = 2.0. The abactinal tubercles are in 3 sizes as in the holotype but the largest tubercles form more or less irregular rows, a carinal with 3 abactinal lateral rows each side, along the length of the arms. The smaller tubercles are irregularly arranged between the larger tubercles. The distalmost superomarginals are more or less circular (vd = 5.5 mm, hd = 5 mm) and fairly broadly contiguous above the terminal plate. Each is ringed with small granules. Proximally 3 superomarginal plates can be discerned when the arm is cleaned of tubercles. They are small (diameter 1.4 mm), being scarcely larger than the adjacent plates. There are 10 inferomarginal plates of which the distalmost 3-4 underline the distal superomarginal plate. The inferomarginals are circular (diameter, 1.5 mm), convex and bear tubercles and granules in similar arrangement to the holotype. The proximal supero-, and inferomarginal plates are separated from each other by 4-5 rows of small plates. The actinal plates are dominated by the single, dome-shaped tubercle. The chevron arrangement of plates from adjacent arms is clear with proximally 6 rows in each arm. The fifth and sixth rows com-

prise 3 and 2 plates respectively. The adambulacral armature is as described for the holotype. However, pedicellariae are entirely absent from the animal.

This species is named for P. FOURMANOIR one of its collectors.

REMARKS

This species appears superficially similar to *A. pinguiculus* from Shark Bay, NW Australia. However the abactinal tuberculation is coarser (hd up to 2.1 mm compared with 1.75 mm for *pinguiculus*) and crowded, the body is more stellate (R/r = 1.6-2.0 compared with 1.6 for *pinguiculus*) and the distalmost superomarginals less elongate (vd/hd = 1.37, compared with 1.7) and more convex. The juvenile specimen indicates 3 proximal superomarginals occur in *fourmanoiri* and the inferomarginal plates can be discerned in the adults. In *pinguiculus* the number of proximal superomarginal plates is unknown but believed to probably number only 2 (see p. 552) and the inferomarginal plates are not discernable in the holotype.

Among the species known to possess 4 superomarginal plates, *fourmanoiri* can be distinguished from *helonotus, tessellatus* and *soelae* (p. 552) not only by the form of tuberculation but by the very large, flat, squarish distalmost superomarginal plates present in those species. The very large tuberculation and strongly convex plates, adambulacral armature, as well as its distribution in temperate waters of southern Australia and New Zealand clearly distinguishes *A. truncatus* (Coleman) from *fourmanoiri*. The loss of recognition of the proximal superomarginal plates in larger animals and form of tuberculation does not allow confusion of *fourmanoiri* with either *lacrimulus* (Arabian Sea), *grayi* (Northern Tasman Sea and Japan) or *tuberculosus* (Hawaii Islands).

Asterodiscides soelae n. sp.
(Fig. 1 ; pl. IV, A-F ; pl. V, A)

Asterodiscides helonotus ; JANGOUX, 1984 : 280 (non *A. helonotus* (Fisher)).

MATERIAL EXAMINED : West side Goss Passage, south of Long Is, Wallabi Group, Houtman Abrolhos, western Australia, 33-36 m, sand and rubble ; 1 specimen (holotype), L. MARSH and S. SLACK-SMITH, 17.iv.1978 (WAM, 191-78). West side Goss Passage, off Long Is, Wallabi Group, Houtman Abrolhos, western Australia, 36 m, sand and rubble ; 1 specimen (paratype), D. M. DEVANEY and C. BRYCE, 15.iv.1978 (WAM, 190-78). Monte Bello Is (19°55' S : 116°00' E-19°54' S : 116°02' E), NW Australia, 78-76 m, many large sponges ; 1 specimen (paratype), L. MARSH and S. SLACK-SMITH (CSIRO, RV " Soela "), 3.xii.1979 (WAM, 382-80). Off NW Cape (20°12' S : 115°19' E), NW Australia, 65 m ; 7 specimens (paratypes), R. B. MARTIN, 25.v.1980 (CSIRO, RV " Soela ") (AM J14508). NE Monte Bello Is (20°17' S : 115°46' E-20°16' S : 115°47' E), NW Australia, 53-57 m ; 1 specimen, L. MARSH and S. SLACK-SMITH, 5.xii.1979 (WAM, 408-80). NE Monte Bello Is (20°01' S : 115°58' E-20°03' S : 115°57' E), NW Australia, 80 m ; 1 specimen, L. MARSH and S. SLACK-SMITH, 2.xii.1979 (CSIRO, RV " Soela " (AM, J13775). 45 n. miles north of Cape Legendre (19°36.3' S : 116°48.0' E-19°37.8' S : 116°46.8' E), NW Australia, 44-46 m, shelly sand ; 2 specimens, L. MARSH and M. BEZANT, 30.ix.1982 (CSIRO, RV " Soela ") (WAM, 1131-82). 33 n. miles north of Rosemary Island, Dampier Archipelago (19°55' S : 116°36' E), NW Australia, 58 m, shell and gravel ; 1 specimen, L. MARSH and M. BEZANT, 29.ix.1982 (CSIRO, RV " Soela ") (WAM, 1130-82). Chenal de l'îlot Maitre, New Caledonia, 20 m (de nuit) ; 1 specimen, A. GERBAULT, 12.iv.1981 (MNHN, EA 166 ; JANGOUX, 1984, as *A. helonotus*).

DIAGNOSIS : Body stellate, R/r = 2.0-2.2. Abactinal tuberculation coarse, tubercles inverted cone-shaped, up to 3.6 mm diameter, longitudinal rows more or less evident, tubercles with basal ring of granules, interstitial granules present ; 4 superomarginal plates, 3 proximal plates discernable in juvenile (R = 45 mm), distalmost squarish, flat, broadly in contact above terminal plate ; 3-4 furrow spines ; subambulacral spines usually single series, second spine (as outer series) irregularly present ; actinal plates dominated by a spatulate (occasionally subspherical) spine ; pedicellariae present or absent.

DESCRIPTION

The holotype is stellate R = 89-92 mm, r = 41.4 mm, R/r = 2.1-2.2. The arms are wide basally (Br = 47 mm) and taper to a rounded tip. Width of the arm at the proximal edge of the distal pair of superomarginals 17.5 mm.

The abactinal tubercles are inverted, cone-shaped with the top slightly convex. The tubercles are crowded and in 3 sizes, mean diameters measuring 1.2 mm, 2.2 mm and 3.6 mm, respectively. The largest tubercles stand slightly higher that the others and are therefore more prominent. They form an irregular carinal row with 2-3 abactinal lateral rows on each side. The largest tubercles are circular in cross-section but the smaller tubercles are angular. All tubercles have a basal ring of small granules and interstitial granules are scattered between the tubercles.

Only the distalmost superomarginal plates are discernable. These are very large, flat, squarish, each measuring vd = 13.4 mm, hd = 10.2 mm, vd/hd = 1.3. They are very broadly in contact above the terminal plate (5 mm = 49 % hd). Each plate has a peripheral ring of small granules.

There are 14 inferomarginal plates of which 7 lie below the distal superomarginal plate. Each plate bears a single large tubercle which on the distal 5-8 plates becomes chisel-shaped, then pointed forming part of a distinctive 'fringe' either side of the arm tip, when viewed from above. Each plate has a ring of small granules.

The actinal plates are in 4 rows, each plate bearing a large, spatulate, flattened tubercle on the abradial half of the plate. Each plate has a ring of granules, several of which (3-4) on the abradial edge are enlarged and peg-like. Interstitial granules occur between the actinal tubercles.

Adambulacral plates bear 4 furrow spines on the first 3-4 plates, then 3. There are often 2 subambulacral spines on each plate, the inner one of which is the larger. The tip of this spine is rounded or more often, slightly widened and flattened. The periphery of the plate bears prismatic granules.

The oral plate bears 6 furrow spines and 3 actinal spines.

No pedicellariae are present.

The colour recorded in life was tan.

Nine paratypes are recorded which show minor differences from the holotype (see Table 2 for size range). In the largest (WAM, 190-78, R = 105 mm) the abactinal tubercles are spaced, there are 16 inferomarginal plates, the actinal plates are in 5 rows on each arm, each plate bears subspherical rather than spatulate tubercles and granules, and several plates bear a pedicellaria. The subambulacral spines occur as 2 more or less equal-sized spines on the first 3-4 adambulacral plates, thereafter only one spine on each plate. In paratype WAM, 382-80 (R = 52.5 mm) there are 14 inferomarginal plates. The first two plates each bear a larger tubercle on the abactinal edge and 1 or 2 smaller

tubercles below it. There is a ring of small granules on the periphery of the plate and one or two granules are placed between the small tubercles on the plate. The remaining infero-marginal plates bear only the single large tubercle and peripheral ring of granules. Most of the adambulacral plates bear a single subambulacral spine though, irregularly, a second, small, pointed outer spine occurs. Pedicellariae are common actinally and abactinally, with a pedicellaria present on many of the adambulacral plates proximal to the subambulacral spine. The 7 small paratypes (AM, J14508) measure R = 34.8-45 mm. The tubercles are closely packed, the largest measures 2.0-2.5 mm diameter. The tubercles form a carinal row with 2 abactinal-lateral rows each side. The smallest tubercles are hidden under the larger sized tubercles.Three proximal superomarginal plates can be distinguished after denuding the arm of tubercles. They are more prominent and slightly larger than adjacent plates. There are 12-14 inferomarginal plates. Actinal pedicellariae are present.

The smallest specimen recorded measures R = 17.4 mm. This is similar in size to two specimens of *A. helonotus* Fisher recorded from the Philippine Islands (Rowe, 1977). The tubercles are of 2 sizes only and are closely packed, with a maximum diameter of 1.5 mm (1.0-1.1 mm in juvenile *helonotus*). The 3 proximal superomarginals each have a dome-shaped tubercle, part of the plate bare, and a peripheral ring of small granules. There are 10 inferomarginal plates. Similar to the proximal superomarginals there is a flattened tubercle on the abactinal edge of the inferomarginal plate, the rest of the plate being bare except for the peripheral ring of small granules. Distally the tubercle becomes pointed. There are 5 rows of actinal plates. There are 4 furrow spines on the first 3-4 adambulacral plates thereafter 3. There are 2 series of subambulacral spines. The outer spine in each series is smaller than the inner spine. There are no pedicellariae. The largest specimen, from New Caledonia, measures R = 135 mm. Abactinal tubercles reach a maximum dia-meter of 3.8 mm. There are 2 subambulacral spines per plate for about 2/3 R, thereafter only 1 per plate.

All other specimens examined fall within the range of variation outlined above.

The species is named for the CSIRO (Australian Commonwealth Scientific and Indus-trial Research Organization) Research Vessel "Soela" by which a large amount of the material forming the basis of this report has be collected.

REMARKS

This species is clearly related to *A. tessellatus* Rowe from the Western Indian Ocean and *A. helonotus* Fisher from the Philippines and Japan. The smaller size (R up to 46.6 mm), angular abactinal tuberculation and relatively enormous size of the distal supero-marginal plates (= 1/3 R) of *tessellatus* easily distinguishes it from *soelae*. *A. helonotus* and *A. soelae* appear very closely related. However, the larger size and the shape of the tuberculation, which is evident also in juvenile specimens, and the usually single subambula-cral series of spines in *soelae* distinguish the two species. Also, the arms of *soelae* do not taper as much as those of the few known specimens of *helonotus*, as estimated from the width of the arm at the proximal end of the distal pair of superomarginal plates, and a larger percentage of the horizontal diameter of the distalmost superomarginals is in contact above the terminal plates (see table 2).

TABLE 2. — Data of specimens of *A. soelae* n. sp. and *A. helonotus* (Fisher).

Reg No.	R	r	R/r	Br at sm	vd of sm	hd of sm	vd/ hd of sm	SM contig. (mm)	% sm contig.	Max. diam. tubs	Locality
A. soelae n. sp.											
WAM, 406-80	17.4	9.0	1.90	4.1	2.7	2.5	1.01	1.3	c50	1.5	Western Australia : Dampier Archipelago
Wam, 1130-82	21.0	9.8	2.10	4.8	3.8	4.4	0.80	1.6	36	1.5	Dampier Archipelago
AM, J13775	28.0	12.8	2.20	7.5	5.2	5.2	1.00	3.3	63	1.9	Monte Bello Ids
WAM, 408-80	28.6	12.8	2.20	7.0	5.0	5.0	1.00	3.0	60	2.0	»
WAM, 1131-82	30.0	13.4	2.20	7.8	5.5	5.8	0.95	3.8	65	2.2	Cape Legendre
AM, J14508 (paratypes)	34.8	17.0	2.00	9.7	7.7	6.7	1.14	4.4	65	2.2	Monte Bello Ids
	34.8	17.0	2.00	9.4	7.5	6.9	1.10	4.5	65	2.2	»
Wam, 1131-82	35.5	14.7	2.40	8.5	6.4	6.4	1.00	4.0	62	2.1	Cape Legendre
AM J14508 (paratypes)	36.5	17.0	2.15	10.0	8.5	8.2	1.04	5.0	60	2.0	Monte Bello Ids
	36.7	17.0	2.15	11.0	7.9	7.2	1.10	4.8	66	2.5	»
	36.7	17.5	2.10	9.4	7.5	7.2	1.04	4.0	55	2.4	»
	40.0	17.1	2.30	10.0	8.0	7.4	1.10	4.4	59	2.5	»
	45.0	20.5	2.20	11.5	9.3	7.8	1.20	4.5	57	2.3	»
Wam, 382-80 (paratype)	52.5	24.9	2.10	13.2	8.7	7.9	1.06	4.5	56	2.5	»
WAM 191-78 (holotype)	91.0	43.0	2.10	17.5	13.4	10.2	1.30	5.0	49	3.6	Houtman Abrolhos
WAM 190-78 (paratype)	105.0	53.0	2.00	23.2	14.3	12.0	1.20	3.0	25	3.2	»
MNHN EA166	135.0	68.0	2.00	25.5	13.4	10.3	1.30	4.5	23	3.8	SW Pacific : New Caledonia
A. helonotus (Fisher)											
WAM, 1081-74	14.4	8.6	1.67	3.8	2.0	2.2	0.90	1.0	45	1.0	Philippines
WAM, 1080-74	16.4	8.0	2.00	3.0	2.7	2.7	1.00	1.3	48	1.1	»
Hayashi 1938 (*A. hirotoi* : holotype)	37.0	18.0	2.05	—	6.0	7.0	0.85	—	—	2.8	Japan
USNM, 32633 (*A. helonotus* : holotype)	98.0	48.0	2.04	—	12.4	10.2	1.20	4.2	41	2.9	Philippines

NEW RECORDS

A grayi Rowe, 1977

MATERIAL : NE Solitary Islands, northern New South Wales, Australia, 108 m ; 1 specimen (R = 98 mm, r = 58 mm, R/r = 1.7), K. GRAHAM, 2.viii.1978 (NSW State Fisheries FV " Kapala ") (AM, J11884). Minabe, Wakayama, southern Japan, 20-100 m, 1 specimen (R = 90 mm, r = 42 mm, R/r-2.1), TOHRU IMAOKA, 16.i.1977. (Doshisha University), Kyoto, Japan).

A. culcitulus Rowe, 1977

MATERIAL (DET. L. MARSH, WAM) : About 82 km west of Dongara (29°14′ S : 114°04′ E-29°14.8′ S : 114°5.1′ E), western Australia, 164.6 m. small stones, sponges and sand ; 1 specimen

(R = 16 mm, r = 13 mm, R/r = 1.2), WAM, M.V. "Sprightly" Cruise, 17.ii.1976 (WAM, 955-77). About 100 km west of Dongara (29°08.5′ S : 113°55.5′ E-29°09′ S : 113°56′ E), western Australia, 165 m, sponges and stone rubble ; 1 specimen (R = 19 mm, r = 16 mm, R/r = 1.2), WAM, M.V. "Sprightly" Cruise, 19.ii.1976 (WAM, 959-77). About 73 km west of Cliff Head (29°31.7′ S : 114°15.5′ E-29°32.5′ S : 114°16.2′ E), western Australia, 145 m ; 2 specimens (R = 23 mm, r = 18 mm, R/r = 1.27 ; R = 34 mm, r = 28 mm, R/r = 1.2), WAM, M.V. "Sprightly" Cruise, 18.ii.1976 (WAM, 956-77). About 92 km west of Dongara (29°11′ S : 113°52.2′ E-29°12′ S : 114°01′ E), western Australia, 137 m, many small and large sponges ; 1 specimen (R = 34 mm, r = 26 mm, R/r = 1.3), WAM, M.V. "Sprightly" Cruise, 17.ii.1976 (WAM 954-77). About 77 km south-west of Dongara (29°21′ S : 114°07′ E-29°21.5′ S : 114°07.5′ E), western Australia, 146 m ; 2 specimens (R = 39 mm, r = 30 mm, R/r = 1.3 ; R = 68 mm, r = 51 mm, R/r = 1.33), WAM, M.V. "Sprightly" Cruise, 18.ii.1976 (WAM, 958-77). About 73 km west of Cliff Head (29°31.7′ S : 114°15.5′ E-29°32.5′ S : 114°16.2′ E), western Australia, 145 m ; 1 specimen (R = 58 mm, r = 46 mm, R/r = 1.26), WAM, M.V. "Sprightly" Cruise, 18.ii.1976 (WAM, 957-77), south-west of Dongara (29°31′-21′ S : 114°12′-08′ E), western Australia, 176-180 m ; 3 specimens (R = 30 mm, r = 28 mm, R/r = 1.07 ; R = 62 mm, r = 50 mm, R/r = 1.24 ; R = 64 mm, r = 52 mm, R/r = 1.23), M. WALKER on "Taiyo Maru 71", 5.viii.1979 (WAM, 488-79). Hommock Island, Zeewyck Channel, Houtman Abrolhos, western Australia, 36-39.6 m ; 1 specimen (R = 64 mm, r = 50 mm, R/r = 1.3), D. HEALD, 10-22.xi.1980 (WAM, 49.81). Bottom of Goss Passage, Wallabi Group, Houtman Abrolhos, western Australia ; 1 specimen (R = 68 mm, r = 55 mm, R/r = 1.23), B. R. WILSON, 6.iv.1978 (WAM, 832-78). About 77 km south-west of Dongara (29°21′ S : 114°07′ E-29°21.5′ S : 114°07.5′ E) western Australia, 146 m, sponges, rubble and sand, with echinoids ; 1 specimen (R = 90 mm, r = 68 mm, R/r = 1.3), WAM, M.V. "Sprightly" Cruise, 18.ii.1976 (WAM, 847-76). East side of Goss Passage, off Beacon Isle, Houtman Abrolhos, western Australia, 31-35 m ; 1 specimen (R = 110 mm, r = 83 mm, R/r = 1.3), B. R. WILSON and others, iv.1978 (WAM, 208-78).

DISCUSSION

Following the description of six new taxa the genus *Asterodiscides* is considered to comprise sixteen nominal species. However, each of the species of *Asterodiscides* appears, on present knowledge, to have a relatively restricted distribution (fig. 1). Of these, four species (*macroplax, culcitulus, truncatus* and *soelae*) have been collected in relatively large numbers. These range from juvenile to adult forms and confirm the relatively small variation occurring in structural features which are used in the identification of each of the species (ROWE, 1977). Within the genus two groups of species are evident (table 3) : those with three superomarginal plates (including the larger distalmost plate) and those with four superomarginal plates (including the larger distalmost plate) (see tabular key). Within these two groups can be seen similar developments of body shape, discernability of the proximal superomarginal plates and skeletal armature. Despite the additional information available at this time, particularly in support of two major species groups, it is still not proposed that the genus *Asterodiscides* be subdivided (ROWE, 1977). A major problem lies in the loss of discernability of the proximal superomarginal plates in adult specimens of some species. Without the benefit of juvenile specimens in which the proximal plates can be distinguished (as is possible in *culcitulus, elegans, soelae, fourmanoiri, helonotus* and *macroplax*) species can be difficult to place within one or other of these two groups. With res-

pect to *A. multispinus, belli* and *pinguiculus*, their close overall similarity to *macroplax* and *elegans* leads me to conclude that all five belong within the same species group. However, until juvenile specimens of *belli, multispinus* and *pinguiculus* are collected, this relationship may still be considered open to question. Despite these problems, and as pointed out by ROWE (1977), within each of the two major groups of species, several subgroups of more closely related species can be recognised (table 3). With the benefit of the present material it has been possible to align the species more satisfactorily into the following subgroups :

1. *tuberculosus, grayi* and *lacrimulus* ; ?*fourmanoiri,* ?*culcitulus ;*
2. *helonotus, soelae, tesselatus,* and *truncatus ;*
3. *elegans, belli, multispinus ; macroplax,* and *pinguiculus ;*
4. *crosnieri* and *cherbonnieri.*

TABLE 3. — Species groups and subgroups of *Asterodiscides.*

3 superomarginals (sms)		4 superomarginals (sms)		
Pentagonal-substellate (R/r = 1.1-1.6)	Substellate-stellate (R/r = 1.5-2.0)	Substellate-stellate (R/r = 1.5-2.0)		Pentagonal-substellate (R/r = 1.1-1.5)
Proximal sms not discernable in adults	Proximal sms discernable in adults	Distalmost sms moderate-very large		Distalmost sms very small
Pentagonal (Adult) *elegans* *belli* *multispinus* *macroplax*	*cherbonnieri* *crosnieri*	Distalmost sms moderate ovate	Distalmost sms v large, squarish	*culcitulus*
		Prox. sms discernable in adults *lacrimulus* *grayi* *tuberculosus*	*helonotus* *soelae* *tessellatus*	
Substellate (Adult) *pinguiculus*			Distalmost large sms very convex *truncatus*	
		Prox. sms not discernable in adults *fourmanoiri*		

Of the doubtfully placed species, *culcitulus* and *fourmanoiri* appear to be allied in the *tuberculosus* group, since both are known from juvenile specimens to possess four superomarginal plates. However, in both species the proximal plates are not discernable in adults. In addition, *culcitulus*, unlike any of the other species in the genus, has very small distal superomarginal plates. *A. pinguiculus* appears most closely related to the *elegans* group for the reasons discussed above.

The only temperate species, *A. truncatus*, has a number of similarities which suggest

close relationship with, possibly evolution from, the *helonotus* group, as discussed below (p. 559).

Within the family Asterodiscididae I regard *Paulia* and *Amphiaster* as the least specialised members of the family (ROWE, 1977), by virtue of their more numerous, prominent and closely aligned marginal plates, the distalmost superomarginal plates not being enlarged. I think it likely that they will prove to be geologically older than *Asterodiscides*. Marginal plates are most numerous in *Paulia* which I believe indicates a more primitive genus. On the basis of the descriptions of *Paulia horrida galapagensis* given by LUDWIG (1905) and DÖDERLEIN (1936), and examination of a specimen in the Australian Museum collections (AM J9654) from the Galapagos Islands, in 1977 I drew up a diagnosis for *Paulia* indicating only four superomarginal plates along each side of the arms (or 3 in juveniles if the type of *Pauliella enigma* is considered conspecific with that of *Paulia horrida*). Following examination of type material of *Paulia horrida* Gray, I have found five plates I interpret as superomarginals and six I interpret as inferomarginals, these being more prominent than adjacent plates along the arms. The number of marginal plates in the holotype of *Paulia horrida* may be debatable and open to different interpretations. Dr. BLAKE (pers. comm.) considers there are up to 29 superomarginal and up to 42 inferomarginal plates. On the other hand Miss A. M. CLARK (pers. comm.) also examined the holotype of *P. horrida* finding the " marginal plating very irregular in position and size so it is almost impossible to determine which are true marginal plates and which are more or less interpolated abactinals. My estimate of the number of true superomarginals is no more than twelve. It might even be as few as four. So I think Dr. Blake's was a considerable overestimate. " Clearly this problem will remain until a good growth series of *Paulia* is recovered. However, it now seems probable to me that *P. horrida galapagensis* is not conspecific with *P. horrida* as DÖDERLEIN (1936), followed by ROWE (1977), concluded. The conspecificity of *Pauliella enigma* Ludwig, 1905, with *Paulia horrida*, suggested by me in 1977, would therefore also be incorrect. On the basis that marginal plate number rarely (? *Amphiaster*) increases with growth (ROWE, 1977), doubt must be raised about the relationship of *P. enigma* having three superomarginal plates with *galapagensis* having four, or *horrida* (?) five superomarginal plates. The inclusion of these taxa in the family Asterodiscididae is, however, still supported.

I regard the restriction of marginal plate number, enlargement of the distalmost superomarginal plates, greater spacing between marginal plates, greater extent of papular distribution and reduction in size of tuberculation exhibited by *Asterodiscides* as derived characters. Whether the enlarged distalmost superomarginal plates are the result of fusion of a number of plates is still undetermined. If such a fusion does occur it must be at metamorphosis, for fusion of plates has not been seen to occur in any growth series I have examined (e.g. *elegans, culcitulus, macroplax, helonotus, soelae, truncatus*). Neither does the number of marginal plates increase in adult specimens from that observed in the juvenile specimens of *Asterodiscides*. Among the species of *Asterodiscides*, I regard retention of recognisable proximal superomarginal plates in adult specimens as a more primitive character than apparent loss during growth. *A. culcitulus* may represent the most advanced condition with the distalmost superomarginal plates not only small and of similar size to the proximal plates, but in adults becoming almost indistinguishable from adjacent plates. Whether *Asterodiscides* has arisen directly from a *Paulia*- or *Amphiaster*-like ancestor, or via a number of

intermediate, and as yet unknown genera, is difficult to determine since no fossil history is known. However, I consider that the extent of the structural differences and even current distribution patterns indicate that direct evolution from either of those genera is unlikely.

Although the family has a present-day 'amphi-Pacific' distribution, I do not believe that this is indicative of a recent origin of the family or that the least specialised genera *Paulia* and *Amphiaster* have traversed the Pacific from the west. Indeed, I contend that there is sufficient circumstantial evidence, at least among echinoderm distributions, to support the view that the family is relatively old (early Tertiary). This also supports McCoy & Heck's (1976) and Heck and McCoy's (1978, 1979) view that, as with corals, seagrasses and mangroves, present-day distributions can be interpreted as being due largely to vicariant events which have occurred since at least the early Tertiary.

The present-day fauna of the Indo-west and central Pacific is quite distinct from that of the tropical Americas, due to the effect of the East Pacific Barrier (Ekman, 1946, 1967). Ekman (1946) concluded that only 2 % and 15 % respectively, of stenothermal species and genera of echinoderms are held in common. Ekman (1967) was not convinced by the Wegener's theory of continental drift. He believed, therefore, that these taxa had been able to surmount the oceanic barrier, arriving in the east via the distribution of long-lived larvae from the west Pacific. However it is debatable whether this could be achieved by echinoderm larvae, the vast majority of which (80 %) have a planktonic life of less than 6 weeks (Thorsen, 1961). Ekman (1946, 1967), concluded however, that genera, having developed over a longer period than species, had a greater opportunity to achieve this transfer.

Briggs (1974) strongly supports a one way, west to east, migration of species across the tropical Pacific. Dana (1975) concluded that the eastern Pacific coral fauna is of Indowest Pacific origin, having become established since the Pliocene closure of the connection in between the Caribbean and eastern Pacific. He considered invasion of the eastern Pacific more likely to have occurred since the northern Line Islands moved into the path of the north Pacific Equatorial Countercurrent by sea-floor spreading. On the contrary McCoy and Heck (1976) and Heck and McCoy (1978, 1979) dispute Dana's (1975) conclusions and have concluded instead that there is no sound evidence for long-distance dispersal of corals, seagrasses or mangroves across the tropical Pacific. Heck and McCoy (1978) also point out that equatorial countercurrents have been found to have been non-existent or of questionable existence in the Pacific during the Tertiary. They (1976) interpret present-day distributions as the result of modification of formerly widely distributed Tethyan faunas by tectonic events, speciation and extinction. As far as coral distributions are concerned they (1976, 1978) contend that the formerly widespread biota has been largely eliminated in the Caribbean but refuges on the west coast of America allowed continued existence of Indowest Pacific associated forms.

Zinmeister and Emerson (1979) support Ekman and Dana's views to explain the occurrence of a small Indo-Pacific molluscan faunal element (1 %) in the Panamic Province. They consider that both the north Equatorial Countercurrent and the Cromwell Current carry the Indo-west Pacific element the necessary minimal 5 000 km to the Panamic region. They conclude that the small number of successful invaders from the west is probably due to lack of number of species with extremely long pelagic lives, lack of suitable panamic habitats and the partial barrier formed by the colder, westward directed currents

from the west American region. Regarding the speed of each of the eastward flowing counter currents in the Pacific, the more northerly Equatorial Countercurrent travels at about 1 knot, whereas the deeper, subsurface Cromwell Current reaches speeds of 2-3 knots at 100 m below the surface (WARREN, 1966). However the velocity of these currents is very variable both in time and longitude (WARREN, 1966). If optimal conditions were maintained, however, time taken to cross the 5 000 km distance from the west to east Pacific would be approximately 130 days in the north Equatorial Countercurrent but only about 43 days at 100 m and 3 knot speeds in the Cromwell Current.

I cannot evaluate the taxonomy and therefore the distributions of other phyla. However I do not believe echinoderm distributions to be supportive of the 'eastward colonisation' movement (BRIGGS, 1974), as was supposed (EKMAN, 1946, 1967), particularly if account is taken of present knowledge of plate tectonics, the relative position of continents through time, the likely effect on ocean current systems and climatic changes (WINDLEY, 1982 ; ADAMS, 1981 ; VAN ANDEL, 1979 ; HAMBREY & HARLAND, 1981). I have re-examined EKMAN's (1946) data and find that of the 159 Pacific echinoid, asteroid and ophiuroid genera he lists, although 25 genera (15 %) occur on both sides of the tropical Pacific, only eight of these (5.3 %) : (*Acanthaster, Mithrodia, Pentaceraster, Leiaster, Ophioplocus, Ophiopteris, Toxopneustes* and *Metalia*) are not known also from Atlantic waters. Of the 159 extant genera in EKMAN's list, no fewer than 41 have been recorded in fossil deposits. These range in age to early Tertiary, possibly even to Upper Cretaceous, and in one case (*Ophiolepis*) possibly the Upper Triassic (SPENCER & WRIGHT, 1966). Thirteen of the 25 'amphi-Pacific' genera are known from fossil deposits, almost all of which include European localities (SPENCER & WRIGHT, 1966 ; DURHAM *et al.*, 1966). There is little doubt, therefore, that these genera were well established at a time when they could be distributed by the predominantly westward directed currents (FELL, 1967 ; VAN ANDEL, 1979), through the Tethyan seaway to the west coast of central America.

I do not consider, however, that lack of fossil representation of the remaining echinoderm genera listed by EKMAN necessarily indicates that they are all of recent origin. Of the eight 'amphi-Pacific' genera (which do not occur in Atlantic waters) included by EKMAN (1946), six, (*Acanthaster, Mithrodia, Pentaceraster, Leiaster, Ophioplocus* and *Ophiopteris*) are not represented in fossil deposits. However, I believe their distribution on the tropical coast of America is more likely to represent relic Tethyan distribution than an 'amphi-Pacific' distribution. This view supports McCOY and HECK's (1976) and HECK and McCOY (1978, 1979) argument. It is relevant that a number of EKMAN's 159 echinoderm genera occur in association with coral reefs. *Acanthaster* and *Mithrodia* are two such genera. If the conclusions of GLYNN (1974) on the conspecificity of *A. planci* and *A. ellisi* and POPE and ROWE (1977) on the conspecificity of *M. clavigera* and *M. bradleyi* are correct, then by implication *A. planci* and *M. clavigera* represent self sustaining relic populations of two very old, phenotypically stable species.

As far as *Acanthaster* is concerned, *A. planci* is reported to have a likely larval life span of 3-4 weeks under natural conditions (YAMAGUCHI, 1973 ; STRATHMANN, 1978). In the laboratory *A. planci* larvae have been shown to have a pre-metamorphosis life span of up to 47 days, with the potential for delaying metamorphosis for up to two weeks under unfavourable conditions (HENDERSON and LUCAS, 1971 : STRATHMANN, 1978). Under certain conditions therefore ; delayed metamorphosis for eight-nine weeks and with sustained opti-

mal conditions of depth (100 m) and current speed (3 knots) in the Cromwell Current over that period, it is conceivable that some larvae of *A. planci* might reach the panamic region. Although the behaviour of *Acanthaster planci* larvae in the water column has not been investigated, the likelihood of this shallow-water, reef-living species having planktotrophic larvae adapted to living in depths of 100 m for prolonged premetamorphic periods seems unlikely. The larvae and larval behaviour of species of *Mithrodia* have not, as far as I am aware, been investigated.

I have found at least nineteen other records of Indo-west Pacific echinoderm species which are described with tropical 'amphi-Pacific' distributions (H. L. CLARK, 1902; A. H. CLARK, 1939; HYMAN, 1955; DEICHMANN, 1958, 1959, 1963), but for only three of these are pre-metamorphic life spans known (CHIA and BURKE, 1978). It is possible that not all of these 'amphi-Pacific' species have been correctly identified. The colour description of a specimen of *Ophiocoma scolopendrina* from Clipperton Island (A. H. CLARK, 1939) relates, rather, to one of the two Panamic species *O. alexandri* or *O. aethiops* whose extension of range to Clipperton Island by means of the westward directed north Equatorial Current may not be unexpected. Also, although MORTENSEN (1937, 1938) found *O. scolopendrina* larvae may survive up to six weeks under laboratory conditions, metamorphosis has not been shown to successfully occur after this time. However, even under optimal conditions in the Cromwell Current, it is unlikely *O. scolopendrina* larvae would survive passage to Clipperton Island. Passage via the slower north Equatorial Countercurrent would almost certainly be out of the question. *Ophiocomella sexradia*, recorded as *O. clippertoni* by A. H. CLARK (1939), may prove to be tropicopolitan if conspecificity of the Caribbean *O. ophiactoides* with *sexradia* is also proved (A. M. CLARK in CLARK & ROWE, 1971). Other tropicopolitan species include *Linckia guildingi, Holothuria (Thymiosycia) impatiens* and *H. (T.) arenicola. H. (T.) impatiens* also inhabits the Mediterranean. The larval life of *H. impatiens* may be extended from two-three weeks to up to about seven weeks, under certain circumstances (lack of food) according to MORTENSEN (1938). The likelihood of a successful crossing of the Pacific seems as equally doubtful as that of both *A. planci* and *O. scolopendrina* in my view. *H. (Halodeima) atra* and *H. (Platyperona) difficilis* are very closely related, if not conspecific with *H. (H.) floridana* and *H. (P.) parvula* (respectively) in the Caribbean and, in the case of *difficilis* with *H. (P.) sanctori* in the Mediterranean. Indeed the record of *difficilis* from Clipperton Island is based on type material of a nominal species (*frequentimentis*) described by H. L. CLARK (1902), which DEICHMANN (1958) considers conspecific with *difficilis*. According to MORTENSEN (1938), under laboratory conditions *H. difficilis* may delay metamorphosis for up to seven weeks. Even if such a delay were to occur under natural conditions it would not be sufficient to allow successful colonisation of Clipperton Island from the west. *H. (Mertensiothuria) leucospilota, H. (M.) fuscocinerea, H. (Thymiosycia) hilla, H. (Lessonothuria) pardalis, H. (Cystipus) rigida, H. (C.) inhabilis*, and *Polyplectana kefersteini* recorded from the Panamic region and *H. (Semperothuria) flavomaculata* from Clipperton Island are otherwise widespread in the Indo-west Pacific, from the Red Sea to Hawaii and (at least *leucospilota*) to Pitcairn Island. *H. (Semperothuria) imitans* is known from Ceylon, Samoa and east tropical Pacific. DEICHMANN's (1963) record of the Indo-west Pacific *Stichopus horrens* from Clipperton Island must be treated with reservation since her description of both colour and spicule form speak against a correct identification. Finally the ophiuroids

Ophiactis kröyeri and *Ophioderma panamense* have been reported from Chile, Peru and Hawaii, and Panama and Hawaii respectively by HYMAN (1955).

Interestingly, there has been no suggestion that taxa have spread across the Pacific from the tropical Americas. Indeed BRIGGS (1974) is very definitely of the view that migration is in one direction, from west to east. ZINMEISTER and EMERSON (1979) explain the absence of east to west distribution as being due to the lack of a westward flowing warm-water current for the tropical panamic species, and the absence of suitable non-coral, hard substrate environments for any cool-water species larvae contained in the currents.

Some 32 extant Indo-west Pacific echinoid species are also known to be represented in fossil deposits (MORTENSEN, 1928-1951). At least half of these are known to date from between the Miocene and Oligocene, with one (*Prionocidaris bispinosa*) possibly dating from the Eocene. BLAKE (1975) commented that estimates of rate of morphological evolution and species in macroinvertebrates are limited, however, following his survey of the literature he found that modern animal species may be considered to exist for up to about 30 million years. EKMAN (1946, 1967) commented that the extant amphi-American warm-water species would be of Middle Miocene-Pliocene age to account for their distribution on either side of the Panamanian Isthmus. DEICHMANN (1957) concluded that holothurians are well suited to be indicators of geographic provinces, stating that " certain tropical shallow-water forms (i.e., aspidochirotes such as *Holothuria*) of older origin have an almost circumtropical range... ". Although fossil remains of *Acanthaster* are unknown, other than the spines of *A. planci* found by FRANKEL (1978) from cores on the Australian Great Barrier Reef, which he dated to about 3 000 years old, a possible forerunner of *Acanthaster* has been found in Eocene deposits in Mexico (BLAKE, 1979).

Although, therefore, west to east migration of some taxa from the west Pacific to the tropical west Americas is supported by some authors in their interpretation of the evidence available for the taxa they study, I have found no convincing data showing that the larvae of existing 'amphi-Pacific' echinoderms are able to survive trans-Pacific transportation. Further, an alternative explanation is available for apparent 'amphi-Pacific' taxa which is reinforced by the distribution of both living and fossil echinoderms. This supports the hypothesis of McCoy & HECK (1976) and HECK and McCoy (1978, 1979) for a "widely distributed biota which has been modified by tectonic events, speciation and extinction... "

Such then is the most probable rationale for the current distribution of the family Asterodiscididae and the following explanation is proposed.

The family probably first arose in the mid- or west-Pacific (?Darwin Rise ; MENARD, 1964, 1972 ; LADD, 1960 ; LADD *et al*, 1974) in the early Tertiary when prevailing water currents would distribute elements of the family, towards the west. The tropical west coasts of the Americas could be reached from the east through the Tethyan seaway since passage would not be inhibited by the presence of the Panamanian Isthmus before the Pliocene. Tectonic and climatic events during the Tertiary have isolated the least specialised genera, *Paulia* and *Amphiaster* on the tropical west coasts of the Americas. Extinction of the earliest members or 'precursors' of the family has apparently occurred in the Atlantic and Indo-west Pacific Oceans but, at least in the latter case, not before the evolution of *Asterodiscides*. The restricted distribution of *Asterodiscides* in the Indo-west Pacific might support a view that it evolved in mid-late Tertiary, after the exclusion of contact between the Atlantic and Mediterranean with the Indian Ocean. The present distribution of the genus

might further support the contention that *Asterodiscides* arose in the central or west Pacific region, prior to the formation of the East Indian Archipelago, in the late Miocene, when it was able to distribute relatively easily through the west Pacific and Indian Oceans.

Turning to the distribution of species of *Asterodiscides*, an interesting pattern exists. The species group with three superomarginal plates is distributed throughout the Indian Ocean and eastward to the Philippines in the north and Queensland, Australia, in the south. The species group with four superomarginal plates is also extensively distributed in the Indian Ocean, but occurs as far east as Hawaii in the north Pacific and from New Caledonia, the Kermadec Islands and New Zealand in the south-west Pacific. Both groups are otherwise absent from the east Indian Archipelago and the west and central Pacific. I believe the more widespread distribution of this latter group supports the implication that the four superomarginal plate group is the older even though fossil evidence is lacking to support this contention. Shuto (1983) concluded more widespread distributions of molluscs in the Indo-Pacific indicates greater antiquity of those taxa.

The absence of *Asterodiscides* in the Malay-New Guinea region of the East Indies, and from the islands of the central-west Pacific is difficult to explain. The most parsimonious explanation is that representatives have simply not been collected from those areas despite such expeditions as the 'Challenger', 'Siboga' and 'Albatross'. In describing the distribution of shorefishes on the Pacific Plate, Springer (1982) proposed two hypotheses to explain the decrease in numbers of marine taxa occurring eastward across the plate. The 'Reality Hypothesis' proposes that taxa absent the Pacific Plate have never been present. The 'Extinction Hypothesis' proposes that taxa absent from the Plate were originally present, but have since become extinct. If Springer's first hypothesis is evoked to account for distributions of the species of *Asterodiscides* then the only implication possible is that the genus predates the formation of the east Indian Archipelago during the late Miocene, but antedates the separation of the Atlantic from the Indian Ocean in the early Miocene. The genus would then have been distributed around the Indo-west Pacific margin of the remaining Tethys by the relevant oceanic currents. After the formation of the east Indian Archipelago, water currents between the Indian and Pacific Oceans were substantially altered, with general water movements in both oceans being both toward and away from the Archipelago (Warren, 1966 ; Fell, 1967 ; Van Andel, 1979). To support the 'Reality Hypothesis' then requires that species of *Asterodiscides* did not invade the east Indian region, nor indeed the islands of the central-west Pacific, at any time.

A more likely explanation for the absence of *Asterodiscides* from the east Indian Archipelago and central-west Pacific may rest with Springer's 'Extinction Hypothesis'. In relatively recent (Pleistocene) times glacial periods, together with land movements, have had major effects on sea level, leading to the emergence of continental shelf areas. This would have led to large scale extinctions in the shelf region of the east Indian Archipelago and, presumably, from the narrow shelf regions around the islands of the central-west Pacific. Re-invasion of those regions (particularly the East Indian Archipelago), does not appear to have taken place even though suitable habitats now appear to exist. This may be due to local water current patterns, vagility in *Asterodiscides* species or both. In isolation, however relatively recent speciation has occurred, particularly on the west and east coasts of Australia. This is exemplified by the remaining close relationships between *belli, macroplax, multispinus, pinguiculus* and *elegans* and between *helonotus* and *soelae*.

The distinctness of *tessellatus* from *helonotus* and *soelae* in the *helonotus — soelae — tessellatus — truncatus* group, and its distribution in the south western Indian Ocean suggests a much longer isolation. Prevailing water currents move towards the east African coast, so the distribution of *tessellatus* among the islands of the western Indian Ocean and even the east coast of Africa might be predicted.

A. truncatus shows closest relationship with *A. helonotus* and *A. soelae*, from which ancestral stock I believe it has arisen. Extension of the ancestral form to the south coast of Australia could have occurred via the Leeuwin Current (LEGECKIS and CRESSWELL, 1980 ; MAXWELL and CRESSWELL, 1980) or its equivalent, at least as early as the early Miocene, when water temperatures were relatively warm (KNOX, 1981 ; STEVENS, 1980). Decline in water temperatures during and since the late Miocene has seen the south Australian coast change to a temperate region with a changed fauna. Such pressures would have promoted the evolution of *truncatus* from the ancestral form. Extension of the range of *truncatus* east to the Kermadec Islands and to northern New Zealand may have occurred across the Tasman Sea at any time, probably by west to east migration (FELL, 1953 ; ROWE & VAIL, 1982). A southern seaway between southern Australia and the Tasman Sea, permitting such a migration, has been established at least since Oligocene to Miocene times (KENNETT, 1980 ; STEVENS, 1980). Initially also, separation of Australia from Antarctica was accompanied by high velocity currents (COOK & CHIMONIDES, 1983) which may have been significant in effecting such a distribution. Migration to both the Kermadec Islands and New Zealand may have been achieved via the Lord Howe Rise and Norfolk Ridge, though *truncatus* has not been recorded from either the Lord Howe or the Norfolk Island regions. Whether larval input maintaining gene flow still occurs between southeastern Australia and the Kermadec/New Zealand region is difficult to determine, even though appropriate current tracts are present in the Tasman Sea. It is possible that populations in the Kermadec/New Zealand region are, in the main, self sustaining and relatively phenotypically stable, though there are some minor morphological differences in specimens I examined from that area (ROWE, 1977).

The distributions of *soelae* in western Australia and New Caledonia, and *helonotus* in Philippines and Japan are interesting. I am in no doubt, at this time, as to the identity of the New Caledonian specimen, which supports the specific differences I have noted between *soelae* and *helonotus*. However, collection of material from the east Indian region will determine whether these structural differences are as important as I have proposed. If I am correct then clearly isolation of populations in the Philippine/Japan region has been sufficient to promote the evolution of *helonotus* from a *soelae* stock. Prevailing wind and surface ocean currents move west-southwestward towards the east Indian and northeastern (Queensland) Australian coastline south of the equator. The occurrence of *soelae* in New Caledonia would therefore permit the prediction that *soelae* will be found at least along the Queensland coast of Australia if not along the northern coast between Queensland and the northwest shelf. Extinction from the northern coast may have occurred due to past emergence of the continental shelf in that region. The occurrence of *soelae* in New Caledonian waters may also support a south-west, if not central Pacific origin for the species.

The distant distributions of the three closely related species *tuberculosus, grayi* and *lacrimulus* are equally perplexing. Interestingly, *lacrimulus* appears isolated in the northwestern Indian Ocean (Arabian Sea) from *tuberculosus* and *grayi* in the Pacific Ocean, in

an equivalent relationship to *tessellatus* with *A. helonotus* and *soelae*. *A. lacrimulus* may represent a relic of a formerly widespread Indo-west Pacific ancestor, or at least have evolved more or less directly from it. The apparent absence of a species related to this group throughout the east Indian Archipelago and central Pacific is ascribed to extinction. The particularly close relationship between *tuberculosus* and *grayi* would tend to support a common ancestor (?*grayi*) in the central-southwest Pacific which, by appropriate westward flowing currents (ROCHFORD, 1958 ; FAIRBRIDGE and VAN DER LINDEN, 1966 ; HEATH, 1973), has been distributed to the coast of Australia and thence, via the east Australian and Tasman Currents to the Norfolk and Kermadec Ridges and islands. The apparent absence of *grayi* from the Lord Howe Rise may be due to lack of collecting, or because of extinction. Alternatively, it is also possible that since both Norfolk Island and Kermadec Islands lie within the region of the tropical convergence (30° S in summer ; 22° S in winter ; HEATH, 1973), *grayi* may have been distributed directly from tropical waters by the westerly directed Trade Wind Drift. This may also account for other tropical species known to occur in those islands.

Interestingly, as with *truncatus*, in 1977 I noted minor morphological differences between specimens of *grayi* from eastern Australia and the specimens from the Norfolk/Kermadec area, the differences lying in the more conical form of the abactinal tubercles of the holotype. Reexamination of the holotype has revealed that the number of tubercles on the actinal plates is similar to that found in the Norfolk/Kermadec specimens. The specimens from New South Wales (AM 11884) and Norfolk Id additionally differ from the holotype in their shorter arms (R/r-1.7-1.8). The Japanese specimen (Doshisha University Collection) has extremely pointed abactinal tubercles. Unlike the more tangible differences I have determined in the species of the *elegans* and *helonotus* groups of species, the differences in specimens identified as *grayi* are seen to be intergrading and not taxonomically significant. The discovery of *grayi* in southern Japan is strongly supportive of the occurrence of the species in the east Indian region. If the species does not occur there, however, then the population isolated in Japanese waters, for whatever reasons, is indicative of a relatively phenotypically stable species, since gene flow from or to southern populations would be lacking. The hypothesis put forward to explain the slightly modified forms of *truncatus* in the Norfolk/Kermadec area might also be applied to *grayi*. These hypotheses can be tested by the collection of more specimens from intermediate localities.

The Hawaiian fauna is generally considered to have originated from the western Pacific by means of larval transport via the Kuroshima southern Extension Current (EKMAN, 1967 ; BRIGGS, 1974 : ZINMEISTER & EMERSON, 1979). It this is the case then either *tuberculosus* or a close relative might be expected in the region of the Philippines and/or southern Japan, from which the Hawaiian species originated. Such a relative, *grayi*, has now been found in southern Japan (new record, herein). Specific differences between *grayi* and *tuberculosus*, pointed out by ROWE (1977), can be confirmed and clearly indicate that gene flow between the Japanese and Hawaiian populations of *Asterodiscides* is not apparently occurring. *A. tuberculosus* would appear to have either speciated in isolation or have become isolated in the Hawaiian Island chain. An alternative mechanism to the Kuroshima Current, which might be applied to explain the occurrence of *A. tuberculosus* in the Hawaiian Islands, is available. ROTONDO *et al.* (1981) explain the endemic element of the

Hawaiian fauna as due to a vicariant mechanism, island integration. They argue that the Hawaiian Island Chain includes at least two elements (Necker Island and Wentworth Seamount) which have originated from south of the equator. This, they consider, would have resulted in the mixing of two biotas, Hawaiian and non-Hawaiian, with isolation leading to high endemism. SPRINGER (1982) gave a detailed discussion of the Hawaiian shorefish fauna, giving support to the ROTONDO *et al.* hypothesis. Considering the close relationship between *grayi* from southern Japan and the southwest Pacific and *tuberculosus* in Hawaii, and given the ROTONDO *et al.* hypothesis, the origin of *tuberculosus* in the Hawaiian Island chain from the central or west Pacific might be explained. If extinction of the ancestral species or one of either *tuberculosus* and/or *grayi* from the central-west Pacific has occurred, then this might be ascribed to recent (Pleistocene) lowered sea-levels, which would have adversely affected the habitat of the species.

The origin and distribution of *culcitulus* appears related to recent (Pleistocene) isolation of the west coast of Australia and its likely relationship lies with the *tuberculosus* group.

Although *fourmanoiri* also appears to belong with the *tuberculosus* group there is insufficient material to determine its closest relationships or distribution, other than to note its apparent isolation in the south western Indian Ocean.

Both *crosnieri* and *cherbonnieri*, by virtue of their superomarginal plate number, are allied to the *elegans* group. The fact that the proximal superomarginal plates are obvious in adult specimens of *crosnieri* and *cherbonnieri* I contend (p. 553) indicates a more primitive condition than that found in the *elegans* group of species, where proximal superomarginals are not discernable in adults. The presently known distribution suggests an early isolation of these species in the western Indian Ocean.

Modification of marginal plate arrangement is described for asteroids in the Lower Ordovician to Lower Carboniferous valvatid suborder Pustulosina (SPENCER & WRIGHT, 1966) with the extreme reduction of the frame confined to a few plates in the arm axils in the Eoactinidae (*Eoactis*, Lower Silurian, England-North America, *Yarravaster*, Silurian, Australia). However the Asterodiscididae has been shown to share most characters with the valvatid granulosin families Goniasteridae (Lower Jurassic to Recent) and Oreasteridae (Recent) by ROWE (1977). Certainly the juveniles show a close resemblance to the goniasterid genus *Tosia*. The origin of the family, particularly in respect to the reduced number and arrangement of the marginal plates, will however, remain obscure until fossil remains are found which may throw some light on the matter.

REFERENCES

ADAMS, C. G., 1981. — An outline of Tertiary Palaeogeography. *In* : L. R. M. COCKS (ed.), The evolving earth. British Museum (Natural History). Cambridge Univ. Press : 221-235, 8 figs.

BELL, F. J., 1909. — Report on the echinoderms (other than holothurians) collected by J. S. Gardiner in the western parts of the Indian Ocean. *Trans. Linn. Soc. Lond.*, (Zool.), **13** (1) : 17-22, pl. 3.

BLAKE, D. B., 1975. — A new west American Miocene species of the modern Australian ophiuroid *Ophiocrossota. Palaeontology,* **49** (3) : 501-507, 1 fig., 1 table, 1 pl.

— 1979. — The affinities and origins of the Crown-of-Thorns sea-star *Acanthaster* Gervais. *J. nat. Hist.*, **13** : 303-314, 10 figs.

BRIGGS, J. C., 1974. — Marine Zoogeography. McGraw-Hill. New York : 475 p., figs.

CHIA, F. S.,and R. D. BURKE, 1978. — Echinoderm metamorphosis : Fate of larval structures. *In* : F.-S. CHIA and M. E. RICE (eds), Settlement and metamorphosis of marine invertebrate larvae. Elsevier. New York : 219-234, 12 figs.

CLARK, A. H., 1939. — Echinoderms (other than holothurians) collected on the Presidential Cruise of 1938. *Smithson. misc. Collns,* **98** (11) : 1-18, 5 pls.

CLARK, A. M., 1974. — Notes on some echinoderms of Southern Africa. *Bull. Br. Mus. nat. Hist.*, (Zool.), **26** (6) : 421-487, 16 figs, 1 map, 3 tables.

CLARK, A. M., and J. COURTMAN-STOCK, 1976. — The echinoderms of Southern Africa. London : 277 p., 276 figs.

CLARK, A. M., and F. W. E. ROWE, 1971. — Monograph of shallow-water Indo-west Pacific echinoderms. London : vii + 238 p., 100 figs, 31 pls.

CLARK, H. L., 1902. — Papers from the Hopkins Stanford Galapagos Expedition, 1898-1899. *XII*. Echinodermata. *Proc. Wash. Acad. Sci.,* **4** : 521-531.

COOK, P. L., and P. J. CHIMONIDES, 1983. — A short history of the Lunulite Bryozoa. *Bull. mar. Sci.*, **33** (3) : 566-581, 4 figs, 1 table.

DANA, T. F., 1975. — Development of contemporary eastern Pacific coral reefs. *Mar. Biol.,* **33** : 355-374, 6 figs, 3 tables.

DEICHMANN, E., 1957. — Holothurians. *Mem. geol. Soc Am.,* n° 67 (1) : 1193-1196.

— 1958. — The Holothurioidea collected by the Velero 111 and 1V during the years 1932 to 1954. Part 2. Aspidochirota. *Allan Hancock Pacif.-Exped.,* **11** : 249-349, pls 1-9.

— 1959. — Ekman's Barrier and the holothurians of the Panama region. *Proc. int. Congr. Zool.,* **15** : 270-272.

— 1963. — The holothurians from Clipperton 1sland in the eastern tropical Pacific. *Breviora*, n° 79 : 1-5.

DÖDERLEIN, L., 1936. — Die Asteriden der Siboga Expedition. *III*. Die Unterfamilie Oreasterinae. *Siboga Exped.*, 46c : 295-369, pls 21-23.

DURHAM, J. W., C. D. WAGNER, R. V. MELVILLE, H. B. FELL, D. L. PAWSON, P. M. KIER and A. G. FISCHER, 1966. — Echinozoans. *In* : R. C. MOORE (ed.), Treatise on 1nvertebrate Palaeontology. Part U. Echinodermata 3 Vols 1 & 2. Geolog. Soc. Amer. 1nc./Univ. Kansas Press : U108-U640, figs 90-517.

EKMAN, S., 1946. — Zur Verbreitungs geschichte der Warmwasser-echinodermen in Stillen Ozean (Asteroidea, Ophiuroidea, Echinoidea). *Nova Acta R. Soc. Scient, upsal.*, (4), **14**, (2) : 1-42.

— 1967. — Zoogeography of the sea. Sidgwick and Jackson. London : 415 p., 121 figs.

FAIRBRIDGE, R. W., and W. J. M. VAN DER LINDEN, 1966. — Tasman Sea. *In* : R. W. FAIRBRIDGE (ed.), The encyclopedia of oceanography. Vol. 1. Dowden, Hutchinson and Ross Inc. Stroudsburg, Penn. : 898-902, 5 figs.

FELL, H. B., 1953. — The origin and migrations of Australasian echinoderm faunas since the Mesozoic. *Proc. R. Soc. N.Z., 81* : 245-255.

— 1967. — Cretaceous and Tertiary surface currents of the oceans. *Oceanogr. mar. Biol. Ann. Rev., 5* : 317-341, 5 figs.

GLYNN, P. W., 1974. — The impact of *Acanthaster* on corals and coral reefs in the eastern Pacific. *Environ. Conserv., 1* (4) : 295-303, 4 figs.

HAMBREY, M. J., and W. B. HARLAND, 1981. — The evolution of climates. *In* L. R. M. COCKS (ed.), The evolving earth. British Museum (Natural History). Cambridge Univ. Press : 137-152, 8 figs.

HAYASHI, R., 1973. — The sea stars of Sagami Bay. Biol. Lab., Imp. Households. Tokyo : 144 p., 13 figs, 18 pl.

HEATH, R. A., 1973. — Present knowledge of the oceanic circulation and hydrology around New Zealand — 1971. *Tuatara, 20* (2) : 125-140, 5 figs.

HECK, Jr., K. L., and E. D. MCCOY, 1978. — Long-distance dispersal and the reef-building corals of the Eastern Pacific. *Mar. Biol., 48* : 349-356, 2 tables.

HECK, Jr., K. L., and E. D. MCCOY, 1979. — Biogeography of seagrasses : evidence from associated organisms. *Proc. lst int. Symp. mar. Biogeog. Evolution in Southern Hemisphere, 1* : 109-127, 5 figs.

HENDERSON, J. A., and J. S. LUCAS, 1971. — Larval development and metamorphosis of *Acanthaster planci* (Asteroidea). *Nature, 232* : 655-657, 4 figs.

HYMAN, L. H., 1955. — The invertebrates : Echinodermata : The coelomate Bilateria. Vol. IV. McGraw-Hill. New York : 763 p., 280 figs.

JAMES, D. B., 1969. — Catalogue of echinoderms in the reference collections of the Central Marine Fisheries Research Institute. *Bull. cent. mar. Fish. Res. Inst.*, no. 7 : 51-62.

JANGOUX, M., 1984. — Les astérides littoraux de Nouvelle-Calédonie. *Bull. Mus. natn. Hist. nat., Paris*, 4ᵉ sér., *6*, section A, (2) : 279-293, 3 pls.

KENNETT, J. P., 1980. — Palaeoceanographic and biogeographic evolution of the southern ocean during the Cenozoic and Cenozoic microfossil datums. *In* : P. F. BALLANCE (ed.), Plate tectonics and biogeography in the southwest Pacific : the last 100 million years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Special Issue, *31* (2-4) : 123-152, 8 figs, 8 tables.

KNOX, G. A., 1980. — Plate tectonics and the evolution of intertidal and shallow water benthic biotic distribution patterns in the southwest Pacific. *In* P. F. BALLANCE (ed.), Plate tectonics and biogeography in the southwest Pacific : the last 100 million years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Special Issue, *31* (2-4) : 267-297, 11 figs.

LADD, H. S., 1960. — Origin of the Pacific Island molluscan fauna. *Am. J. Sci., 258*A : 137-150, 3 figs.

LADD, H. S., W. A. NEWMAN and N. F. SOHL, 1974. — Darwin Guyot, the Pacific's oldest atoll. *Proc. 2nd int. Coral Reef Symp., 2* : 513-522, 11 figs.

LEGECKIS, R., and G. CRESSWELL, 1980. — Satellite observations of sea-surface temperature fronts off the coast of Western and South Australia. *Deep Sea Res., 28*A (3) : 297-306, figs 1-7.

LUDWIG, H., 1905. — Asteroidea. *Mem. Mus. comp. Zool. Zool. Harv., 32* : 291 p., 36 pls.

MACNAE, W., and M. KALK, 1969. — A natural history of Inhaca Island, Mocambique. Revised ed. Johannesburg. : iii + 163 p., 11 pls. (Echinoderms by B. L. BALINSKY : 96-107.)

MAXWELL, J. G. H., and G. R. CRESSWELL, 1981. — Dispersal of tropical marine fauna to the Great Australian Bight by the Leeuwin Current. *Aust. J. mar. Freshwat. Res., 32* : 493-500, figs. 1-5.

McCoy, E. D., and K. L. Heck, Jr., 1976. — Biogeography of corals, seagrasses and mangroves : an alternative to the center of origin concept. *Syst. Zool.,* **25** (3) : 201-210, 2 figs.

McNamara, K. J., 1982. — Taxonomy and evolution of living species of *Breynia* (Echinoidea : Spatangoida) from Australia. *Rec. West. Aust. Mus.,* **10** (2) : 167-197, 15 figs.

Menard, H. W., 1964. — Marine geology of the Pacific. McGraw-Hill. New York : 271 p.

— 1972. — History of the ocean basins. *In* : E. C. Robertson (ed.), The nature of the solid earth. McGraw-Hill, New York : 440-460.

Mortensen, T., 1928-1951. — Monograph of the Echinoidea. Copenhagen : **1** : 1-551, 173 figs, 88 pls (1928) ; **2** : 1-647, 377 figs, 89 pls (1935) ; **3** (1) : 1-370, 196 figs, 77 pls (1940) ; **3** (2 & 3) : 1-533, 321 figs, 56 pls (2) ; 1-446, 215 figs, 66 pls (3) (1943) ; **4** (1 & 2) : 1-371, 326 figs, 14 pls (1) ; 1-471, 256 figs, 72 pls (2) (1948) ; **5** (1) : 1-432, 315 figs, 25 pls (1950) ; **5** (2) : 1-593, 286 figs, 64 pls (1951).

— 1931. — Contributions to the study of the development and larval forms of echinoderms. I-II. *K. danske Vidensk. Selsk. Skr.,* (narturv. — math.), (9) **4** (I) : 1-39, 12 figs, 7 pls.

— 1937. — Contributions to the study of the development and larval forms of echinoderms. III. *K. danske Vidensk. Selsk. Skr.,* (naturv. — math.), (9) **7** (1) : 1-65, 51 figs, 15 pls.

— 1938. — Contributions to the study of the development and larval forms of echinoderms. IV. *K. danske Vidensk. Selsk. Skr.,* (naturv. — math.), (9) **7** (3) : 1-59, 30 figs, 12 pls.

Pope, E. C., and F. W. E. Rowe, 1977. — A new genus and two new species in the family Mithrodiidae (Echinodermata : Asteroidea) with comments on the status of the species of *Mithrodia* Gray, 1840. *Aust. Zool.,* **19** (2) : 201-216, 17 figs.

Rochford, D. J., 1958. — The seasonal circulation of the surface water masses of the Tasman and Coral Seas. *C.S.I.R.O. Aust. Div. Fish. Oceanogr.,* Rep. 16 : 1-3, 5 figs.

Rotondo, G. M., V. G. Springer, G. A. J. Scott and S. O. Schlanger, 1981. — Plate movement and island integration : a possible mechanism in the formation of endemic biotas, with special reference to the Hawaiian Islands. *Syst. Zool.,* **30** (1) : 12-21, 2 figs, 1 table.

Rowe, F. W. E., 1977. — A new family of Asteroidea (Echinodermata), with the description of five new species and one new subspecies of *Asterodiscides. Rec. Aust. Mus.,* **31** (5) : 187-233, figs 1-5.

Rowe, F. W. E., and L. L. Vail, 1982. — The distributions of Tasmanian echinoderms in relation to southern Australian biogeographic provinces. *In* : J. M. Lawrence (ed.), Echinoderms. Proceedings of the International Conference, Tampa Bay. Balkema. Rotterdam : 219-225, 1 fig.

Shuto, T., 1983. — Larval development and geographical distribution of the Indo-west Pacific *Murex. Bull. mar. Sci.,* **33** (3) : 536-544, 3 figs, 1 table.

Spencer, W. K., and C. W. Wright, 1966. — Asterozoans. *In* : R. C. Moore (ed.), Treatise on Invertebrate Palaeontology. Part U. Echinodermata 3. Vol. 1. Geolog. Soc. Amer. Inc. Univ. Kansas Press : U4-U107, 89 figs.

Springer, V. G., 1982. — Pacific plate biogeography, with special reference to shorefishes. *Smithson. Contr. Zool.,* no. 367 : 1-181, 65 figs.

Stevens, G. R., 1980. — Southwest Pacific faunal palaeobiogeography in the Mesozoic and Cenozoic times : a review. *In* : P. F. Ballance (ed.), Plate tectonics and biogeography in the southwest Pacific : the last 100 million years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Special Issue, **31** (2-4) : 153-196, 5 figs.

Strathmann, R. R., 1978. — Larval settlement in echinoderms. *In* : F.-S. Chia and M. E. Rice (eds), Settlement and metamorphosis of marine invertebrate larvae. Elsevier. New York : 235-246, 4 figs.

Thorsen, G., 1961. — Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. *Am. Ass. Adv. Sci.,* no. 67 : 455-474, 3 figs.

VAN ANDEL, J. H., 1979. — An eclectic overview of plate tectonics, paleogeography and palaeoceanography. *In* : J. GRAY and A. J. BOUCOT (eds), Historical biogeography, plate tectonics and the changing environment. Proc. 37th Ann. Biol. Colloquium and Selected Papers. Oregon State Univ. Corvallis : 9-25, 18 figs.

WARREN, B., 1966. — Ocean circulation. *In* : R. W. FAIRBRIDGE (ed.), The encyclopedia of oceanography. Vol. 1. Dowden, Hutchinson and Ross Inc. Stroudsburg, Penn. : 590-597, 4 figs.

WINDLEY, B. F., 1982. — The evolving continents. John Wiley & Sons. Chichester (U.K.) : 385 p., figs.

YAMAGUCHI, M., 1973. — Early life histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.), *In* : O. A. JONES, and R. ENDEAN (eds), Biology and geology of coral reefs. Vol. 2. Biology. 1. Academic Press. New York : 369-387, figs 1-5.

ZINSMEISTER, W. J., and W. K. EMERSON, 1979. — The role of passive dispersal in the distribution of hemipelagic invertebrates, with examples from the tropical Pacific Ocean. *Veliger,* **22** (1) : 32-40, 3 figs.

PLATE I

A, B, C. — *Asterodiscides belli* Rowe, MNHN ECAS 607, R = 73 mm : A, abactinal ; B, actinal ; C, lateral.
D, E, F. — *A. cherbonnieri* n. sp., MNHN ECAS 2033 (part), holotype, R = 63 mm : D, abactinal ; E, actinal ;
  C, lateral.

PLATE I

PLATE 11
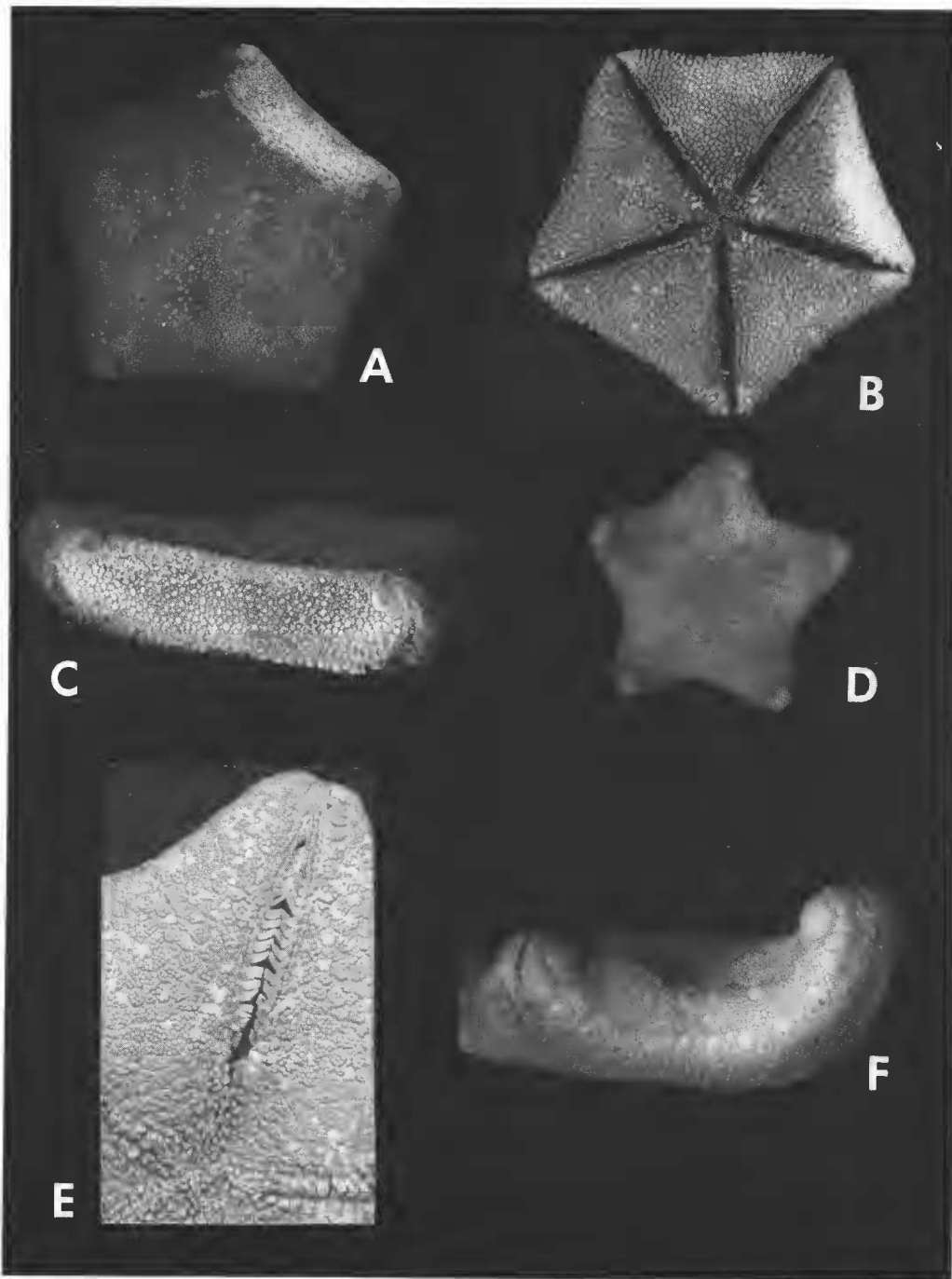
A, B, C. — *Asterodiscides crosnieri* n. sp., MNHN ECAS 1244, holotype, R = 112 mm : A, abactinal ; B, actinal, one arm ; C, lateral.

D, E, F. — *A. macroplax* n. sp., WAM 186-78, holotype, R = 70 mm : D, abactinal ; E, actinal ; F, lateral.
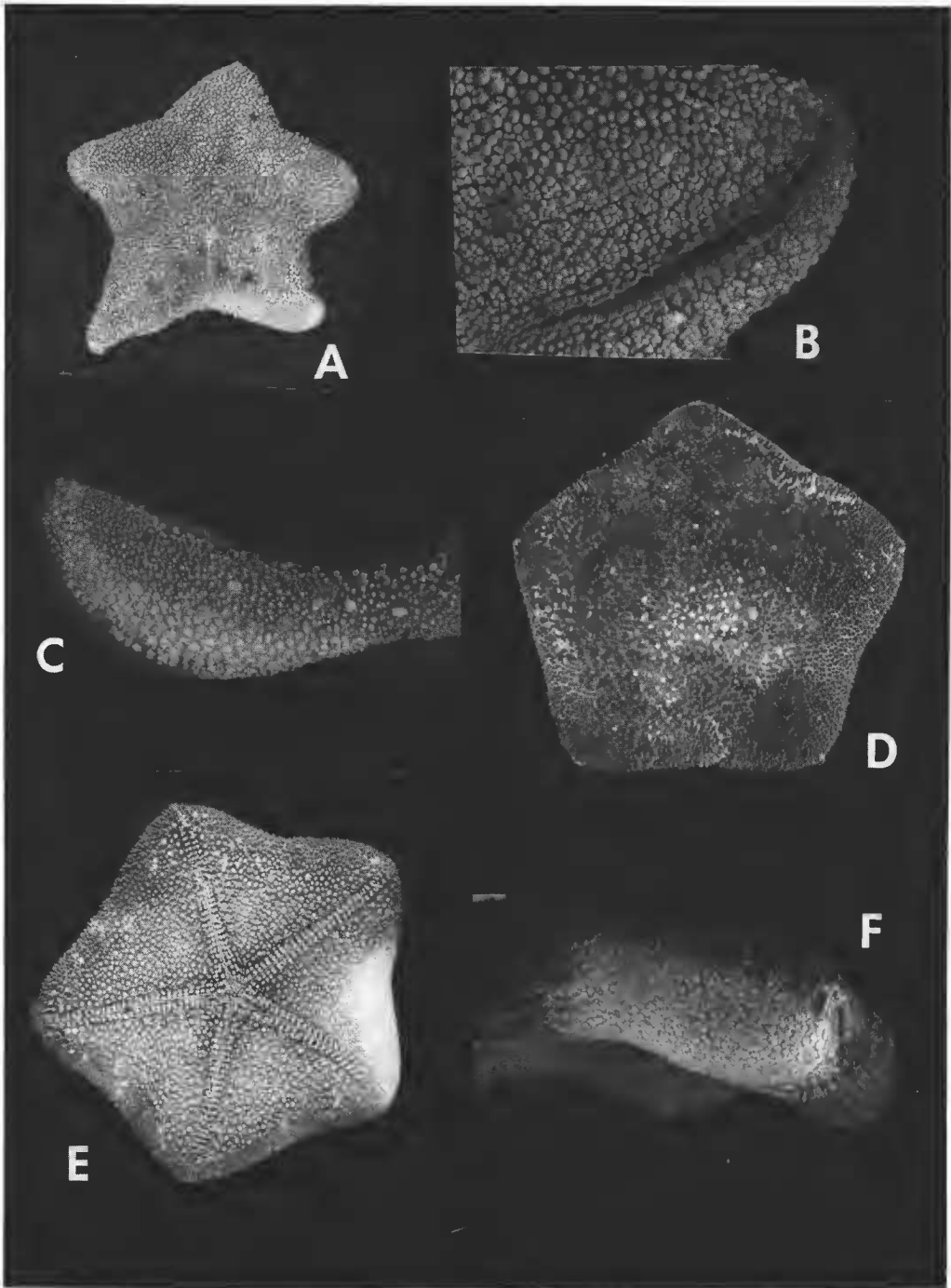
PLATE II

PLATE III

A. — *Asterodiscides macroplax* n. sp., AM J14069, paratype, R = 65 mm, lateral.
B, C, D. — *A. macroplax* n. sp., AMJ 14111, juvenile, R = 24 mm : B, abactinal ; C, actinal ; D, lateral.
E, F. — *A. multispinus* n. sp., QM G2181, holotype, R = 97 mm : E, abactinal ; F, actinal, one arm.
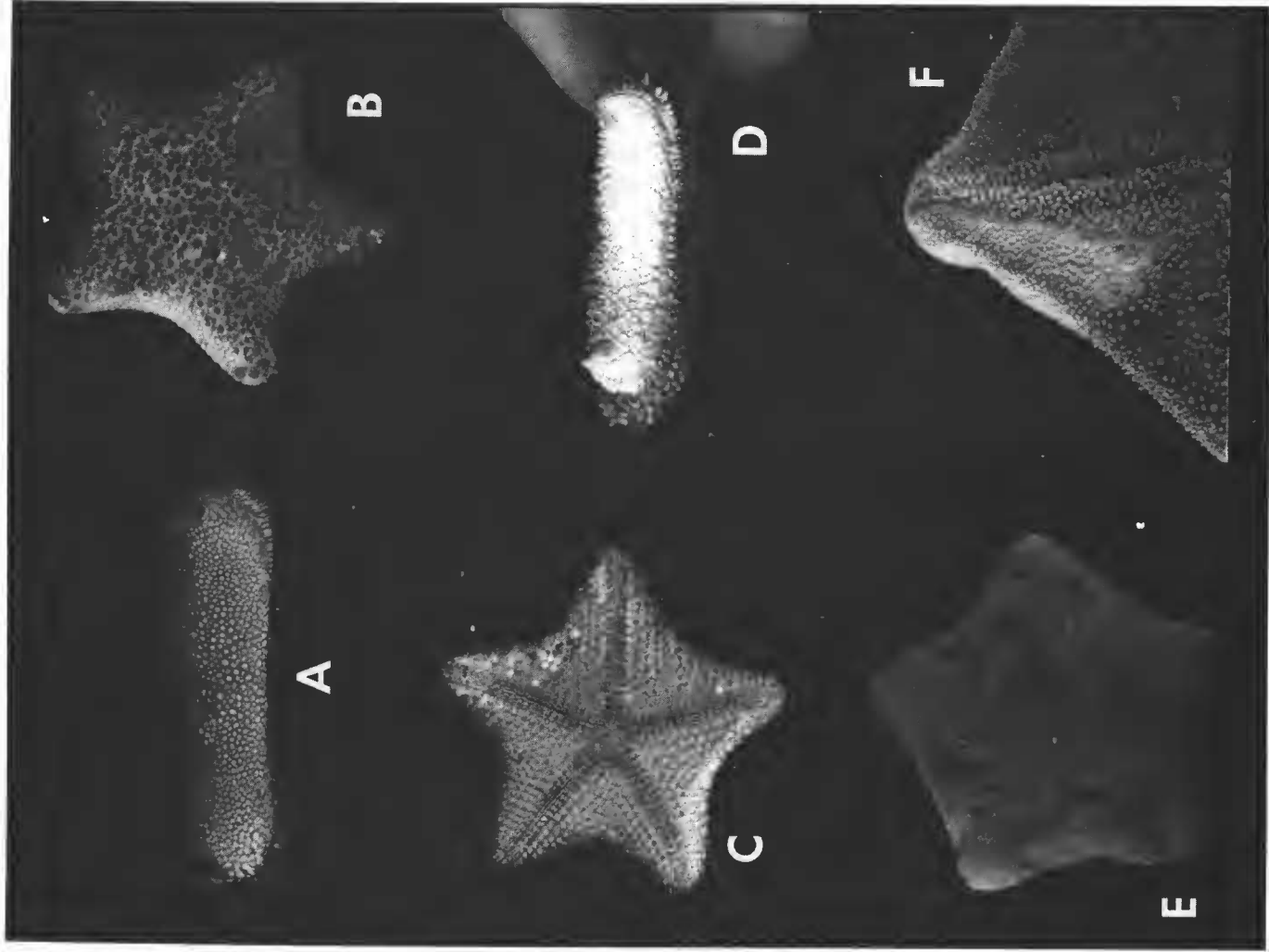
PLATE III

PLATE IV

A, B, C. — *Asterodiscides soelae* n. sp., WAM 191-78, holotype, R = 89-92 mm : A, abactinal ; B, actinal, one arm ; C, lateral.

D. — *A. soelae* n. sp., AM J14508 (part), paratype, R = 35 mm, abactinal.

E, F. — *A. soelae* n. sp., AMJ13775, R = 28 mm : E, oblique abactinal ; F, oblique actinal.
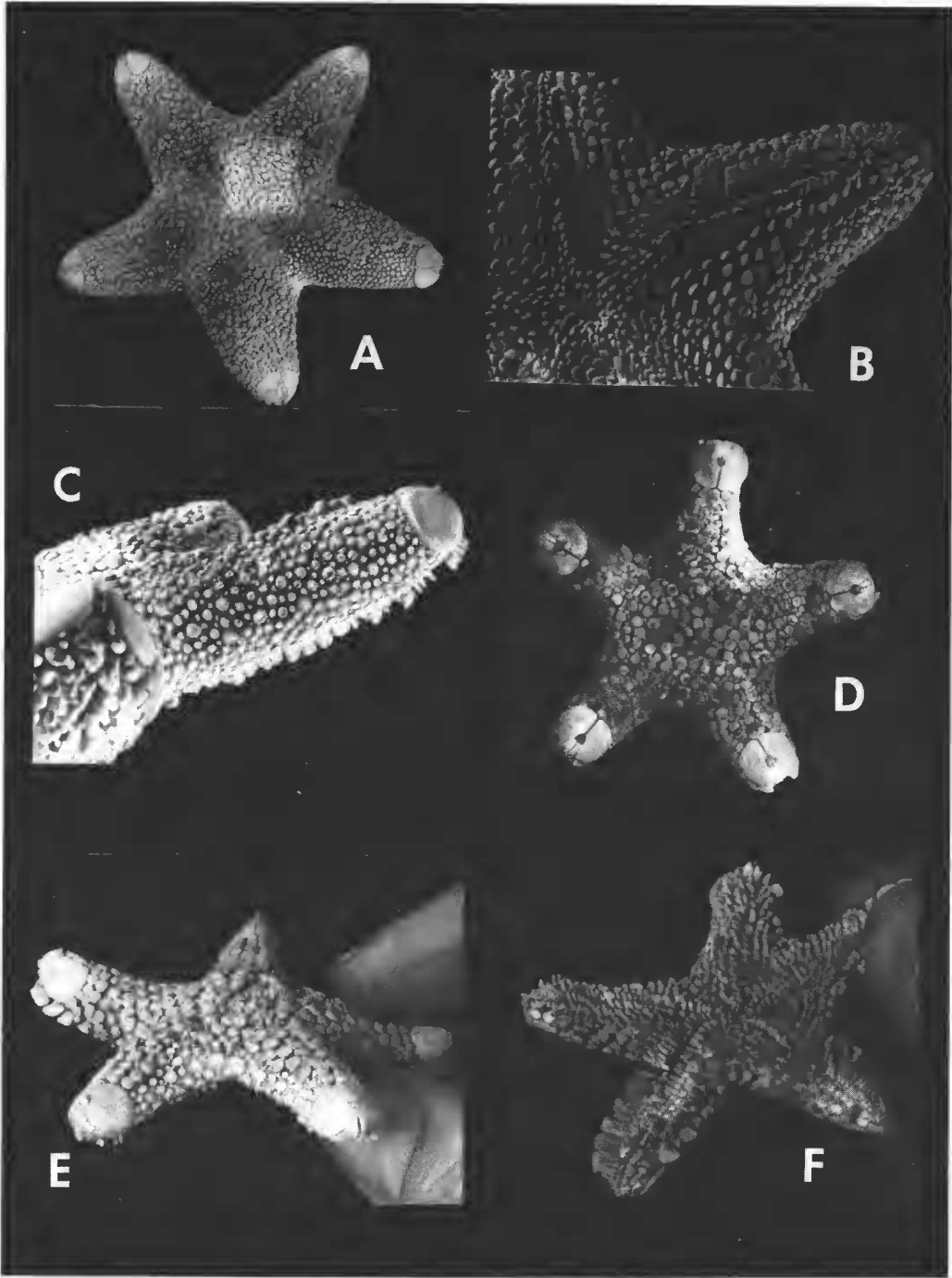
PLATE IV

PLATE V

A. — *Asterodiscides soelae* n. sp., WAM 406-80, juvenile, R = 17.4 mm, abactinal.
B. — *A. helonotus* (Fisher), WAM 1080-74, juvenile, R = 16.4 mm, abactinal.
C, D. — *A. helonotus* (Fisher), USNM 32633, holotype, R = 98 mm : C, abactinal ; D, actinal.
E. — *A. fourmanoiri* n. sp., MNHN ECAS 875, holotype, R = 85 mm, abactinal.
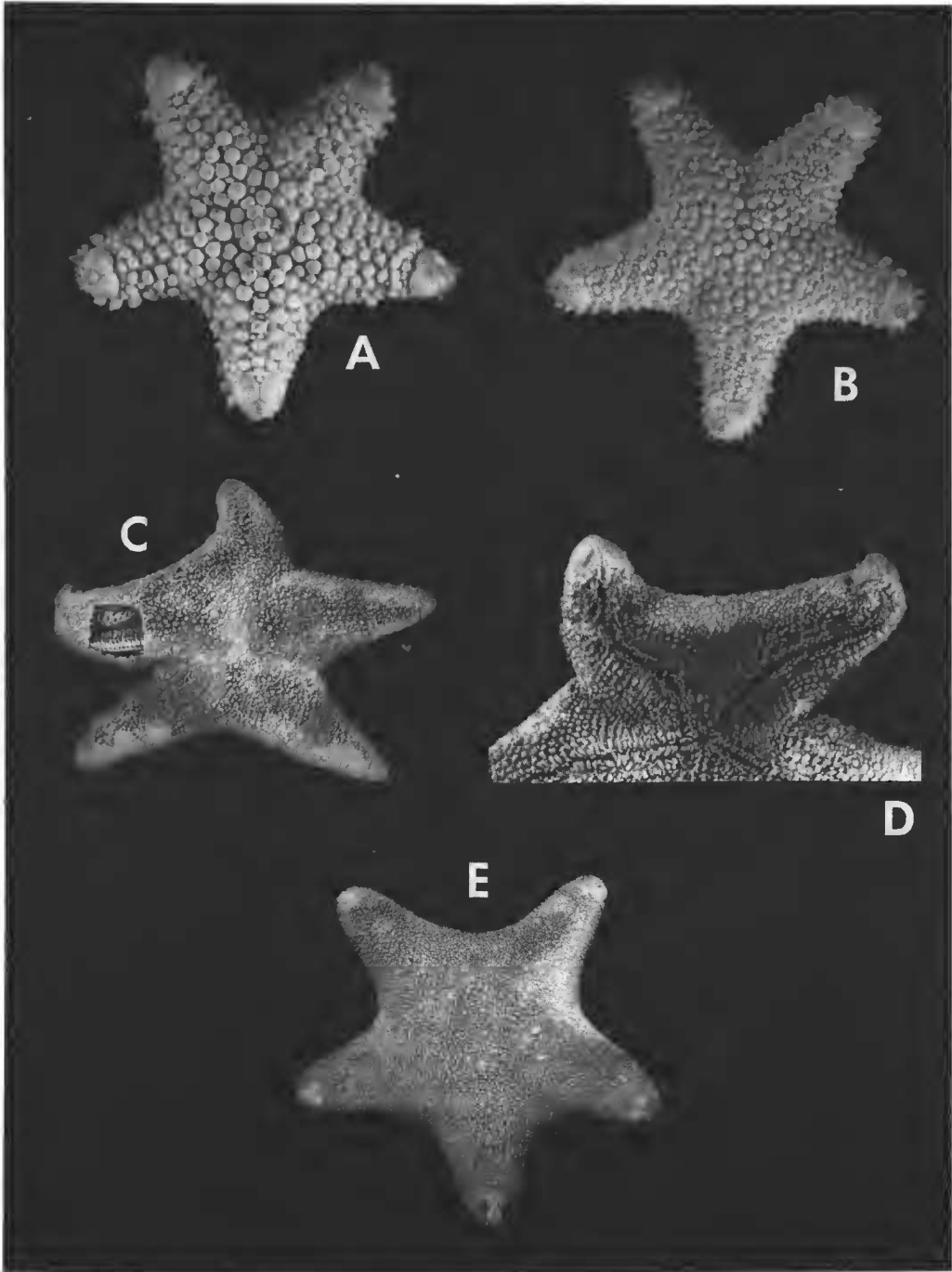
PLATE V

PLATE VI

A, B. — *Asterodiscides fourmanoiri* n. sp., MNHN ECAS 875, holotype, R = 85 mm : A, actinal, furrow ;
   B, oblique actinal.
C, D, E. — *A. fourmanoiri* n. sp., MNHN ECAS 898 (paratype), R = 40 mm : C, abactinal ; D, actinal ; E,
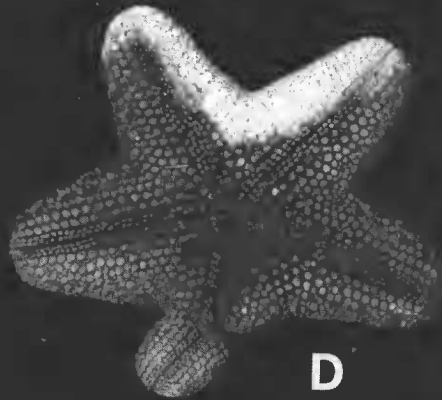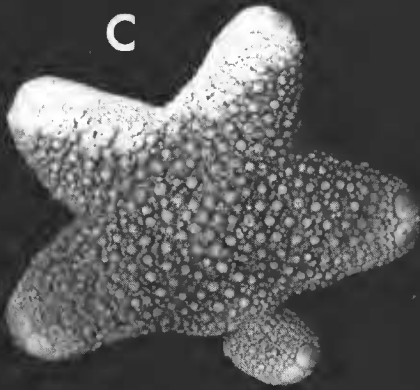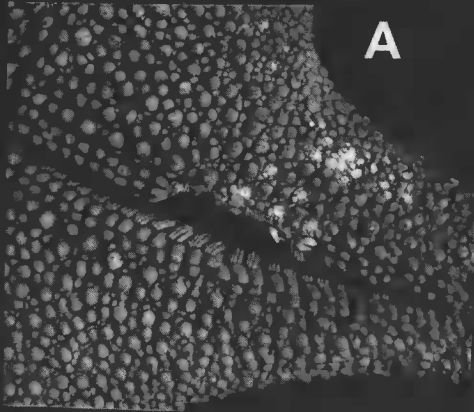   lateral.

PLATE VI