

# ASTEROIDEA

## INTRODUCTION AND GLOSSARY

General accounts of the class are given in A. M. Clark (603 in reference list), Nichols (645) and Hyman (626). For a taxonomic background the best comprehensive work is W. K. Fisher's 'Asteroidea of the North Pacific and adjacent waters' (*Bull. U.S. natn. Mus.* **76** (1): 1-419, 122 pls. [1911]), although the species described in detail are beyond the geographical range of the present monograph. For Indo-tropical Pacific studies Döderlein's 'Siboga' reports (206-208, 211 and 212) provide detailed treatment of the Astropectinidae, Luidiidae, some Goniasteridae and Oreasteridae, while H. L. Clark's Echinoderms of Torres Strait (169) deals monographically with the important family Ophidiasteridae; his Echinoderm Fauna of Australia (180) also includes keys to many of the relevant species.

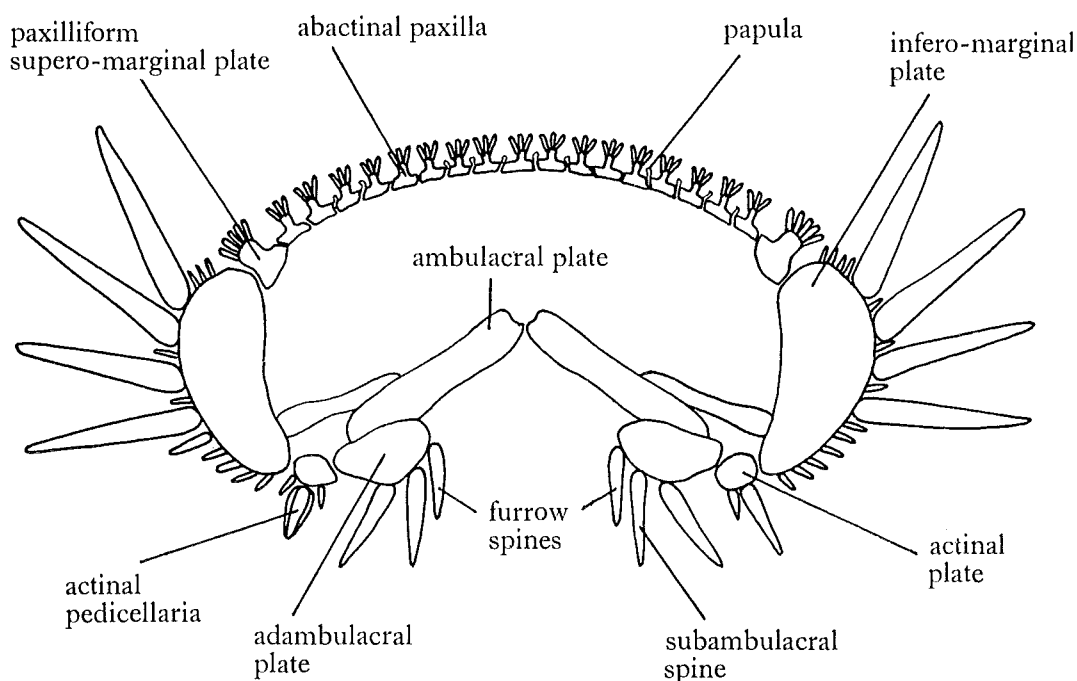


FIG. 10. Introductory figure for asteroids showing stylized transverse section of arm of *Luidia*.

Most of the terms used in describing asteroids are of fairly obvious meaning but the following may need some explanation—

*Abactinal plates*—the superficial plates of the upper side, extending on to the vertical lateral faces of the arms only in species with the arms cylindrical in cross-section (notably most Echinasterids, some Ophidiasterids and the genus *Nepanthia* among the Asterinids) or triangular in cross-section with the oral surface flat and the aboral markedly convex (as in other Asterinids and many Oreasterids); laterally the abactinal plates are bordered by the upper of the two rows of marginal plates—the supero-marginals.

*Actinal plates*—the corresponding plates of the lower side extending between the infero-marginals and the *adambulacral plates* which border the furrows.

*Autotomous*—self-dividing but not necessarily across the disc, for which practice the restricted term *fissiparous* is used.

*Crystal bodies*—minute glassy convex areas projecting slightly from the opaque surface of many plates of certain species.

*Furrow spines*—those on the inner (adradial) edge of the adambulacral plates, usually projecting obliquely over the furrow.

*Madreporite*—the enlarged interradial plate on the upper side of the disc, its surface modified with radiating ridges, which forms the external connection to the sea of the water vascular system. In a few species, usually with more than five arms, there may be more than one madreporite.

*Papulae*—the small, finger-like transparent respiratory processes which project through pores in the body wall, mainly on the upper surface, the arrangement of the pores often characteristic.

*Paxillae*—modified abactinal plates with a median vertical pillar, sometimes quite slender, crowned with spinelets. This form of plate is restricted to certain families, notably the Astropectinidae, while in the Luidiidae the supero-marginal plates as well as the abactinal ones are paxilliform.

*Subambulacral armament*—that of the free surface of the adambulacral plates backing on the furrow spine or spines.

The measurements of asteroids generally used are:  $R$ , the major radius, from centre to arm tip,  $r$ , the minor radius, from centre to the interradial edge and sometimes  $br$ , across the base of the arm.

DISTRIBUTION TABLE  
FOR  
ASTEROIDEA

## DISTRIBUTION TABLE

	Is. of W. Indian Ocean	Mascarene Is.	E. Africa & Madagascar	Red Sea	S.E. Arabia	Persian Gulf
<b>LUIDIIDAE</b>						
<i>Luidia</i> † <i>aspera</i> Sladen	..	..	..	..	..	..
<i>avicularia</i> Fisher	..	..	..	..	(400 *)	..
† <i>hardwicki</i> (Gray) <b>269</b>	(5I)	..	..	..	*	334
† <i>herdmani</i> A. M. Clark	..	..	..	..	..	..
<i>hexactis</i> H. L. Clark	..	..	..	..	..	..
<i>maculata</i> Müller & Troschel	(5I)	..	207 532	*	*	(45I)
<i>magnifica</i> Fisher	..	..	..	..	..	..
<i>mauritiensis</i> Koehler	..	334 * 368	..	..	..	..
<i>penangensis</i> de Loriol	..	..	..	..	..	..
<i>prionota</i> Fisher	..	..	..	(400 *)	45I	45I
<i>savignyi</i> (Audouin)	5I *	207	334 * 532	15 * 50I	..	..
<i>sibogae</i> Döderlein	..	..	..	..	..	..
<b>ASTROPECTINIDAE</b>						
<i>Astropecten</i> † <i>alatus</i> Perrier <b>501</b>	..	..	..	..	..	..
<i>andersoni</i> Sladen	..	..	..	..	..	..
<i>antares</i> Döderlein <sup>1</sup>	..	..	209 *	..	..	..
<i>bengalensis</i> Döderlein <sup>2</sup>	..	..	..	..	..	..
<i>bonnieri</i> Koehler	..	..	..	328	..	..
<i>carcharicus</i> Döderlein	..	..	..	..	..	..
<i>euryacanthus</i> Lütken	..	..	..	..	..	..
<i>fasciatus</i> Döderlein	..	..	..	..	..	..
<i>granulatus</i> Müller & Troschel <b>464</b>	..	..	316 *	..	..	..
<i>hemprichi</i> Müller & Troschel	34 *	..	502 * 507	148 464	*	..
<i>indicus</i> Döderlein	..	..	..	..	316 *	45I *
<i>javanicus</i> Lütken	..	..	..	..	..	..
† <i>mauritianus</i> Gray <sup>2</sup>	..	269 * 316	..	..	..	..
<i>mindanensis</i> Döderlein	..	..	..	..	..	..
† <i>monacanthus</i> Sladen	..	..	206	328	400 *	..
<i>notograptus</i> Sladen	..	..	..	..	..	..
<i>orientalis</i> Döderlein	..	..	..	..	..	..
<i>orsinii</i> Leipoldt <sup>3</sup>	..	..	..	206 (350)	..	..
<i>phragmorus</i> Fisher	..	..	..	..	..	45I *
<i>polyacanthus</i> Müller & Troschel	34 *	368 * 432	501 * 507	274 * 464	316 * (400)	130 * 45I
<i>progressor</i> Döderlein	..	..	..	..	..	..
<i>pugnax</i> Koehler	..	..	..	..	..	(334) * 45I
<i>pulcherrimus</i> H. L. Clark	..	..	..	..	..	..
<i>pusillus</i> Sluiter	..	..	..	..	..	..
<i>sarasinorum</i> Döderlein	..	..	..	..	..	..
<i>triseriatus</i> Müller & Troschel <b>465</b>	..	..	..	..	..	..
<i>umbrinus</i> Grube	..	..	..	..	..	..
<i>vappa</i> Müller & Troschel <b>465</b>	..	..	..	..	..	..
<i>velitaris</i> v. Martens <sup>3</sup>	..	..	..	..	..	..
† <i>zebra</i> Sladen	..	..	..	..	..	..
<i>Craspidaster</i> † <i>hesperus</i> (Müller & Troschel)	..	..	..	..	..	..
<b>ARCHASTERIDAE</b>						
<i>Archaster</i> † <i>angulatus</i> Müller & Troschel	..	368 * 464	532 *	..	..	..
† <i>laevis</i> H. L. Clark	..	..	..	..	..	..
<i>typicus</i> Müller & Troschel <b>461</b>	(*)	540	..	..	..	..
<b>GONIASTERIDAE</b>						
<i>Anthenea</i> † <i>acanthodes</i> H. L. Clark	..	..	..	..	..	..
<i>acuta</i> Perrier	..	..	..	..	..	..
<i>aspera</i> Döderlein	..	..	..	..	..	..

## FOR ASTEROIDEA

	W. India & Pakistan	Maldiva area	Ceylon area	Bay of Bengal	East Indies	North Australia	Philippine Is.	China & S. Japan	South Pacific Is.	Hawaiian Is.
<i>Luidia</i> † <i>aspera</i> Sladen	..	..	..	..	..	..	142 * 534	..	..	229 (245)
<i>avicularia</i> Fisher	..	..	..	..	207	..	247 * 248	(207)	(142 534)	..
† <i>hardwicki</i> (Gray) <b>269</b>	..	..	306 *	40 334	207 * (534)	359 * 534	..	(142 *)	..	..
† <i>herdmani</i> A. M. Clark	..	..	142 * 306	..	..	..	..	..	..	..
<i>hexactis</i> H. L. Clark	..	..	..	..	..	180	..	..	..	..
<i>maculata</i> Müller & Troschel	..	(48)	40 * 207	50I 533	333 * 37I	180 * 198	216 248	265 * 464	..	..
<i>magnifica</i> Fisher	..	..	..	..	..	..	142 * (534)	..	..	(245)
<i>mauritiensis</i> Koehler	..	..	..	..	..	..	..	..	..	..
<i>penangensis</i> de Loriol	..	..	..	..	23 * 369	..	..	..	..	..
<i>prionota</i> Fisher	..	..	..	..	..	..	(247 248)	..	..	..
<i>savignyi</i> (Audouin)	..	..	142 *	4I 334	..	..	248	..	136	..
<i>sibogae</i> Döderlein	..	..	..	..	207	..	..	..	..	..
<i>Astropecten</i> † <i>alatus</i> Perrier <b>501</b>	..	..	..	..	206 540	..	..	..	..	..
<i>andersoni</i> Sladen	..	..	160	334 533	206 * 373	..	..	..	..	..
<i>antares</i> Döderlein <sup>1</sup>	..	..	..	..	..	..	..	..	..	..
<i>bengalensis</i> Döderlein <sup>2</sup>	..	..	206	(209) 334	..	..	..	..	..	..
<i>bonnieri</i> Koehler	..	..	..	..	..	..	..	..	..	..
<i>carcharicus</i> Döderlein	..	..	..	..	..	206	..	206	..	..
<i>euryacanthus</i> Lütken	..	..	160 306	334 * 391	..	..	..	..	..	..
<i>fasciatus</i> Döderlein	..	..	..	..	209	..	..	..	..	..
<i>granulatus</i> Müller & Troschel <b>464</b>	..	..	..	..	333 (* 534)	169 * 198	(248)	..	..	..
<i>hemprichi</i> Müller & Troschel	34 *	..	196 306	533 *	206	..	..	..	..	..
<i>indicus</i> Döderlein	..	..	196 * 206	334 *	23 *	..	..	..	..	..
<i>javanicus</i> Lütken	..	..	..	..	333 * 391	..	..	..	..	..
† <i>mauritianus</i> Gray <sup>2</sup>	..	..	160?	64?	..	..	..	..	..	..
<i>mindanensis</i> Döderlein	..	..	..	..	..	..	206 * 248	..	..	..
† <i>monacanthus</i> Sladen	..	..	..	..	..	..	248 (* 656)	*	..	..
<i>notograptus</i> Sladen	..	..	..	..	533	..	..	..	..	..
<i>orientalis</i> Döderlein	..	..	..	..	206	..	..	..	..	..
<i>orsinii</i> Leipoldt <sup>3</sup>	..	..	..	..	..	..	..	..	..	..
<i>phragmorus</i> Fisher	..	..	..	..	..	..	..	..	..	..
<i>polyacanthus</i> Müller & Troschel	34 *	368 * 432	501 * 507	274 * 464	316 * (400)	130 * 45I	248 612	..	..	..
<i>progressor</i> Döderlein	..	..	..	..	..	..	216 248	265 * 534	136 *	229 (245)
<i>pugnax</i> Koehler	..	..	..	..	..	..	206	..	..	..
<i>pulcherrimus</i> H. L. Clark	..	..	..	..	..	..	..	..	..	..
<i>pusillus</i> Sluiter	..	..	..	..	..	..	206 537	..	..	..
<i>sarasinorum</i> Döderlein	..	..	..	..	..	..	206	..	..	..
<i>triseriatus</i> Müller & Troschel <b>465</b>	..	..	..	..	..	..	..	..	316 *	250
<i>umbrinus</i> Grube	..	..	..	..	..	..	..	..	..	..
<i>vappa</i> Müller & Troschel <b>465</b>	..	..	..	..	..	..	..	278 *	..	..
<i>velitaris</i> v. Martens <sup>3</sup>	..	..	..	..	..	..	..	..	..	..
† <i>zebra</i> Sladen	..	..	..	..	..	..	..	..	..	..
<i>Craspidaster</i> † <i>hesperus</i> (Müller & Troschel)	..	..	..	..	..	..	..	..	..	..
<i>Archaster</i> † <i>angulatus</i> Müller & Troschel	..	368 * 464	532 *	..	..	..	216 248	..	550	..
† <i>laevis</i> H. L. Clark	..	..	..	..	..	..	180 *	..	..	..
<i>typicus</i> Müller & Troschel <b>461</b>	(*)	540	..	..	..	..	133 * 248	(44 *) 647	119 * 29I	250
<i>Anthenea</i> † <i>acanthodes</i> H. L. Clark	..	..	..	..	..	..	180 23I	..	..	..
<i>acuta</i> Perrier	..	..	..	..	..	..	180 501	..	..	..
<i>aspera</i> Döderlein	..	..	..	..	..	..	180 * 204	..	445 56I	..

## DISTRIBUTION TABLE

	Is. of W. Indian Ocean	Mascarene Is.	E. Africa & Madagascar	Red Sea	S.E. Arabia	Persian Gulf
<i>australiae</i> Döderlein 204	..	..	..	..	..	..
<i>conjugens</i> Döderlein	..	..	..	..	..	..
<i>crassa</i> H. L. Clark	..	..	..	..	..	..
† <i>elegans</i> H. L. Clark	..	..	..	..	..	..
† <i>flavescens</i> Gray <sup>4</sup> 269	..	..	..	..	..	..
<i>godeffroyi</i> Döderlein	..	..	..	..	..	..
† <i>grayi</i> Perrier 501	..	..	..	..	..	..
<i>mertoni</i> Koehler	..	..	..	..	..	..
<i>pentagonula</i> (Lamarck) 344	..	..	..	..	..	..
<i>polygnatha</i> H. L. Clark	..	..	..	..	..	..
<i>regalis</i> Koehler	..	..	..	..	..	..
<i>rudis</i> Koehler	..	..	..	..	..	180
<i>sibogae</i> Döderlein <sup>5</sup>	..	..	..	..	..	..
† <i>tuberculosa</i> Gray	..	..	..	..	..	..
<i>viguieri</i> Döderlein <sup>6</sup>	501?	..	..	..	..	..
<i>Anthenoides dubius</i> H. L. Clark	..	..	..	..	..	..
<i>Calliaster</i> † <i>childreni</i> Gray <sup>7</sup>	..	..	..	..	..	..
<i>Goniodiscaster</i> † <i>acanthodes</i> H. L. Clark	..	..	..	..	..	..
<i>australiae</i> Tortonese	..	..	..	..	..	..
† <i>bicolor</i> H. L. Clark	..	..	..	..	..	..
<i>foraminatus</i> Döderlein	..	..	..	..	..	..
† <i>forficulatus</i> (Perrier)	..	..	..	..	..	..
† <i>granuliferus</i> (Gray) <sup>8</sup> 618	..	..	..	..	..	..
<i>integer</i> Livingstone	..	..	..	..	..	..
<i>pleyadella</i> (Lamarck) 344	..	..	..	..	..	..
<i>porosus</i> (Koehler)	..	..	..	..	..	..
† <i>rugosus</i> (Perrier) 501	..	..	..	..	..	..
<i>scaber</i> (Möbius)	..	..	..	..	..	..
<i>vallei</i> (Koehler)	..	..	..	..	..	..
<i>Gymnanthenea globigera</i> (Döderlein)	..	..	..	..	..	..
<i>Iconaster longimanus</i> (Möbius) 431	..	..	..	..	*	..
<i>Mediaster praestans</i> Livingstone	..	..	..	..	..	..
<i>Monachaster sanderi</i> (Meissner)	..	..	211 * 424	..	..	..
<i>Ogmaster capella</i> (Müller & Troschel)	..	..	..	350	..	..
<i>Pseudogoniodiscaster wardi</i> Livingstone	..	..	..	..	..	..
<i>Pseudoreaster obtusangulus</i> (Lamarck) <sup>9</sup> 344	..	310?	..	..	..	..
<i>Siraster tuberculatus</i> H. L. Clark <sup>10</sup>	..	..	..	..	..	..
<i>Stellaster equestris</i> (Retzius) 514	..	..	532 *	148 * 328	327 (*400)	(334)
† <i>princeps</i> Sladen	..	..	..	..	..	..
<i>squamulosus</i> (Studer)	..	..	..	..	..	..
<i>Stellasteropsis</i> † <i>colubrinus</i> Macan	..	..	400 *	..	400 *	..
† <i>fouadi</i> Dollfus	..	..	..	148 * 213	..	..
<i>Styphlaster notabilis</i> H. L. Clark	..	..	..	..	..	..

## ASTEROIDEA

## FOR ASTEROIDEA

W. India & Pakistan	Maldiva area	Ceylon area	Bay of Bengal	East Indies	North Australia	Philippine Is.	China & S. Japan	South Pacific Is.	Hawaiian Is.
..	..	..	..	..	180	..	..	..	..
..	..	..	..	..	180 * 211	..	..	..	..
..	..	..	..	..	180 231	..	..	..	..
..	..	..	..	..	180 *	..	..	..	..
..	..	..	..	23 * 211?	..	..	..	..	..
..	..	..	..	..	204 211	..	..	..	..
..	..	..	..	..	..	501 *	..	..	..
..	..	..	..	(333)	180 204	..	..	..	..
..	..	160	64	..	..	..	180 * 269	..	..
..	..	..	..	..	180	..	..	..	..
..	..	180 * 40	41 * (334)	..	..	..	..	..	..
*	..	160 * 204	334	..	..	..	..	..	..
..	..	..	..	(211)	169? 180?	..	..	..	..
..	..	..	..	211 237	180 * 618	..	..	..	..
..	..	..	..	209	180	..	204 * ?	..	..
..	..	..	..	..	180	..	..	..	..
..	..	..	..	..	..	..	269 *	..	..
..	..	..	..	..	180 *	..	..	..	..
..	..	..	..	..	180 * 562	..	..	..	..
..	..	..	..	..	180 *	..	..	..	..
..	..	..	..	..	180 205	..	..	..	..
..	..	..	(334)	(211)	..	(248) * 501	..	..	..
..	..	..	..	211 431	..	..	*?	..	..
..	..	..	..	..	180 357	..	..	..	..
..	..	..	..	..	34 * 198	..	..	..	..
..	..	..	334	..	198	..	..	..	..
..	..	..	..	..	34 * 180	..	..	..	..
..	..	..	64 533	209 * 431	..	..	..	..	..
..	..	*	(334) *	..	..	..	..	..	..
..	..	..	..	..	180 * 204	..	..	..	..
..	..	..	..	237 320	169 * 198	248	..	..	..
..	..	..	..	..	632	..	..	..	..
..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..
..	..	..	(334)	(211)	(159) *	..	411 * 464	..	..
..	..	..	..	..	356	..	..	..	..
..	..	..	..	..	180 * 204	..	..	..	..
..	(48 *)	160 * 306	(334) *	..	..	..	..	..	..
..	..	160 * 334	64 * 334	211 * 619	169 * 359	217 248	265 * (411)	..	..
..	..	..	..	..	180 * 534	..	..	..	..
..	..	..	..	320 *	(550) *	..	..	..	..
..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	180	..	..	..	..

## DISTRIBUTION TABLE

	Is. of W. Indian Ocean	Mascarene Is.	E. Africa & Madagascar	Red Sea	S.E. Arabia	Persian Gulf
<i>Tosia †queenslandensis</i> Livingstone	..	..	..	..	..	..
<b>OREASTERIDAE</b>						
<i>Asterodiscus †elegans</i> Gray <sup>11</sup> 618	(51 *)	..	..	..	..	..
<i>helonotus</i> Fisher	(51 *)	..	..	..	..	..
<i>Choriaster granulatus</i> Lütken	..	..	..	(148*)	..	..
<i>Culcita coriacea</i> Müller & Troschel	..	..	503?	464 * 624	..	..
<i>grex</i> Müller & Troschel <sup>12</sup> 464	..	..	..	..	..	..
<i>novaeguineae</i> Müller & Troschel	..	..	..	..	..	..
<i>schmideliana</i> (Retzius) <sup>13</sup> 514	51 * 198	198 * 368	198 * 624	..	*	..
<i>Halityle regularis</i> Fisher	..	..	..	..	..	..
<i>Pentaceraster affinis</i> (Müller & Troschel) <sup>14</sup>	..	..	..	..	..	..
<i>alveolatus</i> (Perrier)	..	..	..	..	..	..
<i>†chinensis</i> (Gray)	..	..	..	..	..	..
<i>†decipiens</i> (Bell)	..	..	..	..	..	..
<i>gracilis</i> (Lütken)	..	..	..	..	..	..
<i>horridus</i> (Gray) 269	212	368 * 540	186 415	..	..	..
<i>mammillatus</i> (Audouin)	..	..	212 * 561	15 * 148	561 *	(451) *
<i>multispinus</i> (v. Martens) <sup>15</sup>	..	..	..	..	..	..
<i>regulus</i> (Müller & Troschel)	..	..	..	..	..	..
<i>tuberculatus</i> (Müller & Troschel)	..	..	503 * 540	464 * 560	334	..
<i>westermanni</i> (Lütken)	..	..	..	..	..	..
<i>Pentaster hybridus</i> Döderlein	..	..	..	..	..	..
<i>obtusatus</i> (Bory de St. Vincent) 60	..	..	..	..	..	..
<i>Poraster superbus</i> (Möbius) <sup>16</sup>	..	..	532?	..	..	..
<i>Protoreaster lincki</i> (de Blainville) 56	(51) * 501	501*	388 * 565	..	327	..
<i>nodosus</i> (Linnaeus) 354	(51)	..	310	..	..	..
<i>nodulosus</i> (Perrier)	..	..	..	..	..	..
<b>OPHIDIASTERIDAE</b>						
<i>Bunaster lithodes</i> Fisher	..	..	..	..	..	..
<i>ritteri</i> Döderlein	..	..	..	..	..	..
<i>uniserialis</i> H. L. Clark	..	..	..	..	..	..
<i>Celerina heffermani</i> (Livingstone)	..	..	..	..	..	..
<i>Certonardoia carinata</i> (Koehler)	..	..	..	..	..	..
<i>semiregularis</i> (Müller & Troschel)	..	..	..	..	..	..
<i>Dactylosaster cylindricus</i> (Lamarck) <sup>17</sup> 344	*	368 * 501	415 532	..	327*	..
<i>Ferdina †flavescens</i> Gray	..	269 * 432	..	..	..	..
<i>Fromia armata</i> Koehler <sup>18</sup>	..	..	..	..	..	..
<i>balansae</i> Perrier	..	..	..	..	..	..
<i>elegans</i> H. L. Clark <sup>19</sup>	..	..	..	..	..	..
<i>†ghardaana</i> Mortensen	..	..	..	141 * 449	..	..
<i>hadracantha</i> H. L. Clark	..	..	..	..	..	..
<i>hemiopla</i> Fisher	..	..	..	..	..	..
<i>indica</i> (Perrier) 651	..	..	..	..	..	..
<i>milleporella</i> (Lamarck) <sup>20</sup> 344	..	310 * 368	186 310	368? 561?	..	..

## FOR ASTEROIDEA

W. India & Pakistan	Maldiva area	Ceylon area	Bay of Bengal	East Indies	North Australia	Philippine Is.	China & S. Japan	South Pacific Is.	Hawaiian Is.
..	..	..	..	..	142 * 359	..	..	..	..
..	..	..	*	..	..	(248) * 534	*?	..	..
..	..	..	..	..	..	247 248	..	..	..
..	..	..	..	248 436	..	216 * 534	265 647	291 * 390	..
..	..	..	..	..	..	..	..	..	..
..	..	..	..	135 371	..	..	..	360	..
..	..	..	38 * 334	198 * 464	169 * 359	248 * 534	265 647	198 * 291	250 651
..	147 *	160? * 306?	..	..	..	..	..	..	..
..	..	..	..	..	..	247 248	..	..	..
..	..	160 * 212	334 * 464?	..	..	..	..	..	..
..	..	..	..	33 534	..	212 248	..	335 * 501	..
..	..	..	..	..	..	..	33 269	..	..
..	..	..	..	33 *	..	..	..	..	..
..	..	..	64	237 391	180 * 534	..	..	..	..
..	..	..	..	..	..	..	..	..	..
..	..	267?	..	391 * 412	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..
..	..	..	334 464	33 * 209	182 * 359	212 216	647	359	..
..	..	..	..	..	..	..	..	..	..
..	..	..	334 391	..	..	..	..	..	..
..	..	..	..	..	..	..	..	212	..
..	..	..	..	198 237	..	248 * 501	..	205 * 212	..
..	..	40 * 334	64 334	212 * 431	..	534 *	212	..	..
..	..	212 * 306	334 * 388	540	..	..	..	..	..
..	..	205 306	..	169 * 237	34 * 198	248 * 534	265 573	46 * 291	..
..	..	..	..	..	180 501	..	..	..	..
..	..	..	..	..	..	248 613	..	..	..
..	..	..	..	198	..	..	..	..	..
..	..	..	..	..	169 233	..	..	..	..
..	..	..	..	..	..	..	(44 * 150)	358	..
..	..	..	334	..	..	..	..	..	..
..	..	..	..	464 540	..	(248)	289 * 568	..	..
..	48 * 147	306	..	371	†	..	..	136 * 391	169 * 250
..	..	..	..	..	..	..	..	..	..
..	..	..	38 * 334	..	..	..	568?	..	..
..	..	..	..	..	..	..	..	501 568	..
..	..	..	..	..	169 182	133? 217?	..	..	..
..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	169	288	..	..
..	..	..	..	..	..	247 248	..	136	..
..	147 *	29 *	38 * (334)	237	..	216 217	288 289	150 * 291	..
..	48 * 147	196 *	40 64	237 371	169 * 359	248	288 (*) 647	46 * 388	..



## DISTRIBUTION TABLE

	Is. of W. Indian Ocean	Mascarene Is.	E. Africa & Madagascar	Red Sea	S.E. Arabia	Persian Gulf
† <i>megaloplax</i> (Bell)	..	..	..	..	..	..
<i>pusilla</i> Müller & Troschel <sup>29</sup>	..	..	..	..	..	..
<i>tumescens</i> (Koehler)	..	..	..	..	..	..
<b>METRODIRIDAE</b>						
<i>Metrodira</i> † <i>subulata</i> Gray	..	..	..	..	..	..
<b>CHAETASTERIDAE</b>						
<i>Chaetaster</i> <i>vestitus</i> Koehler	..	..	..	..	..	..
<b>ASTEROPIDAE</b>						
<i>Asteropsis</i> <i>carinifera</i> (Lamarck) <b>344</b>	34 * 51	368 * 432	385 * 503	350 * 464	327*	..
<b>ASTERINIDAE</b>						
<i>Anseropoda</i> <i>rosacea</i> (Lamarck) <b>344</b>	..	..	..	..	..	..
<i>Asterina</i> † <i>burtoni</i> Gray	51	368 * 432	503 * 565	269 * 569	*	451 *
<i>coronata</i> v. Martens	..	..	..	..	..	..
<i>crassispinata</i> H. L. Clark	..	..	..	..	..	..
<i>granulosa</i> Perrier	..	..	..	..	..	..
<i>lorioli</i> Koehler	..	..	..	..	..	..
† <i>lutea</i> H. L. Clark	..	..	..	..	..	..
<i>nuda</i> H. L. Clark	..	..	..	..	..	..
<i>orthodon</i> Fisher <sup>31</sup>	..	..	..	..	..	..
<i>sarasini</i> (de Loriol)	..	..	..	..	..	..
<i>Disasterina</i> <i>abnormalis</i> (Perrier)	..	..	..	..	..	..
<i>leptalacantha</i> H. L. Clark	..	..	..	..	..	..
<i>praesignis</i> Livingstone	..	..	..	..	..	..
<i>spinosa</i> Koehler	..	..	..	..	..	..
<i>spinulifera</i> H. L. Clark	..	..	..	..	..	..
<i>Nepanthia</i> † <i>belcheri</i> (Perrier) <b>501</b>	..	..	..	..	..	..
† <i>brevis</i> Perrier	..	..	..	..	..	..
<i>joubini</i> Koehler	..	..	..	..	..	..
† <i>maculata</i> Gray	..	..	..	..	..	..
<i>magnispina</i> H. L. Clark	..	..	..	..	..	..
<i>suffarcinata</i> Sladen	..	..	..	..	..	..
<i>tenuis</i> H. L. Clark	..	..	..	..	..	..
† <i>variabilis</i> H. L. Clark	..	..	..	..	..	..
<i>Patiriella</i> <i>exigua</i> (Lamarck) <sup>32</sup> <b>344</b>	..	..	317	..	..	..
<i>Tegulaster</i> <i>ceylanica</i> Döderlein	..	..	..	..	..	..
<i>emburyi</i> Livingstone	..	..	..	..	..	..
<b>ACANTHASTERIDAE</b>						
<i>Acanthaster</i> <i>planci</i> (Linnaeus)	51	198 * 368	275 442	569 * 616	169 * 400	..
<b>VALVASTERIDAE</b>						
<i>Valvaster</i> <i>spinifera</i> H. L. Clark	..	..	..	..	..	..
<i>striatus</i> (Lamarck)	..	344 * 368	..	..	..	..
<b>PTERASTERIDAE</b>						
<i>Euretaster</i> <i>cribrosus</i> (v. Martens) <sup>33</sup>	51	..	415 * 501	*	..	..
† <i>insignis</i> (Sladen) <sup>33</sup>	..	..	..	..	..	..

## FOR ASTEROIDEA

W. India & Pakistan	Maldiva area	Ceylon area	Bay of Bengal	East Indies	North Australia	Philippine Is.	China & S. Japan	South Pacific Is.	Hawaiian Is.
..	..	..	..	..	34 * 534 (209?)	..	..	..	..
..	..	..	..	237?	..	466	..	137? 501?	..
..	..	..	..	150 * 333	180 * 361	..	..	..	..
..	..	160 306	334	333 373	180 * 534	(248) * 269	..	..	..
..	..	..	334	..	..	..	..	..	..
..	..	196	..	198 237	169 * 359	217	265 647	501 * 534	169 * 229
..	..	..	64 (334)	23 *	180 * 232	..	..	..	..
334 *	48 * 147	196 267 *	334 533	501 * 537 412	169 * 231 180 *	248 * 501 217 * 248	(*) 265 288	136 250 136 248	226 229 ..
..	..	..	..	..	178 182	..	..	..	..
334 * 522	..	40 *	..	..	..	..	..	..	314 501
..	..	..	..	..	180 *	..	..	..	..
..	..	..	..	..	169 232	..	..	..	..
..	..	..	..	..	(209?)	..	249 445	..	..
..	..	40 * 634	334	..	..	..	..	..	..
..	..	..	..	..	169 363	..	..	501	..
..	..	..	..	..	163 * 363	..	..	..	..
..	..	..	..	..	182 363	..	..	..	..
..	..	..	334	..	..	..	..	..	..
..	..	..	..	137	180	..	..	..	..
..	..	..	..	..	209 * 232	..	..	..	..
..	..	..	..	..	169 * 501	..	..	..	..
..	..	..	..	..	..	248	330	..	..
..	..	..	..	(550) *	(534 *)	(248) * 269	..	..	..
..	..	..	..	..	180	..	..	..	..
..	..	..	(334) 533	333	..	..	..	..	..
..	..	..	..	..	180	..	..	..	..
..	..	..	..	..	180 *	..	..	..	..
..	..	..	334 *	237 * 248	169 * 180	217 * 248	192	169 291	..
..	..	196	..	..	..	..	..	..	..
..	..	..	..	..	363	..	..	..	..
354	48 51	196	38 *	129 * 198	169 * 359	217 * 248	286 573	136 * 405	169 229
..	..	..	..	..	169	..	..	..	..
..	..	..	334	..	..	133	..	*	(245)
..	..	196? 306?	64?	23 *?	..	..	..	..	..
..	..	..	..	*	180 * 655	(248)	*	198	..

## DISTRIBUTION TABLE

	Is. of W. Indian Ocean	Mascarene Is.	E. Africa & Madagascar	Red Sea	S.E. Arabia	Persian Gulf
<b>MITHRODIIDAE</b>						
<i>Mithrodia clavigera</i> (Lamarck) 344	*	368 * 426	239 385	148 * 569	..	..
<i>fisheri</i> Holly	..	..	..	..	..	..
<b>ECHINASTERIDAE</b>						
<i>Cistina columbiae</i> Gray 269	..	370*	..	..	..	..
<i>Echinaster callosus</i> v. Marenzeller	34 *	..	49 *	*	..	..
† <i>luzonicus</i> (Gray) <sup>34</sup>	..	..	..	..	..	..
† <i>purpureus</i> (Gray) <sup>34</sup>	(51) *	269 * 368	385 * 503	15 * 437	..	..
<i>superbus</i> H. L. Clark	..	..	..	..	..	..
† <i>varicolor</i> H. L. Clark	..	..	..	..	..	..
<b>SPHAERASTERIDAE</b>						
<i>Podosphaeraster polyplax</i> A. M. Clark	..	..	..	..	..	..
<b>ASTERIIDAE</b>						
<i>Coscinasterias calamaria</i> (Gray) <sup>35</sup>	..	269 * 368	415	..	..	..

## NOTES TO ASTEROID TABLE

<sup>1</sup> *Astropecten antares*. This species could possibly be omitted since its known range is only from the eastern side of the Cape of Good Hope to Mozambique (the type-locality). However, Mortensen (1933a) has suggested that it will prove to have a more extended range on the east African coast.

<sup>2</sup> *Astropecten bengalensis* and *mauritanus*. Since Döderlein (1917) referred Koehler's material from the Bay of Bengal to his new species *Astropecten bengalensis* from *A. mauritanus*, it seems likely that a similar disposition is preferable for both H. L. Clark's Sinhalese specimens (1915a) and those of Brown (1910) from Mergui; John (1948) has queried the identity of the latter.

<sup>3</sup> *Astropecten velitaris*. A species of *Astropecten* occurs in the Gulf of Suez, where it has recently been taken by Mr. John Pearse, formerly of the American University in Cairo, which is more closely related to *A. velitaris* than to any other described Indo-West Pacific species in my opinion. (However, James (1969) thinks this *Astropecten* is identifiable with *A. orsinii*.) A similar specimen is also in the British Museum collections from Robert M'Andrew, collected more than a hundred years ago.

<sup>4</sup> *Anthenea flavescens*. H. L. Clark (1938) has queried Döderlein's identification of 1935.

<sup>5</sup> *Anthenea sibogae*. H. L. Clark himself (1938) was uncertain about the specific identification of his Australian specimens which were considerably smaller than the holotype. In the earlier reference (1921) he used the name *tuberculosa* of which he then thought *mertonii* and *sibogae* were synonyms.

<sup>6</sup> *Anthenea viguieri*. Döderlein (1915) notes that Perrier's *A. articulata* of 1875 (but not his *Goniodiscus articulatus* of 1869) is conspecific with the holotype of *A. viguieri*. The only locality which Perrier gave was the Seychelles which seems improbable. The holotype of *A. viguieri* is one of the specimens named *Goniodiscus pentagonula* by Müller and Troschel (1842), which were said to have come from China, like the two old specimens in the British Museum collections.

<sup>7</sup> *Calliaster childreni*. There are no depth records for any of the six old dry specimens in the British Museum collections, only one of which, labelled Swatow, Chinese Fisheries Exhibition of 1883, has any more precise locality than 'China'. The other Indo-Pacific species of *Calliaster* are all from depths of 50 metres or more, though the South African *C. baccatus* was first taken in 9-33 metres.

<sup>8</sup> *Goniodiscaster granuliferus*. Gray gives no locality though the two syntypes are labelled as from 'China'. As with so many old specimens in the British Museum and other collections with this locality which were purchased from dealers, I regard this as suspect.

<sup>9</sup> *Pseudoeaster obtusangulus*. The western Indian Ocean records need verification.

<sup>10</sup> *Siraster tuberculatus*. Koehler's record (1910a) of *Stellaster squamulosus*, negated by Döderlein (1935) as belonging to that species, is here referred to *tuberculatus* after study of the variable development of infero-marginal spines in the British Museum material. (In fact this study had suggested the possibility that the holotype of *Siraster tuberculatus* might be only an immature specimen of *Stellaster equestris*.) Bell's records (1902 and 1904) of Gardiner's and Herdman's specimens as *Stellaster incei* (incorrectly given as *S. equestris* by me in 1966 in the Maldivian Islands fauna list), are based on material since renamed *Siraster tuberculatus*, with the type of which they agree also in size.

<sup>11</sup> *Asterodiscus elegans*. Gray gives no locality for the type; Perrier (1875) says that it is from NE China, which seems highly improbable. At least one of Gray's three specimens originated from Cuming, which makes a Philippine locality more likely. Since one of Gardiner's four specimens from the western Indian Ocean recorded by Bell (1909) runs down to *A. helonotus*, I suspect that, when sufficient material is available for a true appreciation of the range of variation, only a single species will be recognized.

<sup>12</sup> *Culcita coriacea*. Peters' record (1852) from Mozambique is more likely to be based on material of *C. schmideliana*.

## FOR ASTEROIDEA

W. India & Pakistan	Maldivian area	Ceylon area	Bay of Bengal	East Indies	North Australia	Philippine Is.	China & S. Japan	South Pacific Is.	Hawaiian Is.
..	(48) * 239	..	..	135 412	..	133 * 369	288 * 289	239 * 534	..
..	..	..	..	..	..	239	..	239 540	250 * 311
..	..	..	..	..	..	..	..	..	..
..	..	(334)	334	248 *	..	(248)	*	46 * 408	..
..	..	..	..	237 * 561	169 * 359	248 * 269	44 * 192	291 * 501	..
..	..	160? * 306	64 * 334?	..	..	..	..	..	..
..	..	..	..	..	163 180	..	..	..	..
..	..	..	..	..	180	..	..	..	..
..	..	..	..	..	..	..	(44 602)	46	..
..	..	..	..	..	[182]	..	610	*	..

<sup>13</sup> *Culcita schmideliana*. Herdman's record (1904) from Ceylon is more likely to have been based on specimens of *Culcita novaeguineae*; H. L. Clark (1915a) also notes that his Sinhalese specimens are not 'perfectly typical'. See also note 33 to the Asteroid key.

*Goniodiscus studeri* de Loriol from Mauritius was based on a specimen with R only 35 mm. and closely resembles '*Goniodiscus sebae*'—the name given to immature forms of *Culcita*; the interradial are rather deeply indented, as in *Hippasteria philippinensis* Domantay, a synonym of *C. novaeguineae*, though similarly stellate forms probably occur also in the western *C. schmideliana*, of which I believe *G. studeri* must be a synonym.

<sup>14</sup> *Pentaceraster affinis*. Müller and Troschel (1842) give the type-locality as 'India'; judging from the frequency of subsequent records this is most likely to have been the Bay of Bengal, as surmised here.

<sup>15</sup> *Pentaceraster multispinus*. Gravely's record (1927) from the Gulf of Manaar needs confirmation.

<sup>16</sup> *Poraster superbus*. Simpson and Brown's record (1910) needs confirmation.

<sup>17</sup> *Dactylosaster cylindricus*. Lamarck (1816) gives the type-locality as 'les mers australes' but Perrier (1875) as 'Ile de France' (Mauritius).

<sup>18</sup> *Fromia armata*. Tortonese (1955) has recorded as *armata* a specimen in the British Museum collections from Macclesfield Bank, which cannot now be traced.

<sup>19</sup> *Fromia elegans*. H. L. Clark (1946) doubts Domantay and Roxas' record from the Philippines; A. H. Clark's record (1949c) from the same area may therefore also be a mistake. See my notes (1967c) under the heading of *F. indica*.

<sup>20</sup> *Fromia milleporella*. The Red Sea records of de Loriol (1885) and Tortonese (1936) made prior to Mortensen's distinction of *F. ghardaqana* are probably based on material of the latter.

<sup>21</sup> *Fromia pacifica*. Domantay's records from the Philippines need confirmation.

<sup>22</sup> *Linckia guildingi*. I am not convinced that Müller and Troschel's record (1842) of *Ophidiaster ehrenbergi* from the Red Sea was really based on material of *L. guildingi* as H. L. Clark (1921) postulates. Tortonese (1937) has also recorded *L. ehrenbergi* from the Red Sea. The locality of the British Museum specimen labelled 'Red Sea' needs confirmation.

<sup>23</sup> *Linckia multifora*. Although there are 24 specimens labelled 'Flinders Bank, N. Australia' and one 'Capricorn Group' (Queensland) in the British Museum collections which I have identified as *L. multifora*, both lots date from the last century and since H. L. Clark with his great experience of Australian echinoderms did not find this otherwise extremely common species there I think this labelling needs confirmation.

<sup>24</sup> *Nardoa frianti*. As expressed in 1967(c), I am uncertain of Hayashi's identification of this species.

<sup>25</sup> *Nardoa lemonnieri*. The doubtful Maldivian records of Bell (1902) and myself (1966) refer to identifications as *N. variolata* subsequently (1967) doubted as being conspecific with the Mascarene species. The Philippine records of Fisher (1919) and Domantay and Roxas (1938) were also discussed briefly by me in 1967(c).

<sup>26</sup> *Neoferdina cumingi*. As noted by H. L. Clark (1921), the type-locality was more likely to have been the Philippine Islands, where Cuming also collected extensively, than the west coast of Colombia.

The specimen from North-West Islet, Capricorn Group, Queensland described by Livingstone (1930) under the name of *Ferdina ocellata* is probably referable to *cumingi*, however, Endeian (1953) has found further Queensland specimens which he says are intermediate between *ocellata* and *cumingi*.

<sup>27</sup> *Ophidiaster lorioli*. Hayashi himself (1938b) doubts the identity of his specimen.

<sup>28</sup> *Ophidiaster squameus*. H. L. Clark (1946) throws some doubt on the Philippine record of Domantay and Roxas (1938) on the grounds of colour difference.

<sup>29</sup> *Tamaria dubiosa* and *pusilla*. See note 52 to the Asteroid key to account for the queries.

<sup>30</sup> *Tamaria fusca*. Livingstone (1932) believes that the "Gazelle" specimens from north-west Australia determined as *fusca* by Studer (1883) are referable to *T. hirsuta*.

<sup>31</sup> *Asterina orthodon*. The record of Döderlein (1926) from north-west Australia is more likely to have been based on one of H. L. Clark's nominal species, *A. lutea* or *nuda*, if these are distinct from *orthodon*. See also note 86 to the Asteroid key.

<sup>32</sup> *Patiriella exigua*. This species has a most unusual distribution, being known from St. Helena in the South Atlantic, South Africa, apparently stopping short in southern Mozambique but occurring again in the Andaman and Nicobar Islands, in the Pacific islands and on the entire east coast of Australia from tropical Torres Strait to temperate Bass Strait, but not on the north coast or the south-west. Old records from the Red Sea (Müller and Troschel, 1842) are probably erroneous; that of Gray (1872) from the Gulf of Suez is certainly based on material of *Asterina burtoni*. Sladen (1889) also mentions records from Mauritius and Madagascar which have been perpetuated in the literature but have never been repeated. Dartnall (personal communication) believes that more than one species is represented in the remaining records, which may account for the apparently anomalous distribution.

<sup>33</sup> *Euretaster cribrosus* and *insignis*. As stated in note 96 to the Asteroid key, these may be synonymous. Until further material is available for comparison, the western Indian Ocean records may be arbitrarily referred to *cribrosus* and the Pacific ones to *insignis*. The intermediate records from Ceylon to Singapore are doubtfully referred to *cribrosus*.

<sup>34</sup> *Echinaster luzonicus* and *purpureus*. The records of H. L. Clark (1915a) and Koehler (1910b) from Ceylon and the Bay of Bengal as *E. eridanella* are probably based on *E. purpureus* rather than *luzonicus* (of which *eridanella* is considered a synonym), since both remark on the five-armed condition. See also note 94 to the Asteroid key.

<sup>35</sup> *Coscinasterias calamaria*. This is another species which appears to have a discontinuous distribution, being known from Mauritius (and East Africa) and from temperate but not tropical Australia. The British Museum record from the South Pacific is based on the 'Challenger' specimen determined as *Asterias gemmifera* (a South American species) by Sladen. The locality label 'Kandavu, Fiji' is tied on to it and so is difficult to refute.

## KEY TO THE ASTEROIDEA

- |     |  |  |
|-----|--|--|
| 1   | Tube feet tapering to a rounded or conical knob, no terminal disc . . . . .  | 2  |
| 1'  | Tube feet cylindrical and with a terminal disc . . . . .   | 40   |
| 2   | Edge of the body defined by the large infero-marginal plates alone, the supero-marginals indistinguishable from the paxillae (pl. 4, figs. 1-3) . . . . .  | <b>LUIDIIDAE</b> 3                                     |
| 2'  | Edge of the body defined by the two series of marginal plates, the supero-marginals sometimes smaller than the infero-marginals but always conspicuously different from the paxillae (pl. 5, figs. 1-3)  | <b>ASTROPECTINIDAE</b> 14                              |
| 3   | No large bivalved pedicellariae at the apices of the jaws close to the mouth; most of the arm breadth taken up by the larger, quadrangular lateral paxillae, up to five longitudinal rows of which each side also tend to form transverse rows, often many of these bearing single enlarged spines; colour with a bold pattern on the upper side, retained in preserved specimens, rarely the darker colour predominating                      | <b>LUIDIA</b> (Alternata-group) 4                      |
| 3'  | Large bivalved pedicellariae present close to the mouth on the vertical face of the oral plates (fig. 11a) (p. 48); about half the arm width made up by smaller, more irregular paxillae, only two or three rows of larger lateral ones each side aligned transversely as well as longitudinally; no conspicuous enlarged paxillar spines (though <i>penangensis</i> has the central spinelet as much as 1 mm. long); no marked colour pattern | <b>LUIDIA</b> (Quinaria-group) 11                      |
| 4   | No conspicuous single paxillar spines, though the smaller proximal paxillae may have a large blunt central spinelet about twice as high as the peripheral spinelets . . . . .  | 5  |
| 4'  | Some or many of the lateral paxillae armed with large sharp single spines . . . . .  | 7  |
| 5   | Seven to nine arms (pl. 4, fig. 3) . . . . .   | <b>Luidia maculata</b> Müller & Troschel, 1842         |
| 5'  | Six arms . . . . .   | 6  |
| 6   | Arms slender and long, R/br c. 9/1; paxillae with fine granules, no one of which is enlarged conspicuously   | <b>Luidia hexactis</b> H. L. Clark, 1938 <sup>1</sup>  |
| 6'  | Arms stout and expanded beyond the base, then tapering sharply, R/maximum br 4-5/1; paxillae convex, those of the disc with one or sometimes several of the central granules markedly higher as well as thicker than the rest . . . . .  | <b>Luidia herdmani</b> A. M. Clark, 1953a <sup>2</sup> |
| 7   | Nearly all the lateral paxillae with spines; eight to ten arms . . . . .   | 8  |
| 7'  | Dorsal spines scattered, rarely present on consecutive paxillae and not very numerous; seven, sometimes fewer, arms . . . . .  | 10   |
| 8   | Eight arms (at least in the holotype and in Fisher's specimen); two actinal plates in series with each adambulacral, most of them bearing a rather slender pedicellaria, length:basal breadth 2.5-3.0:1; three adambulacral spines at R c.200 mm. . . . .  | <b>Luidia aspera</b> Sladen, 1889                      |
| 8'  | Nine or ten arms; three or four actinal plates corresponding to each adambulacral, their pedicellariae short and stout, length:basal breadth 1.5-2.0:1; only two adambulacral spines when R is c. 200 mm., though larger specimens (R > 300 mm.) may have three . . . . .  | 9  |
| 9   | Mauritius . . . . .  | <b>Luidia mauritiensis</b> Koehler, 1910b <sup>3</sup> |
| 9'  | Pacific . . . . .  | <b>Luidia magnifica</b> Fisher, 1906 <sup>3</sup>      |
| 10  | Pedicellariae present on the arms; regularly seven arms (though Koehler in 1910 referred two five-armed specimens from Madagascar to this species) (pl. 4, fig. 1) . . . . .   | <b>Luidia savignyi</b> (Audouin, 1826)                 |
| 10' | Pedicellariae present only in the interradii; six arms in the holotype and only known specimen   | <b>Luidia sibogae</b> Döderlein, 1920 <sup>4</sup>     |

<sup>1</sup> H. L. Clark referred *Luidia hexactis* to the Quinaria-group but its resemblance in paxillae and colour pattern to *maculata* argues against this. Nor has it the true bi-valved oral pedicellariae diagnostic of the Quinaria-group.

<sup>2</sup> Originally described as *Luidia maculata* forma *herdmani* and now raised to specific rank.

<sup>3</sup> I cannot distinguish between *Luidia mauritiensis* and *L. magnifica* on the basis of the available information. Fisher's holotype of *magnifica* is very large with R 330 mm., whereas the Philippine specimen which I referred to the same species in 1953 has R only c.180 mm. This probably accounts for its possession of two rather than three adambulacral spines. However, a Mascarene specimen in the British Museum collections from de Robillard, presumably conspecific with the type of *mauritiensis* from the same source, also has only two adambulacral spines though R was probably at least 300 mm. (It is very difficult to estimate the true size since pieces of arm have been splinted back on to a large disc which might have been from another individual.) This specimen has four actinal plates each side of most segments and their pedicellariae appear to be mostly three-valved. Koehler noted that the type has only one pedicellaria outside the second adambulacral spine and this is bi-valved but he may not have examined it closely; in side view many three-valved pedicellariae appear to be bi-valved. It is probable, I believe, that further collecting will show that a single species extends from Hawaii, the type locality of *L. magnifica*, to Mauritius. Koehler believed that there is a difference in the armament of the infero-marginal plates but his description of the plates of *mauritiensis* is rather obscure and the condition of the British Museum specimens is too poor to help in determining the armament.

<sup>4</sup> Since the holotype of *Luidia sibogae* has R only 19 mm., Döderlein himself expressed a doubt (which seems to me more than justified) about the status of *sibogae* as a species distinct from *savignyi*. The presence or absence of pedicellariae is rarely a character of much weight, in my opinion.

- 11 Nine or ten arms . . . . . *Luidia avicularia* Fisher, 1913a 12
- 11' Five or six arms . . . . . *Luidia penangensis* de Loriol, 1891 13
- 12 Madreporite very large and conspicuous; each paxilla with an enlarged wart-like central spinelet; six arms . . . . . *Luidia hardwicki* (Gray, 1840) 13
- 12' Madreporite obscured by paxillae; no wart-like central spinelet on the paxillae; five arms . . . . . *Luidia prionota* Fisher, 1913a 13
- 13 Long slender pedicellariae on the outer part of some adambulacral plates<sup>5</sup> (pl. 4, fig. 2) . . . . . *Craspidaster hesperus* (Müller & Troschel, 1840a) 14
- 13' No pedicellariae on the adambulacral plates<sup>5</sup> . . . . . *ASTROPECTEN* 15
- 14 Periphery of the body appearing smooth, the spines at the upper end of the infero-marginal plates appressed and inconspicuous . . . . . *ASTROPECTEN* 15
- 14' Periphery fringed with conspicuous large spines . . . . . *ASTROPECTEN* 15
- 15 Three to five actinal plates in longitudinal series each side of each interradius . . . . . 16
- 15' Usually only two actinal plates, sometimes one or three . . . . . 17
- 16 Lower surface of the infero-marginal plates uniformly covered with flattened scale-like spinelets; paxillar area not less than half the arm breadth, the supero-marginals being only moderately wide . . . . . *Astropecten euryacanthus* Lütken, 1872a 16
- 16' Lower surface of infero-marginals loosely covered with easily detached small granuliform tubercles; supero-marginals very wide, the paxillar area between making up less than half the arm breadth . . . . . *Astropecten alatus* Perrier, 1875 17
- 17 Four to six infero-marginal spines arising at the same level near the upper edge of the plate . . . . . *Astropecten progressor* Döderlein, 1917 18
- 17' Only one large infero-marginal spine at the upper edge of the plate, though one or more smaller spines may also be present below it . . . . . 18
- 18 Supero-marginal plates aligned on the sides of the arms, high vertically, even the distal ones appearing relatively narrow when viewed from above, not wider than long; all or most of the plates with a well-developed supero-marginal spine at the upper (inner or adradial) edge (except in *A. andersoni* and *fasciatus* where only the proximalmost spines are inner ones) . . . . . 19
- 18' At least the distal supero-marginal plates, if not the whole series, extending sufficiently on to the upper surface to appear broader than long when viewed from above; supero-marginal spines present or absent, if present then all but the basal few arise from the middle or outer part of the plate . . . . . 24
- 19 All the supero-marginal spines arising close to the upper edge of the plate . . . . . 20
- 19' The supero-marginal spines after the basal few arising from the middle or outer part of the plate . . . . . 23
- 20 Only the first two or three infero-marginal plates with a series of spines along the distal edge on the ventral surface . . . . . *Astropecten mindanensis* Döderlein, 1917 21
- 20' Infero-marginal plates with a series of spines arising close to the distal edge on the ventral side . . . . . 21
- 21 Supero-marginal spines short, only the first one of each series distinctly longer than the plate; main (uppermost) infero-marginal spine markedly flattened and almost truncated at the tip . . . . . *Astropecten javanicus* Lütken, 1872a 22
- 21' Most of the supero-marginal spines exceeding the corresponding plate in length; main infero-marginal spine sometimes rather flattened but not conspicuously so and more or less tapering to a usually sharp tip . . . . . 22
- 22 A continuous series of supero-marginal spines present, no proximal gap in the sequence . . . . . *Astropecten phragmorus* Fisher, 1913a<sup>6</sup> 22
- 22' Several of the proximal supero-marginal plates after the first one reduced in size and spineless (pl. 5, fig. 3) . . . . . *Astropecten polyacanthus* Müller & Troschel, 1842<sup>6</sup> 23
- 23 A series of spines present along the distal ventral edges of the infero-marginal plates . . . . . *Astropecten fasciatus* Döderlein, 1927 23

<sup>5</sup> This difference correlated with the presence of extra adambulacral spines in place of pedicellariae in *Luidia prionota* is the only character given by Fisher to distinguish it from *forficera* Sladen, a synonym of *hardwicki*. As already stated, I doubt whether this is of specific weight.

The two small specimens (R c.25 mm.) from Muscat shown in the Arabian column of the distribution table as *hardwicki* have no adambulacral pedicellariae but the general resemblance to Gray's holotype is so close that I cannot bring myself to re-identify them as *prionota*.

If *Luidia longispina* Sladen comes within the ten fathom line, the least recorded depths at present being 10-15 fathoms off Singapore by Bedford (1900) and 12 fathoms at Batavia by Sluiter (as *hardwicki*), it should run down to this section of the key. It can be distinguished by the much longer uppermost infero-marginal spines, four or more times as long as the infero-marginal plate in *longispina*, as opposed to about twice as long as the plate (or about equal to its width) in *hardwicki* and *prionota*.

<sup>6</sup> Like Mortensen (1940a) I have found that some specimens of *Astropecten* from the Persian Gulf have supero-marginal spines intermediate in form and occurrence between those described for *A. polyacanthus* and for *phragmorus*, thus throwing doubt on the specific validity of the two; nevertheless, one can usually refer specimens from any one station to one nominal species or the other with little hesitation. The solution of this problem needs more field work.

- 23' Ventral infero-marginal spines only present on the first two or three plates *Astropecten andersoni* Sladen, 1888 24
- 24 The distal supero-marginal plates each with a spine on the outer (abradial) part of the plate<sup>7</sup> . . . . . 25
- 24' The distal supero-marginals rarely with any large spines<sup>7</sup> . . . . . 32
- 25 A conspicuous large spine present on the inner edge of the first supero-marginal plate . . . . . 26
- 25' If any spine arises from the first supero-marginal then it is not conspicuously large compared with the other supero-marginal spines . . . . . 28
- 26 Most of the supero-marginal plates with three spines, sometimes more . . . . . *Astropecten triseriatus* Müller & Troschel, 1843 27
- 26' Not more than two spines on each supero-marginal . . . . . 27
- 27 Two similar spines below the main infero-marginal one<sup>8</sup> . . . . . *Astropecten bengalensis* Döderlein, 1917 27
- 27' Two markedly dissimilar spines below the main infero-marginal one, the proximal at least twice as long as the distal<sup>8</sup> . . . . . *Astropecten vappa* Müller & Troschel, 1843 28
- 28 Paxillae relatively broad, the larger ones with numerous (up to c.35) central granules besides the peripheral ones and the midradial arm paxillae also with multiple central granules . . . . . *Astropecten pugnax* Koehler, 1910b 29
- 28' Paxillae rarely with more than a dozen central granules or spinelets (though up to 18 have been recorded when R exceeds 100 mm.), the larger ones often with a granule in the middle ringed by about seven others and the midradial arm paxillae often reduced to only a single central granule or spinelet . . . . . 29
- 29 Arms more or less blunt at the tip, the paxillar areas ending abruptly; ventral sides of the infero-marginal plates usually with few spines among the small rounded scales, sometimes only on the interradiial plates or, when R < 30 mm., none at all, the appearance of these plates rather smooth; size not known to exceed R 45 mm.<sup>9</sup> . . . . . *Astropecten indicus* Döderlein, 1889 30
- 29' Arms tapering evenly to acute tips, the paxillar areas very narrow terminally; ventral surface of the infero-marginal plates appearing more or less 'shaggy', the spines being fairly numerous and the scales often pointed and somewhat outstanding; R often >70 mm. or even >100 mm. . . . . 30
- 30 Supero-marginal plates relatively narrow, the paxillar area making up about three-quarters of the basal arm breadth . . . . . *Astropecten carcharicus* Döderlein, 1917 31
- 30' Supero-marginal plates broad, the paxillar area little more than half the total arm breadth basally, if as much as 50 mm. or c.30 at R 80 mm.) . . . . . *Astropecten mauritianus* Gray, 1840 31
- 31 Supero-marginal plates relatively long and few, up to 35 recorded (and this at R 111 mm., c.23 when R is nearly 40 at R 80 mm.) . . . . . *Astropecten hemprichi* Müller & Troschel, 1843 32
- 31' Supero-marginal plates shorter and more numerous, up to 43 known (this at R 99 mm., c.32 at R 50 mm. or nearly 40 at R 80 mm.) . . . . . 33
- 32 A spine usually present on the inner edge of at least the first supero-marginal plate<sup>10</sup> . . . . . 33
- 32' No proximal supero-marginal spines . . . . . 34

<sup>7</sup> In view of the great range of variation in occurrence and size of the supero-marginal spines shown by Koehler (1910b) and John (1948) to occur in *Astropecten indicus* and *A. zebra*, both referable to 24' according to Döderlein, whose scheme is necessarily followed to some extent here, the great usage by Döderlein of characters to do with these spines is unfortunate.

<sup>8</sup> Specimens of *Astropecten indicus* with a full series of supero-marginal spines, such as the types of *A. koehleri* de Loriol, shown by Koehler (1910b) and John (1948) to be a synonym, may run down here. This is also true of the little-known *A. orsinii* Leiboldt, 1895, which I suspect will prove to be synonymous with some other nominal Red Sea species, since the largest of the three syntypes has R only 25.5 mm. The low rounded middle and distal supero-marginal spines found in *orsinii* may also occur in some specimens of *A. indicus*, as shown in Koehler's pl. iv, fig. 8 but the arms appear to be relatively longer in *orsinii*, R/r being 3.6-4.3/1 compared with usually 2.8-3.5/1 in *indicus*, which can similarly be distinguished from *A. bengalensis* by the relatively shorter and blunter arms, the latter having R/r c.4.0-5.5/1. *A. bengalensis* also grows to a larger size, R even exceeding 100 mm., whereas *A. indicus* is not known to exceed R 45 mm. See also table note 3.

Yet another species which may fall here is *A. zebra*, occasional individuals of which may have almost complete series of supero-marginal spines, according to John.

<sup>9</sup> *Astropecten bonnieri* Koehler, 1906, also falls here. The supero-marginals beyond the first six bear spines but for some reason Döderlein referred the species to the Monacanthus-group, though he did say that it was probably related to *A. hemprichi* (Scoparius-group). The type from SW Arabia within the Red Sea, has R only 28 mm. The arms appear blunt in Koehler's figure, more like those of *A. indicus*.

<sup>10</sup> A few specimens of *Astropecten monacanthus* besides the holotypes of *A. savasinorum* Döderlein, 1917 (R only 16 mm.) from Ceylon and *A. notograptus* Sladen, 1888 (R only 16.5 mm.) from the Mergui Archipelago, Burma, would probably run down here rather than to 32' since certain individuals of *monacanthus* have some small supero-marginal spines, as John (1948) has described and both the others have a spine or at least an enlarged tubercle on each first supero-marginal plate. I believe that *A. notograptus* is in fact a synonym of *monacanthus*. Several of the specimens in the British Museum collections named or left as *monacanthus* by John share the colour pattern with dark interradiial chevrons and distal transverse bands found in the holotype of *notograptus*. This is true of specimens from Burma and from Tuticorin and Pearl Bank in the Gulf of Manaar, those from Tuticorin being labelled as *notograptus* by Bell though in his published report on Thurston's collection they are listed as *Astropecten hemprichi*. One of the two Burmese specimens has both dark chevrons and dark midradial lines. Fisher has given the colour of specimens from the Philippines (the type-locality of *monacanthus*) as light brown with the centre of the disc and a narrow midradial stripe darker. Most of the other British Museum specimens have no trace of colour pattern left but one from the Andaman Islands has dark midradial lines alone. (It should be noted that *A. granulatus* Müller and

- 33 Ventral surface of infero-marginal plates covered with slender spinelets and a series of distal slender spines; usually only a single but conspicuous pair of supero-marginal spines in each interradius but when  $R > 60$  mm. the second plate also often bears a spine *Astropecten velitaris* von Martens, 1865
- 33' Infero-marginal plates with flattened, round-tipped spinelets and a few flattened distal spines; often several supero-marginal plates beyond the basal ones bearing spines *Astropecten zebra* Sladen, 1883
- 34 Several spines present on each infero-marginal plate as well as the main one, at least along the distal edge on the ventral side and usually also associated with the main spine at the upper end (sometimes absent in small specimens,  $R < 20$  mm.) 35
- 34' Only diminutive spines below the main infero-marginal one, not more than a quarter as long as the big spine, giving a very clear-cut outline to the fringe of spines; no enlarged ventral infero-marginal spines (except sometimes on the first two plates only) 38
- 35 R/r usually c.3.0/1, arms markedly flattened and petaloid in shape, the distal supero-marginals narrowing rather abruptly; the infero-marginals usually projecting laterally beyond the supero-marginals; ventral infero-marginal spines slender; often the central spinelet of the distal mid-radial paxillae enlarged<sup>11</sup>  
*Astropecten antares* Döderlein, 1926
- 35' R/r usually 3.5-4.5/1, arms relatively narrow and tapering evenly, the margin thick, at least basally, and vertical, the infero-marginals not projecting farther than the supero-marginals to a very noticeable extent (it should be noted that small specimens,  $R < 20$  mm., at least of *granulatus*, have relatively shorter and flatter arms); no enlarged distal paxillar spinelets 36
- 36 Supero-marginal plates extremely broad, at least in the holotype and only known specimen, each about equal in breadth to the paxillar area; infero-marginals with the second spine below the main one almost as large  
*Astropecten orientalis* Döderlein, 1917
- 36' Supero-marginal plates only moderately broad, paxillar area about half the arm breadth; infero-marginal spine with a much smaller one below it, if any 37
- 37 Large infero-marginal spines flattened and at least the proximal ones truncated  
*Astropecten pulcherrimus* H. L. Clark, 1938
- 37' Marginal spines slender and acute *Astropecten granulatus* Müller & Troschel, 1842
- 38 Supero-marginal plates relatively narrow, the paxillar area at the base of the arm distinctly more than half the total arm breadth, usually about two-thirds; ventral side of the infero-marginals superficially appearing very smooth, being covered with short, rounded, more or less appressed squamules; two very broad and flattened spatulate spines on the middle part of each adambulacral plate (pl. 5, figs. 1, 2)  
*Astropecten monacanthus* Sladen, 1883

Troschel also has dark interradial markings and transverse arm bands and H. L. Clark (1938) found that at Broome, NW Australia, both *granulatus* and *monacanthus* share this colour pattern.) As for morphological characters, Sladen notes *Astropecten notograptus* presents several points of affinity with *A. monacanthus* mihi; but the broad marginal plates, the large paxillae, the simple spinulation of the infero-marginal plates and the difference in the character of the adambulacral armature (although only slight) serve to distinguish the Mergui species [i.e. *notograptus*]. Comparing the two syntypes of *A. monacanthus* with Sladen's description of *notograptus* (the type of which is in the Indian Museum), the armament of the infero-marginal plates seems equally 'simple' owing to the short rounded scale-like spinelets or squamules and the absence of spines while the arrangement of the adambulacral spines appears indistinguishable. Fisher notes (1919) that the paxillae of *monacanthus* are fairly large. Also I find that a specimen from Tuticorin, with colour pattern similar to that of the type of *notograptus* but size similar to that of the types of *monacanthus*, has paxillae not significantly larger than those of the latter. However, this Tuticorin specimen does have relatively broader supero-marginals than the types of *monacanthus*; its measurements R, total arm br (level with the second and third supero-marginals), corresponding paxillar area br and supero-marginal br are respectively 27, 8.2, 5.2 and 1.5 mm., while in the larger syntype they are 27, 6.5, 4.5 and 1.0 mm., the arm in this type-specimen being unusually narrow. Sladen describes the holotype of *notograptus* as having the paxillar breadth three times that of the supero-marginals (presumably the individual supero-marginal not the two corresponding ones combined), giving a ratio of arm breadth:paxillar area breadth of 1:0.60 compared with 1:0.62 in the Tuticorin specimen and 1:0.69 in the syntype of *monacanthus*. However, there is clearly considerable variation in the relative breadth of the supero-marginals judging from other specimens in the British Museum collections; one of the two from 'Burma' (no details) has the four measurements (R, br, pax. br and s.m. br) 38, 11, 9.5 and 0.75, while in the other they are 51, 12.5, 8.5 and 2.0, the two ratios being 1:0.86 and 1:0.68. Further and larger specimens from the Mergui Archipelago (the type-locality of *notograptus*) are needed to settle this problem but I strongly suspect that *notograptus* will prove to be a synonym of *monacanthus*. Both can be distinguished from *A. velitaris* and *A. zebra* by the small size of the spine (or enlarged squamule) below the main infero-marginal spine and by the absence of enlarged ventral spines on these plates. As for *A. sarasinorum*, its affinities are less clear to me; the more spiniform armament of the infero-marginals distinguishes it from *monacanthus*. Possibly it is related more closely to *indicus*, of which Döderlein failed to appreciate the range of variation. It is omitted from the key, the holotype and paratype being immature (R 16 and 27.5 mm.).

<sup>11</sup> Specimens of *Astropecten indicus* without proximal supero-marginal spines such as the holotype may run down here, since they also have two spines accessory to the main infero-marginal one though ventral infero-marginal spines are usually deficient, except interradially. The holotype has R/r 3/1 and even in larger specimens the ratio is usually less than 3.5/1, which, coupled with the rather flattened form, gives *indicus* a considerable superficial resemblance to *A. antares*. The latter can most easily be recognized by the large paxilla obscuring the madreporite, that of *indicus* not being so covered.

- 38' Supero-marginal plates wide, paxillar area rarely more than half the total breadth; infero-marginals with slender or at least tapering spinelets; subambulacral spines numbering three and similar in form to the furrow spines
- 39 Coarse granules on the supero-marginal plates *Astropecten umbrinus* Grube, 1866 39
- 39' No coarse granules on the supero-marginals *Astropecten pusillus* Sluiter, 1889
- 40 Abactinal plates paxilliform (i.e. with a narrow central elevation crowned with spinelets); the midradial row of paxillae distinctly enlarged without being raised above the surface; interradii angular, the arms narrow basally, flat above and with the supero-marginal plates almost completely vertical in alignment (pl. 5, fig. 5) **ARCHASTERIDAE** 41
- 40' Abactinal plates of different forms, tabulate (i.e. with a broad elevation crowned or ringed by short spinelets or granules), convex, flat, forming a reticulum, or obscured by skin, rarely paxilliform and then either the ventro-lateral areas are large and the interradii rounded (*Mediaster*) or the arms are cylindrical and the marginal plates inconspicuous (*Chaetaster*); arms either flattened or more or less cylindrical; midradial row of plates not enlarged and at the same time flush with the rest of the dorsal surface, though they may be distinguished by elevations, tubercles or other projections 43
- 41 Infero-marginal plates with a single large spatulate spine projecting from the upper end (rarely reduced or absent) (pl. 5, fig. 5) *Archaster typicus* Müller & Troschel, 1840a
- 41' Infero-marginal plates with two or three (sometimes four) enlarged flat scales or short appressed spines at the upper end 42
- 42 Paxillae armed with short prismatic truncated spinelets, fitting closely together in preserved specimens so that their tips form a smooth continuous pavement<sup>12</sup> *Archaster laevis* H. L. Clark, 1938
- 42' Paxillae armed with cylindrical round-tipped spinelets *Archaster angulatus* Müller & Troschel, 1842
- 43 Marginal plates large, forming a conspicuous side-wall to the body, the upper surface usually almost flat, rarely somewhat convex; no papulae on the lower side; interradial arcs rounded<sup>13</sup> **GONIASTERIDAE** 44
- 43' Marginal plates rarely very conspicuous when viewed from above (except in a few Ophidiasterids such as *Fromia* or in immature Oreasterids), usually moderate in size or small, when defining the edge of the body this edge is usually thin and low down, the oral side being flat and the aboral very convex; alternatively the arms are narrow and more or less cylindrical; papulae often present on the lower side; interradial arcs rounded or angular 89
- 44 Abactinal plates, at least in the radial areas, paxilliform, crowned with angular granules  
*Mediaster praestans* Livingstone, 1933
- 44' Abactinal plates not paxilliform, though sometimes more or less convex and granule-covered 45
- 45 Abactinal plates conspicuously naked, sometimes with single high conical tubercles occupying the radial plates (*Calliaster*) or with a bumpy surface and thick skin (*Ogmaster*); coarse angular granules only around the periphery of each plate (absent in *Ogmaster*)<sup>14</sup> 46
- 45' Abactinal plates obscured by granules (sometimes rather sparse and easily rubbed off in dry specimens) or by skin so thick as to conceal the underlying plates (except in some small and dried specimens), often both granules and thickened skin present 49
- 46 Arms narrow terminally with several if not most of their supero-marginal plates contiguous aborally; peripheral granules of abactinal plates reduced on some sides or absent altogether 47
- 46' Arms broad terminally, only one or two of the distal-most supero-marginals contiguous aborally; all the abactinal plates completely ringed by coarse angular granules 48
- 47 Supero-marginals contiguous aborally almost from the base of the arm; abactinal plates restricted to the disc and many with complete series of peripheral granules though the radial plates have their tangential sides directly contiguous; aboral skin not thickened (pl. 5, fig. 4) *Iconaster longimanus* (Möbius, 1859)
- 47' Supero-marginals only contiguous aborally in the distal part of the arm, the abactinal plates extending between them proximally; no distinct series of granules bordering the abactinal plates; aboral skin somewhat thickened but not so much so as to conceal the limits of the plates *Ogmaster capella* (Müller & Troschel, 1842)
- 48 Some midradial plates at least bearing single high conical tubercles *Calliaster childreni* Gray, 1840

<sup>12</sup> *Mediaster praestans* may run down here since it has the midradial plates somewhat paxilliform as well as enlarged. It can easily be distinguished from *Archaster* by the curved interradii and the much greater encroachment of the supero-marginal plates on to the upper surface, the two series of each arm coming together distally so that even the midradial series of abactinal plates stops well short of the terminal plate.

<sup>13</sup> *Valvaster* (pl. 9, figs. 10, 11) from the Spinulosa may run down here since the marginals do define the edge of the body. It can be distinguished from the genera of Goniasteridae by the reticulate aboral skeleton with single conical spines on the plates and the huge spinelet-fringed bivalved pedicellariae on the supero-marginals.

<sup>14</sup> Flattened juvenile specimens of *Asteropsis carinifera* may run down here. Lacking granules on the upper surface, they are easily distinguished from *Ogmaster* by the short triangular arms and prominent single marginal spines.

- 48' No conspicuous aboral tubercles . . . . . *Tosia queenslandensis* Livingstone, 1932a
- 49 No modified subambulacral spines or granules developed, the adambulacral plates bearing only furrow spines backed by granulation similar to that of the actinal plates . . . . . 50
- 49' Subambulacral armament distinct from that of the actinal plates, consisting of enlarged granules, tubercles or spines, usually in a longitudinal row . . . . . 52
- 50 Marginal plates covered with a smooth plastering of flattened granules of varying sizes, usually with more or less enlarged granules or tubercles projecting slightly from the middle of the upper surface; numerous well-defined bivalved pedicellariae present both above and below but not reaching a very large size, most being about as wide as a quarter of the diameter of the plates bearing them
- Monachaster sanderi* (Meissner, 1892)<sup>15</sup>
- 50' Marginal and abactinal plates with fine even granules not flattened on to the plates; no enlarged tubercles or spines on the supero-marginals . . . . . **STELLASTEROPSIS** 51
- 51 Distal infero-marginal plates with an enlarged tubercle or short spine at the upper distal edge
- Stellasteropsis colubrinus* Macan, 1938
- Stellasteropsis fouadi* Dollfus, 1936
- 51' No tubercles or spines on the distal infero-marginals . . . . .
- 52 No conspicuous large bivalved pedicellariae present, only minute ones hardly if at all larger than the granules (fig. 11b); aboral skeleton compact, primary plates polygonal or stellate with pores singly or in small groups interstitially, accompanied by few superficial secondary plates and these usually in the form of calcareous rings associated with the alveolar pedicellariae; the limits of the abactinal plates distinguishable from their slightly convex contours and the positions of the papular pores, though often obscured by thickening of the skin or high density of the granulation<sup>16</sup> . . . . . 53

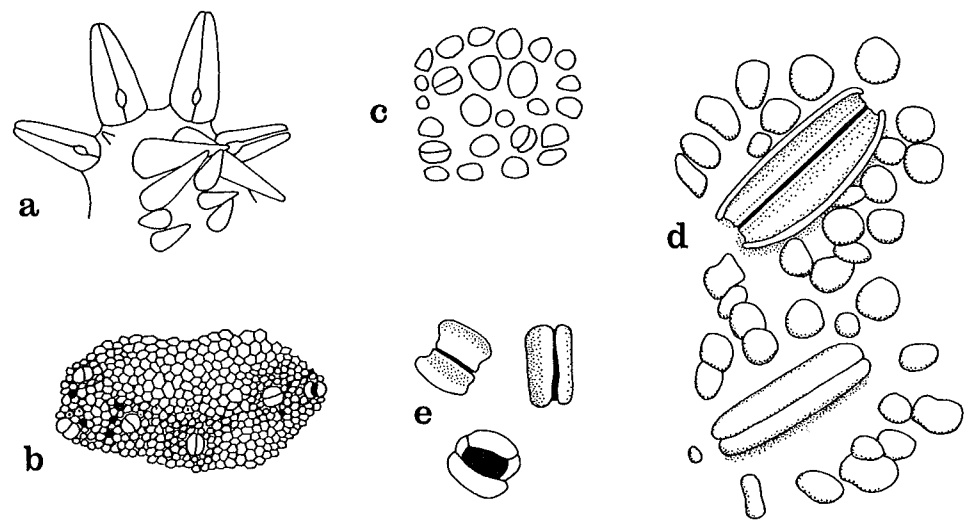


FIG. 11. Pedicellariae of: a. *Luidia penangensis*, proximal part of one jaw, the suboral spines displaced, b. *Goniiodiscaster vallei*, an actinal plate adjoining the adambulacrals, c. *Anthenea pentagonula*, two actinal plates, d. the same, abactinal pedicellariae open, closed and with the valves lost, e. *Nardoia pauciforis*, abactinal pedicellariae among the granules.

- 52' Bivalved pedicellariae large and conspicuous, especially on the plates adjacent to the ambulacral furrows, the valves usually about five or six times as wide as the pedicellaria is thick and often well over half the

<sup>15</sup> The systematic position of *Monachaster* is in doubt. Döderlein (1935) allies it with the Oreasterids and the close plastering of flattened granules and moderate-sized bivalved pedicellariae certainly agree with those of *Pentacaster* and *Protoreaster*. However, the flattened body form and the massive marginal plates as well as the relatively small poriferous areas with few secondary plates suggest an affinity with *Stellaster* and *Goniiodiscaster*. The enlarged granules around the pores resemble those of *Stellasteropsis* and *Siraster* and the absence of subambulacral spines also links it with *Stellasteropsis*. However, it should be remembered that the largest specimens of *Monachaster* recorded have  $R < 40$  mm., which is relatively small in comparison with the size reached by most Oreasterids.

Tortonese (1951) has recorded *Monachaster umbonatus* Macan (type-locality the Gulf of Suez in 65–68 metres) from off Somalia, depth not stated, which nominal species should perhaps be included on the strength of this record. However, I am not perfectly convinced of the distinctness of *M. umbonatus* from *sanderi*, especially as Tortonese found that one of Macan's distinguishing characters—the enlargement of the granules around the pores in *sanderi* also occurred in his specimen in combination with the absence of projecting tubercles on the supero-marginal plates, as in *umbonatus*. The other supposed differences in the shape of the arms and the number of supero-marginal plates are variable in related genera and do not seem to me to be of sufficient degree to justify a specific distinction. However, more material is needed before this can be decided. The type-locality of *M. sanderi* is Zanzibar and on geographical grounds the identity of the Somalian specimen with it is more likely.

- diameter of the underlying plate (fig. 11c; pl. 7, fig. 2); aboral skeleton of larger specimens ( $R > c.60$  mm.) reticulate with secondary plates linking the stellate primaries (though in smaller specimens the skeleton is more compact as in some of the genera included in 52); the abactinal plates concealed by granulation or skin or both, except in *Pseudogonioidiscaster* and in immature, particularly dried, specimens<sup>16</sup> . . . . . 70
- 53 Arms slender and acute at the tips; abactinal plates only slightly convex, if at all; aboral granulation fine, more or less imbedded in the skin, which may be thickened and semi-opaque; infero-marginal spines or stumps often present; superficial secondary abactinal plates mostly solid rather than annular . . . . . 54
- 53' Arms blunt at the tip and usually broad throughout; skin thin and inconspicuous; abactinal plates often conspicuously convex; secondary plates nearly all in the form of calcareous rings associated with the alveolar pedicellariae<sup>17</sup> . . . . . 58
- 54 Granulation of abactinal plates very sparse and no trace of infero-marginal spines or tubercles, at least at  $R$  only 18 mm. (as in the holotype and largest known specimen) . . . . . *Anthenoidea dubius* H. L. Clark, 1938
- 54' Granulation either continuous or slightly spaced so as to leave uncovered the glassy knobs or crystal bodies on the underlying plates; at least the distal infero-marginals with a spine or enlarged tubercle at their upper distal ends, even at  $R$  only c.20 mm.<sup>18</sup> . . . . . 55
- 55 Radial areas flat, supero-marginal plates forming a very broad border to the upper side, their interradial width approximately a third of  $r$ ; arms relatively broad basally and triangular in shape, br at half  $R$  equal to about one third of  $R$ ; granules around the papulae distinctly enlarged and scale-like
- Siraster tuberculatus* H. L. Clark, 1915a
- 55' Radial areas, if not the whole upper side, distinctly convex; supero-marginals narrower, not more than about a fifth of  $r$  interradially; arms slender, br at half  $R$  usually less than a fifth of  $R$ ; granules around the papulae usually similar to the rest (except in *squamulosus*) (pl. 5, fig. 6) . . . . . **STELLASTER** 56
- 56 Granules around the papulae conspicuously enlarged, visibly different, even with the naked eye, when  $R$  is only c.20 mm. . . . . *Stellaster squamulosus* Studer, 1885
- 56' All the granules similar in size . . . . . 57
- 57 At least the proximal infero-marginal plates with two enlarged spines . . . . . *Stellaster princeps* Sladen, 1889
- 57' Not more than one infero-marginal spine, sometimes none<sup>19</sup> . . . . . *Stellaster equestris* (Retzius, 1805)
- 58 Papular areas of the upper side with coarse flattened polygonal granules contrasting with the spherical ones on the convex plates . . . . . *Styphlaster notabilis* H. L. Clark, 1938
- GONIODISCATER** 59
- 58' Granules of the papular areas unspecialized . . . . .
- 59 Supero-marginal and abactinal plates covered with a smooth coat of flattened or rounded even-sized granules, sometimes with blunt, usually single, tubercles interspersed; few, if any, of the pedicellariae of the upper side with valves much longer than the granules are high, most resembling split granules . . . . . 60
- 59' Supero-marginal and aboral armament consisting of more or less spaced conical granules or short spinelets, rather variable in size, with some larger conical tubercles as well (except in some smaller specimens,  $R < c.30$  mm.); numerous tong-shaped alveolar pedicellariae with long curved valves projecting above the general armament of the upper side. . . . . 67
- 60 Arms pointed, narrow at the tip and tapering to some extent for their whole length . . . . . 61
- 60' Arms blunt at the tip, usually with parallel sides for at least part of their length, tapering abruptly from about the fourth from last marginals so that the tip is finger-like . . . . . 63
- 61 No enlarged tubercles on the supero-marginal plates . . . . . *Gonioidiscaster granuliferus* (Gray, 1847a)
- 61' One or more large flattened tubercles at the upper end of each supero-marginal . . . . . 62
- 62 Abactinal and supero-marginal plates with conspicuous single enlarged tubercles; pedicellariae not especially numerous<sup>20</sup> . . . . . *Gonioidiscaster vallei* (Koehler, 1910b)
- 62' Tubercles rather irregular in arrangement and inconspicuous in size; pedicellariae very numerous<sup>20</sup> . . . . . *Gonioidiscaster porosus* (Koehler, 1910b)

<sup>16</sup> Flattish specimens of *Pentaster obtusatus* (Oreasteridae) may cut across this dichotomy, having small valvate pedicellariae but a reticulate aboral skeleton. Also young specimens of *Culcita*, once known under the name of *Gonioidiscus sebae*, may run down here. One of the latest in the long list of synonyms of *C. novaeguineae* is *Hippasteria philippinensis* Domantay, as stated by A. H. Clark (1949). The great extent of the pore-areas distinguishes *Culcita*.

<sup>17</sup> This is hypothetical for *Styphlaster* since H. L. Clark did not denude the aboral skeleton and could not detect any pedicellariae in the intact specimen.

<sup>18</sup> It should be noted that juvenile specimens of *Stellaster* have the granulation very fine and spaced; in fact Döderlein (1935) notes that the youngest specimens (size unspecified) may be completely bare. However, at  $R$  c.15 mm. or more, there are numerous granules, though these may be easily rubbed off.

<sup>19</sup> Some juvenile specimens of *Gonioidiscaster*, which tend to have narrower arms than the adults, may run down here; they belong to those species of *Gonioidiscaster* which have slightly spaced, unequal, conical granules on the marginal and abactinal plates, contrasting with the smooth even granulation of *Stellaster*.

<sup>20</sup> I doubt whether the number of pedicellariae provides a significant distinction, particularly as all the specimens of *Gonioidiscaster porosus* described have  $R$  85–105 mm., whereas the largest known *G. vallei* has  $R$  65 mm. Nor am I sure that the abundance of enlarged tubercles is of importance. Although he compared *porosus* and *vallei* individually with *granuliferus*, Koehler failed to compare one with the other.

- 63 The five primary radial plates usually each with a large conical tubercle, sometimes a small cluster<sup>21</sup> . . . . . 64  
 63' No conspicuous primary tubercles<sup>21</sup> . . . . . 65  
 64 Arms relatively wide nearly to the rounded tip; R/r usually c.2.5/1 or less  
*Goniodiscaster pleyadella* (Lamarck, 1816)  
 64' Arms tapering evenly to a blunt tip; 'R/r c.2.5/1 or more' (in fact in Livingstone's five specimens it ranges from 2.3 to 2.7/1, so this is hardly worth inclusion) . . . . .  
*Goniodiscaster integer* Livingstone, 1931a  
 65 Abactinal plates without coarse granules and pointed tubercles but with very numerous small pedicellariae  
*Goniodiscaster foraminatus* Döderlein, 1916  
 65' Abactinal plates with coarse granules and small, pointed tubercles, small pedicellariae not excessively numerous . . . . . 66  
 66 Upper surface bluish grey in life, with marginal plates and coarsest granules and tubercles bright brick red  
*Goniodiscaster acanthodes* H. L. Clark, 1938  
 66' Disc and arm bases clear grey, remainder of arms bright rose red . . . . .  
*Goniodiscaster bicolor* H. L. Clark, 1938  
 67 Arms long and fairly narrow, though blunt tipped, R/r usually exceeding 2.5/1 and sometimes even 3.0/1<sup>22</sup> . . . . . 68  
 67' Arms of moderate length or short so that the form is stellate, R/r rarely exceeding 2.5/1<sup>22</sup> . . . . . 69  
 68 Upper surface rough, with many coarse conical granules and pointed tubercles easily visible with the naked eye<sup>23</sup> . . . . .  
*Goniodiscaster australiae* Tortonese, 1937b  
 68' Upper surface more finely granulated, the tubercles barely visible with the naked eye<sup>23</sup> (pl. 5, fig. 7)  
*Goniodiscaster rugosus* (Perrier, 1875)  
 69 Few enlarged tubercles on the upper side (possibly correlated with the relatively small size of the known material, R up to only 45 mm.)<sup>24</sup> . . . . .  
*Goniodiscaster forficulatus* (Perrier, 1875)  
 69' Many enlarged aboral tubercles<sup>24</sup> . . . . .  
*Goniodiscaster scaber* (Möbius, 1859)  
 70 Skin covering the upper side thin, not obscuring the limits between the plates and papular areas (even at R 77 mm.); marginal granulation fine; the five primary radial plates and tubercles conspicuously enlarged . . . . .  
*Pseudogoniodiscaster wardi* Livingstone, 1930

<sup>21</sup> Here again I doubt whether this is a reliable character, insufficient allowance having been made for variation. There are three syntypes of *Pentagonaster validus* Bell (acknowledged by H. L. Clark (1909), Livingstone (1931a) and Döderlein (1935) as a synonym of *G. pleyadella*), in the British Museum collections; of these, one has no trace of enlarged primary tubercles, another has single small ones and the third has several tubercles on each primary. A fourth syntype, in the Museum of Comparative Zoology, Harvard, seen and figured by Livingstone (1931, pl. xix, figs. 3 and 4), resembles the second one, as does Döderlein's largest specimen of *pleyadella* (1896, pl. xviii, fig. 34). Müller and Troschel (1842) also describe primary tubercles in Lamarck's types of *G. pleyadella*. Livingstone and H. L. Clark both concluded from this evidence that these tubercles are characteristic of the species, the latter using them in his key of 1946 to separate *pleyadella* and *integer* from the rest of the genus. However, of the specimens which Livingstone referred to *G. integer*, the largest paratype (pl. xviii, fig. 3) has no primary tubercles. (Since it also has tapering arms it closely resembles the holotype and other B.M. specimen of *G. granuliferus*.) Among the other nominal species of *Goniodiscaster* from northern Australia, *G. bicolor* H. L. Clark also shows variation in the primary tubercles. These were not present in the holotype and accordingly H. L. Clark placed *bicolor* in his key among the species lacking tubercles. However, the paratype of *bicolor* which he presented to the British Museum does have well-developed primary tubercles. If Livingstone was correct in considering as conspecific all the specimens he figured under the name of *integer*, then the distinctions between *pleyadella*, *integer*, *granuliferus*, *bicolor*, *acanthodes* H. L. Clark and *foraminatus* Döderlein are very hard to lay down. Clark pointed out that the morphological variation in *bicolor* and *acanthodes* is such that only the different colour pattern would serve to differentiate them; also Döderlein's *foraminatus* is only distinguished from *pleyadella* by the absence of primary tubercles and the convexity of the abactinal plates. Without extensive samples of material from northern Australia it is impossible to settle the specific limits satisfactorily and I can only repeat the dichotomies given by H. L. Clark or Döderlein for these nominal species, with reservations on their true value.

<sup>22</sup> This is a poor distinction since *Goniodiscaster scaber* (Möbius) should run down to 69. It should be pointed out that the holotype, figured by Döderlein (1935), has R/r 56/22 mm. = 2.6/1 and he also mentions a specimen with a ratio of 2.75/1 (though this has R only 37 mm. and the arms do tend to be relatively longer in smaller specimens of *Goniodiscaster*). The other specimens of *G. scaber* described or in the British Museum collections have R/r 2.6, 2.1, 2.05, 1.9, 1.7, 2.2, 2.0 and 2.2/1, the last four being our material from the vicinity of Singapore. There is a great resemblance in armament of the plates between the two syntypes of *G. rugosus* (Perrier) (of which *coppingeri* Bell is here considered to be a synonym) and the holotype of *G. scaber*. However, the more pentagonal shape of most of the other specimens which have been referred to *scaber* gives them such a different facies that I hesitate to synonymize *rugosus*. Perrier's types were of unknown locality; they have R/r 77/28 mm. = 2.75/1 and 73/29 mm. = 2.5/1, whereas in the syntypes of *coppingeri* from Queensland it is 91/33 mm. = 2.75/1 and 79/25 mm. = 3.2/1; in another Queensland specimen it is 55/17 mm. = 3.2/1 and a specimen referred by H. L. Clark (1938) to *coppingeri* has the ratio 93/26 mm. = 3.6/1. Until larger samples are available the specific limits must remain uncertain. Possibly Australian specimens will prove to have a greater tendency to develop relatively longer arms than those from Malaysia.

<sup>23</sup> I have little faith in this distinction either; it is taken from H. L. Clark's key to *Goniodiscaster australiae* and *coppingeri* (1946). A specimen from Broome, NW Australia (with R/r 3.2/1) identified as *G. australiae* by H. L. Clark is in the British Museum collections; it does have the tubercles of the upper side more conspicuous than those of the types of *rugosus* as well as having more pedicellariae, but as both are differences of degree I doubt whether they are enough to warrant a specific distinction.

<sup>24</sup> *Goniodiscaster forficulatus* and *scaber* I consider will also prove to be conspecific when better samples are available.

- 70' Larger specimens at least with the abactinal plates more or less completely hidden beneath the thick skin (even in small dry specimens, R < c.30 mm., the edges of the plates are not sharp); marginal granules usually more or less coarse; primary plates and tubercles rarely larger than at least the other carinal ones . . . . . 71  
 71 Three (or more) series of spines on the adambulacral plates (at least when R > c.25 mm.); arms usually triangular or tapering to a blunt tip; carinal rows of tubercles not conspicuously enlarged  
**ANTHENEAE** . . . . . 72  
 71' Only two series of adambulacral spines, the outer parts of the plates bare and smooth (except in the distal parts of the arms of some specimens of *Pseudoreaster*); arms broadly rounded at the tip; carinal plates with conspicuously enlarged low rounded single tubercles . . . . . 88  
 72 The five primary radial plates each with a conspicuous enlarged pointed tubercle; distal marginal plates also with single tubercles. (R not known to exceed 40 mm.) . . . . .  
*Anthenea rudis* Koehler, 1910b  
 72' The primary tubercles not conspicuously enlarged, often many abactinal plates bearing similar ones . . . . . 73  
 73 Arms more or less pointed at the tips, the breadth at one-tenth R from the tip often c.0.15 R; arms usually relatively long, R/r c.2/1, though tending to be less in some very large specimens, R > 80 mm.<sup>25</sup> . . . . . 74  
 73' Arms broad and rounded at the tips, breadth at one-tenth R from the tip usually c.0.2 R or more; arms usually relatively short, R/r about 1.7/1 but sometimes exceeding 2.0/1<sup>25</sup> . . . . . 81  
 74 Interradial supero-marginal plates mainly horizontal in alignment . . . . . 75  
 74' Interradial supero-marginals more or less vertical, not forming a broad rim to the body when viewed from above . . . . . 78  
 75 Abactinal plates and upper surfaces of the supero-marginals predominantly bare<sup>26</sup>  
*Anthenea flavescens* (Gray, 1840)  
*Anthenea grayi* Perrier, 1875  
 75' Upper side covered with a more or less continuous armament of granules, tubercles and pedicellariae . . . . . 76  
 76 Infero-marginal plates closely covered with small granules and each with only one pedicellaria, if any  
*Anthenea elegans* H. L. Clark, 1938  
 76' Infero-marginals with coarse granules, at least on the more distal part, usually two or more pedicellariae on each plate . . . . . 77  
 77 Abactinal plates with numerous coarse tubercles; the upper part of each supero-marginal plate with a few coarse granules in the middle, sometimes in a vertical row, but bare towards the edges  
*Anthenea crassa* H. L. Clark, 1938  
*Anthenea aspera* Döderlein, 1915  
 77' Aboral tubercles few and inconspicuous; no bare areas on the upper parts of the supero-marginals  
*Anthenea edmondi* nom. nov.<sup>27</sup>  
 78 Reticular form of the skeleton often distinct, at least in large dried specimens; supero-marginal plates with granules extending to the upper edge, no bare areas . . . . .  
*Anthenea edmondi* nom. nov.<sup>27</sup>  
 78' Skeleton not obviously reticular; supero-marginal plates with reduced armament in the upper part, particularly towards the proximal and distal edges which are noticeably bare . . . . . 79  
 79 Extremely numerous and relatively small bivalved pedicellariae present on the lower side, often about ten on each infero-marginal . . . . .  
*Anthenea polygnatha* H. L. Clark, 1938  
 79' Pedicellariae not extremely numerous, rarely more than three or four on each infero-marginal . . . . . 80  
 80 Supero-marginal plates low (dorso-ventrally), with the upper part quite bare; the tubercles of the abactinal plates low and more or less flattened . . . . .  
*Anthenea australiae* Döderlein, 1915

<sup>25</sup> From paucity of material in comparison with that of H. L. Clark (1938) it is necessary to adopt Dr. Clark's key to the species of *Anthenea* to some extent. The difference in R/r measurement, which tends to decrease inversely with size, is an unfortunate choice for a primary distinguishing character, even with qualifications, particularly as Clark includes the type-species, *A. pentagonula*, among the short-armed species, R/r < c.1.9/1, whereas the fourteen specimens in the British Museum collections show an R/r ratio ranging from 1.7 to 2.3/1, averaging 2.0/1. The same dichotomy also splits up some closely-related pairs of nominal species, such as *A. aspera* and *viguieri* and *A. conjugens* and *godeffroyi*.

<sup>26</sup> The holotype of *Anthenea grayi* is much larger than that of *flavescens*, having R/r 42/18 mm. = 2.3/1, as opposed to 17/9 mm. = 1.9/1. Döderlein (1915) designated *grayi* unseen as type-species of *Pseudanthenea*, which I have no hesitation in referring to the synonymy of *Anthenea*, being convinced that *grayi* and *flavescens* are congeneric, if not conspecific; both may well represent the immature form of species of *Anthenea* known only from larger specimens.

In the holotype of *A. grayi* there are, in fact, four or five furrow spines, not three as Perrier (1875) noted, and the supero-marginal 'spines' are better termed pointed tubercles, being conical and not more than twice as high as wide basally. The registered number written on the specimen, 43.3.29.3, corresponds with an entry in the register with the locality Guimaras, Philippine Islands, Cuming collection; Perrier's statement that the locality is unknown is therefore incorrect.

In *A. pentagonula*, which may also run down here since some specimens have more pointed arms, R/r may exceed 2/1 and the aboral armament may be somewhat spaced, also the supero-marginals may be rather bare at the edges.

There is a superficial resemblance between flattened juvenile specimens of *Asteropsis carinifera* with their rounded primary plates contiguous and the holotype of *Anthenea grayi* but *Asteropsis* can be distinguished by the complete absence of armament on the upper surface (except for a tubercle or spine on each primary radial plate) and the single marginal spines.

<sup>27</sup> *Anthenea edmondi* is a new name for *Goniodiscus acutus* Perrier, 1869, a junior primary homonym of *G. acutus* Heller, 1863, which is a synonym of *Sphaeriodiscus placenta*.

Some specimens of *A. elegans* with more vertical supero-marginals than usual may run down here.

- 80' Supero-marginals high and narrow, with a large granule near the top, crowning a wedge-shaped area of progressively less coarse granules; aboral tubercles often as high as wide<sup>28</sup>
- 81 At least the distal supero-marginals predominantly lateral in position, not forming a border to the body when viewed from above; primary abactinal plates, together with their armament, more or less distinctly enlarged near the arm tips . . . . . 82
- 81' All the supero-marginals extending on to the upper side and more or less conspicuous when viewed from above; except in *A. mertoni* the distal abactinal plates similar to the rest . . . . . 85
- 82 Armament of enlarged distal abactinal plates consisting of fairly numerous (5-10) granules, contrasting with the single tubercles of the rest of the upper side . . . . . *Anthenea sibogae* Döderlein, 1915<sup>28</sup>
- 82' Armament of the distal plates not dissimilar to that of the other abactinal plates, though the tubercles may be somewhat enlarged or more numerous than proximally . . . . . 83
- 83 Primary aboral tubercles stout, flat-topped and widely spaced (even the distal plates rarely with more than one tubercle), only about five longitudinal series in the distal half of the arm (at least in larger specimens,  $R > c.70$  mm.)<sup>29</sup> . . . . . *Anthenea tuberculosa* Gray, 1847a
- 83' Primary aboral tubercles numerous and often bluntly pointed, forming about nine series along each arm in larger specimens . . . . . 84
- 84 Aboral tubercles 'big' (exact size not given) and bluntly pointed . . . . . *Anthenea acanthodes* H. L. Clark, 1938
- 84' Aboral tubercles relatively small (about 1 mm. high when  $R = 79$  mm.) and blunt . . . . . *Anthenea godeffroyi* Döderlein, 1915<sup>30</sup>
- 85 Aboral skeleton stout, the spaces between the secondary plates being relatively small; at least on the distal parts of the arms the flat rounded primary plates more or less conspicuously bare . . . . . *Anthenea pentagonula* (Lamarck, 1816)
- 85' Aboral skeleton superficially appearing fairly open (at least in larger specimens,  $R > 50$  mm.), the reticular spaces between the plates relatively large (though sometimes obscured by numerous pedicellariae with their alveoli); distal primary plates bearing tubercles or enlarged granules and sometimes themselves enlarged and convex . . . . . 86
- 86 Abactinal plates near arm tips enlarged and convex, approximating in form to the supero-marginal plates . . . . . *Anthenea mertoni* Koehler, 1910a
- 86' Distal abactinal plates not conspicuously enlarged . . . . . 87
- 87 Aboral pedicellariae small and inconspicuous, not more than 1.5 mm. wide (pl. 7, figs. 1, 2) . . . . . *Anthenea regalis* Koehler, 1910b<sup>31</sup>
- 87' Aboral pedicellariae numerous, some exceeding 2 mm. in width . . . . . *Anthenea viguieri* Döderlein, 1915<sup>31</sup>
- 88 Supero-marginal armament restricted to a few (up to c.6) very coarse granules on the lateral face of each plate, the uppermost one distinctly larger than the rest and forming an abrupt edge to the upper surface since the horizontal part of each supero-marginal is bare in contrast . . . . . *Gymnanthenea globigera* (Döderlein, 1915)
- 88' Supero-marginals with fairly numerous coarse granules on both lateral and upper surfaces (though tapering off on the latter), no single upper one regularly enlarged; the aboral side of the body rounded off at the margin (pl. 6, fig. 1) . . . . . *Pseudoreaster obtusangulus* (Lamarck, 1816)
- 89 Form massive, adults with  $R$  often well in excess of 100 mm.; interradial areas extensive, the arms tapering and stellate or short (sometimes so much so as to be non-existent (pl. 7, figs. 3-5); body almost flat below

<sup>28</sup> *Anthenea sibogae* may run down here since the arms of the holotype are relatively narrow (in contradiction to its position in H. L. Clark's key). However, the arm tips are moderately acute at the same time. It differs from *A. conjugens* in the relatively small size of the aboral tubercles.

<sup>29</sup> I think it quite likely that *Anthenea acanthodes*, with type-locality also in Queensland, may prove to be synonymous with *tuberculosa*, which H. L. Clark failed to recognize among the many Australian specimens studied by him.

<sup>30</sup> Possibly *Anthenea conjugens* Döderlein, 1935 is a synonym of *A. godeffroyi* though it comes in the first half of the key to *Anthenea* as given by H. L. Clark. Döderlein distinguished *conjugens* only by the smaller supero-marginal plates, making it intermediate between *godeffroyi* and *australiae*. Out of several specimens in the British Museum collections from the Broome area (NW Australia), one with  $R$  c.50 mm. has a very close resemblance to the holotype of *godeffroyi*, which Döderlein (1935) thought was probably from Australia and not Samoa. The larger Broome specimens unlike this one, however, lack the enlarged distal dorsal plates and have more pointed arms and larger aboral tubercles, thus resembling the Broome specimen which H. L. Clark identified as *conjugens*, also in our collections.

<sup>31</sup> Döderlein distinguished *Anthenea regalis* and *viguieri* by the supposedly shorter arms ( $R/r$  c.1.5/1) of *viguieri*, of which there are two specimens in the British Museum collections from 'North China' named *A. articulata* by Perrier. The larger of these has  $R/r$  68/40 mm. = 1.7/1 and the smaller 36/18 mm. = 2.0/1. Conversely, one of the three specimens of *A. regalis* from southern India (the type-locality is north of Madras) has  $R/r$  75/50 mm. = 1.5/1 though the two others do have relatively longer arms,  $R/r$  1.7/1 and 1.95/1. I doubt whether the difference in abundance of pedicellariae should be used as a specific character but only additional material will show the truth of this. *A. viguieri* seems to be intermediate in body form and number of pedicellariae between *A. regalis* and *A. aspera*, the latter having relatively longer and more pointed arms, thus coming in the other half of the key (nos. 74-80).

- but usually markedly convex above, often highest at the five primary radial plates which may each be crowned by a high conical prominence; aboral skeleton reticular with secondary plates linking the larger primary ones and leaving conspicuous large poriferous areas between; armament usually of spaced conical tubercles, rarely few or absent; marginal plates well-developed but not very conspicuous in aboral view (except in juvenile *Culcita*, pl. 7, fig. 4) and sometimes more or less completely concealed by thickened skin (in *Choriaster* the thick smooth skin covers the entire body with no protuberances except the small adambulacral spines)<sup>32</sup> . . . . . **OREASTERIDAE** 90
- 89' Size showing a wide range, if the arms are short and the body form stellate or pentagonal with the under side flat and the upper convex, then either the size is small,  $R$  rarely exceeding 30 mm., the aboral skeleton consists of closely imbricated plates with usually single interstitial pores and the armament is of numerous fine, sometimes granuliform spinelets (Asterinidae, pl. 9, figs. 3-8), or the body is covered with thick smooth skin raised into conical eminences by series of single spines along each carinal and supero-marginal row of plates so that the arms are acutely triangular in cross-section (Asteropidae, pl. 9, fig. 9); other families with more or less cylindrical arms and small interradial areas . . . . . 116
- 90 A pair of conspicuous supero-marginal plates visible at the tip of each arm (pl. 6, fig. 4), the other marginals more or less concealed under very coarse granules and tubercles; body form approaching the pentagonal . . . . . **ASTERODISCUS** 91
- 90' The distalmost supero-marginals not conspicuously different from the other marginal plates, which are either all distinct or else more or less concealed by thick skin; arms usually well-developed but some genera stellate or even pentagonal or circular in outline . . . . . 92
- 91 Arms very short, form often pentagonal,  $R/r < 1.8/1$ ; tubercles of upper side and margins tapering from the base to pointed, blunt or somewhat truncated tips (pl. 6, fig. 4) . . . . . *Asterodiscus elegans* Gray, 1847
- 91' Arms better-defined,  $R/r$  c.2/1; aboral and marginal tubercles broader at or near the apex than the base . . . . . *Asterodiscus helonotus* Fisher, 1913a
- 92 Entire surface covered by opaque smooth skin, interrupted only by the relatively small adambulacral spines and the papular areas; arms well-developed but short and broadly rounded at the tip,  $R/r$  c.2/1 (see frontispiece) . . . . . *Choriaster granulatus* Lütken, 1869b
- 92' If skin obscures the plates then it is rough in texture, often with more or less numerous tubercles and the actinal plates are conspicuously granule-covered, also the body form is pentagonal or even circular with  $R/r$  less than 2/1, sometimes almost 1/1; alternatively the limits of the abactinal plates are more or less distinct owing to their contours or armament and the arms are well-developed,  $R/r$  usually 2-3/1, but sometimes exceeding 4.5/1 . . . . . 93
- 93 Body pentagonal or almost circular in outline (according to age and state of preservation, young or badly-preserved and shrunken adult specimens being more angular) . . . . . 94
- 93' Arms well-developed . . . . . 98
- 94 Marginal plates clearly distinguishable, even in larger specimens with  $R > 100$  mm.; no tubercles at all on the upper side; pore-areas very well-defined and triangular in shape; granules of actinal plates markedly flattened and forming a smooth plastering following the contours of the plates . . . . . *Halityle regularis* Fisher, 1913a
- 94' Marginal plates concealed by thickened skin, at least when  $R > c.60$  mm. (pl. 7, fig. 3); some enlarged tubercles often present on the upper side; pore-areas usually rather irregular and sometimes indistinct or more or less continuous; actinal granules mostly coarse and individually distinct, often obscuring the limits of the plates . . . . . **CULCITA** 95
- 95 Papulae almost uniformly distributed all over the upper side and the margins, interspersed with numerous small (c.1 mm. high) tubercles or spinelets; non-poriferous areas very small and inconspicuous . . . . . *Culcita coriacea* Müller & Troschel, 1842
- 95' A distinct pore-free area at least towards the lower side at the margins as well as more or less extensive reticular areas on the upper side, though some of the pore-areas may be somewhat confluent; some larger, usually spaced, tubercles often also present . . . . . 96
- 96 No spines or spinelets on the pore-areas . . . . . *Culcita schmideliana* (Retzius, 1805)
- 96' Some spines or tubercles present within the pore-areas . . . . . 97

<sup>32</sup> The genus *Valvaster*, already mentioned in note 13, may be confused with the Oreasteridae although its upper side is flattened. The numerous articulated slender conical aboral spines and the large valvate spine-fringed supero-marginal pedicellariae (pl. 9, figs. 10, 11) should easily distinguish it.

The aberrant and completely spherical asteroid *Podosphaeraster polyplax* (described by A. M. C. in 1962, Clark and Wright, ref. no. 602) should also run down to this dichotomy but fits neither alternative. The holotype was from more than ten fathoms in the South China Sea but a second specimen has recently been found in the British Museum collections taken in Sandal Bay, Lifu, Loyalty Islands, depth not stated. Possibly the species also merits a place in this monograph. Like the holotype, the second specimen was determined only as '*Culcita* sp.' by Bell (1899: 137); the supposed imbrication of the skeletal plates referred to being due to the dorso-ventrally crushed condition of the specimen. *Podosphaeraster* can easily be distinguished from *Culcita* because the latter at a comparably small size,  $R < 10$  mm., is flattened and stellate, unlike the adult.

- 97 Actinal granulation including more or less numerous coarse, irregular, often polygonal granules, often in groups but generally with some finer granules among the coarse ones; pore-areas somewhat irregular and often only narrowly or incompletely separated (pl. 7, figs. 3-5)  
*Culcita novaeguineae* Müller & Troschel, 1842
- 97' Coarse actinal granules only present adjacent to the adambulacral plates, if at all; pore-areas rounded and separated by a continuous, heavy, non-poriferous reticulum  
*Culcita grex* Müller & Troschel, 1842<sup>33</sup>
- 98 At least the distal marginal plates and the convex parts of the larger abactinal plates covered with a smooth plastering of unequal polygonal flattened granules;<sup>34</sup> dorso-lateral areas of the arms rarely with any convexities (except near the arm tip in some larger specimens of *P. lincki*); infero-marginal plates spineless, also the supero-marginals (again except for a few of the distal ones in *P. lincki*) so that the outline is relatively smooth; actinal granulation always smooth; only two rows of adambulacral spines well-developed  
**PROTOREASTER** 99
- 98' The distal marginals and other plates covered with more individually-distinct and even-sized, usually projecting, granules;<sup>34</sup> dorso-lateral areas usually distinctly reticulate, the primary plates at the nodes often more or less convex or capped with rounded or conical tubercles and arranged in longitudinal series; some at least of the distal infero-marginal plates usually with enlarged single spines or conical projections, the outline consequently rather irregular; actinal plates often with some of the central granules more or less elongated into short spines; larger specimens,  $R > c.75$  mm., often with a third row of adambulacral spines. 101
- 99 A few of the distal supero-marginal plates bearing laterally-projecting, usually conspicuous, tapering spines or at least knobs<sup>35</sup>  
*Protoreaster lincki* (de Blainville, 1834)
- 99' Marginal plates lacking conspicuous spines or knobs (though at  $R < 40$  mm. the distalmost plates may each have an enlarged tubercle) 100
- 100 Disc usually of only moderate height ( $R$ : maximum height (to apex of primary tubercles) usually  $> 3.0:1$ );<sup>36</sup> carinal plates with very broad low rounded cushion-like tubercles, many of them broader than long (i.e. compressed tangentially); pore-areas well separated from each other  
*Protoreaster nodulosus* (Perrier, 1875)
- 100' Disc markedly elevated ( $R$ : height usually  $< 2.5:1$ );<sup>36</sup> some of the carinal plates with very conspicuous, more or less high, rounded or conical elevations, particularly huge on the five primary radial plates, the consecutive carinal tubercles usually spaced from each other and not broadened; pore-areas confluent (pl. 6, fig. 3)  
*Protoreaster nodosus* (Linnaeus, 1758)
- 101 The two series of marginal plates separated by small pore-areas and a few inter-marginal plates in each interradial angle; arms narrow,  $R/r$  often about or exceeding  $4/1$   
*Poraster superbus* (Möbius, 1859)
- 101' No extensive development of inter-marginal pore-areas, though a few intermarginal plates may occur; arms variable in length but  $R/r$  rarely  $> 3/1$  102
- 102 Entire upper side covered with numerous small low rounded, usually irregularly-placed warts, formed by the smaller plates (even within the pore-areas) as well as by the primary plates; pore-areas not well marked-off from each other  
**PENTASTER**<sup>37</sup> 103
- 102' Only the primary plates of the upper side with elevations and these tending to form regular longitudinal series; pore-areas usually well-defined  
**PENTACERASTER**<sup>37</sup> 104
- 103 Abactinal convexities so numerous as to obscure the longitudinal arrangement of the primary plates  
*Pentaster obtusatus* (Bory de St. Vincent, 1827)
- 103' Abactinal convexities fewer, distinctly arranged in longitudinal series  
*Pentaster hybridus* Döderlein, 1936

- 104 No spines on the first two to four supero-marginal plates in each interradial angle<sup>38</sup> 105
- 104' Some of the interradial supero-marginals with spines, at least at  $R > 50$  mm. 109
- 105 Dorso-lateral elevations or spines developed along the arms (rarely few in number)  
*Pentacaster regulus* (Müller & Troschel, 1842)
- 105' Dorso-lateral armament only on the disc, if present at all 106
- 106 Pore-areas more or less confluent; few, if any, supero-marginal spines present;  $R/r$  usually  $c.2.5/1$ <sup>39</sup>  
*Pentacaster tuberculatus* (Müller & Troschel, 1842)
- 106' Pore-areas distinctly separated (though again in large specimens,  $R > c.130$  mm., some of them may be partially confluent); some supero-marginal plates, especially distally, usually with prominent, laterally-directed elevations or spines (if these are reduced or absent then the arms are relatively long,  $R/r > 3/1$ ) 107
- 107 Few if any elevations on the carinal plates other than the five primaries, or on the supero-marginal plates; arms very slender,  $R/r$   $3.4/1$  in the holotype and only known specimen<sup>40</sup>  
*Pentacaster decipiens* (Bell, 1884)
- 107' A number of carinal spines well-developed and usually at least some distal supero-marginal spines also;  $R/r$   $2-3/1$  108

<sup>38</sup> As Döderlein (1936, p. 332) points out in his detailed and painstaking 'Siboga' Report, the genus *Pentacaster* includes a continuous chain of forms some of which may be distinguished as qualified "species" although their limits are much obscured by the existence of intermediate specimens. Consequently, since I cannot do better with the available material, the following part of the key, adapted from Döderlein's with only minor modification, should be used with caution, particularly in the identification of small samples, as is usual with these large sea-stars since their very bulk prevents the average collector from preserving more than a few from any one locality. I should point out that even the primary dichotomy is unsatisfactory since, not only does it separate the closely-related sympatric "species" *P. mammillatus* and *tuberculatus* (intermediates of which are not uncommon, possibly due to hybridization), but also it necessitates the inclusion of *P. regulus* on both sides because of the extent of variation in occurrence of the interradial supero-marginal spines, as demonstrated by Livingstone (1932a) in the Great Barrier Reef Expedition material and also shown by other Queensland specimens in the British Museum collections besides four dry ones from Billiton, near Java, all of which were named *Oreaster gracilis* by Bell. I believe that *O. gracilis* Lütken was based on large specimens of *regulus*, the type having  $R$  200 mm., while neither H. L. Clark (1921) nor Döderlein (1936) identified as *gracilis* any specimens with  $R < 110$  mm. Döderlein synonymized *O. australis* Lütken with *regulus* Müller and Troschel (type-locality India) but H. L. Clark thought the evidence for this was insufficient. Nevertheless I think it was a move in the right direction. Where the specific identification of *Pentacaster* is concerned it is as well to take the locality into consideration since parallel modifications seem to have appeared in different parts of the Indo-Pacific to which separate names have been given, thus *tuberculatus* from East Africa and the Red Sea with reduced aboral and marginal armament has a Pacific counterpart in specimens like the holotype of *Pentaceros bedoti* Koehler, 1911, which Döderlein considers is conspecific with *Pentacaster alveolatus* Perrier. It may be noted here that the holotype of *Oreaster troscheli* Bell, from Billiton is certainly conspecific with Fisher's Philippine specimen of *P. alveolatus*, though it has less resemblance to most of the specimens figured under that name by Döderlein. The types of two of Bell's other nominal species from Billiton, *Oreaster huetkeni* and *muelleri* I would refer rather to *P. regulus*, since they are more extensively armed, although I suspect that *regulus* and *alveolatus* may prove to be not specifically distinguishable. Yet another Billiton specimen, the poorly-preserved type of *O. grayi* Bell, has been considered by Döderlein and by Engel (1938) as referable to *P. multispinus*, which could also fall within the range of variation of *P. regulus*. The state of preservation may account for some of the supposed differences which have been put forward, the unnatural flattening of the upper side found in many museum specimens giving a very different impression of the proportions to that derived from well-preserved specimens.

The oldest specific name within the genus is *mammillatus* Audouin, 1826, for the species from the Red Sea and East Africa with moderate development of the dorso-lateral spines, at least proximally, somewhat larger carinal spines and a complete series of interradial supero-marginal spines (pl. 6, fig. 2). A number of specimens from within the range of *mammillatus* have this armament more or less extensively reduced, correlated with a greater continuity of the pore-areas. These specimens can be distinguished as *tuberculatus* but this could well be at the infra-specific level. Conversely, Mascarene specimens tend to have a much stronger development of the dorso-lateral spines and can be marked off as at least a subspecies *horridus* (Gray). In southern India, *affinis* and *regulus*, both of Müller and Troschel, have been recognized, *affinis* very similar to *mammillatus* but with the carinal spines said to be not conspicuously larger than the dorso-lateral ones (though out of eight specimens with  $R$  100-120 mm. from Madras State in the British Museum collections no less than four do have the carinal tubercles or spines distinctly larger, just as in *mammillatus*). *P. regulus* appears to have narrower arms and less well-developed proximal supero-marginal spines than *affinis* (judging from Koehler's photographs) but here again the difference is poorly marked and only in variable characters. If Döderlein is right, *regulus* extends into the Pacific as far as northern Australia and New Caledonia (reported by Livingstone, 1932a, under the name of *alveolatus*).

<sup>39</sup> Since intermediates occur between this relatively smooth form with only a few carinal elevations coupled with almost continuous pore-areas and *Pentacaster mammillatus* with numerous carinal, dorso-lateral and marginal spines, this distinction will not always hold good.

<sup>40</sup> The smooth and slender form of the holotype of *Pentacaster decipiens* is clearly intermediate between that of the holotypes of *Oreaster troscheli* (i.e. *P. alveolatus*, see note 38) and *O. productus* (a variety of *Poraster superbus* according to Döderlein), both new nominal species of Bell, 1884 and also from Billiton; the absence of intermarginal plates distinguishes *P. decipiens* from *Poraster*. Döderlein (1916, p. 433) notes that his new species *Pentacaster sibogae* is probably identical with *P. troscheli* but I consider that the type of *sibogae* (figured by Döderlein, 1936, pl. xxx, fig. 2) has an even greater resemblance to the type of *P. decipiens*, differing only in the presence of small dorso-lateral spines on the disc of the Siboga specimen. *P. sibogae* may also run down to 107 in this key since some specimens, including the holotype, have very deficient marginal armament.

<sup>33</sup> The British Museum collections include no specimens answering to Hartlaub's description of *Culcita grex* in having the ventral granulation almost uniformly fine. The one from the Andaman Islands named *grex* by Bell does have a fairly extensive non-poriferous reticulum on the upper side but the actinal granules include many coarse ones interspersed with fine, though with some tendency to grouping; I think this would be better identified as *C. novaeguineae* forma *arenosa*, which similarly lacks enlarged tubercles on the upper side. Two other large Andaman specimens, named *C. schmideliana* by Bell, differ in having fairly numerous abactinal tubercles and their coarse actinal granules are more distinctly grouped, the finer granulation tending to be excluded from within the groups, a condition characteristic of *schmideliana* according to Döderlein.

<sup>34</sup> Even with qualifications, this character used by Döderlein to distinguish *Protoreaster* is unsatisfactory since at least some Australian specimens of *Pentacaster regulus* share the mosaic-like condition of the granulation. Young specimens of *Pentacaster*, notably *P. mammillatus*,  $R < c.70$  mm., have the dorso-lateral areas and marginal plates almost flat, like adult *Protoreaster*.

<sup>35</sup> *Pentacaster alveolatus* superficially resembles *Protoreaster lincki* in the development of the abactinal and supero-marginal spines but differs in having infero-marginal spines and distinctly separated pore-areas.

<sup>36</sup> This ratio varies in 11 specimens of *Protoreaster nodulosus* from 2.7 to 3.8:1, compared with 1.9 to 3.0:1 in 19 specimens of *nodosus*.

<sup>37</sup> The distinction between *Pentaster* and *Pentacaster* is poorly-marked, as can be seen from the following dichotomy (103) and the use of the specific name *hybridus* by Döderlein.

- 108 Abactinal and marginal spines slender and conical; arm tips relatively narrow; R/r 2.4-3.0/1  
*Pentaceraster alveolatus* (Perrier, 1875)<sup>41</sup>
- 108' Abactinal and marginal spines stout; arm tips rounded; R/r 2.2-2.5/1  
*Pentaceraster multispinus* (von Martens, 1866)<sup>41</sup>
- 109 At least the carinal spines considerably enlarged, sometimes also the dorso-lateral ones; western Indian Ocean. . . . . 110
- 109' Many small abactinal spines developed but only the apical ones of any size, the other carinal spines little, if at all, larger than the dorso-lateral ones; southern India and eastwards . . . . . 111
- 110 Dorso-lateral spines numerous on the arms as well as the disc and often almost as large as the carinal ones, many spines separated by less than their own width; Mauritius and the Seychelles  
*Pentaceraster horridus* (Gray, 1840)
- 110' Dorso-lateral spines distinctly smaller than the carinal ones, only a few extending on to the arms and all well separated from each other; East Africa and the Red Sea (pl. 6, fig. 2)  
*Pentaceraster mammillatus* (Audouin, 1826)
- 111 Arms relatively short and triangular, R/r 2.0-2.3/1 . . . . . *Pentaceraster affinis* (Müller & Troschel, 1842) 112
- 111' Arms longer, R/r rarely less than 2.5/1 . . . . . 112
- 112 4-6 subambulacral spines in the row behind the furrow spines . . . . . *Pentaceraster chinensis* (Gray, 1840)<sup>42</sup> 113
- 112' 2 or 3, rarely 4, inner subambulacral spines . . . . . 113
- 113 R/r 2.3-2.8/1; some interradial intermarginal plates often developed (fig. 12) . . . . . 114
- 113' R/r c.3/1; no intermarginal plates described . . . . . 115

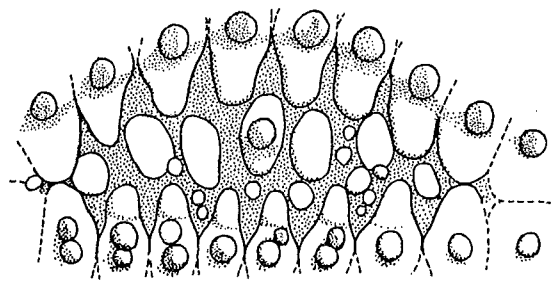


FIG. 12. *Pentaceraster gracilis*, lateral view of partly denuded interradius showing the intermarginal plates, one with a spine.

- 114 The two main series of marginal plates arching apart from each other interradially (fig. 12)  
*Pentaceraster gracilis* (Lütken, 1872a)<sup>43</sup>
- 114' Intermarginal plates, if present, not separating the two main series interradially to any extent but simply interstitial . . . . . *Pentaceraster regulus* (Müller & Troschel, 1842)<sup>43</sup>
- 115 Dorso-lateral spines well-developed, at least one series extending well out on the arms  
*Pentaceraster westermanni* (Lütken, 1872a)
- 115' Dorso-lateral spines diminutive and restricted to the disc . . . . . *Pentaceraster sibogae* Döderlein, 1916<sup>44</sup>
- 116 Arms cylindrical or slightly flattened and interradial areas small; skeleton fairly solid, the abactinal plates tessellate or forming a compact irregular reticulum, rarely (larger specimens of *Metrodira*, fig. 13a) imbricating outwards, often in more or less regular longitudinal series, the pore-areas relatively small compared with the area of the plates; marginal plates quite distinct, sometimes (in flatter genera such as *Fromia* and *Ferdina*) (pl. 8, figs. 8-10) forming a conspicuous border to the body in aboral view<sup>45</sup> . . . . . 117
- 116' Arms varying from flat and triangular to narrow and cylindrical but in the latter case the aboral skeleton has the form of an open reticulum (Echinasteridae), or the plates regularly imbricate inwards (fig. 16) and

<sup>41</sup> As Döderlein (1936) comments, *Pentaceraster alveolatus* and *multispinus* are hard to separate and some of the apparent differences may be attributable to the state of preservation, artificially-flattened specimens having the appearance of *multispinus*. I also find it difficult to distinguish between these two and *P. regulus* considering the variation in armament.

<sup>42</sup> Döderlein (1936) places *Pentaceraster chinensis* Gray in the synonymy of *Pentaceraster orientalis* (Müller and Troschel, 1842), in spite of its obvious two years priority.

<sup>43</sup> As already noted<sup>38</sup>, the similarity between *Pentaceraster gracilis* and *regulus* coupled with the consistently large size of the few recorded specimens of *gracilis* suggests to me that the latter is based simply on large specimens of *regulus*. This is supported by a series of four specimens in the British Museum collections from Port Denison, Queensland, named *gracilis* by Bell and having R 95-145 mm.; the smallest has the appearance of *regulus* and the largest of *gracilis*.

<sup>44</sup> *Pentaceraster sibogae* is omitted from the distribution table since the only records are too deep but is included here for the sake of completeness, all the other species of *Pentaceraster* from within the area covered being known from shallow water.

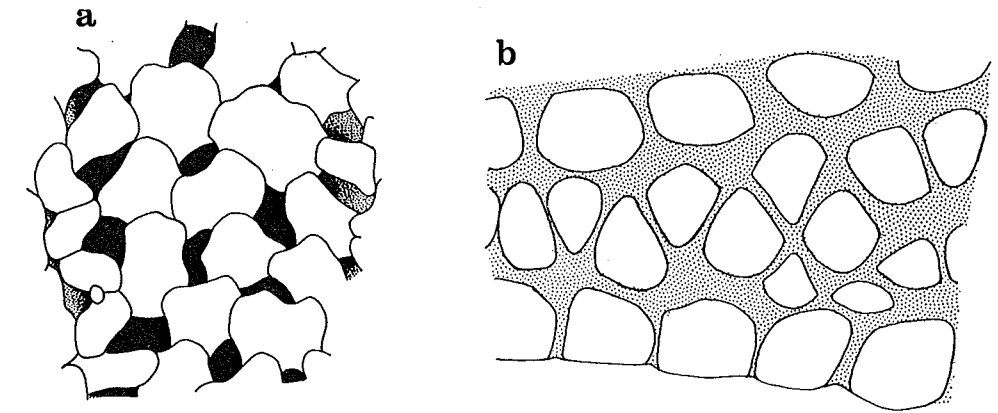


FIG. 13. *Metrodira subulata*. a. Proximal midradial abactinal plates, the more distal towards the top. b. One side of the base of an arm showing the supero-marginal, intermarginal and infero-marginal series, which are denuded though the tissue remains between the plates.

- there is a slight ventro-lateral angle (*Nepanthia*), or else the plates are paxilliform (*Chaetaster*); marginal plates inconspicuous<sup>45</sup> . . . . . 183
- 117 Armament consisting of small widely-spaced skin-covered spines, usually one or two at the distal end of each skeletal plate, producing a prickly texture;<sup>46</sup> the two series of marginal plates separated to some extent (for much of the arm at R > 50 mm. but otherwise only proximally) by irregular intermarginal plates (fig. 13b); all three marginal series noticeably lacking in armament basally so that the skin covering the sides of the arms proximally is quite smooth (pl. 10, figs. 5, 6) . . . . . *Metrodira subulata* Gray, 1840
- 117' Armament predominantly granuliform, usually continuous, though sometimes increasing in size or modified into tubercles, or rarely even small spines, in the centres of the plates, no spines in isolation (in *Leiaster* the adambulacral spines form the only armament of any kind present, the rest of the body being covered with thick naked skin); basal as well as distal marginals bearing granules (again excepting *Leiaster*); intermarginal plates rarely present and then only basally . . . . . **OPHIDIASTERIDAE** 118
- 118 Abactinal plates in more or less regular longitudinal series for the whole length of the arm . . . . . 119
- 118' Abactinal plates irregular in arrangement, though proximally there may be a tendency for longitudinal series to appear . . . . . 143
- 119 Body entirely covered with thick smooth skin, obscuring the limits of the plates (at least in spirit specimens); armament lacking except on the adambulacral plates . . . . . **LEIASTER** 120
- 119' Granules or tubercles present on all the plates; skin thin and inconspicuous, except in *Dactylosaster* (pl. 8, fig. 5) where the armament is restricted to the centres of the plates . . . . . 124
- 120 Furrow spines each with a longitudinal groove on the inner face for almost their entire length  
*Leiaster coriaceus* Peters, 1852
- 120' Furrow spines simply spatulate, flat inwardly (rarely slightly grooved near the base) . . . . . 121
- 121 Skeletal plates smooth, lacking crystal-bodies embedded in the surface (in spirit specimens this may be hidden by the thick skin so that a test area of skin should be removed with bleach)  
*Leiaster glaber* Peters, 1852<sup>47</sup>
- 121' Plates with crystal-bodies embedded, giving a bumpy texture, at least centrally . . . . . 122
- 122 Furrow spines short and broad, length: breadth c.2:1 and length only c.1 mm. (at least at R 130 mm.), becoming tubercle-like on the distal plates . . . . . *Leiaster brevispinus* H. L. Clark, 1921

<sup>45</sup> *Cistina columbiae* Gray (pl. 11, figs. 1, 2), now recognized as conspecific with *Echinaster sladeni* de Loriol which brings it within the scope of this work, necessitates some qualification of this dichotomy. It has the aboral and marginal skeleton forming regular transverse and longitudinal series like *Ophidiaster*, with which Gray allied it, but the meshes between the plates are relatively large and the identity of the marginal plates is obscure since the lowest plates of the main transverse series, abutting on the more numerous single series of actinal plates, are discontinuous longitudinally and spineless. These two characters, together with the presence of spaced articulated spines on the primary plates, prompt me to refer *Cistina* to the Echinasteridae rather than the Ophidiasteridae. (See also note 92.)

At this point in the key *Valvaster* may also cause confusion, for which see notes 13 and 32.

<sup>46</sup> Superficially there is great resemblance between *Metrodira subulata* (pl. 10, figs. 5, 6) and *Echinaster purpureus* (pl. 10, figs. 3, 4) owing to the similar sparse armament. The latter can most easily be distinguished by the extension of the armament on the sides of the arms right to the interradius and of the papulae to the oral side, coupled with the lack of differentiation of the marginal plates.

<sup>47</sup> I support Döderlein (1926) in considering that the relative length of the arms and the occurrence of pedicellariae are characters of little weight in separating the species of *Leiaster*. Evidently H. L. Clark reached the same conclusion by 1946, though in 1921 he had made use of both. I agree with Döderlein too that the development of crystal-bodies on the plates is of taxonomic value and accordingly follow him now in restoring *L. glaber* from the synonymy of *leachi*.

- 122' Furrow spines narrow, length: breadth usually 4-5:1 and length c.2 mm. in large specimens . . . . . 123  
 123 'Colour variegated, orange-yellow and red, with or without magenta'.<sup>48</sup> *Leiaster leachi* (Gray, 1840)  
 123' 'Colour uniformly crimson'.<sup>48</sup> *Leiaster speciosus* von Martens, 1866  
 124 Pore-areas in up to six longitudinal series, none (or only isolated pores) on the lower side below the infero-marginals<sup>49</sup> . . . . . **TAMARIA** 125  
 124' Pore-areas in eight or more series on each arm, at least one below the infero-marginals on each side . . . . . 130  
 125 Carinal plates markedly convex, broader than long and conspicuously broader than the dorso-lateral plates *Tamaria tumescens* (Koehler, 1910a)<sup>50</sup> . . . . . 126  
 125' Carinal plates not markedly broader than long or larger than the other abactinal plates . . . . . 126  
 126 Subambulacral 'spines' (fig. 14d) poorly developed, if present at all then tuberculiform and in a single series, low, rounded and not more than equal in size to the larger of the two furrow spines so that the whole oral aspect tends to resemble that of *Linckia multifora* (fig. 14a); abactinal granulation almost uniformly fine . . . . . 127  
 126' Subambulacral spines in one or two series, if two then the outer ones at least are distinctly larger than either of the furrow spines, the series sometimes with more or less extensive gaps; abactinal granulation variable, often with coarser granules or tubercles in the centres of some or all of the plates<sup>51</sup> . . . . . 127  
 127 Denuded skeletal plates distinctly blue;<sup>52</sup> 3-5 pores in each area only at R < 30 mm., 6-15 pores at R 30-50 mm. . . . . *Tamaria marmorata* (Michelin, 1844)  
 127' Skeleton probably white;<sup>52</sup> still only 3-5 pores in each area at R 55 mm. (according to Fisher) *Tamaria dubiosa* (Koehler, 1910b)  
 128 Granulation of the oral side coarse, often an enlarged granule approximating in size to the subambulacral spine sandwiched between it and the row of furrow spines, so that in effect there are three tangentially contiguous rows of adambulacral spines (fig. 14c)<sup>53</sup> . . . . . *Tamaria megaloplax* (Bell, 1884)  
 128' Granulation of the oral side becoming fine towards the furrow, where it is dwarfed by the subambulacral spines, no enlarged granule filling the space between the subambulacral spine and the furrow spine opposite to it<sup>53</sup> . . . . . 129

<sup>48</sup> This is the revised distinction between *Leiaster leachi* and *speciosus* given by H. L. Clark (1946). However, variation in shades of red is so great in other species of asteroids that I am rather dubious of its worth in this case and think that the two will prove to be synonymous.

<sup>49</sup> Döderlein (1926) expresses doubts about the distinctness of *Tamaria* from *Ophidiaster*, suggesting that the occurrence of actinal pores is sufficiently variable to allow synonymy of *O. granifer* with *T. pusilla*. However, Livingstone's similar doubts about the rank of *Tamaria* were based on incorrectly identified specimens of *Ophidiaster*, as shown in note 53 below.

<sup>50</sup> With synonyms *Tamaria propetumescens* and *ajax* Livingstone (1932c); see A. M. C., 1967c.

<sup>51</sup> Specimens of *Cytonardoa* with particularly regular arrangement of the abactinal plates may run down here. They can easily be distinguished from *Tamaria* by the large adambulacral plates with big fans of furrow spines and multiple subambulacral spines like *Goniasterids*.

<sup>52</sup> Fisher's Philippine specimen of *Tamaria dubiosa* appears to have had many of the abactinal plates rubbed clear of granules but he makes no mention of any colour so revealed, which is a remarkable feature of all the six specimens of *marmorata* in the British Museum collections where a patch of granules has been removed with bleach.

The position of *T. pusilla* (Müller and Troschel, 1844) in this key is difficult to determine since the description of the holotype was brief, the specimen itself is lost (according to Döderlein, 1926) and the specimens subsequently referred to the species and described by Perrier (1875), Döderlein (1926) and Engel (1938) are none of them from the type-locality, the Philippines; Perrier's from New Caledonia lack the uniform aboral granulation of the type but agree more with *T. fusca* in having enlarged granules in groups on the centres of the plates. It is also suggestive that the types of both *pusilla* and *fusca* were collected in the Philippines by Cuming. Engel's specimen from the Banda Sea certainly agrees with Müller and Troschel's description of *pusilla* as regards the presence of two series of subambulacral spines (though the outer could be an actinal series) and fairly uniform aboral granulation; for lack of a Philippine specimen of similar form, this one might well be designated as neotype of *T. pusilla*. Meanwhile it can only be said that *pusilla* may fall between *T. dubiosa* and *megaloplax*, since the adambulacral spines appear to be diminutive.

<sup>53</sup> Koehler (1910b) has described two species from depths beyond 10 fathoms, *Ophidiaster ornatus* from southern Ceylon and *O. hirsutus* from the Andaman Islands, both of which are referable to *Tamaria*. I have only seen one small specimen, R 15 mm. (in the Cambridge Museum collections from the Maldive Islands) which may be referable to *T. ornata*, though it has one row of subambulacral spines rather than the two shown by the holotype (R 17 mm.). H. L. Clark (1921) includes both *hirsuta* and *ornata* together with *megaloplax* in the synonymy of *T. fusca* on the advice of Fisher and supported by the evidence of some specimens from Holothuria Bank, NW Australia, which he recognizes as agreeing with one or other of Koehler's descriptions of his Indian Ocean specimens. Livingstone (1932a) has restored all three as valid species, narrowing the concept of *T. fusca*. I fully agree that *megaloplax* is a distinct species marked off from *T. fusca* by its much coarser granulation on the oral side and tendency for contiguous double series of subambulacral spines as well as much larger aboral pore-areas. However, among the Holothuria Bank specimens in the British Museum collections I find, like H. L. Clark, several that superficially agree with the type of *hirsuta* in having single central tubercles on the abactinal plates, which tubercles are particularly large and conical, almost spine-like and more widespread than in the types of *Ophidiaster tuberifer* Sladen, which is acknowledged as a synonym of *megaloplax* by Livingstone and by H. L. Clark (1946). It is significant that Koehler refers to *tuberifer* another specimen from the Andaman Islands, distinguishing it from *hirsuta* by the lesser development of the tubercles as well as by the occurrence of pedicellariae (rarely reliable as a specific character unsupported). Koehler also believed there is a difference in the adambulacral armament and, as I think that this does afford a useful distinction at least between *megaloplax* and *fusca*,

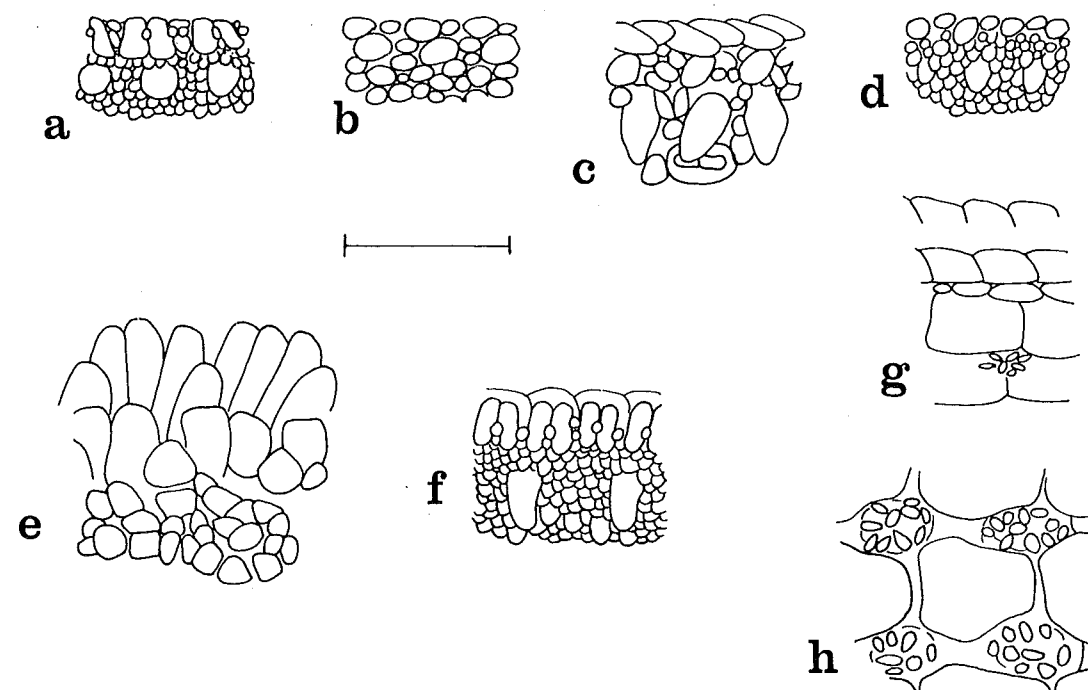


FIG. 14. a-f. Adambulacral armament of: a. *Linckia multifora*, b. *L. guildingi*, c. *Tamaria megaloplax*, holotype, d. *T. marmorata*, e. *Nardoa novaecaledoniae* and f. *Ophidiaster hemprichi*. The furrow spines in a and f are in the reflexed position, revealing the granules between them, the furrow spines in b and d are viewed end on. g. *Tamaria marmorata*, one side of a proximal part of an arm denuded and viewed obliquely from below showing an intermarginal pore area. h. The same species, part of midradial and adjoining supero-marginal series on each side denuded. In each case the mouth is towards the right. The scale measures 2 mm.

- 129 Pore-areas small, only 5-8 pores in each, even at R 45 mm.; subambulacral spine series often with extensive gaps; pedicellariae usually numerous . . . . . *Tamaria fusca* (Gray, 1840)  
 129' 10-16 pores in each area at R > 45 mm., though only 6-8 at R 20-35 mm.; only small gaps in the sequence of subambulacral spines; pedicellariae rare . . . . . *Tamaria lithosora* H. L. Clark, 1921  
 130 Armament restricted to a cluster of coarse granules or tubercles in the centre of each plate, the remaining surface covered with skin (in dry specimens the crystal-bodies embedded in the plates under the skin may produce a slightly bumpy texture but there is no continuity of true superficial granulation) (pl. 8, fig. 5) *Dactyloaster cylindricus* (Lamarck, 1816)  
 130' True granulation continuous all over the plates, skin not conspicuous . . . . . 131  
 131 Ten longitudinal series of pore-areas, the lowest each side developed between adjoining series of actinal plates and consequently including twice as many pore-areas as the other series *Hacelia inarmata* (Koehler, 1895)<sup>54</sup>

I hesitate to refer *hirsuta* to the synonymy of *megaloplax* without seeing any Indian Ocean material. Nevertheless, it certainly appears that *T. megaloplax* is extremely variable with regard to the armament of the marginal and abactinal plates, which ranges from almost uniform granulation to conical, usually single, enlarged central tubercles, varying in height and in the number of plates which bear them, sometimes occurring on most of the plates. Such variation is paralleled by *Tamaria tumescens* (described in A.M.C., 1967c). Conversely the available material of *T. marmorata* suggests that uniform fine granulation is constant in that species, while in *T. lithosora* and *fusca* the reverse holds good, clusters of central granules on all the plates being enlarged in all specimens seen. Better sampling is needed to show the true worth of this character.

Immature specimens of *Ophidiaster helicostichus* (R < c.70 mm.) with the actinal pore-areas lacking or barely developed, may run down to 129; they can be distinguished from the Australian species of *Tamaria* by the more attenuated arms and more particularly from *T. fusca* and *T. lithosora* by the armament, enlarged central granules on the plates being rarely developed and then usually single. *T. megaloplax* differs in the adambulacral armament and the relatively larger aboral pore-areas.

<sup>54</sup> Described by Koehler as *Ophidiaster helicostichus* var. *inarmatus*, this was raised to specific rank within the genus *Hacelia* by H. L. Clark (1921). Since *helicostichus* has been found to lack the two extra intra-actinal series of pore-areas found in *Hacelia attenuata* and evidently also in Koehler's type of *inarmata*, it has been referred back to *Ophidiaster* (A.M.C., 1967c).

- 131' Only eight series of pore-areas, the lowest each side between the infero-marginals and the outermost actinal plates and so no more numerous than the other series<sup>55</sup> . . . . . **OPHIDIASTER** 132
- 132 No granules on the vertical faces of the furrows between the furrow spines . . . . . 133
- 132' One or more granules developed between the consecutive furrow spines, though sometimes only between alternate pairs (fig. 14f) . . . . . 139
- 133 Some of the marginal and abactinal plates, particularly the distal ones, with one or more enlarged central granules or tubercles or even a short spinelet . . . . . 134
- 133' Granulation of the distal plates fairly uniform . . . . . 135
- 134 Arms stout, R/br usually 4.0-4.5/1; many abactinal plates with several coarse central granules or low tubercles, though these are particularly noticeable on the distal plates, some of which may have an even broader low cone centrally though this hardly projects above the surface . . . . .  
*Ophidiaster granifer* Lütken, 1872a
- 134' Arms more slender, R/br 5-7/1; some marginal plates, particularly distal ones, with single projecting central spinelets . . . . . *Ophidiaster armatus* Koehler, 1910a
- 135 Subambulacral spines short and rounded, similar in magnitude to the larger of the two corresponding furrow spines; pedicellariae probably rare . . . . . *Ophidiaster perrieri* de Loriol, 1885<sup>56</sup>
- 135' Subambulacral spines larger than the furrow spines and tapering to a blunt point; pedicellariae usually more or less numerous . . . . . 136
- 136 Arms stout, R/r or R/br 4.0-4.5/1 . . . . . *Ophidiaster chinensis* Perrier, 1875
- 136' Arms slender, R/r or R/br c.7/1 . . . . . 137
- 137 Arms tapering from the base to attenuated tips; pedicellariae with almost straight valves, proximally constricted but distally broadening to a wide digitate 'head' (fig. 15c)  
*Ophidiaster helicostichus* Sladen, 1889<sup>57</sup>  
*Ophidiaster astridae* Engel, 1938<sup>57</sup>

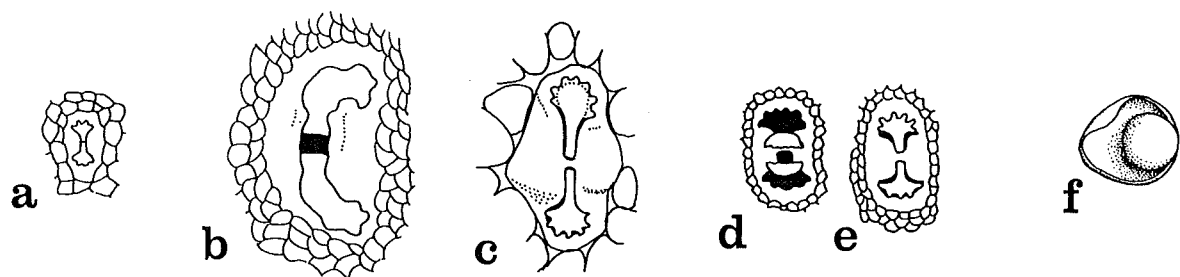


FIG. 15. a-e. Pedicellariae of *Ophidiaster* spp.: a. *O. cribrarius*, actinal, b. *O. duncani*, abactinal, c. *O. helicostichus*, actinal, d and e. *O. lorioli*, actinal. f. Ball and socket organ of *Bunaster ritteri*, after Döderlein, 1896.

- 137' Arms cylindrical for about two-thirds of their length, then tapering slightly to a blunt tip; pedicellariae with curved valves (fig. 15b) . . . . . 138
- 138 Alveolae of each pedicellaria forming a semi-circle (fig. 15b)<sup>58</sup> . . . . . *Ophidiaster duncani* de Loriol, 1885
- 138' Alveolae only moderately curved<sup>58</sup> . . . . . *Ophidiaster lioderma* H. L. Clark, 1921

<sup>55</sup> Some small specimens of *Linckia* spp. (R < 30 mm.), with the abactinal plates still retaining a degree of longitudinal arrangement, may run down here. They can be distinguished from *Ophidiaster* by the position of the lowermost pore-areas above the infero-marginals, not below, though the areas similarly tend to form eight series.

<sup>56</sup> A specimen in the British Museum collections from Zanzibar (Crossland collection) is identifiable as *Ophidiaster perrieri*, which was hitherto known only from the holotype taken in Mauritius. This specimen has similar very squat subambulacral armament, as found in *Linckia multifora* and *Tamaria marmorata*, and also resembles the latter in the bluish colour of the denuded skeleton. However, it differs in the large aboral pore-areas and the extra series of areas below the infero-marginal plates, though there are no isolated pores between the actinal plates themselves such as de Loriol found in the somewhat larger holotype of *O. perrieri* (R 63 mm. compared with 45-50 mm. in the Zanzibar specimen). Like the type, the latter has no pedicellariae.

<sup>57</sup> Provisionally regarded as synonymous in A.M.C., 1967c.

<sup>58</sup> This is the distinction used by H. L. Clark (1921) and certainly some of the pedicellariae in a specimen of *Ophidiaster duncani* with R up to 145 mm. in the British Museum collections from Mauritius, the type-locality, are strongly curved; however, other pedicellariae in the same specimen are nearly straight. Two other individuals, one (in which pedicellariae are rare) also from Mauritius and the other from Madagascar, are in the collections but none from northern Australia, the type-locality of *lioderma*. Nevertheless, the description given by H. L. Clark suggests a close affinity, even to the very fine squamiform granulation and the looseness of the skin bearing the granules resulting in some folding in one of the dried specimens.

- 139 Madreporite single; normally five arms . . . . . 140
- 139' Two madreporites; sometimes more than five arms and often partially regenerating . . . . . 141
- 140 Two series of low rounded subambulacral spines present; granulation even; abactinal plates rather irregular in arrangement<sup>59</sup> . . . . . *Ophidiaster propinquus* Livingstone, 1932a
- 140' One series of elongated subambulacral spines; granulation markedly uneven, some granules (often forming distally-pointing chevrons) distinctly flattened and more or less squamiform, having the appearance of imbricating with the free edges distally; longitudinal arrangement of plates fairly regular (pl. 8, fig. 3)  
*Ophidiaster hemprichi* Müller & Troschel, 1842<sup>60</sup>  
*Ophidiaster squameus* Fisher, 1906<sup>60</sup>
- 141 Pore-areas mostly with ten to twelve pores (at least at R > 30 mm.); pedicellariae relatively narrow, each valve about twice as long as broad with only a slightly broadened head bearing usually two indistinct digits at the free end though there is usually another one each side (fig. 15a)  
*Ophidiaster cribrarius* Lütken, 1872a<sup>61</sup>
- 141' Pore-areas each with only three or four pores (even at R 50 mm.); pedicellariae with markedly short valves, many of them hardly at all longer than broad and with very wide truncated heads bearing a well-developed row of about five digits across the free end, the whole alveolus of each pedicellaria usually only two or three times as long as wide (fig. 15d, e) . . . . . 142
- 142 Arms cylindrical for most of their length, the tips blunt . . . . . *Ophidiaster lorioli* Fisher, 1906
- 142' Arms tapering and flattened below . . . . . *Ophidiaster robillardi* de Loriol, 1885
- 143 Adambulacral armament superficially appearing granuliform (fig. 14a, b); arms cylindrical, disc small . . . . . 144
- 143' Adambulacral armament spiniform, though the spines are usually short, blunt and more or less prismatic (fig. 14e); arms either cylindrical or more or less flattened and wider basally . . . . . 149
- 144 Marginal and abactinal plates with conspicuous obliquely ovate convex bare areas and with interstitial granulation between the plates; pores present on the lower side as well as the upper and usually isolated though sometimes in groups of two or three; size small, R not known to exceed 22 mm. . . . .  
**BUNASTER** 145
- 144' Plates rounded and completely granule-covered, not markedly swollen; pores in groups, rarely occurring on the lower side; R often >50 mm., sometimes even 100 mm. . . . . **LINCKIA** 147
- 145 Only a single series of abactinal plates between the two supero-marginal series of each arm; actinal plates also in a single series . . . . . *Bunaster uniserialis* H. L. Clark, 1921
- 145' Abactinal plates irregular proximally, usually two or three across the arm width; also a second series of actinal plates present proximally . . . . . 146
- 146 Subambulacral spines short, length: breadth < 2:1; odd 'ball-and-socket' organs (fig. 15f) adjacent to some of the pores. . . . . *Bunaster ritteri* Döderlein, 1896
- 146' Subambulacral spines longer, length: breadth c.2:1; no cup-shaped organs observed in the holotype and only known specimen . . . . . *Bunaster lithodes* Fisher, 1917
- 147 Subambulacral spines in two series; those of each plate contiguous with each other and with the furrow spines but aligned slightly obliquely so as to give a herring-bone pattern to the under side of each arm; no granules between the furrow spines within the furrow (fig. 14b) (pl. 8, fig. 7).<sup>62</sup> . . . . .  
*Linckia guildingi* Gray, 1840
- 147' Subambulacral 'spines' or tubercles very low, set back from the furrow spines and surrounded by the granulation, usually only a single series present but, even when there are two series, all the spines isolated

<sup>59</sup> Except that it evidently has only one row of subambulacral spines (or tubercles), *Ophidiaster perplexus* A. H. Clark, 1954, may run down here, though, since the abactinal plates increase from three series between the basal supero-marginals to seven or eight irregular series distally, it is more likely to be confused with *Linckia* (and with some justification). Mr. Clark himself notes that 'there appear to be no papulae on the oral surface', also 'in general appearance it resembles *Linckia multifora* more closely than it does any other species of *Ophidiaster*', thus making its inclusion in *Ophidiaster* a matter of considerable doubt. As no illustration of the type was given it is difficult to reach a firm conclusion about the generic position.

I suspect also that *O. propinquus* may be based on an immature specimen of *Linckia multifora* since the actinal plates are in three series, no pore-areas are described on the lower side and those of the upper are indistinct and irregular like the abactinal plates themselves. The holotype is in the Australian Museum.

<sup>60</sup> Döderlein (1896 and 1926) has shown that *Ophidiaster purpureus* Perrier (type-locality the Seychelles) and *pustulatus* von Martens (from Amboina) are synonyms of *O. hemprichi* (from the Red Sea); in doing this he rejected the occurrence of pedicellariae as a specific character. I have referred single specimens from Tanganyika, the Chagos Archipelago and Christmas Island (all in the Indian Ocean) to *hemprichi* and am convinced that two Pacific specimens, from northern Australia and from the South China Sea, are conspecific with these. However, H. L. Clark (1921) decided that specimens from northern Australia are conspecific with others from the Hawaiian Islands, the type-locality of *O. squameus* Fisher, and named them accordingly. I suspect that *squameus* will prove to be yet another synonym of *hemprichi*, when a comparison can be made between material from the Red Sea and from Hawaii.

<sup>61</sup> The British Museum collections include a specimen of *Ophidiaster cribrarius* from Tonga, the type-locality, received from the Godeffroy Museum. This is a regenerating five-armed comet and the original arm, R 33 mm., has ten to twelve pores in most areas whereas the smaller regenerating arms have only three to seven.

- from each other; granules extending down between the furrow spines, especially numerous in large specimens,  $R > 100$  mm., rarely few<sup>62</sup> . . . . . 148
- 148 Arms normally five in number and madreporite single, rarely otherwise; arms fairly stout and blunt at the tips,  $R/br$  5-10/1; colour in life blue or bluish-green . . . . . *Linckia laevigata* (Linnaeus, 1758)
- 148' Arms often irregular in length and number, normally two madreporites; arms more slender and attenuated towards the tips,  $R/br$  often exceeding 10/1; colour in life often variegated, purplish, reddish, brownish, or khaki-coloured with yellowish, sometimes more nearly uniform . . . . . *Linckia multifora* (Lamarck, 1816)
- 149 Papular pores present on the oral side<sup>63</sup> . . . . . 150
- 149' No pores below the infero-marginals<sup>63</sup> . . . . . 173
- 150 Pores single; form more or less flattened, the marginals usually defining the edge of the body;  $R$  rarely exceeding 40 mm. . . . . *FROMIA* 151
- 150' Pores in groups; arms usually almost circular in cross-section; marginal plates inconspicuous in dorsal view;  $R$  often exceeding 70 mm. . . . . *NARDOA* 161
- 151 Supero-marginal plates of at least the distal half of the arm alternately large and convex and small and flat 152
- 151' Supero-marginals decreasing in size distally fairly regularly, though odd plates may be reduced . . . . . 154
- 152 A series of spaced enlarged and uniformly convex mid-radial or carinal plates present, resembling the swollen alternate supero-marginals, with which they are almost in contact; denuded plates with smooth surface (pl. 8, fig. 8) . . . . . *Fromia nodosa* A. M. Clark, 1967c
- 152' Carinal plates not conspicuously enlarged (though in *ghardaqana* some may stand out slightly above the general surface) and widely separated from the supero-marginals; denuded plates with bumpy surface due to embedded crystal-bodies . . . . . 153
- 153 Actinal pores few or absent on the disc; abactinal granulation very fine, only c.10 granules/mm. length; few, if any, carinal plates raised above the surface<sup>64</sup> . . . . . *Fromia monilis* Perrier, 1875
- 153' Actinal pores present at most of the angles of even the basal actinal plates; abactinal granulation less fine, c.7/mm. and coarser on some isolated carinal plates which are raised slightly above the surface though flattened on top (pl. 8, fig. 9) . . . . . *Fromia ghardaqana* Mortensen, 1938
- 154 Abactinal plates markedly unequal in size, usually two longitudinal series of distinctly enlarged plates on each arm<sup>65</sup> . . . . . 155
- 154' Abactinal plates somewhat irregular but similar in size<sup>65</sup> . . . . . 156
- 155 Armament of actinal plates consisting of short blunt spinelets (or elongated granules), length: breadth c.2:1, not appreciably shorter than the adambulacral spines when seen with the naked eye and usually numbering about five to a plate, radiating outwards, though the central space may be occupied by an additional spinelet on some plates . . . . . *Fromia indica* (Perrier, 1869)<sup>66</sup>
- 155' Armament of actinal plates abruptly lower than that of the adambulacrals, consisting of rounded or polygonal granules not appreciably higher than wide and usually numbering seven to nine, there being no central space on any of the plates . . . . . *Fromia elegans* H. L. Clark, 1921<sup>66</sup>

<sup>62</sup> Ely (1942) has published some beautiful photographs illustrating the characters used in this dichotomy.

The validity of *Linckia diplax* (Müller and Troschel, 1842) should be taken into account here. It was referred to the synonymy of *L. guildingi* by Fisher (1919), provisionally restored without actual examination by H. L. Clark (1921) and considered as valid by Hayashi (1939) on the basis of two specimens from the Caroline Islands. These two have no granules between the furrow spines but Hayashi did not describe the subambulacral spines or compare the specimens with *guildingi*. However, in 1938 he had referred some specimens from Seto, Japan, to *guildingi* and noted that they differ from *diplax* in the purple colour, the usual occurrence of five rays and one madreporite and the broader rays. This contradicts H. L. Clark's statements about *guildingi* (1921) that it commonly has two madreporites and that the colour tends to vary with the habits, which themselves alter with age. A re-examination of the holotype of *diplax* in the Berlin Museum is needed before its validity can be determined. In 1942, Engel was able to examine the type of *L. rosenbergi* von Martens from the same museum, concluding from this that it is synonymous with *L. laevigata*, though H. L. Clark (1921) had included it in his key among the species like *diplax* which lack granulation between the furrow spines, for lack of information to the contrary.

There are a few specimens in the British Museum collections with the superficial ventral appearance of *Linckia multifora* or *laevigata* but with few furrow granules, however, I do not think that these can be distinguished specifically.

<sup>63</sup> Unfortunately this distinction used by H. L. Clark does not hold good for all specimens of *Nardoa*, individuals of several species having the pore-areas below the infero-marginals reduced or absent.

<sup>64</sup> *Fromia pacifica* may run down here since H. L. Clark (1921) notes that small intercalary supero-marginals may occur irregularly in the distal parts of the arms.

<sup>65</sup> Another difference between these two groups of species may be provided by the occurrence of crystal-bodies embedded in the plates; these are certainly absent in *Fromia indica* and *elegans* but present in *F. milleporella*, *armata* and *balansae*; however, the condition in *hemiopla*, *hadracantha* and *pacifica* remains to be seen.

<sup>66</sup> I am indebted to Mr. James F. Clark for re-examining the holotype of *Fromia elegans* for me with respect to the actinal granulation. He states that this is compact, length: breadth of the granules being c.1:1 and his photographs show that the appearance of the oral side is very different from that of *F. indica*. I consider therefore that Hayashi (1939) was wrong in relegating *elegans* as well as *andamanensis* to the rank of forms of *indica*, though I concur that the latter is conspecific with *indica*, having studied specimens from the Andaman Islands, all of which have the actinal armament elongated. Another synonym of *F. indica* is *F. tumida* Bell, 1882, the supposed differences being due to the distortion of the two syntypes and the

- 156 Arms relatively long and slender,  $R/r > 4.5/1$ , only about three abactinal plates across the width between the supero-marginals in the proximal half of the arm; the third series of actinal plates hardly developed before  $R$  reaches 35 mm. . . . . 157
- 156' Arms broad-based and tapering,  $R/r$  rarely  $> 3.5/1$ ; usually five or more plates across the arm width proximally; three rows of actinal plates basally even at  $R$  c.25 mm. . . . . 158
- 157 Most adambulacral plates with 2, rarely 3, furrow spinelets and one larger subambulacral spine; distal marginal plates with an enlarged tubercle<sup>67</sup> . . . . . *Fromia hadracantha* H. L. Clark, 1921
- 157' 3 furrow spinelets backed by 2 subambulacral ones which are shorter though stouter than the furrow spinelets; distal marginal plates with the central granules somewhat enlarged but no single tubercles developed<sup>67</sup>. . . . . *Fromia pacifica* H. L. Clark, 1921
- 158 Abactinal granulation uneven with one or more enlarged tubercles in the middle of many plates<sup>68</sup> . . . . . *Fromia armata* Koehler, 1910b
- 158' Abactinal granulation even<sup>68</sup> . . . . . 159
- 159 Distal marginal plates with enlarged central granules or tubercles . . . . . *Fromia hemiopla* Fisher, 1913a
- 159' Marginal granules evenly fine . . . . . 160
- 160 Aboral side convex; carinal row of plates usually distinct . . . . . *Fromia balansae* Perrier, 1875
- 160' Aboral side flat; carinal series of plates indistinguishable (pl. 8, fig. 10) . . . . . *Fromia milleporella* (Lamarck, 1816)
- 161 A number of isolated abactinal plates abruptly more convex and projecting than the rest, often hemispherical<sup>69</sup> . . . . . 162
- 161' Abactinal plates all similar in contour, though often variable in size, none markedly projecting<sup>69</sup> . . . . . 166
- 162 Some of the supero-marginal plates hemispherical as well as some abactinal plates, the height of these often equal to the basal diameter. . . . . *Nardoa frianti* Koehler, 1910b<sup>70</sup>
- 162' No supero-marginal plates conspicuously tubercular though alternate ones may be somewhat convex; the tubercular abactinal plates distinctly wider than high, if broader than the unspecialized flatter plates. . . . . 163
- 163 Tubercular abactinal plates low, broad and cushion-like, absent from the distal parts of the arms, often transversely elliptical, measuring 3-4 mm. in diameter at  $R > 50$  mm. . . . . *Nardoa tumulosa* Fisher, 1917
- 163' Tubercular plates relatively small, rarely much exceeding 2 mm. in diameter, even at  $R > 70$  mm., often present distally as well as (or rather than) proximally . . . . . 164
- 164 Arms not attenuated but more or less blunt at the tip,  $R/r$  5.0-7.0/1; the main actinal row of plates extending the whole length of the arm; tubercular plates inconspicuous, tending to be fewer proximally and restricted to the dorso-lateral areas in the distal halves of the arms; supero-marginal plates all similar in size (pl. 8, fig. 1) . . . . . *Nardoa tuberculata* Gray, 1840
- 164' Arms very attenuated distally,  $R/r$  7.5-9.2/1 (in the only four specimens); the main actinal row of plates terminating at half to two-thirds  $R$  from the base; tubercular abactinal plates well developed, proximally as well as distally; some of the supero-marginals, often alternate ones, reduced in size . . . . . 165
- 165 Intermarginal plates present in the arm angles; the majority of abactinal plates markedly convex, particularly mid-radially<sup>71</sup>. . . . . *Nardoa sphenisci* A. M. Clark, 1967c
- 165' No intermarginal plates; tubercular abactinal plates widely spaced, as well-developed dorso-laterally as mid-radially . . . . . *Nardoa gomophia* (Perrier, 1875)
- 166 Supero-marginal plates tending to alternate large and small for some part of the series . . . . . *Nardoa rosea* H. L. Clark, 1921
- 166' No regular alternation in size of the supero-marginals . . . . . 167

inadequacies of Bell's description. Domantay and Roxas (1938) and A. H. Clark (1949) have extended the geographical range of *F. elegans* to the Philippines and the latter extends the  $R/r$  range up to as much as 5/1. The photographs given by the Philippine authors could well be of *elegans* but the specimen from Banda Neira referred by Engel (1938) to *elegans* is certainly referable to *indica*, his drawing of the actinal plates showing the same distinctive elongated armament.

<sup>67</sup> *Fromia eusticha* Fisher, 1913a, also runs down here but the only depth record is 24 fms. (44 metres). Fisher and H. L. Clark distinguish it by the numerous pedicellariae on the under side.

<sup>68</sup> This distinction used by H. L. Clark may prove to be unsatisfactory since a specimen in the British Museum collections from the Fiji Islands, which has been identified as *Fromia milleporella*, has distinctly coarser central granules on many abactinal plates, though there is not the abrupt contrast in size between granules and tubercles shown by a specimen of *armata* from the Andaman Islands.

<sup>69</sup> A revision of the genus *Nardoa* is given in A.M.C., 1967c.

Although H. L. Clark (1921) included his own species *Nardoa rosea* in the section of *Nardoa* lacking tubercular plates, the holotype has some of the abactinal plates distinctly convex, though not over 1 mm. high. The alternation in size of the supero-marginal plates supposedly characteristic of *rosea* may also be partially evident in some specimens which I have referred to *N. frianti*, the most markedly tubercular species, as well as more regularly in *N. gomophia* and *N. sphenisci*.

<sup>70</sup> *Nardoa mamillifera* Livingstone (1930) is very probably a synonym of *N. frianti*. See A. M. Clark, 1967c.

<sup>71</sup> The two localities at which *Nardoa sphenisci* has been taken off NW Australia are both from beyond the ten fathom line, nevertheless the species is included in the key for the sake of completeness, all the other known members of the genus *Nardoa* having been found at lesser depths.

- 167 Abactinal plates for the proximal half of each arm forming fairly regular longitudinal and transverse series, though this breaks down distally . . . . . *Nardoa fouazii* Macan, 1938
- 167' Abactinal plates irregular in arrangement throughout . . . . . 168
- 168 Adambulacral plates each bearing two rows of spines, four furrow spines and four subambulacral ones (though the granulation backing on to these is transitional to the spines, at least in my interpretation of Lütken's danish)<sup>72</sup> . . . . . *Nardoa galathea* (Lütken, 1864)
- 168' Granulation of the outer part of each adambulacral plate usually modified to form a third row of spines, numbering three like the two inner rows, though the furrow series may consist of four spines . . . . . 169
- 169 Many of the abactinal plates more or less conspicuously broadened and alternating to form an almost continuous pavement, the interstitial pore-areas being very small, the larger plates markedly bigger than the supero-marginal plates, exceeding 3 mm. in diameter, even at R only c.40 mm., and numbering only c.5 across the width of the arm basally at R up to c.50 mm. though there are usually two additional short rows of small plates each side above the marginals basally when R reaches 100 mm.; the distal abactinal plates similar to the proximal ones though gradually becoming smaller (pl. 8, fig. 2) . . . . . *Nardoa variolata* (Retzius, 1805)
- 169' Few if any of the abactinal plates conspicuously larger than the supero-marginals and rarely broadened transversely to exceed c.2.5 mm. in diameter; if some large plates are present proximally then the distal plates are relatively much smaller, often with an abrupt change in magnitude<sup>73</sup> . . . . . 170
- 170 All the abactinal plates, both proximally and distally, small in comparison with the marginal plates, numbering about 13 across the arm width basally, at least at R > 90 mm.; granuliform pedicellariae distinctly coarser than the granules often present between the abactinal plates; actinal papulae few or even absent . . . . . *Nardoa pauciforis* (von Martens, 1866)
- 170' The proximal abactinal plates, especially midradially, distinctly larger than the distal ones, rarely more than 11 plates across the width, usually c.9; pedicellariae not observed, either inconspicuous or absent; usually a number of pore areas developed between infero-marginal and actinal plates . . . . . 171
- 171 R/r usually 5.0-6.0/1 (13 specimens including six from New Caledonia having a mean of 5.4/1) . . . . . *Nardoa novaecaledoniae* (Perrier, 1875)
- 171' Arms more attenuated, R/r usually 5.5-8.5/1 (with a mean of 6.5/1 for 12 specimens of *lemonnieri* and a value of 6.4/1 for the only specimen of *mollis* available compared with 6.9/1 in the type) . . . . . 172
- 172 Distal abactinal plates conspicuously smaller than the proximal ones, their positions shown by rounded groups of coarse granules among the fine interstitial granulation . . . . . *Nardoa mollis* de Loriol, 1891
- 172' Distal abactinal plates becoming gradually somewhat smaller than the proximal ones but markedly elongated in form with ovate groups of coarse granules . . . . . *Nardoa lemonnieri* Koehler, 1910b
- 173 Some abactinal plates abruptly and conspicuously conical in shape and often crowned with an enlarged nipple-like tubercle (pl. 8, fig. 4)<sup>74</sup> . . . . . *Gomophia egyptiaca* Gray, 1840
- 173' If any abactinal plates are enlarged and projecting, their shape is low and cushion-like . . . . . 174
- 174 Adambulacral plates completely granule-covered except for the single row of furrow spines, though on the distal parts of the arms a single granule may be enlarged into a tubercle on each plate; no longitudinal arrangement of the abactinal plates except the carinal (mid radial) series . . . . . 175
- 174' Two or three rows of spines on the adambulacral plates; proximal abactinal plates tending to form longitudinal rows<sup>75</sup> . . . . . **CERTONARDOA** 182
- 175 Some of the marginal and usually also abactinal plates conspicuously bare and convex, the granulation stopping short near their edges . . . . . **NEOFERDINA** 176
- 175' Abactinal and marginal plates all with continuous granulation . . . . . 181
- 176 Arms relatively long and narrow, R/r c.5/1 . . . . . *Neoferdina kuhli* (Müller & Troschel, 1842)
- 176' Arms relatively shorter, R/r c.3/1 . . . . . 177
- 177 Some of the dorso-lateral plates slightly enlarged and tending to form spaced transverse series together with certain carinal and supero-marginal plates; supero-marginals numbering 12 or more at R > 20 mm. and tending to zig-zag in position and to alternate in form, larger more aboral bare plates alternating with smaller convex granule-covered plates slightly lower on the arms, though these are often irregular in occurrence . . . . . 178
- 177' No distinct transverse rows of plates across the arms and no regular alternation of the supero-marginals, which are large and few, up to only c.10 in each series . . . . . 180

<sup>72</sup> Lütken's description of *Nardoa galathea* might apply to several of the species of *Nardoa* now recognized, particularly to *N. novaecaledoniae* and *lemonnieri*, of which I have seen several specimens with four (sporadically even five) furrow spines, and at least one of the latter with four subambulacral spines on many plates.

<sup>73</sup> Since these species of *Nardoa* seem very liable to damage and loss of parts of the arms, an abrupt reduction in size of the distal plates may be correlated with regeneration, though it appears to be natural in some specimens.

<sup>74</sup> Specimens of *Nardoa frianti* such as the holotype, with deficient actinal papulae, may run down here owing to the great prominence of the tubercular abactinal plates, though these lack terminal tubercles.

<sup>75</sup> Small individuals of such species as *Nardoa pauciforis* which are deficient in pores below the infero-marginals may run down here. They can be distinguished from *Certonardoa* by the irregular proximal as well as distal abactinal plates.

- 178 None of the carinal plates as large as the larger supero-marginals; only 13-15 supero-marginals altogether at R c.40 mm. . . . . *Neoferdina ocellata* (H. L. Clark, 1921)<sup>76</sup>
- 178' Some of the carinal plates similar in size to the larger supero-marginals; supero-marginals more numerous (18-20 altogether at R c.40 mm. though there are only c.15 at R c.30 mm.) . . . . . 179
- 179 Dorso-lateral plates of the transverse series bare like the enlarged carinal and supero-marginal plates . . . . . *Neoferdina cancellata* (Grube, 1857)<sup>76</sup>
- 179' Dorso-lateral plates nearly all fully granule-covered, only a few irregular ones bare . . . . . *Neoferdina cumingi* (Gray, 1840)<sup>76</sup>
- 180 Granulation coarser on the centres of the granulated abactinal plates than between the plates . . . . . *Neoferdina offreti* (Koehler, 1910b)
- 180' Granulation coarser interstitially than in the centres of the abactinal plates<sup>77</sup> . . . . . *Neoferdina insolita* Livingstone, 1936
- 181 Papulae isolated and fairly evenly spaced between the abactinal plates; aboral skeleton tessellate; supero-marginals regularly alternating large and small; granulation markedly coarser in the centres of the actinal plates . . . . . *Celerina heffernani* (Livingstone, 1931b)
- 181' Papulae tending to form small groups of two or three, though some are spaced; aboral skeleton a compact reticulum (though normally concealed by granulation); no regular alternation of the ill-defined supero-marginal plates; actinal granulation fairly uniform . . . . . *Ferdina flavescens* Gray, 1840
- 182 Abactinal plates of arms quadrangular, forming both longitudinal and transverse series; granules no larger on the pore-areas than elsewhere . . . . . *Certonardoa semiregularis* (Müller & Troschel, 1842)
- 182' Abactinal plates rounded, only forming longitudinal series on the proximal half of the arm, distally irregular; granulation coarser on the pore-areas than elsewhere . . . . . *Certonardoa carinata* (Koehler, 1910b)
- 183 Skeletal plates paxilliform; arms cylindrical; the two series of marginal plates alternating; mouth plates each with a single downwardly-directed hyaline-tipped suboral spine . . . . . *Chaetaster vestitus* Koehler, 1910b
- 183' Plates not paxilliform (except in the Pterasteridae where the paxillae are completely hidden beneath the supra-dorsal membrane); arms of various form, ranging from cylindrical to markedly tapering and flattened below; no regular alternation of the marginals; no hyaline suboral spines . . . . . 184
- 184 Body flat below, sometimes also above but usually the aboral side rising, often steeply, from a more or less well-defined ventro-lateral angle; arms ranging from very short and triangular (so that the body is almost pentagonal) to almost cylindrical and narrow but still with a ventro-lateral angle or flange (some species of *Nepanthia*); skeleton compact, spaces between the plates often small . . . . . 185
- 184' Body with cylindrical arms or sometimes cushion-like, rounded ventro-laterally; aboral skeleton usually reticular with relatively large spaces between the plates . . . . . 206
- 185 Body covered by smooth skin obscuring the non-imbricating oval or circular abactinal plates which are nearly all quite naked, though bearing crystal-bodies embedded in their surface (which may give a granular appearance to dried specimens); larger specimens, R > c.30 mm., with arms triangular in cross-section, the carinal plates forming a mid-radial ridge emphasized by a series of spines and the pores in small groups (at R < 30 mm. the upper side is flatter and the spaces between the plates smaller so that many of the pores are single); the edge of the body formed by the supero-marginal plates with prominent conical single spines (pl. 9, fig. 9) . . . . . *Asteropsis carinifera* (Lamarck, 1816)
- 185' The quadrangular or crescentic abactinal plates more or less obviously imbricating in the proximal direction (fig. 16a, b), usually armed with fine spinelets or granules, rarely naked except around the anus and madreporite; arms flattened or rounded above, occasionally somewhat carinate but then with no mid-radial series of conspicuous spines; papulae isolated; the ventro-lateral edge formed by the infero-marginal plates armed only by multiple spinelets or granules (pl. 9, figs. 1-8) . . . . . **ASTERINIDAE** 186
- 186 Body extremely flat, almost leaf-like and very fragile, height less than a tenth of the maximum diameter; 11-17, usually 15 or 16 rays; maximum size >100 mm. R . . . . . *Anseropoda rosacea* (Lamarck, 1816)
- 186' Body often more or less flattened but still fairly solid centrally and midradially, the height more than a tenth of the diameter; up to eight rays or arms but rarely more than seven, when these are short (R/r < c.1.5/1) usually small, R rarely exceeding 20 mm. . . . . 187
- 187 Arms well-developed, finger-like, high midradially and rounded above in cross-section, sometimes almost cylindrical; R/r at least 3/1, sometimes >5/1 . . . . . **NEPANTHIA** 188
- 187' Body pentagonal or stellate with short arms, flattened above or rarely somewhat carinate, R/r usually 1.5-2.5/1, rarely up to 3/1 . . . . . 193

<sup>76</sup> As Fisher (1925) and Livingstone (1931b) surmise, a good series of specimens will probably show that the types of *N. ocellata* and *cancellata* are conspecific with those of *cumingi*. The few available specimens suggest that the characters which have been used to separate them, such as the occurrence of enlarged bare plates, are variable.

<sup>77</sup> *Neoferdina glyptodisca* (Fisher, 1913a) known only from 44 metres off Celebes, may run down here. It differs from *N. insolita* in having most of the carinal plates enlarged and bare.

- 188 Arms long and cylindrical, R/r > 5/1; ventro-lateral angle slight; secondary abactinal plates few or absent (pl. 9, fig. 1) . . . . . *Nepanthia maculata* Gray, 1840<sup>78</sup>  
*Nepanthia tenuis* H. L. Clark, 1938<sup>78</sup>
- 188' Arms shorter, R/r 3-5/1; ventro-lateral angle well-marked; usually one or more secondary plates corresponding to most primary plates on the adradial areas, though these may be lacking (? underscribed in *N. magnispina*) (fig. 16a) . . . . . 189

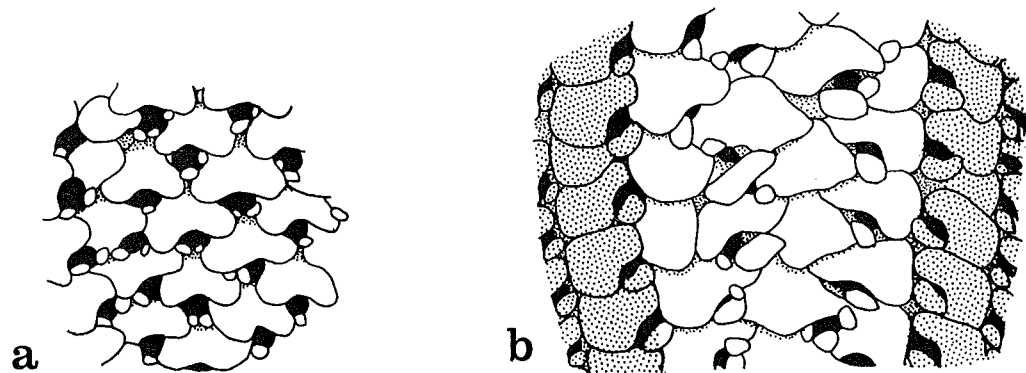


FIG. 16. Denuded proximal midradial abactinal plates of: a. *Nepanthia brevis* and b. *Paranepanthia* sp. from Zanzibar, the latter showing the abrupt transition to the lateral 'field' of plates each side (stippled). The more distal plates are towards the top.

- 189 Abactinal plates bearing coarse spinelets and appearing rugose. . . . . *Nepanthia magnispina* H. L. Clark, 1938
- 189' Abactinal plates with numerous very fine hyaline-tipped spinelets, giving a velvety appearance and texture . . . . . 190
- 190 Multibrachiate and fissiparous (self-dividing) species, arms usually irregular in size and number, most often six or seven and with additional madreporites, sometimes as many as there are radii, even the occasional five-armed specimens having more than one . . . . . *Nepanthia belcheri* (Perrier, 1875)<sup>79</sup>  
*Nepanthia joubini* Koehler, 1908<sup>79</sup>
- 190' Normally five arms and only a single madreporite, rarely more, except in small fissiparous specimens of *N. variabilis*, R < 15 mm. . . . . 191
- 191 Arms bulging near the base<sup>80</sup> . . . . . *Nepanthia suffarcinata* Sladen, 1888
- 191' Arms with parallel or evenly tapering sides<sup>80</sup> . . . . . 192
- 192 Primary abactinal plates small (at br 10 mm. c.7 longitudinal rows in the lateral field on each side of the arm basally and c.7-9 in an oblique line across the radial field); adambulacral spines 'numerous, very slender, acute'.<sup>81</sup> . . . . . *Nepanthia brevis* (Perrier, 1875)
- 192' Primary plates larger (at br 10 mm. c.5 longitudinal series in the lateral fields and 5 or 6 obliquely across the radial field); adambulacral spines 'fewer, coarse, blunt'<sup>81</sup> . . . . . *Nepanthia variabilis* H. L. Clark, 1938
- 193 Abactinal plates either naked or with very fine, easily detached, spinelets, often completely lost in museum specimens;<sup>82</sup> actinal spinelets usually single, elongated and needle-like . . . . . 194

<sup>78</sup> I believe that *Nepanthia tenuis* will prove to be a synonym of *maculata* when the range of variation can be worked out. H. L. Clark's distinction of the two by the presence of secondary abactinal plates in *maculata* is incorrect, being based on Sladen's specimen from Torres Strait, whereas such plates are absent in material from the type-locality of *maculata*—the Philippines. Possibly Sladen's specimen will prove to be an unusually narrow-armed example of *N. brevis*, also known from the Torres Strait area.

<sup>79</sup> H. L. Clark (1938) points out that there is no way of distinguishing *joubini* from *belcheri*, at least on the basis of Koehler's description which omitted to mention Perrier's species. The two will probably prove to be synonymous.

<sup>80</sup> This character used in H. L. Clark's key (1938) is surely of little weight, based as it is on the holotype and only known specimen of *Nepanthia suffarcinata* from the Mergui Archipelago; until further material from that area can be compared with Australian specimens the specific limits of *suffarcinata* as opposed to *brevis* and *variabilis* must remain uncertain; it would of course have priority over *variabilis*, the great variability of which is emphasized by H. L. Clark.

<sup>81</sup> These distinctions are taken from H. L. Clark's key (1938). Unfortunately he omitted to give comparative details of the numbers or lengths of the adambulacral spines. In the holotype of *Nepanthia brevis* (R 24 mm.) and another specimen from Torres Strait (R 44 mm.) there are about 6 furrow spines, while H. L. Clark describes 5 or 6 in the type-material of *variabilis*, R up to 60 mm. However, the size of the abactinal plates does appear to be greater in the paratype of *N. variabilis* in the British Museum collections than in the few specimens of *brevis* available, though the latter may also have a fairly regular longitudinal arrangement of the plates.

- 193' Abactinal armament usually tenacious though sometimes restricted to fine spinelets towards the proximal edges of the plates;<sup>82</sup> actinal spinelets often multiple, in length rarely exceeding the plate bearing them . . . . . 200
- 194 Arms carinate, relatively long, R/r 2-3/1; no marked area of naked skin in the proximal part of each actinal interradius . . . . . **TEGULASTER** 195
- 194' Arms low and rounded above; R/r usually c.2/1; a noticeable patch of uncalcified skin distal to each pair of oral plates . . . . . **DISASTERINA** 196
- 195 Actinal plates with single elongated spines or spinelets; adambulacral plates with 4 or 5 furrow spines and usually 2 subambulacral ones . . . . . *Tegulaster ceylanicus* (Döderlein, 1889)
- 195' Actinal plates with 1-4 spinelets; adambulacrals with c.6 furrow and 2-4 subambulacral spines . . . . . *Tegulaster emburyi* Livingstone, 1933a  
*Disasterina praesignis* Livingstone, 1933a
- 196 Arms relatively short, R/r < 2/1 . . . . . 197
- 196' R/r 2/1 or more . . . . . 197
- 197 Most actinal plates with 2 long slender spines, abactinal plates each with 1-3 similarly slender spines . . . . . *'Disasterina' spinosa* Koehler, 1910b<sup>82</sup>
- 197' Actinal plates each with a single long slender spine; abactinal plates with few, if any, spines or spinelets . . . . . 198
- 198 Abactinal plates more or less obscured by thick naked skin, even when dry . . . . . *Disasterina abnormalis* Perrier, 1875
- 198' The skin over the abactinal plates transparent and inconspicuous . . . . . 199
- 199 Adambulacral plates with c.5 furrow spines (at least at R c.18 mm.) and oral plates with 7-9; abactinal plates near centre of the disc with small spinelets<sup>83</sup> . . . . . *Disasterina leptalacantha* (H. L. Clark, 1916)
- 199' 3 or 4 furrow spines on the adambulacral plates and c.4 on the oral plates (at R 7-8 mm.); abactinal spinelets only found near the interbrachial margins<sup>83</sup> . . . . . *Disasterina spinulifera* H. L. Clark, 1938
- 200 Body form almost or quite pentagonal, R/r < 1.5/1; interbrachial margin fairly rigid and almost straight, in preserved specimens at least; size small, R up to only c.18 mm.; abactinal armament coarse and superficially appearing granuliform<sup>84</sup> (pl. 9, fig. 3) . . . . . *Patiriella exigua* (Lamarck, 1816)
- 200' Body usually stellate with R/r > 1.5/1, but if nearly pentagonal then the margin is thin and pliable, often curling upwards in preserved specimens; R exceeding 20 mm. in some species, up to c.40 mm. (? 65 mm. in *granulosa*, though this may not be a true *Asterina*); abactinal armament usually distinctly spiniform and sometimes fine<sup>84</sup> . . . . . **ASTERINA** 201
- 201 Body almost pentagonal, R/r usually < 1.7/1,<sup>85</sup> often markedly flattened . . . . . 202
- 201' Body stellate, R/r usually > 1.7/1, often > 2/1, interbrachial arcs more or less deep and often angular, always thick midradially . . . . . 203
- 202 Abactinal armament coarse, superficially appearing granuliform, tenacious; papular areas confluent interradially; body more or less thickened . . . . . *Asterina lorioli* Koehler, 1910b
- 202' Abactinal armament very delicate, consisting of fine minute hyaline spinelets, easily rubbed off; few, if any, papulae corresponding to the median row of plates in each interradius, the petaloid radial papular areas linked only to the area in the centre of the disc; body markedly flattened (pl. 9, figs. 7, 8) . . . . . *Asterina sarasini* (de Loriol, 1897)<sup>86</sup>  
*Asterina nuda* H. L. Clark, 1921<sup>86</sup>  
*Asterina orthodon* Fisher, 1922<sup>86</sup>  
*Asterina lutea* H. L. Clark, 1938<sup>86</sup>

<sup>82</sup> However, the group of species of *Asterina* which includes *A. sarasini* has easily dislodged delicate abactinal spinelets. These species can be distinguished from *Tegulaster* and *Disasterina* by the almost pentagonal body form (R/r c.1.5/1) and the flexible thin interbrachial margin and rounded arcs; also from the latter genus by the absence of a naked space distal to the oral plates and the multiple actinal spinelets. *Disasterina praesignis*, the only species with short rays which should run down to no. 194, has markedly angular interradial arcs. Conversely *D. spinosa* (only known from the holotype) has 1-3 long slender spines on each abactinal plate and is doubtfully congeneric with *D. abnormalis*, the type-species.

<sup>83</sup> This distinction used by H. L. Clark (1946) is a very poor one. The abactinal spinelets of the diminutive dried holotype of *D. spinulifera* were probably rubbed and the smaller size could well account for the fewer furrow spines.

<sup>84</sup> It should be noted that the standard character introduced by Verrill (1913) and adopted by Fisher (1919) and others for the distinction of *Patiriella* and *Asterina*, namely the development of secondary abactinal plates in the papular areas of only *Patiriella* is not strictly true. In *A. gibbosa* the type-species of *Asterina*, as Verrill admits, there are some scattered secondary plates present to about the same extent as in specimens of comparable, relatively small, size of *Patiriella exigua*. The larger species of *Patiriella*, such as *P. gummi* and *P. calcar* from temperate Australia do have more numerous and more regularly-arranged secondary plates but they far exceed the size of any species of *Asterina* (except for the little-known *Asterina granulosa* Perrier with R 32-65 mm. in the type-material, which is almost certainly not a true *Asterina*).

<sup>85</sup> H. L. Clark measured the holotype of *Asterina nuda* as having R/r 18/11 mm., giving a ratio of 1.64/1 but the photograph of the preserved specimen looks much more pentagonal than this would suggest and measurements from it give a ratio of 1.4/1. Certainly Fisher (1922) did not think the ratio sufficiently different from that of his holotype of *A. orthodon* (where it is only 1.36/1) for any comment to be needed.

<sup>86</sup> *Palmipes* (or *Anseropoda*) *sarasini* de Loriol was referred to *Asterina* by Livingstone (1933a), whose action is endorsed here after a comparison between eight specimens from Tuticorin, southern India (which are clearly conspecific with the types

- 203 Scattered abactinal plates unusually convex and bearing a cluster of markedly enlarged spinelets (pl. 9, fig. 6)  
*Asterina coronata* von Martens, 1866
- 203' Abactinal plates similar in size and contour, spinelets fairly uniform in magnitude . . . . . 204
- 204 Actinal plates each with 2 coarse spines, sometimes only 1 . . . . . *Asterina crassispina* H. L. Clark, 1928<sup>87</sup>
- 204' Usually 3 or more spines or spinelets on each actinal plate, if only 2 on some of the plates then the shape is slender . . . . . 205
- 205 Adult size large, R 32-65 mm. in the type-series; arms 'fairly acute'; not known to be fissiparous  
*Asterina granulosa* Perrier, 1875<sup>88</sup>
- 205' R rarely much exceeding 30 mm., usually 15-25 mm.; arms blunt-tipped; in certain areas, particularly at the extremities of its range—the Red Sea, Australia and possibly the Hawaiian Islands—often fissiparous (self-dividing across the disc) with six or seven (sometimes eight) arms and several madreporites  
*Asterina burtoni* Gray, 1840<sup>89</sup>

of *sarasini* from Ceylon and Koehler's specimens from the Andaman and Nicobar Islands) and a paratype of *Asterina lutea* from Broome, NW Australia. The two lots are extremely similar, differing only in the slightly flatter form of the abactinal plates and coarser abactinal spinelets in *sarasini*, the latter resembling the spinelets of the type of *A. orthodon* as drawn by Fisher, whereas the spinelets of *lutea* are very slender and almost needle-like. I do not think that these small differences alone justify a specific distinction. Judging from the descriptions, the status of *A. orthodon* and *A. nuda* as distinct from *A. sarasini* is also doubtful. The unique type of *nuda*, described as smooth and shiny above when dry, was probably rubbed in preservation. Some of the Tuticorin specimens are similarly rubbed, the lost spinelets leaving no trace on the plates. In contrast the holotype of *A. orthodon* was well preserved with the spinelets *in situ*, judging from Fisher's photographs. In life, the type-material of all four nominal species probably had a chevron of fine spinelets on each of those abactinal plates that subtend a papula, this being reduced to a small tuft on the middle of the more lateral plates with no corresponding papulae. The actinal plates are armed with a linear series of usually about 3 but up to 6 fine spinelets. In 1946 H. L. Clark distinguished *nuda* from *lutea* by the presence of central groups of 2-4 actinal spinelets in the former, this being in direct contradiction to his description of the holotype as having *linear series* of 3-5 spinelets. The Tuticorin specimens show that there is some variation in the number and arrangement of the actinal spinelets, occasional plates having an offset spinelet giving the appearance of a cluster rather than a fan. The number of longitudinal series of both abactinal and actinal plates also varies to some extent, not necessarily correlated with the size, the abactinal plates numbering from 17 to 21 across the arms basally (omitting only the few odd interradial plates hardly worth recognizing as forming longitudinal series) and the actinal series from 8 to 12. R ranges from 12 to 19.5 mm. in these eight specimens and R/r from 1.25-1.45/r. However, there may be a distinction between *sarasini* and the rest provided by the adambulacral spines, of which there are 6 to 7 furrow spines and 5 or 6 subambulacral ones in these specimens from Tuticorin, whereas the types of the three other nominal species are all described as having 7 or 8 furrow spines and, except for *lutea* with only c.6, also up to 8 subambulacral ones. The type of *A. nuda* was predominantly pearl grey in colour in life with orange margins and anal area, contrasting with that of *A. lutea* which was bright orange all over. Mortensen's specimen of *A. orthodon* was pinkish. The colour of *sarasini* in life remains to be noted.

<sup>87</sup> The locality of the holotype of *Asterina crassispina* is doubtful; it may well have been from southern Australia rather than the north, and so could be excluded from this work.

<sup>88</sup> Verrill (1913) has referred *Asterina granulosa* from the Hawaiian Islands to the genus *Patiria*; this move is certainly supported by the large size but the species could also be referred to *Paranepanthia* on this count; until the type-material has been re-examined the true position of *granulosa* must remain in doubt.

<sup>89</sup> Having recently discovered (A.M.C., 1967d) that the five-armed specimen which Smith (1927) recognized as a syntype of *A. burtoni* has five very small madreporites (revealed by judicious cleaning of the spinelets interradially), indicating that it was potentially fissiparous, I think that the syntype must be conspecific with the fissiparous *A. wega* Perrier, the type-material of which was likewise from the Red Sea. Possibly *Asterina anomala* H. L. Clark (1921) from tropical Australia and the Marshall Isles (A. H. Clark, 1952) is another synonym; it too is fissiparous. A comparison of some specimens from Lord Howe Island, sent by Dr. Clark, with the two syntypes of *A. burtoni* shows a great similarity and the dull blotched colour pattern of *anomala* in life is very similar to that of the live specimens I have seen from the Red Sea. There is a minor difference in the shape of the abactinal spinelets (fig. 17a and g) but these show a considerable range of form in *burtoni* and I do not consider that the distinction they afford merits a specific separation. I have also found a sample of fissiparous specimens of *Asterina* from Hulule, Maldiv Islands, which can be referred to *A. burtoni*, while H. L. Clark (1921) and Edmondson (1935) have also mentioned small fissiparous Asterinids from Hawaiian waters which are quite likely to prove conspecific with *burtoni*. In addition, a fissiparous *Asterina*, which I cannot distinguish from *A. burtoni*, has recently been found on the Mediterranean coasts of Israel and Syria. Mr. Y. Achituv of the Hebrew University, Jerusalem, tells me that he has found no five-armed specimens in Mediterranean samples and the same seems to be true in Hawaii since there are no records of either *A. burtoni* or *A. cepheus* (currently recognized as a synonym) from there. However, in the Red Sea, at the Maldiv Islands and in northern Australia, five-armed non-fissiparous specimens of *A. burtoni* have also been recorded. I cannot find any reason to distinguish these specifically from the multi-armed specimens but the whole problem of the relationship between fissiparous multi-armed and non-fissiparous but otherwise similar five-armed sympatric Asterozoa remains to be properly investigated by studies on living material and breeding experiments.

After examination of the abactinal spinelets of the British Museum specimens which have been referred to *Asterina burtoni* or in earlier days by Bell to *A. cepheus*, I find that there is a strong probability that specimens from the East Indies and Philippines consistently have elongated abactinal spinelets with transparent flanges (fig. 17h), differing from the rather squat and usually fairly opaque spinelets of specimens from the Red Sea, E. Mediterranean, E. Africa, the Persian Gulf and the Maldives (fig. 17a-f), though some specimens from the western Indian Ocean outside the Red Sea are transitional. Also the slender flanged form of spinelet is found in the only three specimens in the collections from Mauritius (fig. 17i). Since Batavia

(Jakarta), the type-locality of *A. cepheus*, comes within the area of the slender-spined form and the three museum specimens from Batavia possess such spinelets, I consider that the name *cepheus* may be used for a non-fissiparous subspecies of *burtoni* with slender abactinal spinelets extending from New Guinea to the Philippines and South China Sea, and possibly also to Mauritius. However, this needs to be supported by study of further and larger samples of *Asterina*. It should be noted that as a proper name, *cepheus* retains the masculine termination.

I have also attempted to correlate other characters with locality, notably the number and arrangement of the actinal spines, whether arranged in fans or clusters, and the number of suboral spines; unfortunately these seem very variable. Most of the values obtained are included in the table on p. 70. Mortensen (1940a) used the presence of as many as five suboral spines on each plate to distinguish the variety *iranica* from the types of *A. cepheus* which he says have only two such spines. The three British Museum specimens from Batavia all have two or three suboral spines, varying on different jaws of the same specimen, but two from Macclesfield Bank in the South China Sea have four or five of these spines and a sample of twelve specimens from

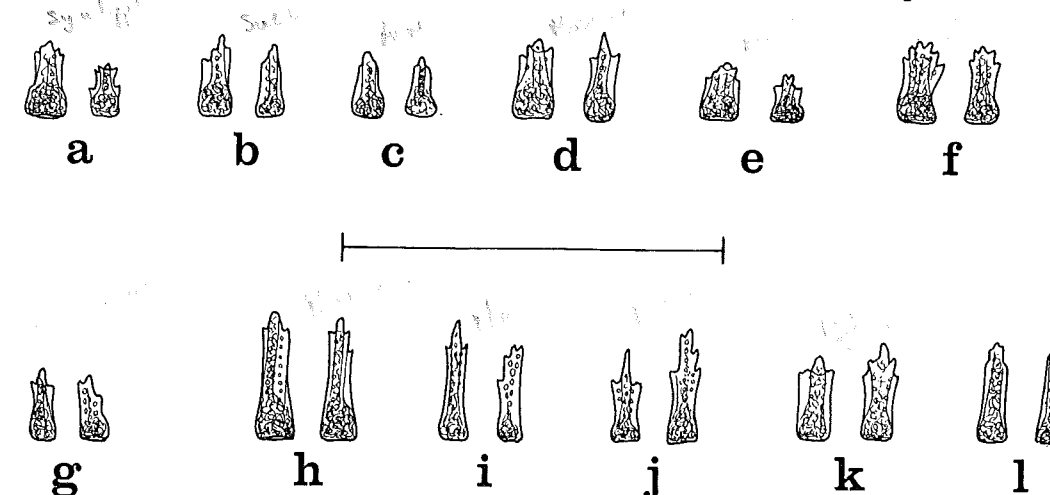


FIG. 17. Abactinal spinelets of a-g. *Asterina burtoni burtoni*, a. syntype, b-g. Suez, Acre (NW Israel), Muscat, the Maldives, Zanzibar and Lord Howe Island (*anomala*); h-j. *A. burtoni cepheus*, from Batavia (Jakarta), Mauritius and Macclesfield Bank; k. *Paranepanthia* sp., Zanzibar; l. *P. brachiata*, Arabia. The scale measures 1 mm.

Zanzibar shows a range from two to five or six spines. Mortensen was misled by Smith's description of the type-material of *A. burtoni* into thinking that his Persian Gulf specimens had little affinity with those from the Red Sea. In fact there is great resemblance, though the abactinal spinelets tend to be a little longer in some of the specimens I have seen from Oman than in any of those from the Red Sea. The table does indicate that there may be a slight correlation between the Persian Gulf and a high number of suboral spines, relative to most Pacific specimens, as well as a rather high frequency in the latter of clustered actinal spines but there is no such consistency as occurs with the abactinal spinelets.

It is possible that a species of *Paranepanthia* occurs in shallow water in East Africa. Two Asterinids taken at Zanzibar by the same collector as the sample of 12 specimens of *A. burtoni* included in the table were at first labelled *burtoni* with the rest but a re-examination shows several correlated differences. The arms are relatively longer and narrower at the tip; R/r is 30/11 mm. = 2.7/r and 20/8 mm. = 2.5/r, in comparison with a mean ratio of 2.0/r in the other twelve, though one of these does have a value as high as 2.5/r. The breadth at the arm tip is c.4.5 mm. in the specimen with R 30 mm., compared with 5.5 mm. in the largest of the twelve, R 25 mm. There are also unusually numerous secondary abactinal plates in the radial areas of the arms among the primary plates (at least in the larger of the two, fig. 16b) and there is a much sharper demarcation between the plates of radial and lateral 'fields' of the aboral side than is usual in *A. burtoni*, resembling rather the arrangement characteristic of *Paranepanthia* (as opposed to *Patiria*), which is also found in *Nepanthia* and to a lesser extent in *Asterina*. Fourthly, the actinal spines of the twelve specimens are nearly always arranged in fans, even on the few proximal plates where the spines number as many as 5 or 6, whereas the two other specimens differ sharply in having 6-12 (in the larger) and 5-8 (in the smaller) actinal spines on each plate and these are arranged in a cluster, or at least in two rows, on each plate. Although some variation in the arrangement and number of actinal spines is common in *A. burtoni*, in this case the difference is very marked. Finally there is a minor difference in the form of the abactinal spinelets, which are blunter and more opaque in the twelve specimens with less marked distal points, though in the two others they are fairly short, 2.5-3.5 times as long as broad.

The shape of the arms in the two specimens is very reminiscent of the South African *Patiria granifera* Gray but in *Patiria* the secondary abactinal plates are usually much more numerous and there is no distinction of radial and lateral fields of plates on the aboral side.

It is possible that these two specimens from Zanzibar are conspecific with Lamarck's *Asterias penicillatus* of unknown type-locality, which was designated as type-species of *Asterinopsis* by Verrill (1913). Mortensen (1933b) ascertained that Lamarck's type-material has been lost and also doubted the distinctness from *Parasterina bellula* Sladen (a synonym of *Patiria granifera* Gray according to me—*Ann. Mag. Nat. Hist.* 9:380, 1956) of Müller and Troschel's material of *Asteriscus penicillaris*. Accordingly H. L. Clark (1946) rejected *Asterinopsis* as a 'heterogeneous group' with uncertain type-species and merged it with *Paranepanthia* Fisher, 1917. Fisher (1919) referred his own species *Nepanthia pedicellaris* (1913a) to *Asterinopsis*, commenting

TABLE I

Reg. No.	Locality	R	Actinal spines		Suboral spine no.	Abactinal spinelet shape
			No.	clustered		
44.12.9.49	Red Sea	15	3, 4	—	2, 3	squat
70.12.23.15	Suez	16	3-5	(—)	5(4)	squat
1927.1.10.41	Suez	16	3, 4	—	3, 4(5)	squat
1949.10.12.14	Gulf of Akaba	14	2-5	(+)/—	4, 5	squat
1949.10.12.13	Gulf of Akaba	12	2, 3	—	3, 4	squat
1951.5.7.12	Sudan	10	3-5	+	1	v. tapering
99.4.17.15	Muscat	26	5-9	+	5	squat-interm.
1904.3.2.11	Oman	25	2-6	—	4	intermediate
1904.3.2.12	Oman	25	3-7	—	4, 5	intermediate
1904.3.2.13	Oman	21	4-7	+	6	—
1962.8.16.36	Persian Gulf	18	2-5	(—)	5	interm.-elongate
1962.8.16.35	Persian Gulf	18	3-6	(+)/—	6	squat-interm.
1963.10.30.4	Trucial Oman	15	2-5	(—)	4(5)	squat
1965.6.1.84	Gan, Maldives	20	2-4	—	4(5)	interm. tapering
1965.6.1.84a	Gan, Maldives	15	2-4	+	3(4)	—
1903.4.2.19	Zanzibar	25	3-5(6)	+ / —	?5	interm. opaque
1965.6.1.734	Zanzibar	25	2-6	—	4	squat
1965.6.1.735	Zanzibar	22	2, 3(4)	—	2(3)	squat
1965.6.1.736	Zanzibar	22	2-5	—	5	squat
1965.6.1.737	Zanzibar	22	3-6	(—)	4	squat
1965.6.1.738	Zanzibar	21	2, 3(6)	—	3	squat
1965.6.1.739	Zanzibar	20	2-5	—	3	squat-interm.
1965.6.1.740	Zanzibar	19	2-4	—	3, 4	squat
1965.6.1.741	Zanzibar	18	2-6	—	3	squat
1965.6.1.742	Zanzibar	18	2-4	—	5, 6	squat
1965.6.1.742a	Zanzibar	17	2, 3	—	4	squat
1965.6.1.742b	Zanzibar	16	2-6	(—)	4	squat
1965.6.1.742c	Zanzibar	14	2, 3(4)	—	2	v. squat
1903.4.2.61	Zanzibar	20	3-6	+	3, 4	squat-interm.
1903.4.2.62	Zanzibar	16	4-8	+	4	squat-interm.
68.3.6.13	Zanzibar	14	2-4	—	3	squat
1913.12.23.3	Tanganyika	24	2-5	—	5	short, opaque
1955.3.25.66	Mozambique	27	6-8	+	2	intermediate
1961.4.12.16	Inhaca	31	3-6	+	5	longish
1939.6.15.88	Lord Howe I.	8.5	3-5	—	4	squat
1953.5.18.7	Queensland	18	5-10	+	4, 5	interm., flanged
1902.8.14.1	New Guinea	15	4-6	+	3	flanged, tapering
89.3.11.7	Mauritius	13.5	3, 4	(—)	5	slender, flanged
89.6.15.16	Batavia	26	2-4	(+)	2(3)	slender, flanged
94.7.5.11	Batavia	21	2-4	+	2(3)	slender
89.6.15.17	Batavia	19	2-5	+	3	—
93.8.25.185	Macclesfield Bk.	12	4-7	+	5	slender, flanged
43.3.29.35	Philippines	10	3	—	3	slender, flanged

*Asterina burtoni* Gray; details of some specimens in the British Museum collections. Brackets signify rare numbers or, in the case of column five, arrangements; negative entries under actinal spines signify linear arrangement.

that the genus is closely related to *Paranepanthia*, although he had diagnosed the latter as having the abactinal plates distinguished into two areas, which is not the case in *N. pedicellaris*. Nor is it so in *Nepanthia brachiata* Koehler, 1910b, from the Indian Ocean, which Fisher nevertheless simultaneously referred to *Paranepanthia* rather than to *Asterinopsis*. Besides the skeletal similarity, *N. pedicellaris* and *brachiata* agree in having six arms and in my opinion are certainly congeneric. Pending a revision of the generic limits within the family Asterinidae, they are probably best included in *Paranepanthia*, while *Asterinopsis* should be officially rejected by the International Commission for Zoological Nomenclature on the grounds of the uncertain identity of its type-species.

The type-species of *Paranepanthia* is *Nepanthia platydisca* Fisher, 1913a, from Celebes in 377 metres; three species from temperate Australia, *grandis*, *praetermissa* and *rosea*, have also been referred to the genus.

One feature which Fisher thought to be characteristic of *Paranepanthia* is the arrangement of the actinal plates in transverse series from the furrow to the margin (fig. 18b), rather than simply in chevrons (fig. 18a). This is clearly noticeable in the holotype of *P. platydisca* and in large specimens of *P. grandis*, where only the basal few transverse series fall short of the margin, since they meet the interradius (fig. 18b). A similar arrangement is evident, though less conspicuous, in *P. brachiata* and *pedicellaris*, as well as in *Asterina burtoni*. However, in the two specimens from Zanzibar the comparable transverse series are indistinct, although they can just be traced (dotted lines in fig. 18c); instead the longitudinal series of adjacent arms

206 Ten to twenty arms and numerous madreporites (sometimes nearly as many as there are arms); aboral armament consisting of large conical isolated spines mounted singly on stalklike pedicels (pl. 11, fig. 3)

## ACANTHASTERIDAE

206' Usually five or six arms and only one madreporite, sometimes two (up to twelve arms in *Coscinasterias calamaria* which differs in having the tube feet in four rows, pl. 12, figs. 5, 6); armament variable but if conical spines are present then these are mounted only on low eminences

207 Aboral spines long and conspicuous, commonly 15-30 mm. long when R exceeds 100 mm., though up to almost half this length may be made up by the pedicel; pedicellariae slender (pl. 11, fig. 3)

207' Aboral spines of the disc only c.2 mm. long, even at R nearly 100 mm. though those on the arms are larger; pedicellariae stout, nearly as broad as long

208 Huge bivalved (occasionally trivalved) pedicellariae present on most of the supero-marginal plates (pl. 9, fig. 11)

208' Pedicellariae inconspicuous, if present at all, with narrow valves

209 Aboral skeleton consisting of a regular reticulum, with plates in straight longitudinal series linked up obliquely, bearing conical spines 2-3 mm. long, which are slightly spaced (at least in most dried specimens) (pl. 9, figs. 10, 11)

209' Aboral reticulum irregular, armament almost continuous

210 Tube feet in four rows; 6-12 arms and usually two madreporites; crossed and straight pedicellariae present (pl. 12, figs. 5, 6)

210' Tube feet in two rows; 5 or 6 arms, rarely 7, usually one madreporite; no pedicellariae

211 Arms elongate, slender and cylindrical, R/r > 5/1; no supradorsal membrane

211' Arms short and blunt, R/r 1.8-2.5/1; a supradorsal membrane present supported by the tips of the aboral spines to form a cavity within (pl. 12, fig. 3)

212 Aboral skeleton more or less concealed by granules or scale-like tubercles, which also cover the often conspicuously large spines; furrow spines in longitudinal fans of 6-12 (fig. 19a)

continue across the interradius obliquely to form a sort of herringbone pattern. A tendency for such an arrangement can also be discerned in some specimens of *P. grandis* at least. Just how far the arrangement of actinal series is of functional and taxonomic importance remains to be investigated. The generic as well as the specific limits within the family Asterinidae

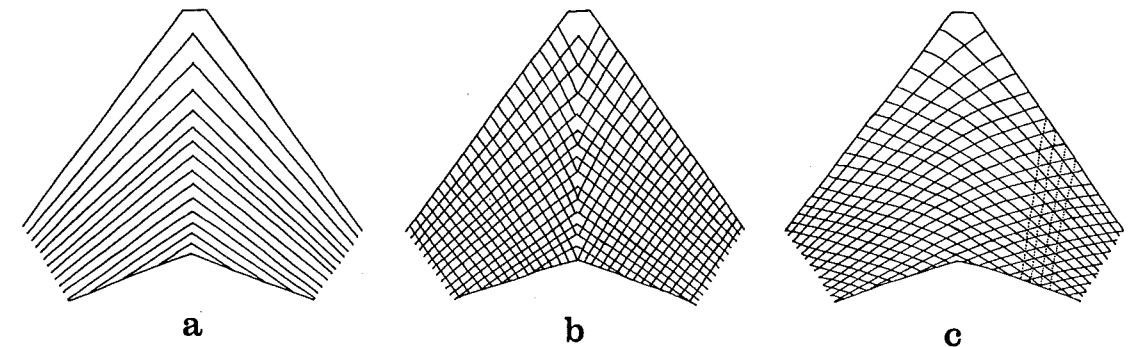


FIG. 18. Diagrams of arrangements of actinal plates in one interradius, a. in chevrons, b. in transverse series also and c. in herringbone series.

have yet to be properly defined. Certainly the abactinal spinelets (fig. 17k) are very much shorter in the Zanzibar specimens than the needle-like ones of *P. grandis*, though in *P. brachiata* (fig. 17l) they are intermediate in length. In *P. platydisca* Fisher describes the abactinal armament as short and papilliform.

<sup>90</sup> Madsen (1955) suspects that the type-material of *A. brevispinus* from the Philippines will prove to be conspecific with the very variable *A. planici*.

<sup>91</sup> If Fisher (1906) was correct in considering his Hawaiian specimen to be conspecific with material of *V. striatus* from Mauritius, the type-locality, it seems likely that the holotype of *V. spinifera* from northern Australia will also prove to be conspecific with *striatus* when more is known about the range of variation of *Valvaster*. The uniform distribution of the aboral spines in the holotype of *spinifera* may well have been correlated with better preservation than that of the dried specimens upon which de Loriol (1885) based his drawings, which appear to have provided the basis for H. L. Clark's concept of *V. striatus*. Fisher noted that the Hawaiian specimen preserved in spirit had the pulpy sheaths of the spines so much expanded as to leave little space between them. A spirit specimen in the British Museum collections from the Solomon Islands with R/r 47/18 mm. also appears to have a fairly dense converging of spines; nevertheless its skeletal reticulum is quite regular with longitudinal and oblique transverse series of plates, as can be seen better when the skin is dissolved, so I have referred it also to *V. striatus*.

<sup>92</sup> The convention throughout these keys of numbering the odd species as they are resolved (e.g. 210 rather than 210') brings *Coscinasterias* as the only forcipulate forward from its proper systematic position at the end.

212' No enveloping aboral granulation; spines sometimes conspicuous but more often diminutive; adambulacral spines few, usually about 3 in number and more often forming series at right angles to the furrow (fig. 19b)

**ECHINASTERIDAE** 214

213 Aboral reticulum open; papular areas large and triangular; spines conspicuous, widely spaced, often clavate or sometimes bifid at the tip, several present mid-radially (pl. 12, figs. 1, 2)

*Mithrodia clavigera* (Lamarck, 1816)

213' Aboral reticulum compact; papular areas small and irregular in shape; spines short and inconspicuous, rare midradially though numerous on the under side.

*Mithrodia fisheri* Holly, 1932

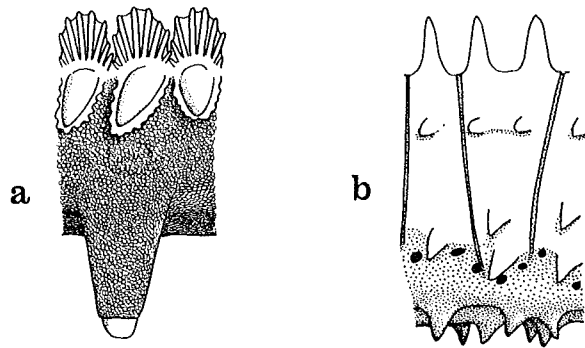


FIG. 19. One side of a proximal part of an arm from below of: a. *Mithrodia clavigera* and b. *Echinaster purpureus*. The mouth to the right.

214 Skeletal plates in regular longitudinal and transverse series; seven longitudinal series of usually single isolated conical spines on each arm (pl. 11, figs. 1, 2); adambulacral spines in longitudinal series, 2 furrow and 1 subambulacral spine on each plate, the furrow spines linked by a continuous web of skin

*Cistina columbiae* Gray, 1840<sup>93</sup>

214' Skeletal reticulum irregular aborally, no well-defined longitudinal and transverse series of plates

**ECHINASTER** 215

215 Abactinal spines large and conspicuous, often 4-5 mm. long and well spaced

*Echinaster callosus* von Marenzeller, 1895

215' Abactinal spines small, up to 2.0 mm. but usually 1.0-1.5 mm. long and fairly numerous

216 Abactinal spines with chisel-shaped or clavate tips; the largest spines lateral to the adambulacral plates and also conspicuously clavate

*Echinaster superbis* H. L. Clark, 1916

216' Abactinal spines tapering and conical or rounded at the tip; spines on the under side no larger

217 Five or six rays, occasionally seven, autotomous with single separated arms regenerating to produce comet forms but apparently not fissiparous (splitting across the disc); arms slender and cylindrical, often relatively long, br normally equal to or less than r; no marked bare strip close to the furrow; colour in life red or brownish, sometimes so dark as to be almost black but not purple (pl. 10, figs. 1, 2)<sup>94</sup>

*Echinaster luzonicus* (Gray, 1840)

<sup>93</sup> With synonym *Echinaster sladeni* de Loriol, 1893. As far as Gray's brief but very distinctive diagnoses of *Cistina* and *C. columbiae* go, they agree perfectly with de Loriol's description and fine figures of *Echinaster sladeni* from Mauritius as well as with a dry specimen in the British Museum also collected by de Robillard. Since 'Isle of France' (i.e. Mauritius) was the second most common source of Gray's material, after Cuming's west American collection, I am convinced that the long-lost types of *C. columbiae* came from the former locality rather than from Colombia so that the specific name is particularly unfortunate. Grey placed *Cistina* between *Tamaria* and *Ophidiaster* and indeed it is difficult to decide whether it should be referred to the Ophidiasteridae on account of the regular serial arrangement of the skeleton, like *Tamaria*, *Ophidiaster* and *Leiaster*, or to the Echinasteridae on account of the more open skeleton, the difficulty in recognizing the two marginal series of plates and the armament, which resembles that of the Echinasterid *Poraniopsis*. This problem must await further and better-preserved material. For the present, I am referring *Cistina* to the Echinasteridae.

<sup>94</sup> I agree with H. L. Clark that there is good justification for maintaining *Echinaster purpureus* and *luzonicus* as distinct species inhabiting the Indian and West Pacific Oceans respectively; in addition to the characters given in the key, the aboral skeleton seems to be more compact and the spines more slender in *luzonicus*, though this remains to be confirmed from comparisons of much larger samples than are available to me. Nevertheless, if a small-spined *Echinaster* is to be found in the geographically intermediate Singapore area, it should be of particular interest. The seven specimens of *E. purpureus* I have seen from southern India have relatively elongated arms, the mean R/r being 7.3/1. The British Museum specimens run down to one species or the other on morphological grounds agreeing with the locality and I have little hesitation in referring earlier Pacific records for *purpureus* to *luzonicus* and vice versa.

The British Museum's material of *E. purpureus* and *luzonicus* is not nearly so abundant as H. L. Clark's (1921), at least for

217' Normally five rays, not autotomous, arms fairly stout proximally and slightly tapering, the basal br normally exceeding r; subambulacral spines often deficient except proximally, leaving a bare strip outside the furrow spines; colour in life often purple

218 Subambulacral spines forming a more or less complete series, leaving no marked bare strip on the under side; maximum size large, R up to at least 190 mm. *Echinaster varicolor* H. L. Clark, 1938<sup>95</sup>

218' Subambulacral spine series often more or less incomplete; R up to c.140 mm. but rarely exceeding 120 mm. (pl. 10, figs. 3, 4) *Echinaster purpureus* (Gray, 1840)<sup>95</sup>

219 Five or more adambulacral spines in the proximal combs even at R only 18 mm. (a specimen with R 12 mm. has four) (pl. 12, figs. 3, 4) *Euretaster insignis* (Sladen, 1882)<sup>96</sup>

219' Only four adambulacral spines proximally, except for only one or two basal combs which may have five *Euretaster cribrosus* (von Martens, 1867)<sup>96</sup>

the latter species. However, the proportions of our specimens differ somewhat from Dr. Clark's as shown in the following table.

	<i>E. purpureus</i>				<i>E. luzonicus</i>					
	No.	R/r		R/br		No.	R/r		R/br	
		Range	Mean	Range	Mean		Range	Mean	Range	Mean
H.L.C.	—	6-7/1	—	5.5-6.5	—	144	7-10.5	—	7-10.5	—
B.M.	20	5.6-9.6	7.3	4.8-8.1	6.3	18	5.6-9.5	6.8	5.6-8.4	6.8

In addition, more than half of H. L. Clark's specimens from Torres Strait had only five arms, whereas only a third of our Pacific ones and a quarter of Fisher's Philippine ones (named *Othilia purpurea* by him in 1919) have five. Inevitably there is a higher r value in six-armed specimens than in five-armed ones with similar R and br values, giving a somewhat lower R/r ratio; our five-armed specimens of *luzonicus* with R > 40 mm. have a mean ratio as high as 7.9/1.

<sup>95</sup> These slight differences are the only ones evident between *Echinaster varicolor* and *purpureus* from H. L. Clark's description and remarks about *varicolor*, which he compares primarily with *luzonicus* since that species approximates geographically more closely (being found in northern Queensland as opposed to north-west Australia for *varicolor*). He also believed that there is a difference in the shape of the arms of *varicolor* and *purpureus*, though I doubt whether this is significant, being probably correlated with the large size of all Dr. Clark's specimens of *varicolor*, R 86-190 mm. He notes that R/r is 8-10/1, whereas the paratype he sent to the British Museum has R/r 100-120/16.5 mm. = 7.3/1 at the most, though the difference might be attributable to drying. The appearance and shape of its arms is very little different from that of the types of *E. purpureus* from Mauritius. Two specimens from the Monte Bello Islands, at the north-west corner of Australia, which I have identified as *varicolor*, have R/r 75/13 mm. = 5.8/1 and 60/9.5 mm. = 6.4/1. It should be noted that the presence of a bare strip along the under side of the arms outside the marginal furrow spines is by no means invariable in specimens from the Indian Ocean and conversely appears on part of one arm of a specimen of *luzonicus* from the Solomon Islands.

<sup>96</sup> I have examined seven specimens of *E. cribrosus* from the Indian Ocean, including two from the type-locality, Zanzibar, as well as thirteen of *insignis* from Singapore or further east, including the holotype from the Torres Strait area. Unfortunately there is very little overlap in size. The Indian Ocean specimens all have R 21-40 mm. Six of the Pacific specimens have R > 40 mm. and in four it is < 20 mm., leaving only three of comparable size to the material of *cribrosus*. One of the three is from Singapore and has R 35 mm. and six adambulacral spines on the proximal plates, though in the two others (R 25 mm. and c.38 mm.) from Australian waters the number of spines is five proximally (except on one or two basal plates which have six). As for the number of spiracular pores in each area, this is in the neighbourhood of 45-50 in the larger proximal areas of the two Pacific specimens with R 35 and c.38 mm., as well as in those from East Africa of similar size. However, von Martens gives the number as up to only 40 in the type of *E. cribrosus* at R 54 mm. Two specimens of *insignis* from the East Indies (Billiton) with R 50 and 65 mm. have respectively c.55-60 and 80-100 pores in the larger areas, while the holotype with R 45 mm. also has 80-100. Clearly the number is rather variable and Fisher's assertion (1919) that it provides a distinction between the two remains to be proved from larger samples of comparable size. He also states that the groups of pores are regularly subdivided into triangular areas in *insignis* but not in *cribrosus*. This is not necessarily so, though the areas do appear to be better defined in *cribrosus*, the supra-dorsal membrane being apparently thicker. However, this varies considerably with the state of preservation. Fisher found only three adambulacral spines in the specimen of *cribrosus* he studied but there are four proximally in all the British Museum specimens, even at R only 21 mm. Also the number of spines projecting through the supra-dorsal membrane at the nodes depends on the state of preservation; in life probably none project. Dissection of three specimens shows that the usual number of spines on each pseudopaxilla is four in both Indian Ocean and Pacific specimens and there is no obvious difference in the spines microscopically. Altogether I think that there are some grounds for Döderlein's action in synonymizing *cribrosus* and *insignis* but comparison of much larger and more uniformly-preserved specimens from both oceans is needed to settle the problem.

## SUMMARY OF TAXONOMIC CHANGES—ASTEROIDEA

- Luidia maculata* forma *herdmani* A. M. Clark, 1953, raised to specific rank—see key note 2.  
*Luidia hexactis* H. L. Clark, 1938, referred to the Alternata-group of Döderlein from the Quinaria-group—see note 1.  
*Goniodiscaster coppingeri* (Bell, 1884), a synonym of *G. rugosus* (Perrier, 1875)—see note 22.  
*Anthenea edmondi* nom. nov. for *Goniodiscus acutus* Perrier, 1869, non *G. acutus* Heller, 1863—see note 27.  
*Oreaster luetkeni* and *muelleri* Bell, 1884, synonyms of *Pentaceraster regulus* (Müller & Troschel, 1842)—see note 38.  
*Leiaster glaber* Peters, 1852, a valid species distinct from *L. leachi* (Gray, 1840)—see note 47.  
*Fromia elegans* H. L. Clark, 1921, a valid species distinct from *F. indica* (Perrier, 1869)—see note 66.  
*Fromia tumida* Bell, 1882, a synonym of *F. indica* (Perrier, 1869)—see note 66.  
*Echinaster sladeni* de Loriol, 1893a, a synonym of *Cistina columbiae* Gray, 1840—see notes 45 and 92.

## SUMMARY OF RELATIONSHIPS NEEDING FURTHER INVESTIGATION

- Luidia mauritiensis* Koehler, 1910b and *magnifica* Fisher, 1906—see note 3.  
*Luidia sibogae* Döderlein, 1920 and *savignyi* (Audouin, 1826)—see note 4.  
*Luidia prionota* Fisher, 1914 and *hardwicki* (Gray, 1840)—see note 5.  
*Astropecten phragmorus* Fisher, 1913 and *polyacanthus* Müller & Troschel, 1842—see note 6.  
*Astropecten orsinii* Leipoldt, 1895, probably based on an immature specimen of another Red Sea species—but see table note 3 and key note 8.  
*Astropecten notograptus* Sladen, 1888 and *monacanthus* Sladen, 1883—see key note 10.  
*Monachaster umbonatus* Macan, 1938 and *sanderi* (Meissner, 1892)—see note 15.  
*Goniodiscaster australiae* Tortonese, 1935, *rugosus* (Perrier, 1875), *forficulatus* (Perrier, 1875) and *scaber* (Möbius, 1859)—see notes 22, 23 and 24.  
*Anthenea grayi* Perrier, 1875 and *flavescens* (Gray, 1840)—see note 26.  
*Anthenea acanthodes* H. L. Clark, 1938 and *tuberculosa* Gray, 1847—see note 29.  
*Anthenea conjugens* Döderlein, 1935 and *godeffroyi* Döderlein, 1915—see note 30.  
*Asterodiscus helonotus* Fisher, 1913c and *elegans* Gray, 1847—see table note 11.  
*Siraster tuberculatus* H. L. Clark, 1915a and *Stellaster equestris* (Retzius, 1805)—see table note 10.  
*Protoreaster* and *Pentaceraster*, generic limits—see key note 34.  
*Pentaster* and *Pentaceraster*, generic limits—see note 37.  
*Pentaceraster* spp. included, notably *P. gracilis* (Lütken, 1871) and *regulus* (Müller & Troschel, 1842)—see notes 38 and 43; *P. alveolatus* (Perrier, 1875) and *multispinus* (von Martens, 1866)—see notes 38 and 41. *P. sibogae* Döderlein, 1936 and *decipiens* (Bell, 1884)—see note 40.  
*Leiaster speciosus* von Martens, 1866 and *leachi* (Gray, 1840)—see note 48.  
*Ophidiaster perplexus* A. H. Clark, 1954, almost certainly not an *Ophidiaster*; possibly a *Linckia*—see note 59.  
*Ophidiaster propinquus* Livingstone, 1932, possibly an immature *Linckia multifora*—see note 59.  
*Ophidiaster squameus* Fisher, 1906 and *hemprichi* Müller & Troschel, 1842—see note 60.  
*Ophidiaster lorioli* Fisher, 1906 and *cribrarius* Lütken, 1872a—see note 61.  
*Linckia diplax* (Müller & Troschel, 1842) of doubtful standing in relation to *L. guildingi*—see note 62.  
*Nardoa mamillifera* Livingstone, 1930 and *frianti* Koehler, 1910b—see note 70.  
*Neoferdina ocellata* (H. L. Clark, 1921), *cancellata* (Grube, 1857) and *cumingi* (Gray, 1840)—see note 76.  
*Nepanthia tenuis* H. L. Clark, 1938 and *maculata* Gray, 1840—see note 78.  
*Nepanthia joubini* Koehler, 1908 and *belcheri* (Perrier, 1875)—see note 79.  
*Asterina lutea* H. L. Clark, 1938, *nuda* H. L. Clark, 1921, *orthodon* Fisher, 1922 and *sarasini* (de Loriol, 1897)—see note 86.  
*Euretaster insignis* (Sladen, 1882) and *cribrosus* (von Martens, 1867)—see note 96.