

ECHINOIDEA

INTRODUCTION AND GLOSSARY

As with the other classes, elementary general accounts are given in A. M. Clark (603 in reference list), Nichols (645) and a more detailed one by Hyman (626). Mortensen's fine 'Monograph of the Echinoidea' (439, 446, 452, 454, 455, 643 and 459) provides keys and detailed descriptions of most of the species concerned, or references to where such descriptions can be found.

The following terms may need some clarification—

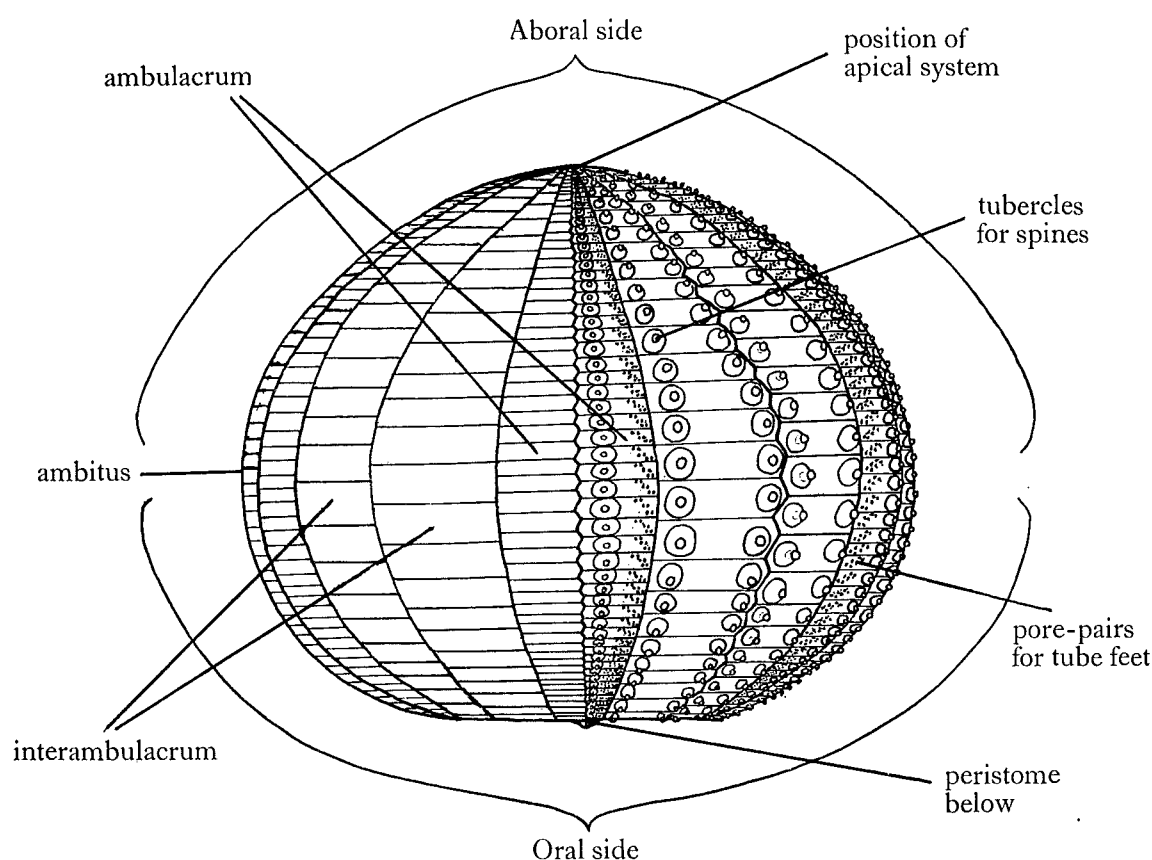


FIG. 58. Introductory figure of regular echinoid test in side view.

Ambitus—the broadest part of the test, through which the horizontal diameter (h.d.) is measured.

Apical system—the double ring of five radially-situated *ocular plates* (opposite the apical ends of the ambulacral series of plates) and five interradial *genital plates*, together with the periproct (q.v.) which they encircle. Some or all of the oculars may make contact with the periproct, in which case they are called insert, alternatively, if excluded by the adjoining genital plates meeting radially, then the condition is exsert (see figs. 59 and 68).

Corona or *test*—the usually rigid main part of the series of five pairs of ambulacral plates and five pairs of interambulacrals, extending from the peristome up to the apical system.

Labrum—in the Spatangoida the lip behind the asymmetrical mouth.

Lunule—in certain Clypeasteroida a slot or hole, usually elongated, perforating the test dorso-ventrally.

Pedicellariae—the minute stalked grasping organs, each with usually three calcified valves, found on various parts of the surface, even the largest barely visible with the naked eye. These are divisible into several kinds of which the most important are—*globiferous*, with associated poison glands and the middle part of the valves tubular, terminating in one or more prominent teeth for injection [pl. 31 figs. 13, 14 (pt.), 15 (pt.), 16 (pt.), 18 (pt.), 19 (pt.)]; *tridentate*, with relatively large parallel-sided or petaloid valves, often meeting only near the tip [pl. 31 figs. 14 (pt.), 15 (pt.), 17 (pt.), 18 (pt.), 19 (pt.)]; *triphylous*, with short broad-tipped valves [pl. 31 figs. 17 (pt.), 18 (pt.), 19 (pt.)]; *ophicephalous*, with broad often waisted valves of medium length and rounded tips [pl. 31 figs. 16 (pt.), 18 (pt.), 19 (pt.)]. The exact shape of the first two kinds, globiferous and tridentate, is important in the distinction of many species, especially of regular echinoids.

Periproct—the circular or oval extensible area immediately surrounding the anus bearing a variable number of small plates embedded in the skin, one of which may be enlarged as the *suranal plate*.

Peristome—the area of skin between the mouth and the test; usually with only a few widely-spaced plates embedded in it but sometimes with articulated plates.

DISTRIBUTION TABLE
FOR
ECHINOIDEA

DISTRIBUTION TABLE

	Is. of W. Indian Ocean	Mascarene Is.	E. Africa & Madagascar	Red Sea	S.E. Arabia	Persian Gulf
CIDARIDAE						
<i>Chondrocidaris †brevispina</i> (H. L. Clark)
<i>Eucidaris metularia</i> (Lamarck)	51 * 385	344 * 367	49 * 505	5 * 175
<i>Phyllacanthus dubius</i> Brandt
<i>forcipulatus</i> Mortensen
<i>imperialis</i> (Lamarck)	175 *	367 * 439	310 * 345	5 * 344
<i>longispinus</i> Mortensen
<i>Prionocidaris baculosa</i> (Lamarck)	175 *	344 * 439	5 * 385	254 * 421	175 * (450)	..
<i>bispinosa</i> (Lamarck)
<i>pistillaris</i> (Lamarck) ¹	(175 * 310)	344 427	171 * 439	..	(450 *)	..
<i>verticillata</i> (Lamarck) 344	51 * 175	175 * 367	49 * 310
ECHINOTHURIIDAE						
<i>Asthenosoma intermedium</i> H. L. Clark
<i>varium</i> Grube ²	148 * 446
DIADEMATIDAE						
<i>Astropyga radiata</i> (Leske) 351	34 * 51	175 * 367	505 * 507	..	327	..
<i>Centrostephanus rogersi</i> (A. Agassiz) ³ 2
<i>Chaetodiadema granulatum</i> Mortensen	(148*)
<i>Diadema paucispinum</i> A. Agassiz
<i>savignyi</i> : Michelin ⁴	11 * 34	175 * 427	310 * 434	..	(450 *)	..
<i>setosum</i> (Leske) ⁴	..	175 * 367	385 * 505	148 * 452	175 * 339	137
<i>Echinothrix calamaris</i> (Pallas)	*	367 * 427	317 * 507	200 * 274	(450 *)	..
<i>diadema</i> (Linnaeus) 354	11 51	367 * 452	385 507	5	175 *	..
<i>Lissodiadema lorioli</i> Mortensen
STOMOPNEUSTIDAE						
<i>Stomopneustes variolaris</i> (Lamarck) 344	..	5 * 367	317 * 507	..	175 *	..
TEMNOPLEURIDAE						
<i>Mespilia globulus</i> (Linnaeus) 354
<i>Microcyphus †ceylanicus</i> Mortensen
<i>excentricus</i> Mortensen
<i>maculatus</i> L. Agassiz ⁵ 11	..	367 * 454
<i>rousseaui</i> L. Agassiz	345 * 454	148 560	11	..
<i>Paratrema doederleini</i> (Mortensen)
<i>Salmaciella dussumieri</i> (L. Agassiz) ⁶	(175 *)	..	157 * 454	148 *	(450 *)	..
<i>Salmacis belli</i> Döderlein
<i>bicolor</i> L. Agassiz	(51)	200 * 367	65 * 171	5 * (148)
<i>sphaeroides</i> (Linnaeus)
<i>virgulata</i> L. Agassiz
<i>Temnopleurus †alexandri</i> (Bell) ⁷
<i>decipiens</i> (de Meijere)

FOR ECHINOIDEA

	W. India & Pakistan	Maldiva area	Ceylon area	Bay of Bengal	East Indies	North Australia	Philippine Is.	China & S. Japan	South Pacific Is.	Hawaiian Is.
	439	46 * 175	..
	..	48 * 147	(306)	(339)	344 537	175 *	423 * 438	194 * 439	45 * 137	7 * 59
	61 439
	447
	175 * 196	40	200 423	169 * 180	132	194	136 * 439	..
	180 435
	175 *	51 * (339)	160 306	40 * 64	200 * 423	..	423 * 438	195 * 285
	306	..	(202) * 434	200 * 344	..	200

	..	51 175	..	38 * 175	439 * 538	6 * 435	438 * 518	194 586	5 * 176	7
	180 233
	..	48 * 175	175 * 196	40 64	200 * 371	..	6 * 453	621
	..	147 175	37 196	38 * 339	423 * 434	163 552	216 453	80	452 547	6 * 8
	235 * 452
	..	452	..	339	423 * 433	(6) * 163	453	(44 * 175)
	137	3 225
	..	*	160	..	135 412	169 179	453	80 * 570	452 *	..
	196 * 580	38 * 339	351 * 434	169 * 231	423 * 518	285 445	8 512	..
	..	48 * 667	..	40 * 339	371 * 487	169 * 200	5 453	80 * 586	6 * 136	8 452
	..	48 * 147	160 (306)	175 339	423 *	169 232	132	2 80	45 * 136	174 452
	371 452
	*	339	306 * 580	175 * 268	155 423	169 * 232	..	446 586	119 * 175	..
	64 339	423 * 537	180 182	6 * 518	194 * 585	136 * 454	..
	196 641	175 * 454
	453 454

	339	434	..	454	339	434	..
	306 * (339)	224 * 339	11 * 434	34 * 175	(6 * 453)	5 200
	202 * 454	179 * 200
	11 * 175	(48)	196 * 339	64 * 224	23 (423)	..	6 * 454	(44 * 175)
	155 * 200	180 * 454	434 * 453	445	175 *	..
	11 * 339	200 224	23 * 537	..	(453)	454
	202 454	34 * 180
	(423)	..	453 454

DISTRIBUTION TABLE

	Is. of W. Indian Ocean	Mascarene Is.	E. Africa & Madagascar	Red Sea	S.E. Arabia	Persian Gulf
<i>cyclostomus</i> Leske 351	*	175 * 367	49 * 504	..	(456 *)	..
CLYPEASTERIDAE						
<i>Clypeaster amplificatus</i> Koehler	338 455
<i>eurypterus</i> H. L. Clark
<i>fervens</i> Koehler	455	..	455? *	141 *	456 *	..
<i>humilis</i> (Leske) ¹⁴ 351	65? * 171?	254 * 338	175 * 456	130 * 451
<i>ohshimensis</i> Ikeda
<i>rarispinus</i> de Meijere	158 * 171	254 * 566	456 *	451
<i>reticulatus</i> (Linnaeus) 354	34 * 175	367 * 432	65 * 505	5 * 254	327 * (456)	451 *
<i>telurus</i> H. L. Clark
ARACHNOIDIDAE						
<i>Arachnoides placenta</i> (Linnaeus) 354
<i>tenuis</i> H. L. Clark
FIBULARIIDAE						
<i>Echinocyamus australis</i> (Desmoulins) ¹⁵ 191	271?
<i>crispus</i> Mazetti ¹⁵	455	421 * (456)	(456) *	..
<i>incertus</i> H. L. Clark ¹⁵
<i>megapetalus</i> H. L. Clark	..	158?
<i>planissimus</i> H. L. Clark
<i>Fibularia acuta</i> Yoshiwara
<i>angulipora</i> Mortensen
<i>cribellum</i> de Meijere
<i>oblonga</i> Gray ¹⁵
<i>ovulum</i> Lamarck ¹⁶ 344	*	175 * (456)
<i>volva</i> L. Agassiz ¹⁵	5 12	*	..
LAGANIDAE						
<i>Laganum centrale</i> H. L. Clark
<i>decagonale</i> (de Blainville)
<i>depressum</i> Lesson	(175*)	367 * 432	5 * 455	148 * (456)
<i>joubini</i> (Koehler)	..	455 458	338 *	455
<i>laganum</i> (Leske) 351
<i>Peronella lesueurii</i> (Valenciennes) 10
<i>macroproctes</i> Koehler
<i>merguiensis</i> Koehler
<i>minuta</i> de Meijere
<i>oblonga</i> Mortensen
<i>orbicularis</i> (Leske) 351	158
<i>rubra</i> Döderlein
<i>tuberculata</i> Mortensen
SCUTELLIDAE						
<i>Astriclypeus manni</i> Verrill
<i>Echinodiscus auritus</i> Leske 351	..	367 * 432	65 * 200	10 * 560	456 *	130 * 451
<i>bisperforatus</i> Leske ¹⁷ 351	..	171?	5 * 385	175 * 254	*	*
<i>tenuissimus</i> (L. Agassiz)
ECHINOLAMPADIDAE						
<i>Echinolampas alexandri</i> de Loriol	(51 458)*	175 * 366	*	..
<i>ovata</i> (Leske) ¹⁸ 351	..	455	..	12 254

FOR ECHINOIDEA

W. India & Pakistan	Maldiv area	Ceylon area	Bay of Bengal	East Indies	North Australia	Philippine Is.	China & S. Japan	South Pacific Is.	Hawaiian Is.
..	51 * 338	37 * (306)	38 * 175	135 519	180 * 232	132 (457)	455 586	136 * 165	174
..
..	174
..	..	175 * 338	455	455	..	(457)	(175 458)
*	..	160 * 306	..	(6) * 423	34 * 182	6 * (457)	..	5 428	..
..	313	(455)?	..
(338) *	(338)	175 *	338	422 455
(338)	(338)	306 (338)	(338)	423 * 455	(175 *)	457 * 518	(175 *)	3 137	158 174
..	159 * 455
..	5 * 338	412 * 423	180 * 455	175 * 518	77 * 545	46 * 169	..
..	180 *
..	136 * 455	5 * 174
..	*	..	(338)	(423) 455	..	(457)	(175) * 455	..	(158)
..	(158) 455
..	137 * 455	455
..	180
..	455	..	(457)	664 666	136	..
..	455 458
..	..	338?	..	(422 455)	..	457
..	..	*?	..	455 458	271 * (435)	..	(*)?
..	175 * (338)	..	(338)	423 455	..	5 (457)	455	136 * 455	..
..	..	160?	41? (338)?	(423) 455	169 * 180	..	158? 540?	136?	..
..	175 *	..
343	5 338	55 * 423	6 * 455	158 (457)	412 * 445
..	(48 * 458)	196 * 306	224 338	10 * 423	179 * 232	457 * 518	(175) * 445	136 * 558	..
..
..	338?	10 * 455	175 * 182	5 * 457	..	158 338	..
(338)	338	(338)	64	175 * 458	180 * 435	158 (457)	77 * 455
..	..	(338)	..	455	..	(457)
..	338
..	..	455 458	423 457	570
..
..	175 *	23 * 423	180 * (235)	175 * (457)	5 * 455
..	455	(158 194)
..	180 * 435
..
..	455 * 567
175 * 343	..	160 * 306	41 338	371 (423)	180 435	5 518	285 455
..	..	37 *	338 * 412	200 * 455
..	12 537	180 200	132	2 455	175 * 428	..
..	..	165	338	423 455	136	..
..	..	165 * 267	(338) 455	5	175 * 180

DISTRIBUTION TABLE

	Is. of W. Indian Ocean	Mascarene Is.	E. Africa & Madagascar	Red Sea	S.E. Arabia	Persian Gulf
SPATANGIDAE						
<i>Marelia carinata</i> Bolau
<i>planulata</i> (Lamarck) 344	(51)	367 429	65 * 459	(456) * 558	(456) *	..
<i>Pseudomarelia alta</i> (A. Agassiz) ¹⁹	(51) * 175	367
PALAEOSTOMATIDAE						
<i>Palaeostoma mirabile</i> (Gray)	643 652
LOVENIIDAE ²⁰						
<i>Breynia australasiae</i> (Leach) ²¹ 349
<i>desori</i> Gray ²¹ 270
<i>vredenburgi</i> Anderson
<i>Lovenia doederleini</i> Mortensen
<i>elongata</i> (Gray)	49 * 459	15 * 254	175 * (456)	130 *
† <i>subcarinata</i> (Gray)	65
PERICOSMIDAE						
<i>Pericosmus melanostomus</i> Mortensen
SCHIZASTERIDAE						
<i>Diploporaster barbatus</i> Mortensen	459 642
<i>savignyi</i> (Fourtau) ²²	345 *	254 * 336
<i>Hypseleraster tjukesi</i> (Gray)
<i>Moira lethe</i> Mortensen
<i>stygia</i> Lütken	5	4 * 254
<i>Paraster gibberulus</i> (L. Agassiz) ²³	49 65	13 * 557
<i>Protenaster rostratus</i> (Smith) ²⁴
<i>Prymnaster investigatoris</i> Koehler	..	459
<i>Schizaster lacunosus</i> (Linnaeus) ²⁵ 354	(171) 459
BRISSIDAE						
<i>Brissopsis luzonica</i> (Gray) ²⁶	65 * 175	148 (* 456)
<i>persica</i> Mortensen	451 * 459
<i>Brissus latecarinatus</i> (Leske) 351	51 * 175	344 367	345*	175? * ?
<i>Metalia dicrana</i> H. L. Clark
† <i>latissima</i> H. L. Clark
<i>robillardii</i> (de Loriol)	..	366 367	(456 * 459)
<i>spatagus</i> (Linnaeus) 354	*	5 344	* 504	175 * 254	*	..
<i>sternalis</i> (Lamarck) 344	34 385	367 * 432	(456) * 507	254 *	..	*
† <i>townsendi</i> (Bell)	50 *	130 * 451
<i>Rhynobrissus hemiasteroides</i> A. Agassiz ²⁷
<i>macropetalus</i> H. L. Clark
<i>pyramidalis</i> A. Agassiz

FOR ECHINOIDEA

W. India & Pakistan	Maldiv area	Ceylon area	Bay of Bengal	East Indies	North Australia	Philippine Is.	China & S. Japan	South Pacific Is.	Hawaiian Is.
..	57 459	..
..	(48 * 175)	306	175 * 336	371 * 423	179 * 232	457	5 * 194	6 * 136	..
..	(48)	160 * 580	336	(423)	..	(457 459)	2 5
..	(336)	5 * (537)	..	270 (457)	(175 * 194)	*	..
..	232 * 459
..	435 459
..	14 459
..	202 642	..	(457)
..	48 (336)	196 * 306	336	23 423	180 * 617	5 (457)	80 * 585
..	64 336	175 * 459	..	(457) * 617	5 * 6
..	457 459	(457)
..
..
..	272 * 459
..	232 440
..	38 * 175	459
..	..	(306)
..	544?	..
..	336
..	(175 * 456)?	179 * 270	423	6 * (165)
(336)	(456 *)	..	(336)	423 459	(6 * 179)	270 (* 457)	(175 * 194)	5 * 336	(165)
..
..	175 667	175	..	412 423	175 * 459(?)	5 * 457	155 * 638	136 * 459	165 * 174
..	135	..	165 * 175	..	136 * 165	..
..	..	175 *
..
..	336
..	..	40	38 * 175	135 371	179 * 233	423 457	194 585	45 * 459	(165)
..	23 * 423	175 * 179	457	194 585	5 * 173	5 165
..
..	180 232	(6 587)	175 459
..	180 459
..	..	40 * 459	..	165 459	175 182	..	45

NOTES TO ECHINOID TABLE

- ¹ *Prionocidaris pistillaris*. The type-locality is Mauritius but Mortensen (1928) has designated some specimens from the Seychelles as neotypes, Lamarck's material having been lost.
- ² *Asthenosoma varium*. The precise type-locality is unknown but has been assumed to be in the 'East China Seas'; certainly the neighbouring Philippine area has yielded a number of records.
- ³ *Centrostephanus rogersi*. A. Agassiz (1863a) gives 'Port Jackson' as the type-locality, this being beyond the scope of the table. The inclusion of the species at all rests on one specimen from Port Denison, half-way up the Queensland coast, of which Mortensen (1940b) writes 'I do not venture to say that this specimen does not belong to *Rodgersii*'.
- ⁴ *Diadema setosum* and *savignyi*. Some of the records may be interchangeable—see Clark and Owen (1965).
- ⁵ *Microcyphus maculatus*. Mortensen (1943) notes that this is known with certainty only from Mauritius, other records being based on mistakes in identity or locality. The British Museum record is based on two worn dead tests from Dar-es-Salaam, both lacking the apical system, which appears to have been more or less elongated. It is possible that they are referable to *M. rousseaui*, though the colour of the test agrees with *maculatus*.
- ⁶ *Salmaciella erythracis* (H. L. Clark) is here considered to rank as a western subspecies of *S. dussumieri*, since the colour difference is so small.
- ⁷ *Temnopleurus alexandri*. Bell's type-material was from an unknown source but in 1888 he recorded additional specimens from the Torres Strait, which may well be regarded as the type-locality.
- ⁸ *Nudechinus gravieri*. Mortensen (1943) and H. L. Clark (1946) both comment that the latter's earlier identification of Australian specimens is a doubtful one.
- ⁹ *Nudechinus inconspicuum*. Mortensen (1943) doubts Australian sources for material of this species.
- ¹⁰ *Nudechinus multicolor*. Mortensen (1943) comments that until further material besides the type is available from Japan, the identification of material from other areas remains uncertain.
- ¹¹ *Pseudoboletia maculata*. Mortensen (1943) doubts the Australian locality.
- ¹² *Toxopneustes maculatus*. Lamarck (1816) gives '?L'océan indien' as type-locality and there are also specimens in the British Museum collections with locality 'Indian Ocean'. According to Mortensen's concept of the species (1948a) it is 'known with certainty only from Palmyra and Christmas Islands' (in the north central Pacific), which seems rather improbable as a source for Lamarck's material.
- ¹³ *Heterocentrotus trigonarius*. Lamarck (1816) gives '?La méditerranée' as type-locality. The Red Sea record from the British Museum collections is based on two specimens, one from the Cuming collection, the reliability of which is doubtful since Cuming himself collected only in the Pacific, while the second was received from the Zoological Society more than 100 years ago.
- ¹⁴ *Clypeaster humilis* (Leske). A proposal is before the International Commission on Zoological Nomenclature (A. M. Clark, 1964) for the recognition of Klein's figures C and D of plate 19 (1734) as lectotype; unfortunately no locality was given for the specimen on which the figures were based.
- Mortensen (1948a) doubts the identity of Brown's specimen (1910b) from Mozambique and H. L. Clark's (1923a) from Natal. The East African specimen in the British Museum record is a recently-collected one from Zanzibar.
- ¹⁵ *Echinocyamus australis*, *crispus*, *incertus* and *Fibularia oblonga*. Few reliable records of these species in life exist within our depth range but since dead tests are liable to be washed up into shallower water they are included here. As for *Fibularia volva*, no reliable records exist at all, owing to uncertainties in identification, notably confusion with *F. oblonga*; even from the Red Sea—the type-locality—no specimens have been recorded in the last hundred years.
- ¹⁶ *Fibularia ovulum* Lamarck has been validated as type-species of *Fibularia* by the International Commission (Opinion 207, 1954). Although the description given by Lamarck accords with the Indo-Pacific species, the locality he gives is 'la mer de Norvege'. A neotype of Indo-Pacific origin is here selected (Rowe, pp. 167-170).
- ¹⁷ *Echinodiscus bisperforatus*. The source of H. L. Clark's reference (1923a) to Mauritius as a locality for this species cannot be traced; nor can any other records from the Mascarene Islands. The specimens from New Caledonia in the British Museum collections recorded by H. L. Clark (1925b) came from the Cuming collection (the locality in this case is not in doubt); in my view they agree better with *E. tenuissimus*.
- ¹⁸ *Echinolampas ovata* (Leske). Kier (1962, *Smithson. misc. Coll.* 144[3]) has revived the name *oviformis* Gmelin, 1791 in place of *ovata*, since he considers *ovatus* Leske to be the type-species of *Echinanthus* and anyway of uncertain affinities. In order to avoid such an undesirable change of a well-known name, the International Commission has been asked to place the name *Echinolampas ovata* (Leske) on the Official List (A. M. Clark, 1964, *Bull. zool. Nom.* 21).
- ¹⁹ *Pseudomaretia interrupta* (Studer) has been recorded by H. L. Clark (1938) from about 10 metres near Broome, NW Australia, but only as a dead test, probably washed up from deeper water.
- ²⁰ *Echinocardium cordatum* (Pennant) was originally included in this table on the strength of the locality 'Flinders Island, Queensland' given by H. L. Clark (1925b and 1946) and quoted by Edean (1957). Unfortunately the specimen in the British Museum collections upon which this was based cannot now be found. In the absence of subsequent records from Queensland it seems better to omit *E. cordatum* from the table. The species is also known from Japan but again beyond the strict limits of the present work.
- ²¹ *Breyntia desori*. Although A. Agassiz (1872), followed notably by H. L. Clark (1946) referred *B. desori* to the synonymy of *B. australasiae* (Leach), in 1951 Mortensen restored it for specimens from west and north-west Australia, the type-locality of *B. desori* being 'Swan River' (Fremantle). At the same time he limited *B. australasiae* to material from the eastern side of Australia (Queensland to Lord Howe Island and the type-locality—Port Jackson). The characters used by Mortensen to distinguish the two include the shape and extent of the labrum (long and narrow in *desori*, extending posteriorly for about half the length of the third ambulacral plate on each side, as opposed to shorter in *australasiae*, not reaching beyond the second ambulacral plate), the number of subanal tube-feet or pore-pairs (eight each side in *desori* and only six in *australasiae*) and the number of primary aboral tubercles and spines, particularly in the anterior interambulacra (these being more numerous in *B.*

desori). There is also a colour difference which prompted H. L. Clark to note that the *Breyntia* found at Broome in NW Australia are much lighter in colour than those from the east coast.

Unfortunately the British Museum collections include only one specimen from Broome and none from Port Jackson or Swan River, Gray's holotype of *B. desori* being lost. However, there are eleven specimens from the Monte Bello Islands at the NW corner of Australia which would be expected to belong to *B. desori* if Mortensen is correct in his assumption about the geographical distribution. The test length of the eleven ranges from 38 to 64 mm. and the number of their aboral primary spines increases with size from three or four in each anterior interradius up to 14 or 15, whereas a Torres Strait specimen (of *australasiae*) equal in size to the largest still has only four such spines. The largest Monte Bello specimen has seven subanal tube-feet on one side and six on the other but a dry specimen with test length as much as 62 mm. has only four pore-pairs each side. Only one other out of the eleven has as many as seven pore-pairs (possibly even eight though it is broken in the subanal region and the exact number is uncertain); all the rest have only five or six. The evidence of the labrum is equally unsatisfactory in supporting Mortensen's contention since its shape and extent vary considerably, together with those of the adjoining ambulacral plates, to such an extent that in the same specimen the distal end of the labrum may lie some way along the third ambulacral on one side and no farther than the posterior part of the second ambulacral on the other; in fact several of these specimens show a marked asymmetry in this respect. Out of the eleven, six do run down to *B. desori* on the evidence of the labrum but two agree with *australasiae* and the remaining three are intermediate. The colour of the intact specimens is brownish, agreeing more with *australasiae*. The single Broome specimen is, however, not only paler in colour but does have eight subanal tube-feet each side and the labrum extends to the anterior end of the third ambulacral plate, agreeing throughout in these three characters with its identification as *B. desori*. Thus, if two species can be distinguished, their geographical distribution is not so clear-cut as Mortensen supposed.

Mortensen also suggested that his *Breyntia elegans* might be found off the north coast of Australia as well as in the East Indies, where the only depth records are 85 and 60 metres, the latter for a dead test. The two large specimens measured by Mortensen are very low, the test length being as much as 2.7 and 3.4 times the height. In the Monte Bello specimens the ratio varies from 1.9 to 2.3:1, which makes it improbable that they at least can be referred to *B. elegans*.

²² *Diploporaster savignyi*. Mortensen (1951) queries Lambert's record (1923) from Madagascar. However, the British Museum possesses two specimens from East Africa, one from Zanzibar, the other from Mombasa.

²³ *Schizaster koehleri* Lambert, 1923 has been provisionally referred to *Paraster* by Mortensen (1951). The species was based on a specimen from New Caledonia (depth not stated) identified as *P. gibberulus* by Koehler (1914). In view of the uncertain systematic position as well as the depth, the species is not included here.

²⁴ *Protaster rostrata*. The specimen in the British Museum collections currently labelled as the holotype is not Smith's type but is a *Brissoopsis*—almost certainly *B. lyrifera*. The substitution probably took place since 1923 when H. L. Clark catalogued the collections, since he would surely have noticed the discrepancy. The true holotype, of uncertain locality, cannot now be traced.

²⁵ *Schizaster lacunosus*. The Maldive records of H. L. Clark (1925b) and Mortensen (1948b) are queried because the latter is based on the John Murray Expedition specimens, which have four genital pores and so run down to *Paraster compactus*. The Gardiner specimen (the basis of Clark's record) is too small for positive identification in my opinion.

²⁶ *Brissoopsis luzonica* Gray. The holotype cannot now be traced in the British Museum collections.

²⁷ *Rhynobrissus*. Mortensen (1951) uses Agassiz's subsequent corrected spelling *Rhynobrissus* for this genus. However, according to the Code of Nomenclature (article 32a) 'incorrect transliteration (as in this case), improper latinization, etc., are not to be considered inadvertent errors', i.e. ones meriting correction. Accordingly, Agassiz's original spelling is the one used here.

KEY TO THE ECHINOIDEA

(Partly derived from Mortensen's Monograph)

- 1 Anus aboral in position, within the apical system, mouth in the centre of the oral surface; test usually circular in outline, sometimes oval; spines bristling and erect (pls. 23, 24) 'REGULARIA' 2
- 1' Anus posterior or on the oral side, lying interradially and not within the apical system; mouth either central or when the test is oval anterior; bilateral symmetry more or less evident; most of the spines somewhat appressed (pl. 25) 'IRREGULARIA' 74
- 2 Interambulacral plates high, each with a single massive primary spine, usually ringed by much smaller, often spatulate, secondary spines; the mature primary spines naked and often encrusted with epizoic organisms; ambulacral plates simple so that the pore-pairs form single vertical series, sometimes sinuous; peristome covered with both ambulacral and interambulacral series of overlapping plates but the main part of the test rigid (pl. 23, figs. 1, 2) CIDARIDAE 3
- 2' Interambulacral plates low, the ambital ones at least usually with several primary spines, which are rarely massive, the secondary spines not arranged in rings but scattered among the primaries; spines covered with very thin barely perceptible skin, which prevents the settling of encrusting organisms; ambulacral plates compound, three or more fused together and the pore-pairs correspondingly forming more or less staggered series, rarely a single one; peristome covered with soft skin, or if with plates then these are only ambulacral ones and the whole test is very flexible (pls. 23, figs. 3-7, 24) 12
- 3 Ambulacral pores non-conjugate (no furrow linking the two pores of each pair), a knob between the two pores in larger specimens; apical system bare but for a scattering of minute miliary spinelets and a marginal fringe of larger petaloid ones together with a small cluster on the periproct; the plates of the apical system covered with minute glassy bumps, visible on denuding; size not known to exceed 30 mm. h.d. (horizontal diameter) (pl. 31, fig. 13—pedicellariae) *Eucidaris metularia* (Lamarck, 1816) 4
- 3' Pores conjugate, sunk in a common furrow; apical system with a more or less dense covering of spinelets, or of tubercles visible when denuded; adult size usually considerably exceeding 30 mm. h.d. 4

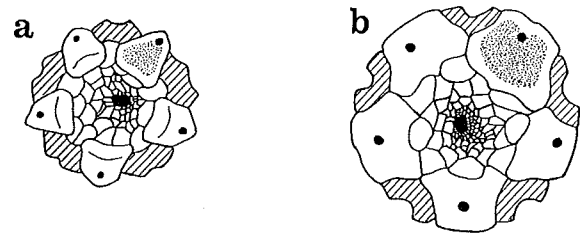


FIG. 59. Apical systems of: a. *Prionocidaris baculosa* with insert ocular plates (cross-hatched) and b. *Phyllacanthus imperialis* with exsert plates.

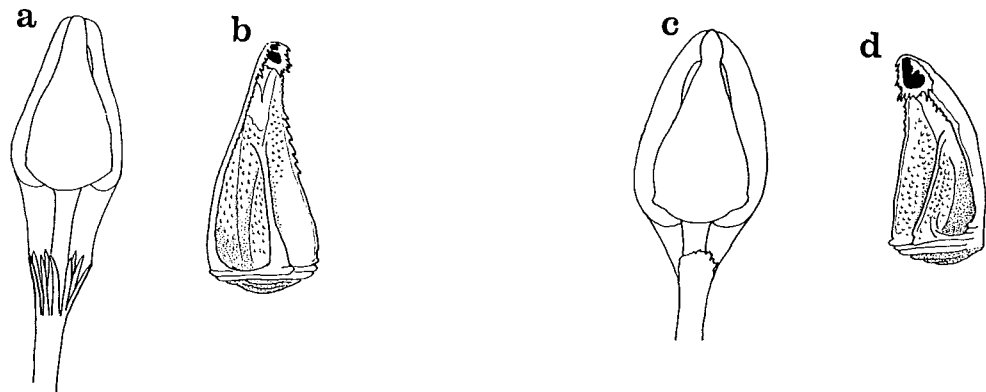


FIG. 60. Globiferous pedicellariae of: a. *Prionocidaris baculosa*, whole pedicellaria and b. single valve. c. *Phyllacanthus imperialis*, whole pedicellaria and d. single valve. (a from Döderlein, 1887, b-d. from Mortensen, 1928.)

- 4 In the apical system the ocular plates usually nearly all insert (fig. 59a); large globiferous pedicellariae usually with a 'limb' or frill of rods on the stalk close to the head (fig. 60a) PRIONOCIDARIS 5
- 4' All the oculars usually exsert (fig. 59b); no limb on the stalk of the globiferous pedicellariae 8

- 5 Primary spines distinctly verticillate, with three or four spaced complete thorny whorls along their lengths (fig. 61a) *Prionocidaris verticillata* (Lamarck, 1816)¹
- 5' Primary spines cylindrical or tapering, sometimes with a terminal 'crown' or with longitudinal series of thorns (fig. 61c) rarely (some specimens of *P. baculosa*) with thorns arranged in distinct whorls but in this case the whorls number six to ten on each spine, the adoral side of which is flattened so that the whorls are incomplete (fig. 61b) 6

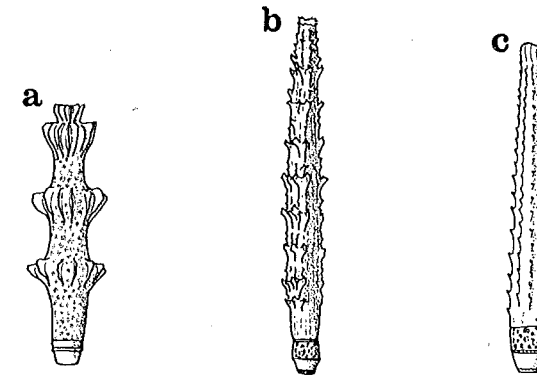


FIG. 61. Primary spines of: a. *Prionocidaris verticillata*, b. *P. baculosa*, semi-verticillate spine and c. more usual spine with smaller thorns in longitudinal series.

- 6 Collar of primary spines without spots or stripes. *Prionocidaris bispinosa* (Lamarck, 1816)
- 6' Purple stripes or spots on the collar 7
- 7 Collar striped *Prionocidaris pistillaris* (Lamarck, 1816)
- 7' Collar spotted (fig. 61b, c; pl. 23, fig. 1; pl. 31, fig. 14—pedicellariae) *Prionocidaris baculosa* (Lamarck, 1816)
- 8 Primary spines with coarse thorns; pores on the peristomial plates continuing in single series *Chondrocidaris brevispina* (H. L. Clark, 1925b)
- 8' Primary spines smooth; peristomial pores zig-zagging to form double series 9
- 9 Primary spines each with about twelve fine longitudinal ridges; peristome not much larger than apical area, its diameter about 40% of the h.d., at least when the latter is c. 60 mm. (as in the holotype); only 17 or 18 ambulacral plates in each series at this size but seven or eight interambulacral *Phyllacanthus forcipulatus* Mortensen, 1936
- 9' Primary spines with 18 or more very fine longitudinal ridges or series of granules; peristome 44-56% of the h.d. when this is 40-65 mm., the apical area usually distinctly smaller; 18-26 ambulacral plates but not more than seven interambulacral 10
- 10 Apical area 35-40% of the h.d. when this is 40-65 mm.; rarely more than six interambulacral plates at this size range; oral primary spines not at all clavate *Phyllacanthus dubius* Brandt, 1835
- 10' Apical area 29-34% of the h.d.; six to seven interambulacral plates; oral primary spines more or less clavate 11
- 11 Primary spines usually exceeding the h.d. in length by nearly a third and their shape slender and slightly tapering; genital pores situated on elevations on the plates *Phyllacanthus longispinus* Mortensen, 1918
- 11' Primary spines usually about equal to the h.d., rarely longer, except in small specimens, h.d. < c.30 mm., spines fusiform in shape; genital pores not elevated (pl. 23, fig. 2) *Phyllacanthus imperialis* (Lamarck, 1816)
- 12 Test very flexible, in life more or less hemispherical in shape but usually collapsing into a flat pancake on preservation; ambulacral plates continuing over the peristome to the mouth ECHINOTHURIIDAE 13

¹ Mortensen (1928) includes *Prionocidaris verticillata* in a separate genus *Plococidaris* established by him in 1909 (Deutschen Südpolar-Expedition) for this species together with *Cidarites bispinosa* Lamarck, the latter being designated as type-species in 1909. However, in 1928 Mortensen followed Döderlein and H. L. Clark in referring *bispinosa* to *Prionocidaris* A. Agassiz, 1863. Thus *Plococidaris* becomes a synonym of *Prionocidaris*, Mortensen's retention of the name with *verticillata* as re-designated type-species being contrary to the Rules of Nomenclature. H. L. Clark (1946) pointed this out but noted that it is superfluous if *verticillata* itself is regarded as being congeneric with *Prionocidaris pistillaris* (Lamarck), the type-species of *Prionocidaris*, which was his considered opinion. Since *Prionocidaris baculosa* often has verticillate primary spines approximating in form to those of *verticillata* (fig. 61b), there are only minor characters of little taxonomic weight to separate *verticillata* from the species of *Prionocidaris*, for instance the indistinctly conjugate pore-pairs, the fewer plates in the periproct, which is not raised into a cone, and the conspicuously green mottled colour of the test. None of these appear to warrant a generic distinction and accordingly *verticillata* is here included in *Prionocidaris*.

- 12' Test rigid, rarely somewhat flexible but then undergoing little if any flattening when preserved; peristome skin-covered 14
- 13 Only a few more aboral interambulacral plates than oral ones; tridentate pedicellariae probably all with narrow valves; madreporic pores extending on to the adjacent plates of the apical system besides genital II in larger specimens (diameter >c.120 mm.) *Asthenosoma intermedium* H. L. Clark, 1938
- 13' More than twice as many aboral as oral interambulacral plates; some or most tridentate pedicellariae with short broad valves; madreporic pores not extending beyond genital II² *Asthenosoma varium* Grube, 1868b
- 14 Primary tubercles perforate and often also crenulate (fig. 62a); spines usually hollow, long, cylindrical and very slender and breakable (in *Astropyga* and *Chaetodiadema* the cavity of each spine is filled with loose meshwork) **DIADEMATIDAE** 15

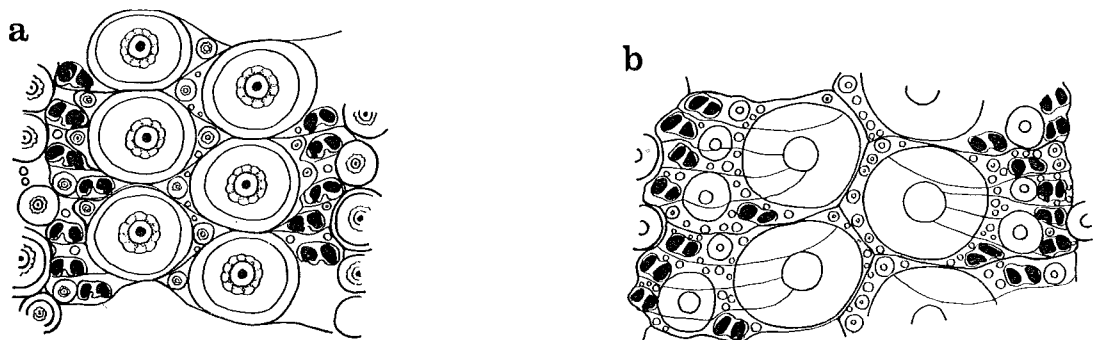


FIG. 62. Tubercles of: a. *Diadema setosum* and b. *Echinometra mathaei*.

- 14' Primary tubercles imperforate (fig. 62b), though sometimes crenulate; spines solid 23
- 15 Tubercles not crenulate; spines smooth *Lissodiadema lorioli* Mortensen, 1903
- 15' Tubercles crenulate; spines with a finely thorny or ridged surface 16
- 16 Primary tubercles of oral side abruptly reduced in size from close below the ambitus and pore-pairs correspondingly becoming widely spaced into a single almost straight series without arcs; test somewhat flexible *Chaetodiadema granulatum* Mortensen, 1903
- 16' Primary tubercles as well-developed on the oral side as at the ambitus and aborally; pore-pairs arranged in arcs throughout; test rigid except in wet specimens of *Astropyga* which are slightly flexible. 17
- 17 Genital plates conspicuously elongated into the interambulacra between the aborally bulging ambulacra (fig. 63a), except in immature specimens, h.d. < c.60 mm.; periproct flat or low conical; adult size very large, up to 180 mm. h.d. (pl. 23, fig. 3) *Astropyga radiata* (Leske, 1778)

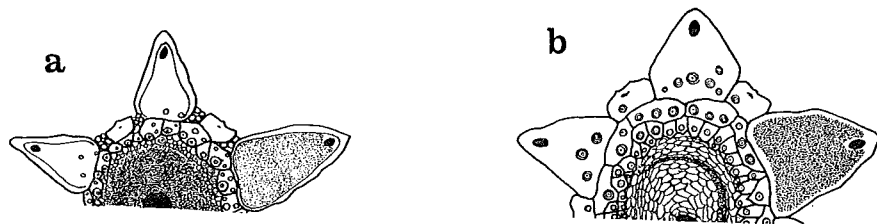


FIG. 63. Parts of apical systems of: a. *Astropyga radiata* and b. *Echinothrix calamaris*. (Both from Mortensen, 1940b.)

- 17' Genital plates not longer than wide; if the ambulacra bulge conspicuously aborally then the slender primary ambulacral spines are distinctly barbed terminally, not smooth; periproct often with a tubular extension; size up to 130 mm. h.d. (*Echinothrix*) or 100 mm. (*Diadema* and *Centrostephanus*) 18
- 18 Ambulacral spines of the aboral side very fine and needle-like, with backwardly-directed barbs near the tip, contrasting with the other spines (fig. 64a) **ECHINOTHRIX** 19
- 18' Aboral spines not dissimilar, the barbs on the ambulacral ones not directed backwards (fig. 64b) 20

² *Chaetodiadema granulatum* may run down here since its test can collapse rather like that of an Echinothuriid. It is distinguished by the conspicuous series of dark spots parallel to the ambulacra on the aboral side and the abruptly smaller and much more numerous spines of the proximal two-thirds of the oral side, apart from the skin-covered peristome.

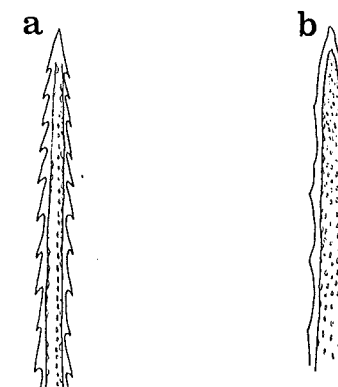


FIG. 64. Tips of aboral ambulacral spines of: a. *Echinothrix diadema* and b. *Diadema setosum*. (Both from Mortensen, 1940b.)

- 19 Ambulacra distinctly bulging aborally, with naked interambulacral areas between them apically; cavity of primary spines large, externally the spines with transverse series of thorns, though longitudinal ridging may also be more or less evident; naked test aborally usually greenish in colour (pl. 31, fig. 17—pedicellariae) *Echinothrix calamaris* (Pallas, 1774)
- 19' Ambulacra not distinctly bulging and no naked interambulacral areas aborally; cavity of primary spines very small, their surfaces with fine longitudinal ridges only; no green colour on the naked test aborally (pl. 24, fig. 2) *Echinothrix diadema* (Linnaeus, 1758)
- 20 Spines present on the buccal plates embedded in the peristome; globiferous pedicellariae present *Centrostephanus rodgersi* (A. Agassiz, 1863a)
- 20' No spines on the buccal plates; no globiferous pedicellariae. **DIADEMA** 21
- 21 Large tridentate pedicellariae mostly with narrow blades only meeting at the tip, the ratio of total length of the valve to breadth of the blade (measured at about the middle of the length) c.20:1 (unfortunately these pedicellariae are never numerous and sometimes lacking); a red ring around the anus (pl. 24, fig. 1) *Diadema setosum* (Leske, 1778)
- 21' Large tridentate pedicellariae with wider valves, more rounded at the tip, length:breadth less than 10:1, usually 4-8:1; no anal red ring 22
- 22 Tridentate pedicellariae hollow spatulate, fairly narrow but widening slightly to a rounded tip, length:breadth of blade 7.7:1 (in the one figured by Mortensen); 12-14 interambulacral plates in each series when the h.d. is 50-60 mm. *Diadema paucispinum* A. Agassiz, 1863b
- 22' Tridentate pedicellariae leaf- or spoon-shaped, tapering slightly to a rounded distal end, length:breadth 3.6-5.1:1 (in the four figured by Mortensen); 14-16 (or 17) interambulacral plates at h.d. c. 50 mm. and the total number of spines correspondingly greater *Diadema savignyi*: Michelin, 1845

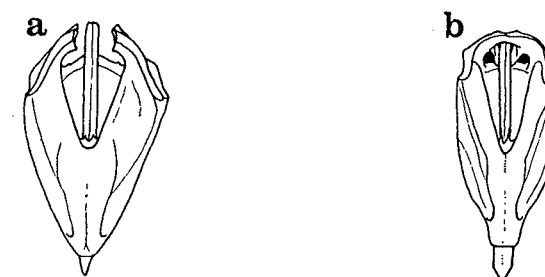


FIG. 65. Pyramids from Aristotle's lantern of: a. *Stomopneustes variolaris*, without complete bridge and b. *Tripneustes gratilla*.

- 23 No complete bridge across the V-shaped space at the upper end of each of the five pyramids forming the frame of the Aristotle's lantern (fig. 65a); ambulacral plates doubly compound so that at the ambitus one very large ambulacral tubercle corresponds to three to six arcs of three pore-pairs (fig. 66; pl. 23, fig. 6) *Stomopneustes variolaris* (Lamarck, 1816)
- 23' Paired rod-like epiphyses bridging across the splayed upper ends of the pyramids (fig. 65b); ambital ambulacral plates either with primary tubercles of small or moderate size corresponding to each arc of pore-pairs or else some arcs with no tubercle alongside 24

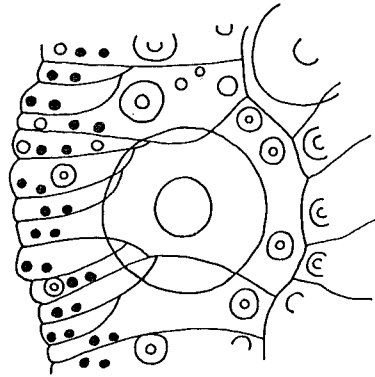


FIG. 66. Doubly compound ambulacral plates of *Stomopneustes variolaris*. (From Mortensen, 1935.)

- 24 Tubercles usually crenulate; test usually with distinct pits, troughs or pores at the angles of the sutures, or the plates more extensively sculptured (fig. 67)³ **TEMNOLEURIDAE** 25
- 24' Tubercles not crenulate; no angular pits or pores³ 46
- 25 Conspicuous pits or troughs at the angles of the sutures, usually extending horizontally, sculpturing sometimes extending over the entire surface of the plates (fig. 67a, c) 26

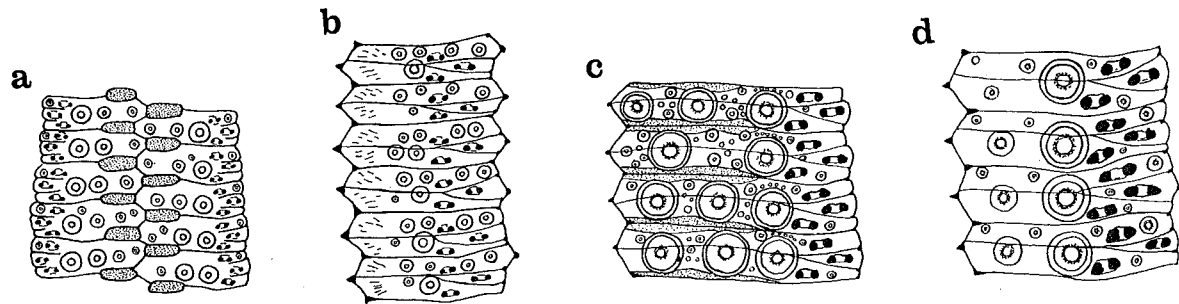


FIG. 67. Ambulacral plates of: a. *Temnotrema bothryoides*, b. *Mespilia globulus*, c. *Temnopleurus alexandri* and d. *Salmacis bicolor*. (All from Mortensen, 1943.)

- 25' Angular pores present only (fig. 67b, d), sometimes inconspicuous or even lacking 36
- 26 Only five buccal plates present with their corresponding tube feet **Paratrema doederleini** (Mortensen, 1904) 27
- 26' Ten buccal plates and ten buccal tube feet. 27
- 27 Crenulation conspicuous; size often exceeding 40 mm. h.d. (except in *T. decipiens*); pore-pairs more or less distinctly in arcs of three (fig. 67c)⁴ **TEMNOLEURUS** 28
- 27' Crenulation hardly, if at all, distinct; h.d. rarely exceeding 20 mm. (except in *T. bothryoides*, the holotype of which has twice this diameter); pore-pairs usually in a straight or slightly sinuous series, sometimes (*bothryoides* and *elegans*) biserial, one out of every three pore-pairs being offset to form a second line (fig. 67a) **TEMNOTREMA** 31
- 28 Anal opening near the centre of the periproct; no distinct enlarged suranal plate 29
- 28' Anal opening very excentric, a suranal plate usually enlarged opposite to it among the other periproctal plates (fig. 68a) 30
- 29 Spines, at least on the oral side, banded white with green, brown or reddish (pl. 24, fig. 3) **Temnopleurus toreumaticus** (Leske, 1778)

³ This distinction is rather unsatisfactory since both characters may not be evident in the genus *Microcyphus*, which comes within the scope of this work. It is otherwise distinguished by the naked pigmented areas around the interradial and horizontal sutures of the interambulacral plates aborally, contrasting with the light-coloured tubercles to form beautiful colour patterns on the cleaned tests (pl. 24, fig. 6).

⁴ *Salmacis* may also run down here and conversely *Temnopleurus* to no. 43; the two are very close. *T. toreumaticus* may be distinguished from *S. bicolor* most reliably by the pair of lateral teeth on the valves of the globiferous pedicellariae, as opposed to no lateral teeth in the larger globiferous pedicellariae of *S. bicolor*, or only a single tooth in the smaller ones. There is also a difference in the relative length of the spines, the longest of which are about equal to the h.d. in *Temnopleurus*, whereas in *Salmacis* they are much shorter.

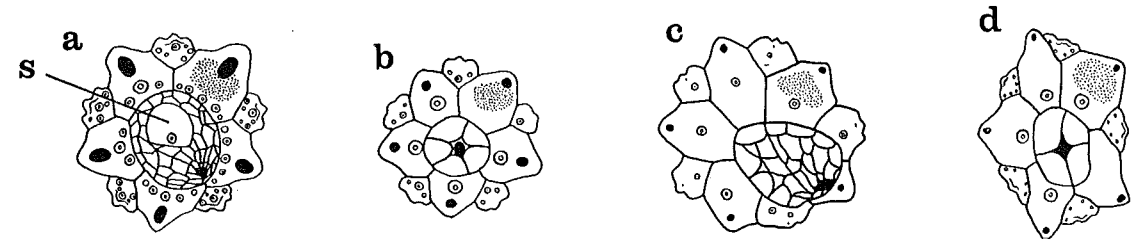


FIG. 68. Apical systems of: a. *Temnopleurus reevesi*, paratype, s—suranal plate, b. *Nudechinus stictus*, c. *Gymnechinus pulchellus* and d. *Parasalenia gratiosa*. (c-d from Mortensen, 1943.)

- 29' Spines not banded but often greenish basally becoming purple distally, or else uniform in colour, green, purple or white **Temnopleurus alexandri** (Bell, 1884)
- 30 Spines banded with reddish-brown; test dark olive in colour; only known at a small size, h.d. < 10 mm. **Temnopleurus decipiens** (de Meijere, 1904)
- 30' Spines not banded, usually pale greenish-brown; size often exceeding 30 mm. h.d. **Temnopleurus reevesi** (Gray, 1855)
- 31 Globiferous pedicellariae with a pair of lateral teeth on each valve 32
- 31' No distinct lateral teeth on the globiferous pedicellariae 33
- 32 Test olive-green, spines with intense scarlet bands; known from north Australia and the Aru Islands **Temnotrema bothryoides** (L. Agassiz in Agassiz & Désor, 1846)
- 32' Test greenish-white, pore zones pinkish; spines banded with reddish-violet; Western Australia **Temnotrema elegans** Mortensen, 1918
- 33 Horizontal series of larger tubercles present on the ambital interambulacral plates; genital plates with a transverse line marking off their distal ends; test whitish **Temnotrema maculatum** (Mortensen, 1904)
- 33' No horizontal series of tubercles; no transverse line on genital plates; test coloured or patterned with green or reddish 34
- 34 Spines usually with narrow greenish or brownish bands **Temnotrema siamense** (Mortensen, 1904)
- 34' Spines not banded though with dark bases and lighter tips 35
- 35 Test greenish, lighter in the interambulacra aborally; spines light grey-green basally **Temnotrema hawaiiense** (A. Agassiz & H. L. Clark, 1907)
- 35' Test reddish-purple, purple in the interambulacra aborally; spines bright red basally **Temnotrema phoinissa** H. L. Clark, 1926b
- 36 Only one in every two or three ambital and aboral ambulacral plates with a primary tubercle **SALMACIELLA** 37
- 36' Each ambital and aboral ambulacral plate with a primary tubercle 38
- 37 Ambital and oral primary spines banded with purple; secondary spines white or greenish, rarely reddish and then at the base only. (Unknown westwards of Ceylon) **Salmaciella dussumieri dussumieri** (L. Agassiz in Agassiz & Désor, 1846)
- 37' Ambital and oral primary spines banded green and whitish (rarely the oral ones with purple bands), secondary spines bright vermilion, at least basally. (Western part of the Indian Ocean) **Salmaciella dussumieri erythracis** (H. L. Clark, 1912)
- 38 Ten conspicuous abruptly spineless vertical areas on the test covered with extremely numerous globiferous pedicellariae, forming a dense carpet, their valves with wide blades bearing two or three lateral teeth each side, the underlying parts of the plates very finely textured with light-coloured striations radiating from the direction of the tubercles on the other end of the plate (fig. 67b; pl. 24, fig. 5) **Mespilia globulus** (Linnaeus, 1758)
- 38' Globiferous pedicellariae less conspicuously developed, the blade fairly narrow and bearing not more than one lateral tooth each side; if bare areas are present aborally then these do not have a textured surface 39
- 39 Tubercles indistinctly crenulate; sutural pores very small and inconspicuous; naked areas conspicuous aborally (pl. 24, fig. 6) **MICROCYPHUS** 40
- 39' Tubercles distinctly crenulate; pores distinct; no extensive bare areas on the test (pl. 24, fig. 4) **SALMACIS** 43
- 40 Apical system elongate (at least in the single specimen known) **Microcyphus excentricus** Mortensen, 1940b
- 40' Apical system rounded 41
- 41 Test reddish, spines green **Microcyphus maculatus** L. Agassiz in Agassiz & Désor, 1846
- 41' Test either patterned with dark purple or with olive green; spines reddish-brown and white or purple and white 42

- 42 Naked aboral areas of test dark purple; spines reddish-brown with pale tip or banded purple and white (forma *purpuratus*) (pl. 24, fig. 6) . . . *Microcyphus rousseaui* L. Agassiz in Agassiz & Désor, 1846
- 42' Test patterned with olive-green; spines banded with reddish-brown and white . . . *Microcyphus ceylanicus* Mortensen, 1942 (and 1943)
- 43 Primary spines not banded . . . *Salmacis virgulata* L. Agassiz in Agassiz & Désor, 1846
- 43' Primary spines more or less conspicuously banded . . . 44
- 44 Globiferous pedicellariae all with a lateral tooth each side . . . *Salmacis sphaeroides* (Linnaeus, 1758)
- 44' Globiferous pedicellariae with only an unpaired lateral tooth, if any (pl. 31, fig. 18) . . . 45
- 45 Base of spines red (pl. 24, fig. 4) . . . *Salmacis bicolor* L. Agassiz in Agassiz & Désor, 1846
- 45' Base of spines green . . . *Salmacis belli* Döderlein, 1902
- 46 Gill slits sharp and deep (fig. 69a); test circular or pentagonal, as viewed from above **TOXOPNEUSTIDAE** 47

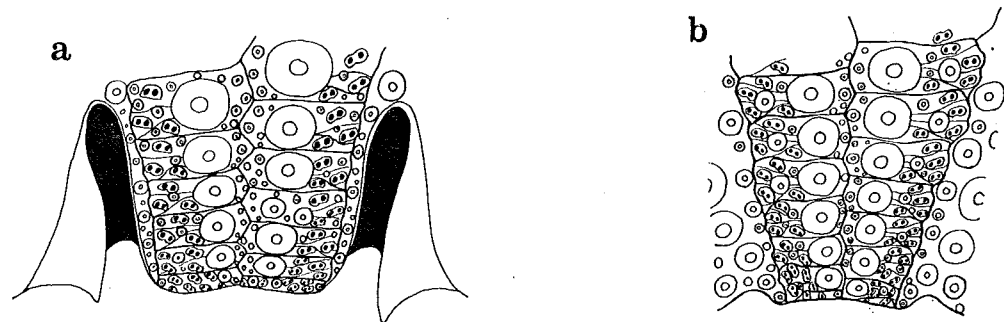


FIG. 69. Gill slits of: a. *Toxopneustes pileolus* and b. *Echinometra mathaei*.

- 46' Gill slits shallow (fig. 69b); test often more or less ovate (fig. 71) . . . Order ECHINOIDA 62
- 47 Ambulacral plates polyporous (i.e. with more than three pore-pairs) . . . **PSEUDOBOLETIA** 48
- 47' Ambulacral plates oligoporous (with three pore-pairs each) . . . 49
- 48 Test uniform in colour, no dark spots . . . *Pseudoboletia indiana* (Michelin, 1862)
- 48' Test with dark spots . . . *Pseudoboletia maculata* Tröschel, 1869
- 49 Only one out of every two or four ambulacral plates with a primary tubercle . . . 50
- 49' Each ambulacral plate with a primary tubercle . . . 52
- 50 Globiferous pedicellariae not enlarged but inconspicuous; only one in three or four ambulacral plates with a primary tubercle; test high, almost globular; pore-pairs in horizontal arcs and spaced to form three distinct vertical series in larger specimens (the h.d. may exceed 100 mm.); preserved material often with a conspicuous dark vertical stripe down each interambulacrum contrasting with the light ambulacral areas and white spines (pl. 24, fig. 8; pl. 31, fig. 16—pedicellariae) . . . *Tripneustes gratilla* (Linnaeus, 1758)
- 50' Globiferous pedicellariae very large and conspicuous, reaching a span of c.3 mm. when gaping open (pl. 24, fig. 7; pl. 31, fig. 15 (pt.)); every second ambulacral plate with a primary tubercle; test low; pore arcs shallow but not obviously forming three spaced vertical series; preserved specimens with only horizontal markings evident, if any . . . **TOXOPNEUSTES** 51
- 51 Gill-slits rather long; test usually sunken towards the mouth; test usually marked with up to six undulating horizontal purple and light bands; geographical range extensive (pl. 24, fig. 7; pl. 31, fig. 15—pedicellariae) . . . *Toxopneustes pileolus* (Lamarck, 1816)
- 51' Gill-slits small; oral surface of test flat; test with only an ambital band of purple besides an aboral blotch or band of colour; known only from Palmyra and Christmas Islands in the central Pacific . . . *Toxopneustes maculatus* (Lamarck, 1816)
- 52 Peristome with some additional plates in the buccal membrane besides the five pairs of buccal plates . . . *Cyrtacanthus verruculatus* (Lütken, 1864)
- 52' Peristome with few if any plates besides the buccal ones . . . 53
- 53 Apical system markedly excentric (fig. 68c) . . . **GYMNECHINUS** 54
- 53' Apical system not excentric (fig. 68b) . . . **NUDECHINUS** 56
- 54 Test and primary spines white or pale yellow . . . *Gymnechinus robillardii* (de Loriol, 1883)
- 54' Spines red, purple or orange, only white at the tips; test usually with coloured markings though sometimes almost uniformly white . . . 55
- 55 Spines mainly dull purple or orange; secondary tubercles well developed so as to form horizontal series on at least the ambital interambulacral plates . . . *Gymnechinus epistichus* H. L. Clark, 1912
- 55' Spines mainly bright purple or red; secondary tubercles rarely so well developed as to form horizontal series . . . *Gymnechinus pulchellus* Mortensen, 1904

- 56 Denuded test radially striped, rarely spotted . . . 57
- 56' Test not striped but either spotted or uniformly greenish . . . 58
- 57 A series of dark spots in the skin (but not on the underlying test) down the middle of each ambulacrum and interambulacrum; valves of tridentate pedicellariae broad, spoon-shaped, the minimum breadth at the 'waist' more than half the maximum breadth of the distal half (at least in the valve figured by Mortensen in 1943); globiferous pedicellariae with stalk glands . . . *Nudechinus darnleyensis* (Tenison Woods, 1878)
- 57' No spots in the skin; valves of tridentate pedicellariae strongly constricted in the middle, the minimum breadth only about a third of the distal maximum (in Mortensen's figure of 1904); stalk glands not observed for the globiferous pedicellariae . . . *Nudechinus inconspicuus* (Mortensen, 1904)
- 58 Primary spines with red or pink bands . . . *Nudechinus gravieri* (Koehler, 1905b)
- 58' Spines banded with greenish or purple or brownish bands, if at all . . . 59
- 59 Test with purplish spots . . . *Nudechinus stictus* H. L. Clark, 1912
- 59' Test green or spotted with green . . . 60
- 60 Spines with purplish-violet bands . . . *Nudechinus multicolor* (Yoshiwara, 1898)
- 60' Spines either uniformly purplish, or banded with other colours, or dark green basally paling distally . . . 61
- 61 Spines dark green basally distally paler or banded with green (rarely with brown) . . . *Nudechinus scotiopremnus* H. L. Clark, 1912
- 61' Bases of spines not dark green, though there may be greenish or brownish banding, alternatively (in forma *purpurascens*) the spines purplish and not banded . . . *Nudechinus ambonensis* Mortensen, 1942 (and 1943)

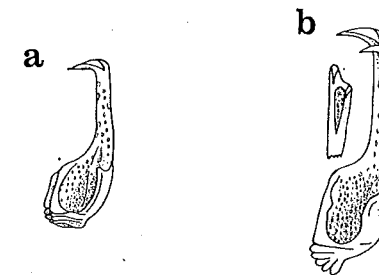


FIG. 70. Globiferous pedicellariae of: a. *Parasalenia gratiosa* and b. *Echinometra mathaei*. (Both from Mortensen, 1943.)

- 62 Shape always markedly elongated; periproct with only four (three to five) plates (fig. 68d); globiferous pedicellariae with no lateral teeth (fig. 70a); size small, h.d. rarely > 30 mm., usually much less . . . **PARASALENIIDAE** 63
- 62' Shape either circular or more or less ovate; periproct with multiple plates; globiferous pedicellariae with an unpaired lateral tooth (fig. 70b); h.d. often > 40 mm. . . **ECHINOSTREPHUS** 64
- 63 Length of primary spines about equal to the maximum h.d. of the test (at least in adults, h.d. > 10 mm.); spines usually uniformly dark-coloured in adults though with a tendency for banding in immature specimens . . . *Parasalenia gratiosa* A. Agassiz, 1863b
- 63' Primary spines only about half as long as the test, distinctly banded with red and white . . . *Parasalenia poehli* Pfeffer, 1887
- 64 Test high, maximum h.d. near the aboral side, which is almost flat; only three or four pore-pairs in each arc; longest spines projecting vertically in an aboral tuft; inhabits deep burrows **ECHINOSTREPHUS** 65
- 64' Maximum h.d. of test at about half the total height or below; test arched aborally; four to sixteen pore-pairs in each arc; longest spines projecting horizontally or only diagonally upwards; lives exposed or in shallow hollows . . . 66
- 65 Three pore-pairs in each arc . . . *Echinostrephus molaris* (de Blainville, 1825)
- 65' Four pore-pairs in all but the adoralmost arcs . . . *Echinostrephus aciculatus* A. Agassiz, 1863b
- 66 Test round, though the spines sometimes shorter on one side . . . *Anthocidaris crassispinata* (A. Agassiz, 1863a)
- 66' Test usually oval . . . 67
- 67 Long axis of the test through ambulacrum I and interambulacrum 3 (fig. 71a); spines slender and acute, all circular in cross section; usually only four pore-pairs per arc aborally (pl. 23, fig. 5; pl. 31, fig. 19—pedicellariae) . . . *Echinometra mathaei* (de Blainville, 1825)
- 67' Long axis though ambulacrum II and interambulacrum 4 (fig. 71b); primary spines often massive and either very long or truncated and very short, but even if they are slender then the lower ones are more or less flattened and some are angular in cross section; eight or more pore-pairs per arc aborally (pl. 23, figs. 4, 7) . . . 68

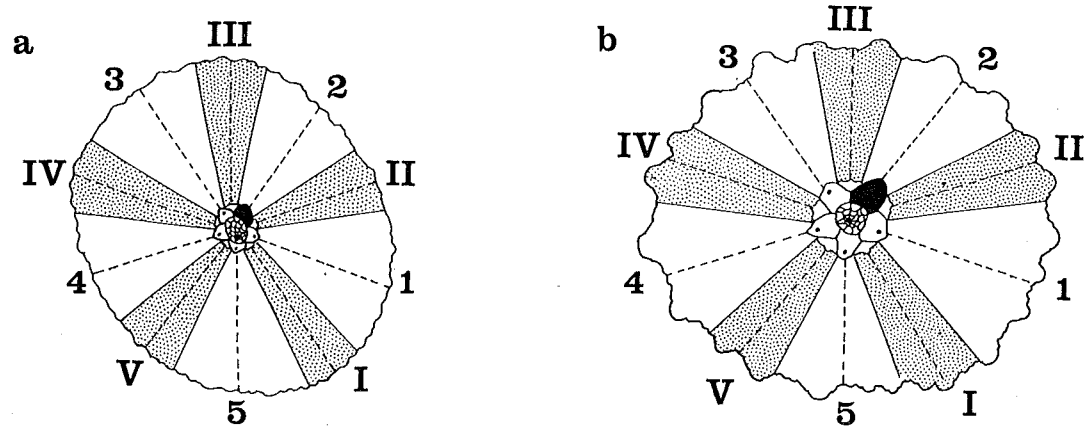


FIG. 71. Orientation of long axis of test in: a. *Echinometra mathaei* and b. *Heterocentrotus mammillatus*.

- 68 The aboral spines all extremely short, similar in length and more or less angular in cross section, often forming a compact mosaic; a single row of short spatulate spines projecting from the ambitus to form a ventro-lateral fringe; the external shape smooth and somewhat limpet-like, adapted for life on surf-beaten shores. **COLOBOCENTROTUS** 69
- 68' The aboral spines very long and radiating laterally, not restricted to a single row, the aboral spines somewhat shorter and fewer but similar in shape to the ambital ones and not forming a mosaic 71
- 69 Aboral spines numerous and short but much less wide than the spines of the marginal fringe and not so angular in cross-section or so closely-fitting as to form a mosaic **Colobocentrotus mertensi** Brandt, 1835
- 69' Aboral spines fewer and larger, their diameter not much less than that of the marginal spines and their cross-section markedly angular so that their truncated distal ends form a smooth continuous mosaic pavement over the convex aboral side, flaring out ventrally to the marginal fringe of spines 70
- 70 Marginal spines with flattened chisel-like tips, forming a continuous fringe; colour usually olive-green aborally **Colobocentrotus pedifer** (de Blainville, 1825)
- 70' Marginal spines with rounded, often swollen, tips, some of them spaced from each other so that the fringe is discontinuous; colour usually dark purple aborally (pl. 23, fig. 7) **Colobocentrotus atratus** (Linnaeus, 1758)
- 71 Primary spines massive, all either rounded and very thick but somewhat flattened towards the tip, or triangular in cross section and slightly tapering ('slate-pencil urchins') **HETEROCENTROTUS** 72
- 71' Primary spines strong and the ventro-lateral ones fairly stout and flattened or angular, but the aboral spines more or less slender **ZENOCENTROTUS** 73
- 72 Usually 9-11 pore-pairs in each arc at the ambital region; primary ambulacral tubercles rather abruptly smaller above the ambitus and their spines truncated like the secondary spines; tridentate pedicellariae with narrow valves, meeting only at the tip (pl. 23, fig. 4) **Heterocentrotus mammillatus** (Linnaeus, 1758)
- 72' Usually 15-16 pore-pairs in each arc in the ambital region; primary ambulacral tubercles gradually decreasing in size aborally and their spines correspondingly only gradually shorter and not truncated; tridentate pedicellariae with leaf-shaped valves, contiguous for their whole lengths **Heterocentrotus trigonarius** (Lamarck, 1816)
- 73 Pore-pairs 'staggered' in arrangement aborally, so as to form double arcs, one within the other; pore zones of the oral side broadened in the middle to form a distinctly petaloid shape; buccal membrane with some small spine-bearing plates **Zenocentrotus kellersi** A. H. Clark, 1931
- 73' Pore-pairs hardly at all staggered, forming single though slightly irregular arcs, at most only a partial secondary arc made up of but two or three pore-pairs; pore zones of the oral side not conspicuously widened in the middle; no spines on the buccal membrane **Zenocentrotus paradoxus** A. H. Clark, 1931
- 74 Ambulacra simple, each consisting of two columns of similar plates with pore-pairs in two more or less parallel vertical series running from apical system to peristome. **ECHINONEIDAE** 75
- 74' Ambulacra expanded aborally to form five petals delimited by enlarged pore-pairs, the petals usually stopping short of the ambitus, though inconspicuous pores can be discovered near and below the ambitus (see pl. 25) 76
- 75 Primary tubercles perforate (fig. 72a) **Echinoneus abnormalis** de Loriol, 1883
- 75' Primary tubercles imperforate (fig. 72b) **Echinoneus cyclostomus** Leske, 1778
- 76 Lantern and teeth present throughout life; test usually more or less flattened with a low, sometimes acute, margin, rarely (in the small Fibulariidae where the length rarely exceeds 10 mm.) the test ovate (pl. 25, figs. 1-10) **Order CLYPEASTEROIDA** 77

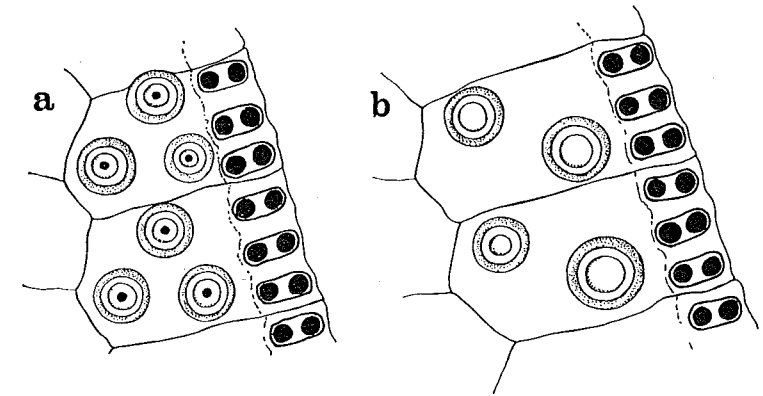


FIG. 72. Primary tubercles of: a. *Echinoneus abnormalis* and b. *E. cyclostomus*; the texture of the plates not shown.

- 76' Lantern and teeth absent altogether or only developed in the very young, at least up to a test length of 5 mm.; test ovate or hemispherical, the margin never very acute (pl. 25, figs. 11-16) 115
- 77 Plates of the petals alternating in form, every second one a demi-plate not extending radially between the inner row of pores unlike the primaries between them (fig. 73a)⁵; aboral miliary spines serrated and often slightly clavate but not markedly flared into a 'crown' or enveloped in a terminal glandular bag (fig. 74a) 78

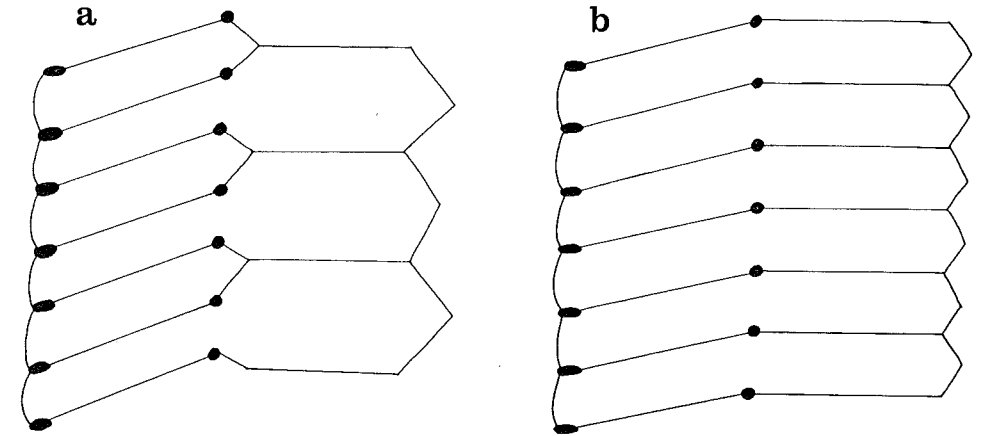


FIG. 73. Outline of plates from petals of: a. a clypeasterid and b. a laganid. (From Mortensen, 1948.)

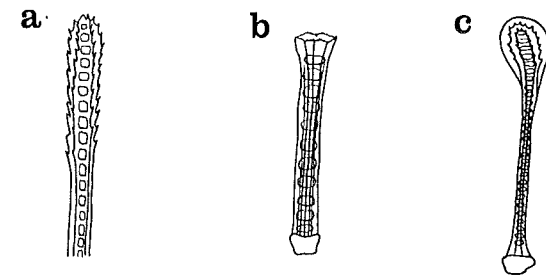


FIG. 74. Miliary spines of: a. a clypeasterid, b. a laganid and c. a scutellid. (From Mortensen, 1948.)

- 77' Plates of the petals all alike and running across half the width of the petal (fig. 73b); aboral miliary spines ending in a crown or a glandular bag 87
- ⁵ Unfortunately the limits of the plates may be difficult to see but can often be revealed by partial drying after wetting with xylol or by viewing from the inside if the test is broken. There is a great superficial resemblance between *Clypeaster* and *Laganum* so both alternatives should be tried if the material available is spineless and the structure of the petals cannot be ascertained, though these two genera, both with five genital pores, can be distinguished by the presence in *Laganum* of sinuous grooves on the apical system.

- 78 Five genital pores; periproct below the margin **CLYPEASTERIDAE**⁶ 79
- 78' Four genital pores; periproct above the margin **ARACHNOIDIDAE** 86
- 79 Interambulacra bulging around the peristome to form bourrelets (fig. 75) *Clypeaster ohshimensis* Ikeda, 1935

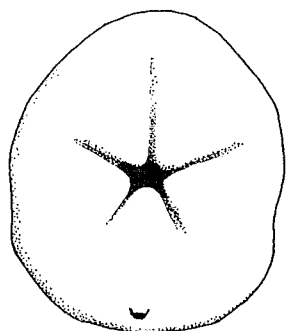


FIG. 75. *Clypeaster ohshimensis* from below, showing bourrelets. (From Ikeda, 1935.)

- 79' No interradiation projections around the peristome 80
- 80 Petals extremely large, almost triangular in shape and reaching nearly to the edge, so covering the major part of the aboral side, the whole of which is convex, though flattened centrally, and rises to a height almost or about equal to a third of the length in the type (fig. 76a) *Clypeaster eurypetalus* H. L. Clark, 1925b

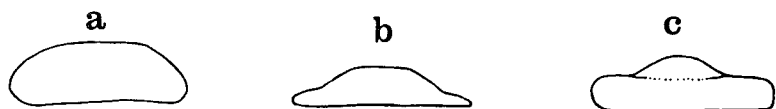


FIG. 76. Lateral profiles of: a. *Clypeaster eurypetalus* (from H. L. Clark, 1925a), b. *C. humilis* and c. *C. reticulatus*.

- 80' Petals oval and small or moderate in size, not covering a significantly greater area of the aboral side than the extra-petalous area, if as much; test low and almost flat aborally or rising more towards the centre than peripherally so that the aboral profile has a double concavity (fig. 76b, c); the height rarely as much as a third the length 81
- 81 Periproct separated from the posterior edge of the test by more than its own diameter; test length up to at least 150 mm. 82
- 81' Periproct separated from the edge of the test by not more than its own diameter; except in *C. humilis* (where it reaches 163 mm.) the maximum recorded test length < 100 mm. 83
- 82 Petals very broad basally so that the interambulacra barely make contact with the apical system *Clypeaster amplificatus* Koehler, 1922b
- 82' Interambulacra narrow proximally but clearly reaching the apical system *Clypeaster telurus* H. L. Clark, 1914a
- 83 Test delicate, often broken in preserved specimens; shape pentagonal, hardly longer than broad, the ratio of length:maximum breadth (which comes at the level of the anterior pair of petals) 1.0-1.05:1, rarely more; petals fairly narrow, angular terminally; margin of the test sometimes abruptly thickened; posterior edge of the test often with a slight bulge opposite the periproct; sutures of the aboral plates often showing up as a dark reticulum *Clypeaster rarispinus* de Meijere, 1902
- 83' Test fairly strong; shape pentagonal or oval but distinctly longer than broad, length:breadth at least 1.1:1 and often over 1.2:1; petals broad, blunt terminally; margin of the test thickened (*reticulatus*) or not (*humilis* and *fervens*); posterior end of the test usually rounded or with a short straight median part, rarely bulging in the middle 84
- 84 Test usually oval with only a slight tendency for a pentagonal shape, rarely exaggerated; length:breadth 1.17-1.46:1 in 10 specimens measured, averaging 1.30:1, usually very thick and rounded at the edge, the centre slightly elevated and projecting (fig. 76c) but sometimes surrounded by a depression encircling the petaloid area so marked that the centre does not always stand out above the thick edge in profile; in some specimens the whole test is much lower but otherwise the shape is similar; maximum length known 75 mm.; oral side of test always markedly and evenly concave (pl. 25, figs. 2-4) *Clypeaster reticulatus* (Linnaeus, 1758)

⁶ As Mortensen (1948a) warns in his key, the species of *Clypeaster* are very variable; accordingly many qualifications are needed in this section of our key.

- 84' Test usually distinctly pentagonal; length:breadth 1.17-1.28:1, averaging 1.21:1 in six specimens of *fervens* and eight of *humilis*; marginal area of test sloping evenly to a rounded edge, the test rising a little more abruptly towards the centre; oral side concave or flat 85
- 85 Petaloid area relatively large, ratio of test length:petaloid area length c.1.5-1.6:1; test concave orally; frontal petal usually open distally; maximum known length 87 mm. *Clypeaster fervens* Koehler, 1922b
- 85' Petals generally smaller, the ratio normally c.2.0:1, though sometimes approximating to 1.6:1, especially in very large specimens, length >80 mm.; test flat orally; frontal petal closed; maximum length known 163 mm. (pl. 25, fig. 1) *Clypeaster humilis* (Leske, 1778)
- 86 Periproct less than its own width from the posterior edge of the test, which is notched and has a groove leading to the periproct on the aboral side *Arachnoides placenta* (Linnaeus, 1758)
- 86' Periproct about twice its own diameter from the edge of the test, which is neither notched nor associated with a groove *Arachnoides tenuis* H. L. Clark, 1938
- 87 Test entire with no lunules perforating it; shape ovate (Fibulariidae) or flattened (Laganidae), though in the latter case often thick marginally; only a single interambulacral plate at the apical end of each double series; miliary spines with a terminal 'crown' (fig. 74b) 88
- 87' Test always very flat and perforated by two or more lunules; a pair of interambulacral plates heading the double series apically; miliary spines ending in a glandular bag (fig. 74c) **SCUTELLIDAE** 112
- 88 Size small, length up to 20 mm., often not more than 10 mm.; shape more or less ovate; petals poorly developed, usually inconspicuous **FIBULARIIDAE** 89
- 88' Adult test length usually 30-50 mm., sometimes more; shape markedly flattened, sometimes angular; petals well developed **LAGANIDAE** 99
- 89 Test high, globular or ovate, length:height from 2.5:1 to almost 1:1; no internal partition walls (pl. 25, figs. 6-8) **FIBULARIA** 90
- 89' Test low, more or less markedly flattened, length:height 2.5-4.7:1; radiating partition walls present, more or less completely developed **ECHINOCYAMUS** 95
- 90 Periproct round (rarely irregularly quadrangular or transversely oval) 91
- 90' Periproct elongated and longitudinally oval 93
- 91 Petals hardly recognizable as such since the rounded pores are so few (only c.30 altogether when the test length is 5.5 mm.) though relatively huge and scattered all over the aboral side of the test, some distinctly larger than the others; test relatively low, length:height 2.0-2.5:1 *Fibularia cribellum* de Meijere, 1902
- 91' Pores much smaller, about 100 altogether (i.e. about five pore-pairs in each side of each petal) and recognizably forming petals; no conspicuous difference in the size of neighbouring pores;⁷ test either low or high and almost globular 92
- 92 Test high, almost globular (pl. 25, figs. 6-8) *Fibularia ovulum* Lamarck, 1816
- 92' Test lower, more or less flattened aborally and tapering at each end, length:height 2.0-2.5:1 *Fibularia volva* L. Agassiz in Agassiz & Desor, 1846
- 93 Pores of petals large and triangular *Fibularia angulipora* Mortensen, 1948a
- 93' Pores usually smaller and rounded in shape (angular only in *F. oblonga* variety *ambonensis*) 94
- 94 Test high, arched and not at all tapering at the ends *Fibularia oblonga* Gray, 1851a
- 94' Test low, flat and tapering to a rounded point at each end *Fibularia acuta* Yoshiwara, 1898
- 95 Petals large, extending to the ambitus, the pore-series diverging *Echinocyamus megapetalus* H. L. Clark, 1914a
- 95' Petals stopping short of the ambitus, the pore-series parallel or converging 96
- 96 Test very flat, the margin somewhat thickened *Echinocyamus planissimus* H. L. Clark, 1938
- 96' Centre of test always higher than margin 97
- 97 Periproct nearer to posterior margin than to the mouth; test flat below *Echinocyamus incertus* H. L. Clark, 1914a
- 97' Periproct mid-way between margin and mouth; test markedly concave below 98
- 98 Periproct with five or six regular radiating spineless plates; largest specimens known only 10.5 mm. long *Echinocyamus crispus* Mazetti, 1893
- 98' Periproct with many irregular spine-bearing plates; known to reach a length of 20 mm. *Echinocyamus australis* (Desmoulins, 1835)
- 99 Genital pores five; madreporic pores situated in a sinuous sometimes branched groove or in pits, not individually distinct (fig. 77) **LAGANUM** 100
- 99' Genital pores four; madreporic pores scattered and individually distinct though inconspicuous **PERONELLA** 104
- 100 Periproct approximately mid-way between posterior margin and mouth, not closer to the edge 101
- 100' Periproct nearer the posterior margin than the mouth⁸ 102
- 101 Periproct much longer than broad *Laganum laganum* (Leske, 1778)

⁷ However, in *Fibularia trigona* Lamarck, which Mortensen (1948a) regards as a variety of *ovulum*, the pores may be larger and fewer, though more central in position.

See p. 167 for description of proposed neotype for *F. ovulum*.

⁸ In *Laganum joubini* the periproct is only a little less than mid-way from the posterior margin.

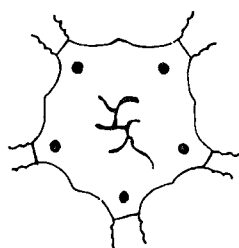


FIG. 77. Apical system of *Laganum depressum*. (From Lovén, 1874.)

- 101' Periproct broader than long *Laganum centrale* H. L. Clark, 1925b
- 102 Test ten-sided or circular, with length and breadth approximately equal; petaloid area just under half as long as the test *Laganum decagonale* (de Blainville, 1827)
- 102' Test pentagonal or elliptical, distinctly longer than broad (rarely almost circular); petaloid area more than half or often more than two-thirds of the test length 103
- 103 Periproct almost mid-way from the posterior margin to the mouth; petaloid area little more than half the test length; test more or less elliptical in shape *Laganum joubini* Koehler, 1922b
- 103' Periproct distinctly closer to the posterior margin; petaloid area often exceeding two-thirds of the test length; test very variable in shape, often elongate pentagonal, the margin more or less conspicuously thickened, though other specimens are more elliptical in shape with lower margins (pl. 25, fig. 10) *Laganum depressum* Lesson in L. Agassiz, 1841
- 104 Periproct mid-way between mouth and posterior margin 105
- 104' Periproct nearer to posterior margin 106
- 105 Colour red, pink or whitish⁹ *Peronella rubra* Döderlein, 1885
- 105' Colour greyish-violet or greyish-yellow⁹ *Peronella merguensis* Koehler, 1922b
- 106 Periproct naked¹⁰ 107
- 106' Periproct covered with spines¹⁰ 109
- 107 Oral ambulacral furrows well-marked; margin of test rarely thickened *Peronella tuberculata* Mortensen, 1918
- 107' Oral ambulacral furrows indistinct; margin of test usually conspicuously thickened, with a ring-shaped depression on the aboral side between margin and apical region. 108
- 108 Test usually almost circular, or sometimes rounded pentagonal, length: breadth c. 1.0-1.1:1; posterior interambulacrum more or less distinctly swollen towards the periproct *Peronella orbicularis* (Leske, 1778)
- 108' Test elongate, length: breadth 1.20-1.25:1 (in the two specimens known); no swelling towards the periproct *Peronella oblonga* Mortensen, 1948a
- 109 Size large, known to reach a test length of 168 mm., the genital pores rarely appearing before a length of 30-40 mm. (pl. 25, fig. 5) *Peronella lesueuri* (Valenciennes in L. Agassiz, 1841)
- 109' Size small, not known to exceed 37 mm., the genital pores appearing when the test is 10-15 mm. long (in *P. oblonga* present at least at 23 mm. test length) 110
- 110 Margin of test thin *Peronella macroproctes* Koehler, 1922b
- 110' Margin of test thickened 111
- 111 Pore-pairs of petals non-conjugate *Peronella minuta* (de Meijere, 1904)
- 111' Pores conjugate, distinct grooves linking the two pores of each pair *Peronella oblonga* Mortensen, 1948a (and 1949)
- 112 Five lunules, one in each ambulacrum *Astriclypeus manni* Verrill, 1867
- 112' Only two lunules, situated in the posterior paired ambulacra **ECHINODISCUS** 113
- 113 Lunules open distally (fig. 78b). *Echinodiscus auritus* Leske, 1778
- 113' Lunules enclosed within the area of the test (fig. 78a; pl. 25, fig. 9) 114
- 114 Lunules very short, only a quarter or a fifth the length of the radius taken through them, shorter than the petals; tubercles and spines of the oral side forming a fairly uniform texture *Echinodiscus tenuissimus* (L. Agassiz in Agassiz & Désor, 1847)
- 114' Lunules at least as long as the petals and often as much as half as long as the radius through them; spines and tubercles of the ambulacral areas of the oral side sharply contrasting with those of the interambulacral areas to form a conspicuous pattern (pl. 25, fig. 9) *Echinodiscus bisperforatus* Leske, 1778

⁹ Mortensen (1948) suspects that *Peronella rubra* and *merguensis* will prove to be synonymous. Koehler made no mention of *P. rubra* when describing *merguensis*.

¹⁰ Despite its uselessness for the identification of dead tests where the periproctal plates are lost, Mortensen (1948a) found that this character is the most reliable for splitting the species of *Peronella*. It should be noted that exceptionally *P. orbicularis* does have a few spines on the periproct, while conversely *P. lesueuri* can have few or none. Since *P. oblonga* is only known from two dead tests it has had to be included twice in this key.

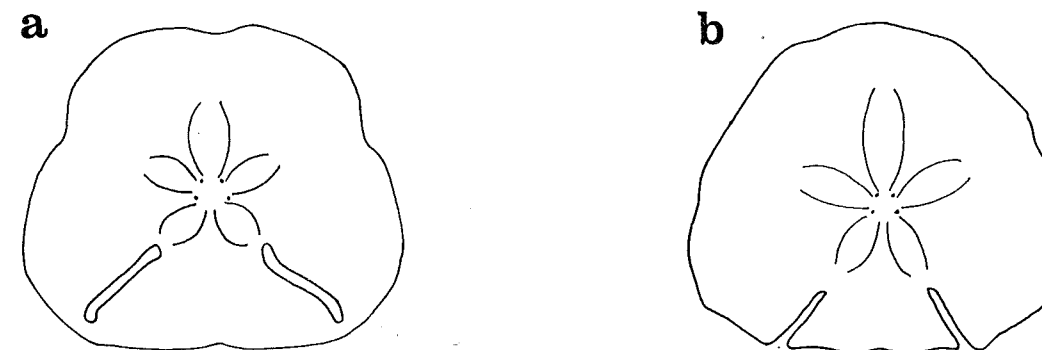


FIG. 78. Outlines of test and petals of: a. *Echinodiscus bisperforatus* and b. *E. auritus*.

- 115 Peristome at or only slightly anterior to the centre of the oral surface; no fascioles (belts of fine ciliated spines) present (pl. 25, fig. 13) **ECHINOLAMPADIDAE** 116
- 115' Peristome distinctly anterior in position; fascioles of some kind present (fig. 79) Order SPATANGOIDA 117

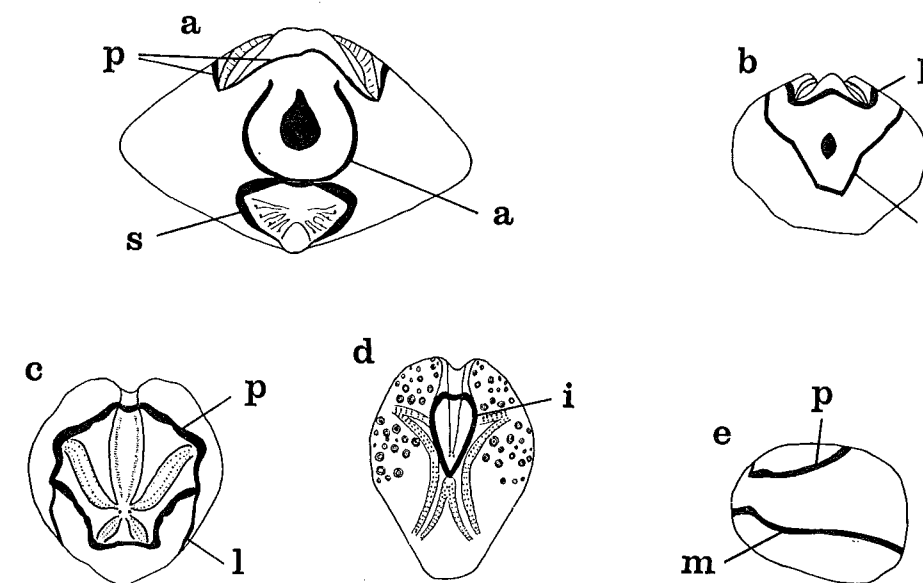


FIG. 79. Fascioles (black) of: a. *Metalia spatagus*, viewed from behind, showing subanal (s), anal (a) and part of peripetalous (p) fascioles, b. *Schizaster lacunosus*, from behind, showing latero-anal (l) and part of peripetalous fascioles, c. the same, from above, d. *Lovenia elongata*, from above, showing inner (i) fasciole and e. *Pericosmus melanostomus*, from the side, showing parts of peripetalous and marginal (m) fascioles. (e from Mortensen, 1951.)

- 116 Peristome pentagonal; interporiferous zone of the petals with crowded tubercles, often about eight in a single transverse series (pl. 25, fig. 13) *Echinolampas ovata* (Leske, 1778)
- 116' Peristome oval; few tubercles between the pores *Echinolampas alexandri* de Loriol, 1876
- 117 Peristome pentagonal, with no labrum posterior to it *Palaeostoma mirabile* (Gray, 1855)
- 117' Peristome crescentic or D-shaped; labrum well-developed 118
- 118 Subanal fasciole present (fig. 79a) 119
- 118' No subanal fasciole 139
- 119 Inner fasciole present (fig. 79d). **LOVENIIDAE** 120
- 119' No inner fasciole 125
- 120 No peripetalous fasciole; sternum (the ventral interradial oval area) almost naked. **LOVENIA** 121
- 120' Peripetalous fasciole present (see fig. 79c) as well as inner and subanal ones; sternum well-tuberculated **BREYNIA** 123

- 121 Posterior end of the test with a deep funnel-like concavity (pl. 25, figs. 14, 15) *Lovenia elongata* (Gray, 1845)¹¹
 121' Posterior end of the test vertical or only slightly concave 122
 122 Labrum reaching posteriorly only to the end of the second ambulacral plates (fig. 80a); posterior side of subanal fasciole widened to cover the entire subanal plates; aboral tubercles irregular in arrangement
Lovenia doederleini Mortensen, 1950¹²

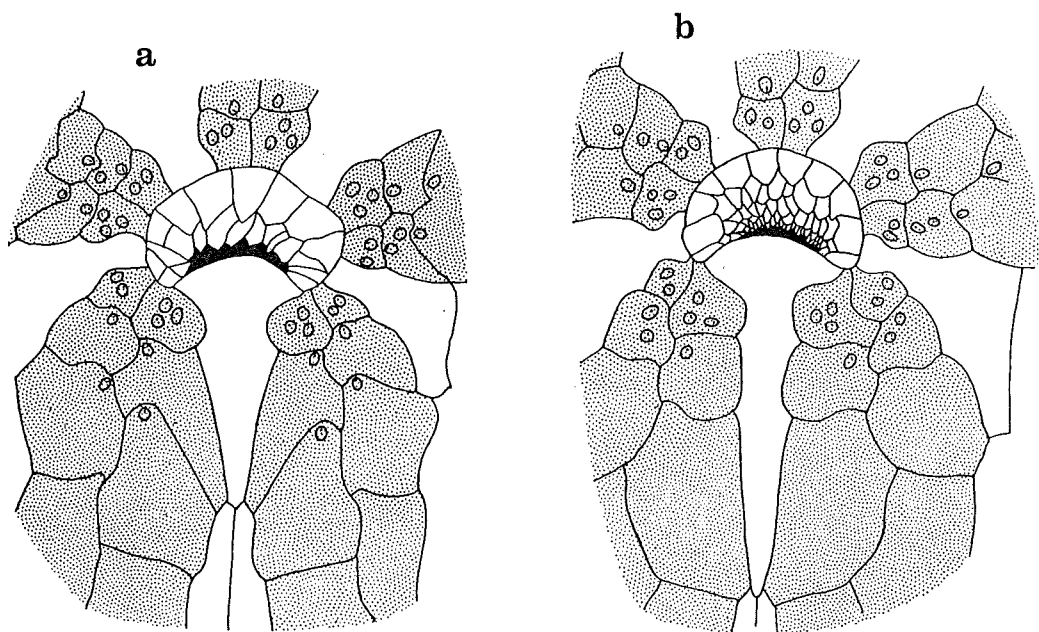


FIG. 80. Peristome, labrum and adjoining ambulacral plates (stippled) of: a. *Lovenia doederleini* and b. *L. subcarinata*. (Both from Mortensen, 1951.)

- 122' Labrum reaching usually to the posterior end of (or at least half-way along) the third ambulacral plates (fig. 80b); posterior part of the subanal fasciole narrow throughout; aboral tubercles arranged in longitudinal series
Lovenia subcarinata (Gray, 1845)
 123 Primary aboral tubercles absent except in the two anterior interradii (at least at a test length of 30 mm.)
Breynia vredenbergi Anderson, 1907
 123' Primary aboral tubercles present in all the interradii (at least when the test length exceeds 20 mm.) 124
 124 Six pore-pairs or tube-feet within the subanal fasciole on each side; labrum short, hardly if at all reaching beyond the second ambulacral plate each side (fig. 81a); spines brownish¹³
Breynia australasiae (Leach, 1815)

¹¹ Unfortunately Gray's type of *Lovenia elongata* can no longer be found in the British Museum collections. In 1917(b) H. L. Clark described the nominal species *Lovenia camarota* from a specimen in the Museum of Comparative Zoology, Harvard, originating from 'Challenger' station 188 (Torres Strait) and identified by Agassiz as *Lovenia elongata*, distinguishing it by the presence of only four or five pairs of pores occurring within the subanal fasciole, rather than six to ten pairs as found in adult *elongata*. In 1925 Dr. Clark relabelled as *L. camarota* two other specimens from 'Challenger' station 188 besides further examples of *Lovenia* from northern Australia, all in the British Museum collections. A re-examination of these has revealed that the two specimens from station 188 both have six pore-pairs each side within the subanal fasciole while one from the 'Alert' Torres Strait collections has nine. These three specimens have test lengths from 42 to 47 mm., while in the holotype of *L. camarota* it is 53 mm. In his key to the Australian species of *Lovenia* (1946), H. L. Clark also distinguishes *L. camarota* by the posterior position of the highest part of the test, contrasting with a supposed anterior position for the apex in *L. elongata*. However, Mortensen (1951) describes *L. elongata* as itself having the highest part posteriorly. The British Museum specimens show some variation in the slope of the aboral side of the test, so that this supposed difference is probably not significant. The holotype of *L. camarota* thus seems to be unique only in its small number of subanal tube-feet and I suspect that it will prove to be an abnormal specimen of *L. elongata*. Since 'Challenger' station 188 had a depth of 50 metres, *L. camarota* is anyway beyond the scope of this work, even if it is valid.

¹² The date of publication of *Lovenia doederleini* as a valid name is open to controversy. It first appeared in 1948 in combination with a new variety *acuminata*, the description of which is almost entirely comparative with the still to be described *doederleini*, and may therefore be regarded as a nomen nudum. By some mishap, Mortensen's preliminary paper to volume 5 of his Monograph, containing the diagnosis of *L. doederleini*, was not published until 1951, after the Monograph itself.

¹³ But see note 21 to distribution table.

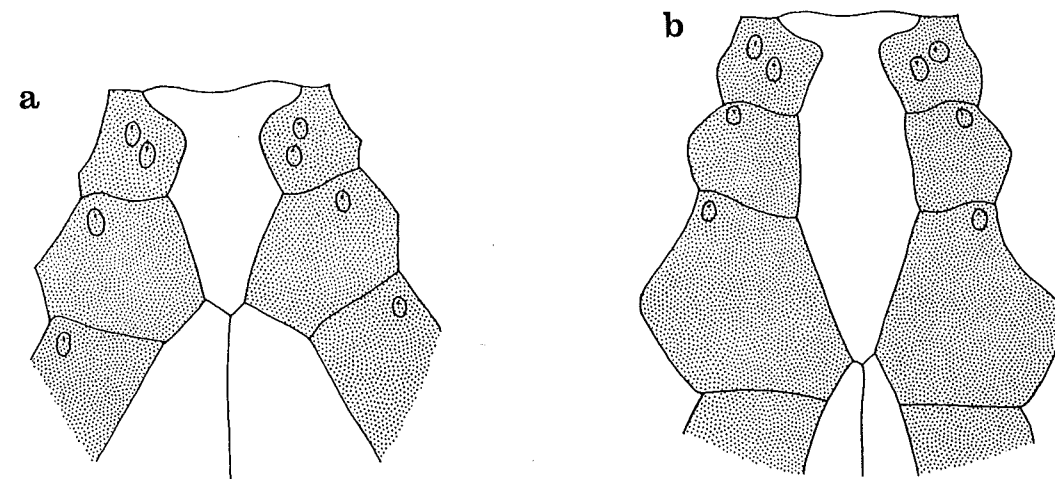


FIG. 81. Extent of labrum of: a. *Breynia australasiae* and b. *B. desori*. (Both from Mortensen, 1951.)

- 124' Eight pore-pairs each side within the subanal fasciole; labrum longer, reaching to about the middle of the third ambulacral plates (fig. 81b); spines pale in colour¹³.
Breynia desori Gray, 1851a
 125 Peripetalous fasciole absent SPATANGIDAE 126
 125' Peripetalous fasciole present BRISSIDAE 128
 126 Three genital pores; the anterior series of pore-pairs of the anterior paired petals developed only in the distal half of the petal (fig. 82b); only one (sometimes two) horizontal series of primary aboral tubercles developed and these limited to the two latero-posterior interambulacra¹⁴
Pseudomaretia alta (A. Agassiz, 1863a)

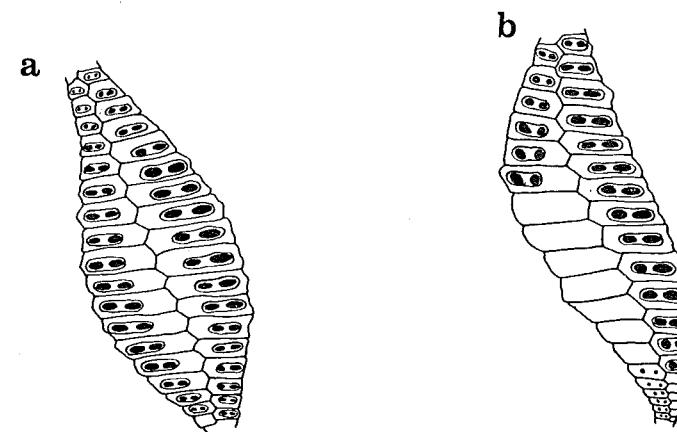


FIG. 82. Right anterior petals of: a. *Maretia planulata* and b. *Pseudomaretia alta*. (Mis-aligned, visualize rotated clockwise about 70°.)

- 126' Four genital pores; the paired petals all with complete series of pore-pairs (fig. 82a); primary aboral tubercles numerous in the anterior as well as posterior interambulacra (pl. 25, fig. 12) MARETIA 127
 127 Test very low, flattened, length:height 3-4:1 (pl. 25, fig. 12) *Maretia planulata* (Lamarck, 1816)
 127' Test fairly high, length:height c.2:1 *Maretia carinata* Bolau, 1873
 128 Subanal fasciole enclosing a reniform (kidney-shaped) area 129
 128' Subanal area shield- or heart-shaped 130
 129 Anterior end of test convex, no frontal notch; posterior paired petals divergent from their bases (pl. 25, fig. 16) *Brissus latecarinatus* (Leske, 1778)
 129' A more or less distinct frontal notch in the test; posterior petals almost parallel proximally, more divergent distally *Brissopsis luzonica* (Gray, 1851a)
 130 No anal fasciole *Brissopsis persica* Mortensen, 1940a¹⁵

¹⁴ But see note 19 to distribution table.

Pseudomaretia interrupta differs from *P. alta* in lacking primary tubercles aborally.

¹⁵ It was only in 1951 that Mortensen noticed the heart-shaped form of the subanal area in *Brissopsis persica*; this prompted him to suggest that it might be better considered as the type-species of a separate genus having affinities with *Metalia* but without knowledge of the pedicellariae he hesitated to take this step.

130' Anal fasciole present (fig. 79a) 131

131 Oral side of the test extended backwards below the anus, culminating in a peak in the subanal plastron 131

RHYNOBRISSUS 132

131' No distinct subanal projection **METALIA** 134

132 Test highest anterior to the apical system *Rhynobrissus hemiasteroides* A. Agassiz, 1879

132' Test somewhat raised posterior to the apical system but not conspicuously so 133

133 Secondary spines coarse and brownish in colour *Rhynobrissus macropetalus* H. L. Clark, 1938

133' Secondary spines fine, silky in appearance and white in colour *Rhynobrissus pyramidalis* A. Agassiz, 1872

134 Posterior petals fusing together or at least very closely approximated apically; no primary tubercles near the apical system in the posterior interambulacrum (pl. 25, fig. 11) *Metalia sternalis* (Lamarck, 1816)

134' Posterior petals distinct throughout; posterior interambulacrum with tubercles adapically 135

135 Apical system near the centre of the aboral side *Metalia townsendi* (Bell, 1904)

135' Apical system markedly anterior 136

136 Frontal ambulacrum conspicuously sunken *Metalia latissima* H. L. Clark, 1925b

136' Frontal ambulacrum only slightly, if at all, sunken 137

137 Posterior end of sternum forming two slight peaks *Metalia dicrana* H. L. Clark, 1917b

137' Only a single median peak at the end of the sternum 138

138 Highest part of the test markedly anterior so that the front of the test is almost vertical *Metalia robillardi* (de Loriol, 1876)

138' Highest part of test not conspicuously anterior in position, the front increasingly sloping backwards *Metalia spatagus* (Linnaeus, 1758)

139 Peripetalous and marginal fascioles present but no latero-anal ones (fig. 79e) *Pericosmus melanostomus* Mortensen, 1948c

139' Peripetalous and usually also latero-anal fascioles present but no marginal one (fig. 79b, c) **SCHIZASTERIDAE** 140

140 Four genital pores 141

140' Two genital pores 145

141 Pore-pairs of frontal ambulacrum zig-zagging in irregular double series, the alternating ones more or less staggered in position (fig. 83b) **DIPLOPORASTER** 142

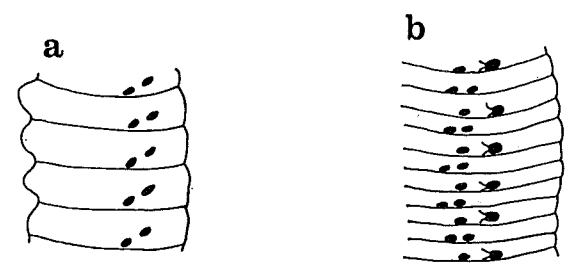


FIG. 83. Plates from frontal ambulacra of: a. *Paraster gibberulus* and b. *Diploporaster savignyi*. (Both from Mortensen, 1951.)

141' Pore-pairs of frontal ambulacrum in regular single series (fig. 83a), though the two pores of each pair may be aligned obliquely 143

142 Posterior end of test low and sloping; anterior interambulacra not overhanging the frontal ambulacrum from the sides so as to hide the frontal pores *Diploporaster barbatus* Mortensen, 1950 (and 1951)

142' Posterior end of test high and truncated; anterior interambulacra bulging inwards over the frontal groove and tending to conceal the pores when viewed from above *Diploporaster savignyi* (Fourtau, 1904)

143 Frontal ambulacrum distinctly sunken, the notch fairly well marked *Paraster gibberulus* (L. Agassiz in Agassiz & Désor, 1847)

143' Frontal ambulacrum hardly at all sunken, notch indistinct 144

144 Petals broad, length: breadth of the anterior ones (from photograph of holotype) 2.7:1 *Prymnaster investigatoris* (Koehler, 1914)

144' Petals narrow, ratio (from very diagrammatic figure of Smith) 5.3:1 *Protenaster rostratus* (Smith, 1878)

145 Petals very deeply sunken and their edges produced inwards so as to constrict them above **MOIRA** 146

145' Petals more or less sunken but their openings not constricted 147

146 A deep hollow in the posterior side of the test just above the subanal area *Moira lethe* Mortensen, 1930

146' Only a slight hollow above the subanal area *Moira stygia* Lütken in A. Agassiz, 1872

147 Latero-anal fasciole distinct (fig. 79b, c) *Schizaster lacunosus* (Linnaeus, 1758)

147' Latero-anal fasciole rudimentary *Hypselaster jukesi* (Gray, 1855)¹⁶

SUMMARY OF TAXONOMIC CHANGES—ECHINOIDEA

Salmaciella erythracis (H. L. Clark, 1912), reduced to a subspecies of *S. dussumieri* (L. Agassiz in Agassiz & Désor, 1846)—see table note 6.

Hypselaster dolosus H. L. Clark, 1938, a synonym of *H. jukesi* (Gray, 1855)—see key note 16 (below).

SUMMARY OF RELATIONSHIPS NEEDING FURTHER INVESTIGATION

Peronella merguensis Koehler, 1922 and *rubra* Döderlein, 1885—see key note 9.

Lovenia camarota H. L. Clark, 1917 and *elongata* Gray, 1845—see key note 11.

APPENDIX TO ECHINOIDEA

Fibularia ovulum Lamarck

fig. 83', pl. 25, figs. 6-8

Fibularia ovulum Lamarck, 1816:16; Mortensen, 1948a:208-210, figs. 102d, 104e, 106, 118, pl. 46, figs. 15-17, 21-24; Opinion 207, *Opin. int. Comm. Zool. Nom.* 3 1954:339-352.

Fibularia craniolaris: H. L. Clark, 1914:57; 1925:163 [Non *Echinocyamus craniolaris* Leske, 1778.]

The traditional concept of the genera of the family Fibulariidae follows L. Agassiz (1841, *Monograph des Scutelles*) who recognized *Echinocyamus* van Phelsum as representing flattened species with internal partitions and *Fibularia* Lamarck for those with more nearly ovate tests unsupported internally. Since the early descriptions of species were often imprecise, limited to the external appearance and rarely supported by preserved specimens, much confusion existed, aggravated by the action of Lambert (1891, *Bull. Soc. géol. Fr.* 29) who reversed the usual concept by treating ovate species as belonging to *Echinocyamus* and flattened ones as *Fibularia*.

H. L. Clark (1911, *Ann. Mag. nat. Hist.* 7) attempted to restore order by designating the first-named of Lamarck's three nominal species, *trigona*, as type-species of *Fibularia*, simultaneously referring it to the synonymy of *craniolaris* Leske. In 1932, Mortensen (*Ann. Mag. nat. Hist.* 10) accordingly submitted to the International Commission on Zoological Nomenclature a proposal for the validation of *Fibularia* Lamarck, 1816, with type-species *Echinocyamus craniolaris* Leske, 1778, as well as of *Echinocyamus* Van Phelsum, 1774, type-species *Spatagus pusillus* O. F. Müller, 1776. However, the Commission deferred making a decision on the case and by

¹⁶ H. L. Clark (1938) has described a new nominal species, *Hypselaster dolosus*, from Broome, NW Australia. He compares it with *H. fragilis*, the type-locality of which is off Japan in deep water, to which species he had previously referred several specimens of *Hypselaster* from Queensland. The latter were subsequently recognized as referable to *H. jukesi* by Mortensen (1951). Dr. Clark distinguishes *dolosus* from *fragilis* by the posterior position of the apical system in *dolosus* but it is only in the Japanese holotype of *H. fragilis* that the apical system is anterior and Mortensen was mistaken in applying this same distinction to *dolosus* and *jukesi* (1951:314). In the holotype of *H. jukesi* (figured by Mortensen, pl. xxii, figs. 15-17) the centre of the apical system is 33 mm. from the anterior end but only 27 mm. from the posterior. Mortensen also attempted to use the relative breadth of the posterior petals to distinguish the two, describing them as broad in *jukesi* but narrow in *dolosus*, as shown by comparison of his figures 6 and 14 of plate xxii (1951). Measurements of the posterior petals in these photographs gives a length: breadth ratio for *dolosus* of 2.4:1 and for *jukesi* of 2.2:1, which hardly seems significant, and in addition the type of *jukesi*, shown in his figure 15, appears to have a ratio of c.2.7:1, or narrower than that of *dolosus*. On this evidence there seems to be little justification for considering *H. dolosus* as anything but a synonym of *jukesi*.

the time it was raised again, about 1946, Mortensen had decided that *craniolaris* Leske was itself referable to *Echinocyamus*. He therefore reviewed Lamarck's three nominal species of *Fibularia*, *trigona* with locality unknown, *ovulum* from 'la mer de Norwège?' and *tarentina* from 'la Méditerranée, dans le golfe de Tarente', rejecting *trigona* as unrecognizable from the description and *tarentina* as a synonym of *Echinocyamus pusillus*. This left only *ovulum*, which he considered to be sufficiently characterized by the inclusion in the diagnosis of the words 'globosa-ovata, basi subangustata', accordingly substituting it for *craniolaris* as proposed type-species of *Fibularia*.

The Commission (Opinion 207) in 1954 accepted Mortensen's proposal and added the names *Fibularia* and *F. ovulum* to the Official Lists of Generic and Specific Names. Evidently Mortensen's taxonomic judgement was rated sufficiently highly for acceptance of his concept of *ovulum* as representing the ovate Indo-Pacific species contrary to Lamarck's provisional European locality, without the support of Lamarck's type-material, which Mortensen (1948) had reported as being untraceable by Dr. Cherbonnier in the collections of the Paris Museum (although the holotype of *F. trigona* was found there at the time and was treated as representing a subspecies of *ovulum* by Mortensen).

In face of Lamarck's locality, provisional though it is, which could only accord with the identity of *ovulum* with the common *Echinocyamus pusillus*, the status of *Fibularia* unsupported by a type-specimen of *ovulum* seems to us fraught with hazard, even though 37 out of 38 of Mortensen's contemporary specialists on echinoderms supported him (Lambert only opposing). The Commission having exerted its plenary powers to set aside designations of type-species other than *ovulum* (such as *trigona* of H. L. Clark in 1911, which would have been much the better solution), the best way to ensure the validity of *Fibularia* seems to be for the Commission to exert its plenary powers again to recognize an undoubted Indo-Pacific specimen, agreeing with Mortensen's description, as neotype of *Fibularia ovulum*. Since previous descriptions, such as those of A. Agassiz and Mortensen, are based on a number of specimens from a wide range of localities, we give here a description of a specimen in the British Museum collections (drawn up by F.W.E.R.), to which we propose to draw the attention of the Commission so that it may be formally designated as neotype of *Fibularia ovulum*. This should secure the accustomed nomenclature as given in the definitive work on the Fibulariidae—namely Mortensen's monograph.

We have ascertained from Dr. Madsen that Mortensen did not designate any of the specimens in the Copenhagen Museum as a neotype, also from Dr. Cherbonnier that there is still no trace of Lamarck's material of *ovulum* in the Paris Museum. Both these specialists support our proposed action, as do Drs. Pawson and Kier, also consulted.

With regard to satisfying the limitations and conditions of Article 75 of the International Code of Nomenclature, the present proposal appears to satisfy all but paragraph c5, relating to agreement between the original type-locality and that of the proposed neotype, which is clearly impossible in this case, the purpose of which is to show that Lamarck's doubt as to the type-locality must have been justified. As far as Lamarck's description goes there is sufficient agreement in our view.

Material. North Male, Maldives Islands; Stanley Gardiner collection; B. M. Reg. No. 1902. 3.13.44; the proposed neotype and one other specimen.

Description of proposed neotype. The test is almost globular in shape, 8 mm. long, 7 mm. broad and 6 mm. high. The apical system and peristome are both slightly posterior of centre aborally and orally respectively. The periproct is closer to the peristome than to the posterior end of the test.

The petals (fig. 83'a) have 5–7 pore-pairs in each series. The pores are quite large, especially the more distal ones, round in shape with each pair aligned obliquely. The two outer series of

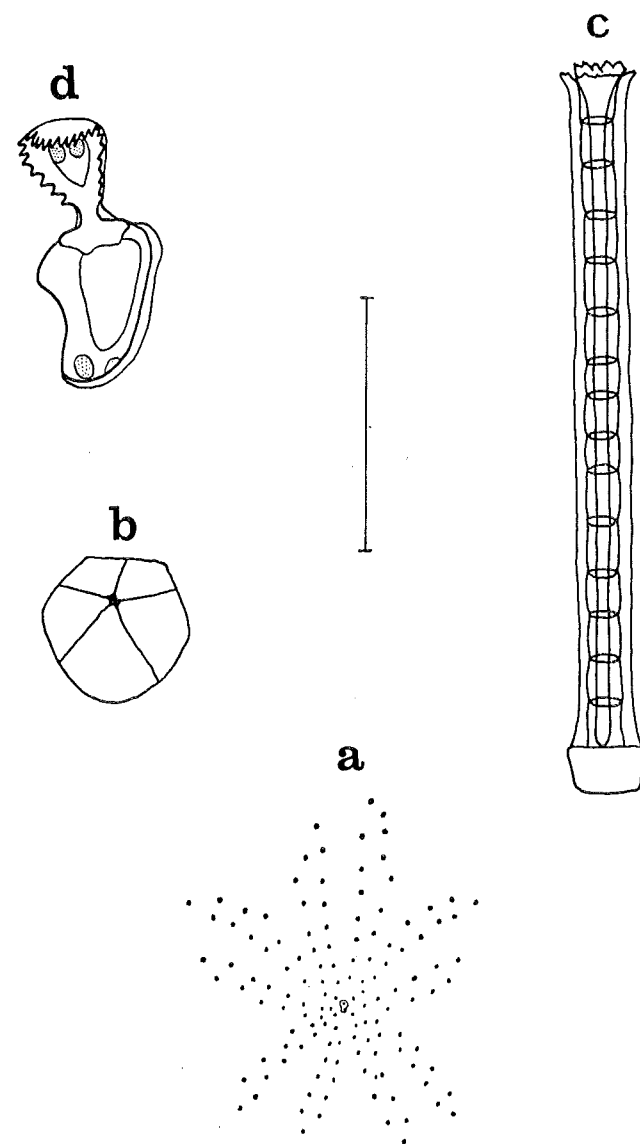


FIG. 83'. *Fibularia ovulum*. a. Petals and apical system of proposed neotype, b. periproct of second specimen, c. miliary spine of proposed neotype and d. ophicephalous pedicellaria valve from the same. The scale equals 5 mm. for a, 1.5 mm. for b and 0.1 mm. for c and d.

pores of each petal form irregular lines though the inner ones are straight and slightly divergent; the individual pore-pairs are only obvious proximally. The test has been partially denuded; primary spine tubercles are distributed in the poriferous as well as interporiferous areas. At least one hydropore is visible in a longitudinal depression between the four genital pores which are about the same size as the adjacent proximal pores of the petals. The interporiferous areas of the petals are slightly elevated but the interambulacral areas between the petals are quite flat.

The peristome is round and the membrane devoid of plates. The periproct is rounded pentagonal. The anal plates have been lost in this specimen but in the other one they number five (fig. 83'b) and are unequal in size, the most posterior one being the largest and the most anterior the smallest.

The primary spines are short, 0.6–0.7 mm. long, tapering to a blunt point. Miliary spines (fig. 83'c) are about 0.3 mm. long, terminating in a horizontal crown of minute thorns.

Only ophicephalous pedicellariae (fig. 83'd), similar to those of other fibulariids, are found.

The tube feet lack a supporting plate in the tip.

The second specimen is similar in size to the proposed neotype but does not appear to have any pedicellariae; also its hydropore depression has completely collapsed so that the number of hydropores cannot be ascertained.

Discussion. Mortensen (1948) includes seven species besides *F. ovulum* in his key to the species of *Fibularia*; of these, *F. oblonga*, *acuta* and *angulipora* belong to the subgenus *Fibulariella* Mortensen, 1948, since they have no ophicephalous pedicellariae but peculiar globiferous ones; also they have more or less well-developed calcareous plates in the peristomial membrane and a well-developed calcareous disc at the end of each tube-foot, unlike *F. ovulum* and the four other species of *Fibularia* sensu stricto. These four species can be distinguished most easily from *F. ovulum* as follows: *F. cribellum* de Meijere, 1902 (maximum known length 7 mm.) is smaller than *ovulum* (of which the length may reach 11.5 mm.), also it has fewer but larger pores in each petal. *F. nutriens* H. L. Clark, 1909, like *F. volva* L. Agassiz, 1847 and *F. plateia* H. L. Clark, 1928, has a lower, more or less flattened, test, with the ratio length:height c.2.0:1 (*nutriens*), c.1.6:1 (*volva*) or c.2.6:1 (*plateia*), compared with c.1.25:1 in *ovulum*. *F. nutriens* is one of the smallest echinoids known, the maximum length so far found being only 3.3 mm.; petals are lacking, though one or two pairs of pores may be detectable at high magnification (at least $\times 70$ according to H. L. Clark) and it possesses tridentate in addition to ophicephalous pedicellariae. *F. volva* (maximum known length 10 mm.) and *F. plateia* (up to 6.25 mm.) are distinguished from each other by their size and shape, *F. volva* being pointed at each end while *F. plateia* is truncated posteriorly, also by the number of hydropores, *volva* having several while *plateia* has only one.

Though treating *trigona* Lamarck as a subspecies of *F. ovulum*, Mortensen was uncertain whether or not to refer *trigona* instead to the subgenus *Fibulariella*, this being impossible to determine in view of the existence of only dead tests of *trigona*, lacking any pedicellariae. It was evidently for this reason that he felt it unwise to select *trigona* as type-species of *Fibularia*. The same doubt exists as to the position of *F. volva*, again known only from naked tests. Pending the discovery of intact material, Mortensen inclined to the inclusion of such species in *Fibularia* sensu stricto by default.

Clearly before the true affinities of the various nominal species of *Fibularia*, and indeed of other fibulariids, can be properly appreciated, much more intact material is needed so that detailed studies can be made of growth changes and variation.