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DISCOVERY REPORTS

VOLUME XX

CAMBRIDGE
UNIVERSITY PRESS
LONDON: BENTLEY HOUSE
NEW YORK, TORONTO, BOMBAY
CALCUTTA, MADRAS: MACMILLAN
TOKYO: MARUZEN COMPANY LTD

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DISCOVERY REPORTS

Issued by the Discovery Committee
Colonial Office, London
on behalf of the Government of the Dependencies
of the Falkland Islands

VOLUME XX



CAMBRIDGE
AT THE UNIVERSITY PRESS

1941

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LARVAE OF DECAPOD CRUSTACEA
PART VI. THE GENUS *SERGESTES*

BY
R. GURNEY AND M. V. LEBOUR

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LARVAE OF DECAPOD CRUSTACEA

PART VI. THE GENUS *SERGESTES*

By R. Gurney and M. V. Lebour

(Text-figs. 1-56)

INTRODUCTION

THE main facts in the development of the Sergestidae are now fully known, and the history of the progress of knowledge has been summarized by Wasserloos (1908) and by Hansen (1922). Of two species only, *S. arcticus* and *S. prehensilis* (by Wasserloos, 1908 and Nakazawa, 1915, 1916), are all the stages known with certainty. While the Acanthosoma stages do in some cases offer characters which make it possible to link them up with the Mastigopus and so with the adult, the Elaphocaris stages are so completely unlike the Acanthosoma that it is generally impossible to connect them with later stages when only preserved material is available.

Among the larvae in the Elaphocaris stage certain types are distinguishable (Gurney, 1924c), and it is of real importance that they should be identified, if possible, since they may help to point to a satisfactory subgeneric grouping of the adults. While it is occasionally possible to link together a series of larvae in a plankton sample with some approach to certainty, a real advance can only be made where living material is available in quantity, and the larvae can be kept alive for moults from one stage to another. The Biological Station in Bermuda offers ideal conditions for such work. In the spring of 1935 one of us (R. G.) devoted much time to study of Sergestid larvae and obtained a number of moults, but the results were not sufficiently complete for publication. In 1938 both of us spent part of the summer in Bermuda, and one of us (M. V. L.) continued to work there for a whole year. For a successful issue to such research a regular supply of living plankton from the open ocean down to depths below 200 metres is necessary, and samples from deep water have been regrettably few. Still, the material that has been obtained permits of connecting up the early stages with the Mastigopus in a number of species, partly by means of colour resemblances and partly by moulting. On the whole the larvae live well in the laboratory; but there are difficulties to overcome. It is generally impossible to make any adequate examination of a larva which it is intended to keep alive, and the moulted skin is so fragile that it is of very little use for subsequent identification. On two occasions in 1935 a larva actually moulted while a drawing was being made of it.

A large amount of material from the 'Discovery', mainly of Mastigopus stages, has been studied, and some of this is dealt with in this report. This material includes some larvae which have not been seen at Bermuda.

Of the sixteen species of *Sergestes* known from the Atlantic and included in Hansen's monograph we have been able to follow the development completely, or in part, of thirteen. The development of *S. mollis*, *S. grandis* and *S. splendens* remains completely unknown. These are species of very deep water, and it is possible that they do not occur in the immediate neighbourhood of Bermuda. We have, both from Bermuda and from the Discovery material, larvae which it is impossible at present to identify. It is suggested that they may belong to species as yet undescribed.

Nakazawa states that *S. prehensilis* starts its life-history as a Nauplius. We have been unable to read the paper, which is entirely in Japanese, and do not know what evidence he is able to give. The figures show the Nauplii to be entirely unlike those of any other Penacid, and they appear to have all the characters of Copepod Nauplii. Wasserloos was unable to find any evidence for the existence of a Nauplius in *S. arcticus*, and we have seen no Nauplii attributable to *Sergestes*. It is by no means impossible that there is such a stage, since there is a Nauplius in *Lucifer* and *Acetes*, but it will be most difficult to prove or disprove its existence. The Nauplius phase may be very rapidly passed through, probably at night, and it would have to be sought in the strata occupied by the adult.

Our main purpose in this report is to describe the Elaphocaris and Acanthosoma stages of the Atlantic species, but we have also included descriptions of the first Mastigopus, and, in some cases, have given figures of later stages also, since we believe that figures of the whole animal are valuable aids to identification. Detailed descriptions of the later Mastigopus stages are unnecessary, since they have been so fully dealt with by Hansen; but he was not usually in a position to determine, as we have done in some cases by moulting, the actual first stage. It is to be understood that we have relied entirely upon Hansen's monograph in the identification of the species dealt with, since this is the most complete and authoritative account of the genus published; but there is some evidence from the larvae that there exist species which Hansen did not discriminate.

Mr Burkenroad informs us that some of Hansen's species (e.g. *S. corniculum*) are certainly composite, and Dr I. Gordon has recently described a new species of the *robustus*-group from the Atlantic.

Hansen has laid great stress upon the depth of colour of the eye pigment, stating that it is always brown up to the end of the Mastigopus phase, and black thereafter. This we do not find to be the case when living material is available. In all species the eye is black or dark brown from the earliest stages, but it becomes lighter, or even colourless, in formol and spirit.

In the descriptions which follow we have found it difficult to decide upon a terminology for the armature of the carapace. While the outgrowths of the carapace are homologous in Elaphocaris and Acanthosoma they have been described as processes in the former and spines in the latter simply as a matter of convenience, since, in the former, they may themselves bear spines. In both cases the outgrowths may also bear spinules or prickles, and the objectionable term "long spinules" has been used when the armature is intermediate between prickles or spinules and longer outgrowths which can definitely be called spines. We have laid stress upon the number of spines on the processes in the

Elaphocaris. When a single number is given it is to be understood that this is taken from one typical specimen; but we have found the number to be variable, though only within narrow limits. Any considerable departure from the number given would render identification very doubtful.

The structure of the mouth parts and thoracic appendages throughout the genus seems to be so uniform that we have omitted all reference to them, apart from the mandibular palp, which appears earlier in some species than in others. They have been fully described and excellently figured by Hansen.

We feel that it is of importance to establish the specific characters of the larvae of the Sergestidae since they are so common in the plankton of the warmer oceanic areas. There is some evidence, though not sufficiently precise to be brought forward, that the Sergestid larval fauna of the waters fished from the Bermuda Biological Station varies with season and year. Since nearly all the larvae can now be identified, at all events in freshly caught material, these changes can now be studied, and it seems probable that they may contribute to throwing light upon seasonal changes in the oceanic currents. It is desirable that the bathymetrical distribution of the larvae in relation to that of the adult should be studied. Nothing is as yet known with certainty as to the oviposition and hatching of the eggs, but it is unlikely that this knowledge can be obtained except by taking plankton at night at depths exceeding 200 metres.

MOVEMENTS OF THE LARVAE

Systematic observation of the swimming habits of the larvae have not been made, but the following points have been noted. The Protozoa, like that of the Penaeidae, swims by slow beating of the antennae in a forward direction, generally back upwards. We have not seen vertical movement such as is described by F. Müller (1863, p. 9) in *Penaeus*.

The *Acanthosoma* swims in exactly the same way as most Carid larvae, namely, back down and tail first.

The swimming of the *Mastigopus* is difficult to observe, since the confinement necessary under laboratory conditions probably upsets its normal habit. As it is not until stage 2 or 3 that the antennal flagellum is fully developed, stage 1, at all events, must have different habits from those of later stages. It would seem that the normal position, at least of some species, is with head upwards, abdomen flexed sharply backwards so that it is almost horizontal and the pleopods widely spread. In this position the legs are held forwards and slightly to either side so that, with the long setae which fringe their two sides, they form an open basket-work perhaps for catching food. The enormously long flagella, armed at each segment beyond the "kink" with a pair of curved setae, the points of which nearly meet, are most efficient organs for suspending the body. It was noticed that, when a specimen jumped backwards by sudden flexure of the abdomen, it was jerked back again by the drag of the flagella.

SYSTEMATIC IMPORTANCE OF THE LARVAE

Perhaps the most interesting feature of the development of *Sergestes* is the striking difference which exists between the larvae of the different species, while the adults are often separable with difficulty. It may well be that knowledge of the larvae, when complete, may give a better indication of the relationships of the species than the adult structure.

The Elaphocaris in stages 2 and 3 may be divided into three types which are quite distinct and have been called *dohrni*, *ortmanni* and *hispidula* respectively (Gurney, 1924c, p. 79). In all cases the carapace has the same number of processes, but they differ as follows:

(1) *Dohrni* type. Supraorbital, lateral and posterior processes with numerous long lateral spines.

S. atlanticus, *cornutus*, *arcticus*, *pectinatus*, *sargassi*, *vigilax*, *armatus*, *diapontius*, *edwardsi*.

(2) *Ortmanni* type. Lateral and posterior processes without lateral spines, but with long spines springing from the carapace at their bases.

S. corniculum.

(3) *Hispidula* type. Lateral and posterior processes without long spines. Sometimes with long spinules at base.

S. tenuiremis, *robustus*, *crassus*, *prehensilis*.

The *ortmanni* type seems to be a derivative of the *dohrni* type rather than of the *hispidula* type, since the supraorbital processes have long spines as in the former.

While *S. corniculum* and the species of the *robustus* group have perfectly characteristic forms of Elaphocaris, the *dohrni* type is found in a number of species which are not supposed to be particularly closely related, and it is not possible to separate them into groups on the structure of this stage. The Elaphocaris of *S. arcticus*, for example, is very distinct in its form of eye and the peculiarly branched spines, but it is otherwise of typical *dohrni* type.

The Acanthosoma cannot be separated into types corresponding to the Elaphocaris. One group comprising *S. vigilax*, *diapontius*, *armatus* and *edwardsi* is, however, characterized by an Acanthosoma of distinctive form with very short telson (see p. 46).

The species of the *robustus* group of which the development is known have Acanthosomas with particularly long telson arms, but no other very distinct common characters, though there appears to be a group of larvae resembling that of *S. robustus* which cannot at present be identified (see p. 33). The Acanthosoma of *S. arcticus* more closely resembles that of the *robustus* group than any other, though the points of resemblance are not particularly significant.

We have given evidence (p. 38) that there are at least three species of Acanthosoma without posterior dorsal spine, and we consider that these larvae belong to species

hitherto confounded with *S. corniculum*, so that it may be correct to speak of the Elaphocaris of *ortmanni* type as representing a *corniculum* group. Apart from the presence of a dorsal spine the Acanthosoma of *S. cornutus* very closely resembles that of *S. corniculum* and not its close ally *S. atlanticus*.

Of the two species *S. pectinatus* and *sargassi* only the Acanthosoma of the former is known with certainty, and this seems to have no near relationship with the type characterizing the other species of Hansen's group II. If we are right in the identification of the Acanthosoma of *S. sargassi* their relationship seems to be with *S. corniculum*. Burkenroad (1937, p. 320) has already pointed to the close resemblance of *S. sargassi* to *S. corniculum*.

The petasma offers the most reliable basis for separation of species and should also serve to distinguish groups within the genus. The evidence here shows very clearly that the *vigilax-edwardsi* group is well founded, but that *S. pectinatus* and *S. sargassi* fall outside it, as their larvae also show that they do. It is also very clear that *S. atlanticus* and *S. cornutus* are most closely related, but in this case the larvae do not appear to corroborate. Within the remainder of the species it is difficult to distinguish any clearly defined groups on the basis of the petasma. All alike tend to have elongated median stems and the same form of uncinat process. The simplified form of the terminal lobes place *S. pectinatus* and *S. sargassi* together and somewhat apart from the rest, while *S. arcticus* and *S. corniculum* are both distinguished by the elaborate armature of the ventral process, though the resemblance is not such as necessarily to imply relationship. The remaining species—*tenüremis*, *robustus*, *grandis*, *crassus*, *splendens*, *mollis* and *prehensilis*—correspond to the *robustus* group, in which the Elaphocaris is, or may be expected to be, of the *hispidus* type.

Burkenroad (1937, p. 317) attaches much importance to the presence or absence of the organ of Pesta. This organ, he says, is present in all species except the *S. mollis*, *S. tenüremis*, *S. robustus* and *S. challengerii* superspecies of Hansen's "Group I", and he also says that *S. arcticus*, of all species which have this organ, comes nearest to those which lack it.

Of the remaining genera of the Sergestidae, *Petalidium*, *Lucifer*, *Acetes* and *Sicyonella*, the development of *Lucifer* has long been known, and Soejima (1926) and Menon (1933) have now described fully that of *Acetes*. *Acetes*, like *Lucifer*, hatches as a Nauplius, and the Elaphocaris is of the same *hispidus* type as that of *S. robustus*, for example, though differing in the much shorter thoracic processes, and shorter telson arms, but there are great differences in later stages. Thus there is only one Acanthosoma stage, which lacks all the spines so characteristic of *Sergestes*, and the fifth leg does not appear at all. Furthermore, the mouth parts are, to a large extent, degenerated. Another remarkable feature is the appearance of pleopods 1 and 2 when those behind are absent, and even in Mastigopus 1 there are only three pairs. Pleopod 4 appears as a non-setose appendage in Mastigopus 2 and pleopod 5 in Mastigopus 3.

The development of *Petalidium* and *Sicyonella* is uncertain. Larvae attributed to *Petalidium* have been described by Gurney (1924), but we are informed by Mr Burken-

road that these larvae really belong to *Sicyonella*. In view of the fact that the genus *Petalidium* is so close to *Sergestes* that it is scarcely separable (Burkenroad, 1937, p. 324) it is most unlikely that the larvae would differ to any great extent, and we feel that Mr Burkenroad's transference of these larvae to *Sicyonella* can probably be accepted.

We have seen no larvae in the Discovery material which can be referred to either of these genera.

IDENTIFICATION OF THE LARVAE

The three Elaphocaris stages differ so much from each other that it is impossible to frame a key which will cover them all, and also our knowledge of them is not yet sufficiently complete for such a key to be useful. The Mastigopus stages, again, change so much with growth in the proportions of the eye, uropod, etc. that a key could only be satisfactory if it could be made to apply to a single stage, and that is neither possible nor desirable. On the other hand, the Acanthosoma stages differ but little from each other and we have made a key to them which we hope may make identification easy.

KEY TO THE ACANTHOSOMA STAGES

1.	Abdominal somites without median ventral spines	2
	Abdominal somites with two or more ventral spines; lateral spine of somite 5 very small	10
2.	Thorax without posterior dorsal spine	3
	Thorax with posterior dorsal spine	4
3.	Margin of carapace not denticulate	<i>S. corniculum</i>	
	Margin of carapace denticulate	<i>S. crassus</i>	
4.	Exopod of uropod with setose part more than $1\frac{1}{2}$ times as long as bare part	5
	Setose part less than bare part or not more than $1\frac{1}{2}$ times as long	6
5.	Carapace with angular projection behind anterior lateral spine	<i>S. pectinatus</i>	
	Carapace without this projection	<i>S. sargassi</i>	
6.	Eye long and slender, eyeball nearly round	7
	Eyeball large, asymmetrical	8
7.	Lateral spines of somites 4 and 5 very long	<i>S. robustus</i>	
	These spines very short	<i>S. arcticus</i>	
8.	Lateral spines of thorax and abdomen very long, with long spinules; eyes short	<i>S. cornutus</i>	
	These spines short, with very small spinules; eyes very long	9
9.	Setose part of uropod shorter than bare part; endopod of uropod wider than exopod	<i>S. tenuiremis</i>	
	Setose part longer than bare part; endopod not wider than exopod	<i>S. atlanticus</i>	
10.	Ventral spines on somites 1 and 2	11
	Ventral spines on somites 1-3	<i>S. armatus</i>	
	Ventral spines on somites 1-5	<i>S. edwardsi</i>	
11.	Lateral spines of somites 4 and 5 very small; eye nearly as long as scale	<i>S. vigilax</i>	
	Lateral spine of somite 4 much larger than 5; eye about half as long as scale	<i>S. diapontius</i>	

GROUP I

Sergestes atlanticus H. M. Edw.

Hansen, 1922, p. 47, Mastigopus.

Illig,¹ 1914, p. 350, Acanthosoma 2 (*S. ovatoculus*).

MATERIAL. Fairly common at Bermuda in water of 100–250 metres or more, the Elaphocaris in the deeper layers. Moults obtained from Elaphocaris 1 to Elaphocaris 2; from Elaphocaris 3 to Acanthosoma; and from Acanthosoma 2 to Mastigopus. Elaphocaris 2 is presumed to belong to this series from similarity in colour² and form of posterior dorsal process.

Acanthosoma and Mastigopus taken at Discovery Stations 701, 708, 709.

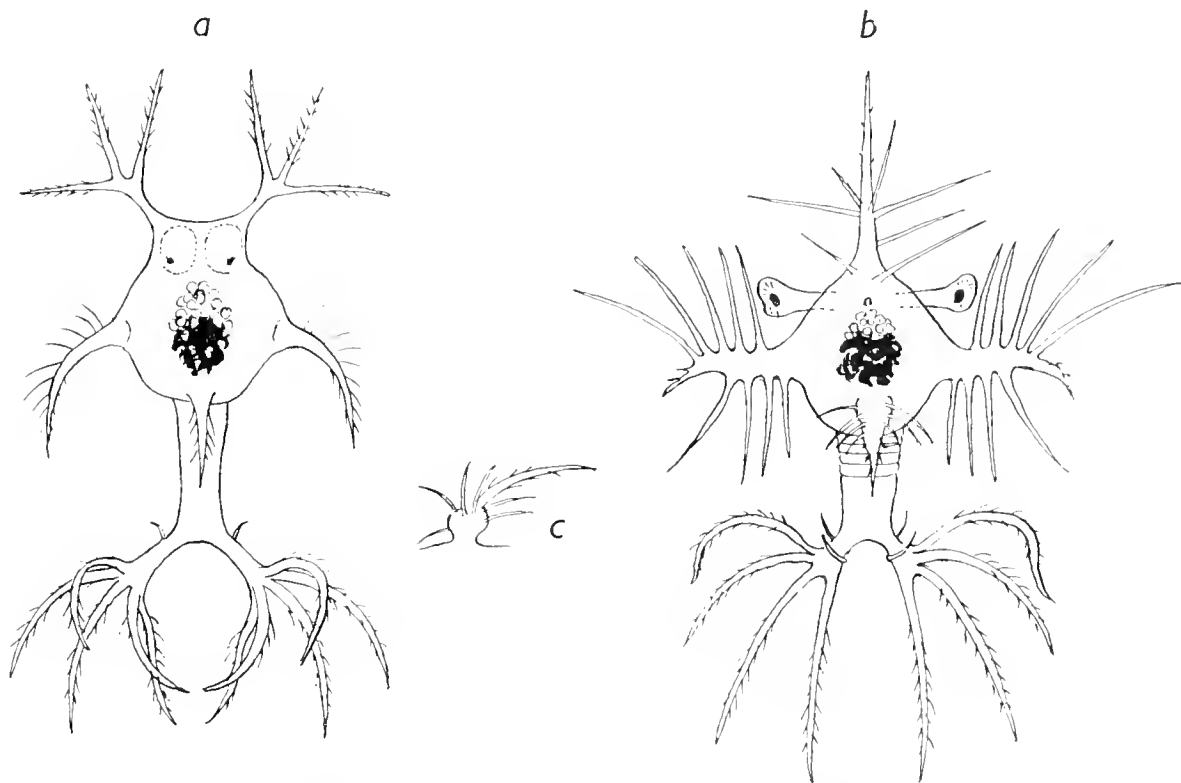


Fig. 1. *S. atlanticus*. a, Elaphocaris 1; b, Elaphocaris 2; c, dorsal spine from side.

DESCRIPTION. Elaphocaris 1 (Fig. 1 a). Length 0.8 mm.

Anterior process dividing into three equal denticulate spines. Lateral process curved backwards, denticulate, and without spines. Posterior process about two-thirds length of abdomen, denticulate, without spines. Telson branches long and narrow, the long spines subequal.

Elaphocaris 2 (Fig. 1 b, c). Length 1.3 mm. Rostrum 0.94 mm.

Rostrum as long as carapace, with seven spines, rather irregularly arranged. Lateral process with five anterior and four posterior spines. Posterior process swollen at base,

¹ We have in all cases omitted references which have already been given by Hansen.

² The colour is indicated by black or stippling in the figures.

with a group of six spines on each side of this basal part, but none on distal part. Labrum with long spine. Eye small, with slender stalk.

Elaphocaris 3 (Fig. 2). Length 1.76 mm. Rostrum 1.0 mm.

Rostrum about $1\frac{1}{2}$ times length of carapace, without lateral spines, but with three long ventral spines. Supraorbital process very long, curving inwards to meet and overlap the process of the opposite side, and armed with about 15 spines. Lateral process long and slender, with 17–20 spines. Posterior process springing from a large swelling which bears 16 spines arranged in a circle.

Abdominal somites with pleural spines. Telson branches very divergent, slender.

Eyeball large asymmetrical, on long slender stalk; total length of eye nearly equalling length of thorax.

The figure of this stage is taken from a specimen which began to moult while the drawing was being made; the abdomen has been drawn in from the moulted skin, and is probably shown too elongated.

Colour of *Elaphocaris*. Body colourless except for a large patch of vermilion in gastric region. The exopod of the antenna in stage 3 may also be red.

Acanthosoma 1 (Fig. 3 *a, b*). Length 2.8–3.2 mm. Rostrum 1.25 mm.

Rostrum longer than antennule, nearly smooth, with very small basal spine. Supraorbital spine very nearly as long as eye. Hepatic spine long. Lateral spines and posterior dorsal spine long, with small prickles. Dorsal organ a small papilla.

Abdominal somites with dorsal spines increasing from 1 to 4, those of 5 and 6 a little shorter than 4; median ventral spines absent. Lateral spines decreasing from in front backwards, each with basal spine and 1–3 with rather large spinules; that of somites 4 and 5 very small. Telson nearly twice as long as wide, with large lateral spines; branches of distal fork slender, parallel, nearly as long as telson, with two outer and two inner small spines.

Eye about one-quarter length of body, with long slender stalk about $1\frac{1}{2}$ times as long as the greatest width of the very asymmetrical eyeball. Pigment in preserved specimens very pale. There is a very small papilla near end of stalk on anterior dorsal surface. Antennal scale with five stout apical setae and a small outer spine near distal end (Fig. 3 *b*); flagellum nearly as long as body, fully segmented. Pleopods small. In one specimen, moulted from the *Elaphocaris*, pleopods 2–5 have very small inner lobes which one would suppose to be rudiments of endopods; but these are absent in next stage from all but pleopod 5. Exopod of uropod slender, setose part 1.6 times as long as bare part.

Colour. Vermilion in gastric region only, and at end of antennal flagellum.

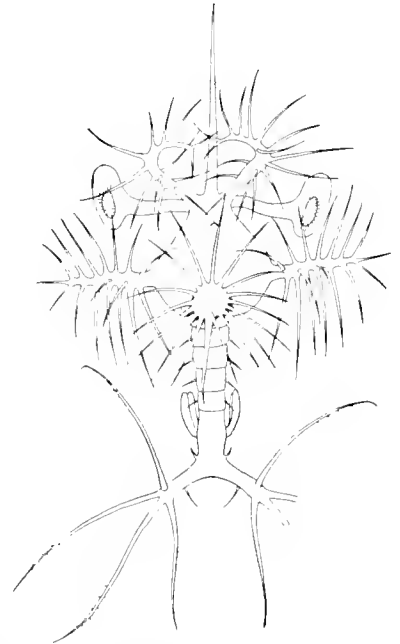


Fig. 2. *S. atlanticus*. *Elaphocaris* 3.

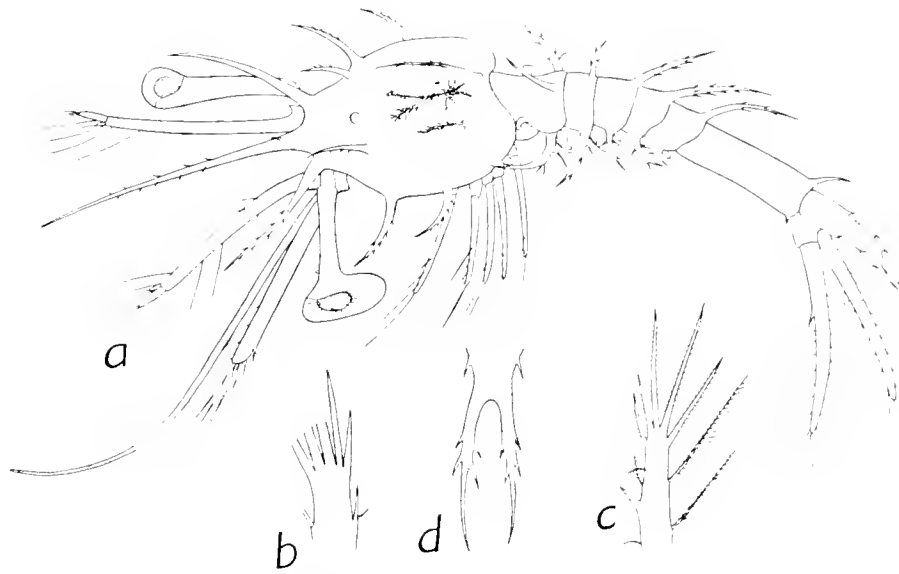


Fig. 3. *S. atlanticus*. a, Acanthosoma 1; b, end of antennal scale; c, Acanthosoma 2, end of antennal scale; d, telson.

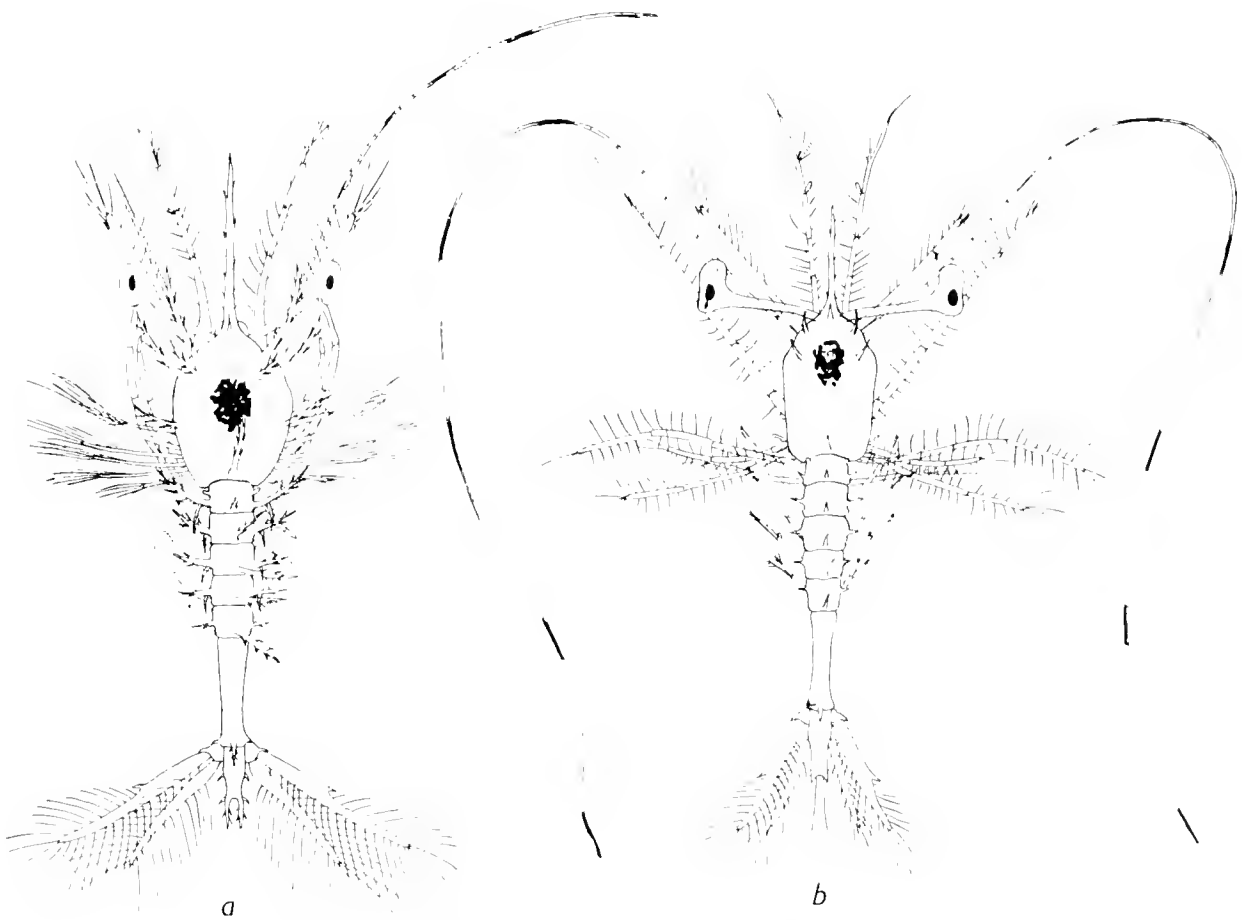


Fig. 4. *S. atlanticus*. a, Acanthosoma 2; b, Mastigopus 1.

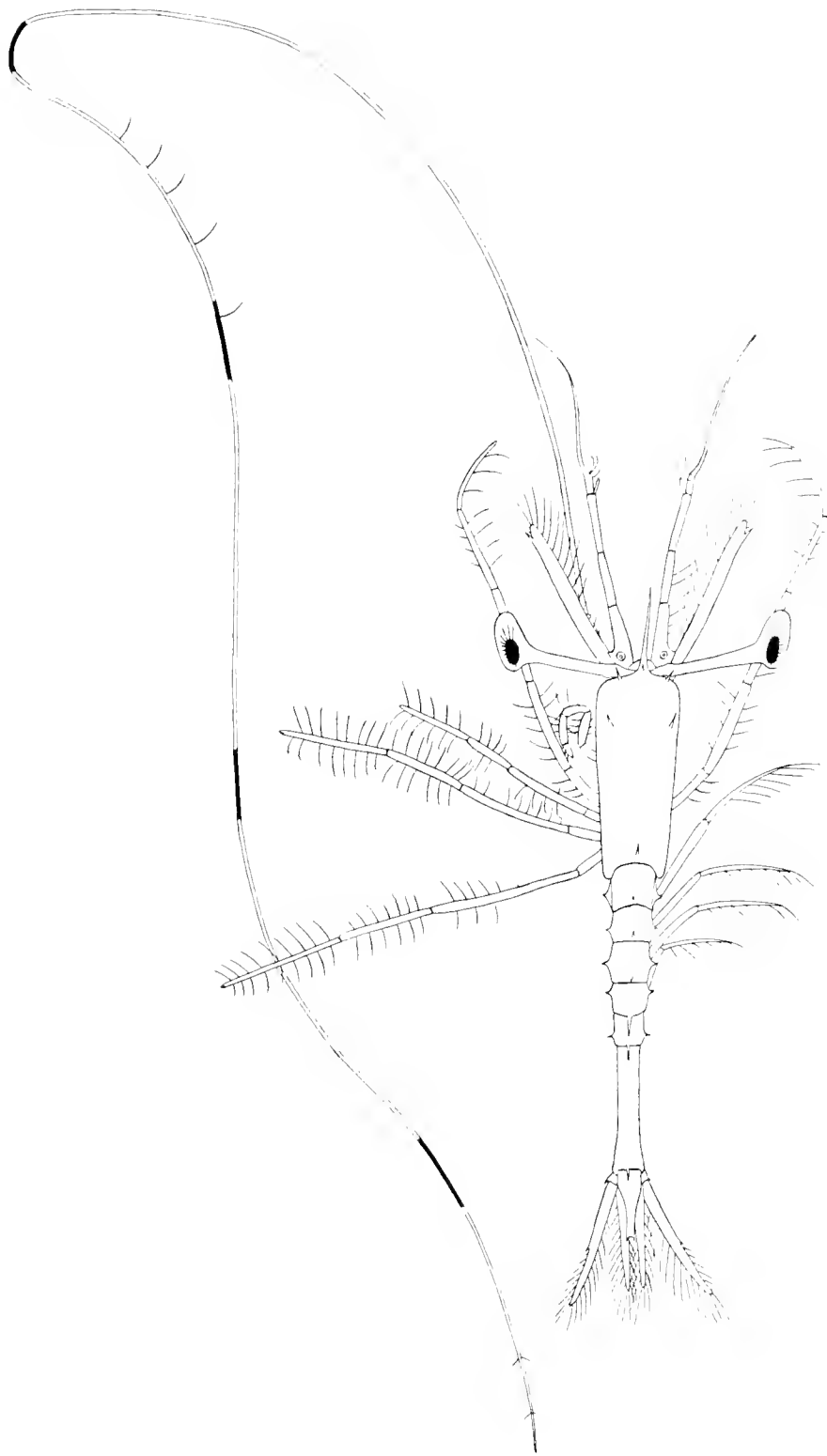


Fig. 5. *S. atlanticus*. Mastigopus, 6 mm.

Acanthosoma 2 (Figs. 3 *c*, *d*, 4 *a*). Length 3.34–4.0 mm. Rostrum 0.83 mm.

General form as in stage 1. Antennal scale differing little from that of stage 1, but having a relatively larger outer distal spine. Pleopods large, with rudiment of endopod on pleopod 5 only. Exopod of uropod with setose part 1.3 times as long as bare part.

Mastigopus 1 (Figs. 4 *b*, 5). Length 3.9 mm. Rostrum 0.7 mm.

Rostrum nearly reaching end of segment 1 of antennule, basal spine large. Supra-orbital and hepatic spines large. Posterior dorsal spine present, small. Dorsal organ a small papilla.

Abdominal somites with small dorsal and pleural spines, the dorsal spines increasing somewhat in length from in front backwards. Telson slender, nearly three times as long as wide, with small apical fork. There may be one, or two, small spines on outer margin at end.

Eye with very long slender stalk and very asymmetrical eyeball. In preserved material the pigment is very pale, sometimes almost absent. Antennal scale very long and slender, about fourteen times as long as wide; flagellum about twice as long as body.

Mandibular palp absent, or represented by a very minute papilla. Legs with vestiges of exopods; endopods of legs 4 and 5 absent. Pleopods very long, with setose endopod on pleopod 5; pleopod 4 may have a rudiment of endopod, but there is no trace of it on 1–3. Exopod of uropod very slender, about ten times as long as wide, the bare part a little longer than the setose part (1.25:1).

Colour as in *Acanthosoma*; colourless except for vermilion mass in gastric region, and red bands on antennal flagellum.

Fig. 5 shows a specimen of 5.2 mm. (rostrum .6 mm.) in stage 2 or 3, in which the antennal flagellum is very much longer and sharply bent, but with the curved setae not yet fully developed. Legs 4 and 5 are beginning to regenerate. The mandibular palp is present, though still rudimentary.

A *Mastigopus* of about 12 mm. moulted to a young male with rudiment of petasma. The two pairs of "organs of Pesta" were noted in the last *Mastigopus*.

Sergestes cornutus Kröyer

Sund, 1920*b*, Pl. 1, fig. 1, *Acanthosoma* 2.

Hansen, 1922, p. 57, *Mastigopus*.

Illig, 1927, fig. 123, *Elaphocaris* 3.

MATERIAL. Common at Bermuda. The three *Elaphocaris* stages can be connected with each other with certainty by their characteristic colour. The connexion of *Elaphocaris* with *Acanthosoma* and *Acanthosoma* with *Mastigopus* was established by moult.

DESCRIPTION. *Elaphocaris* 1 (Fig. 6 *a*). Length 0.9 mm.

Anterior process trifold, the branches with long spinules at end, and posterior branch

again divided at end. Lateral process short, at right angles to carapace, with long spines near base. Posterior process stout, with three pairs of spines. Telson branches slender, very divergent, spine 5 shorter than spine 4.

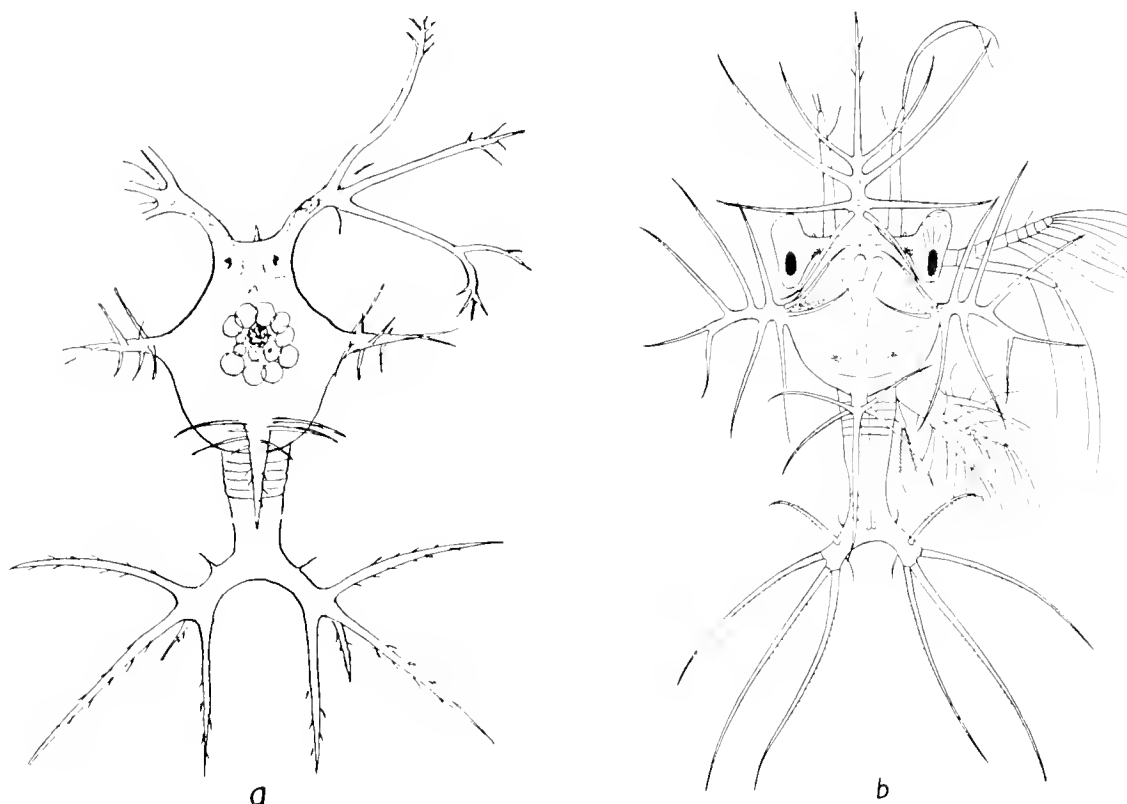


Fig. 6. *S. cornutus*. a, Elaphocaris 1; b, Elaphocaris 2.

Elaphocaris 2 (Fig. 6 *b*). Length 1.3 mm. Rostrum 0.98 mm.

Rostrum very long, with four pairs of lateral and two ventral spines. Posterior process very long, with two pairs of spines. Telson branches divergent, about twice as long as wide, spine 5 shorter than spine 4.

Eye very large, asymmetrical, greatest width of eyeball nearly equal to length of eye. Eyestalk with small anterior papilla. Labral spine large.

Elaphocaris 3 (Fig. 7 *a, b*). Length 2.5 mm. Rostrum 1.0 mm.

Rostrum very much longer than antennule, without lateral spines, but with two long and five short ventral spines. Supraorbital process slender, with numerous spines (12-19). Lateral process slender, with 12-14 spines. Posterior process reaching to end of body; with four pairs of spines.

Abdominal somites with very small pleural points. Telson branches almost at right angles to body-axis; spine 5 shorter than spine 4.

Eye very large, as in stage 2.

Colour. In stage 1 the body is colourless except for a trace of vermilion in gastric region and in eye, and a patch of brownish orange in base of anterior horns. In stages 2

and 3 the brown-orange colour has extended over the sides of the thorax and abdomen, and the red in the gastric region is enlarged. The brown-orange colour is very distinctive.



Fig. 7. *S. cornutus*. *a*, Elaphocaris 3; *b*, rostrum, side view.

Acanthosoma 1 (Fig. 8 *a, d*). Length 3.5 mm. Rostrum 0.96 mm.

Rostrum longer than antennule, with numerous lateral spinules. Supraorbital spines longer than eyes. The two pairs of lateral spines stout, with many long lateral spinules. Hepatic spines very stout, with many spinules. Posterior spine small, spiny. Dorsal organ a very small papilla.

Abdominal somites with very long dorsal spines. Lateral spines very long, that of somite 2 the shortest, and 3–5 increasing in length. No median ventral spines. Telson long and slender, its branches reaching nearly to end of uropods. Length to base of fork twice the width, with long slender lateral spines. Arms of fork slightly divergent, about three-quarters length of telson, with two outer and two inner spinules.

Eye very large and asymmetrical, total length of eye nearly one-quarter of length of body. Antennal scale with four apical setae not very distinct in size from the inner

marginal setae: one slender outer seta near end. Flagellum very long, segmented, with a pair of small spines near base and on penultimate segment. Pleopods very small. Uropods slender, the setose part of the exopod not much longer than the bare part (1.3:1).

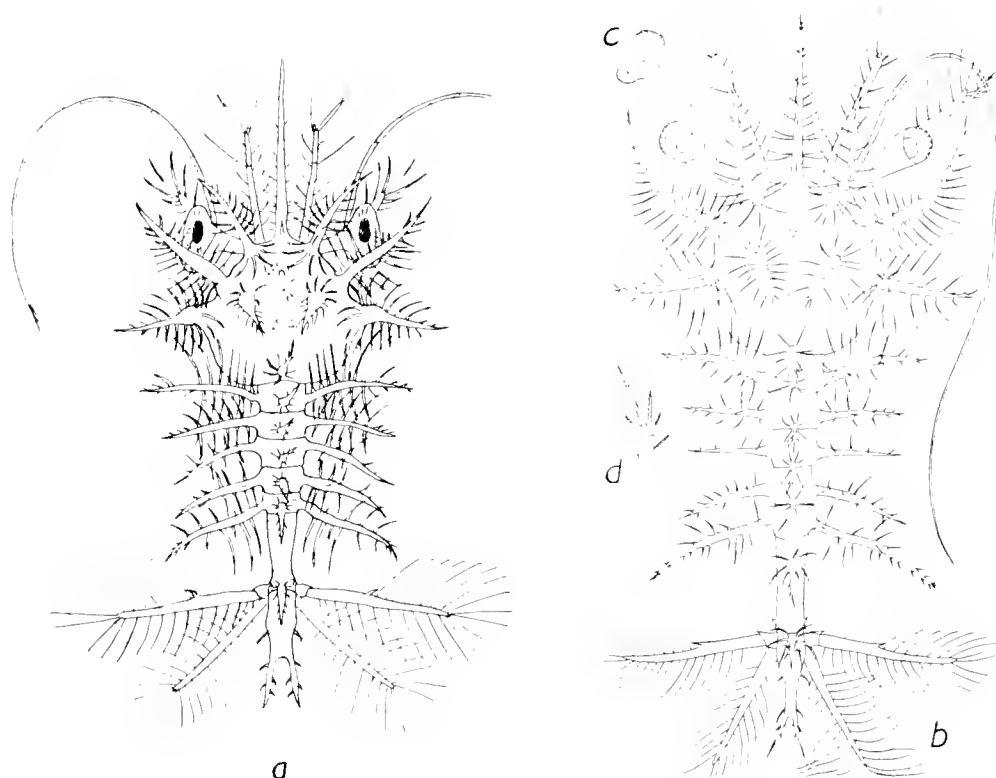


Fig. 8. *S. cornutus*. *a*, Acanthosoma 1; *b*, Acanthosoma 2; *c*, eye in side view; *d*, end of antennal scale in stage 1.

Acanthosoma 2 (Fig. 8 *b, c*). Length 4.2 mm. Rostrum 1.6 mm.

General form as in stage 1. Lateral spine of somite 3 shorter and more slender than the others, and that of somite 5 much the longest. Telson the same but more slender. Antennal scale with very long apical spine; flagellum about as long as body without telson. Pleopods variable, but may be very long. Maxillipede 3 very long, reaching near end of antennule.

Colour. The brown-orange colour of the *Elaphocaris* is lost, and the body is colourless, except for a large patch of vermilion in the gastric region.

Mastigopus 1 (Fig. 9 *a, b*). Length 4.8 mm. Rostrum 0.83 mm.

Rostrum longer than segment 1 of antennule; basal spine very small. Supraorbital and hepatic spines small; posterior dorsal spine minute. Dorsal organ present.

Abdominal somites with small dorsal spines, of which the fourth is the longest, and long pleural points somewhat procurved. The large hook-shaped pleural spine of somite 5 is a striking character by which the species may be easily recognized. Telson long and slender, more than three times as long as wide, and reaching to near end of

uropod. The apex is truncate, with a very small spine at each angle and a pair of setae and spines between.

Eye with very long stalk, the whole about one-third the length of the body. Antennal scale very long and slender, with long apical spine; flagellum nearly twice length of body, without curved setae.

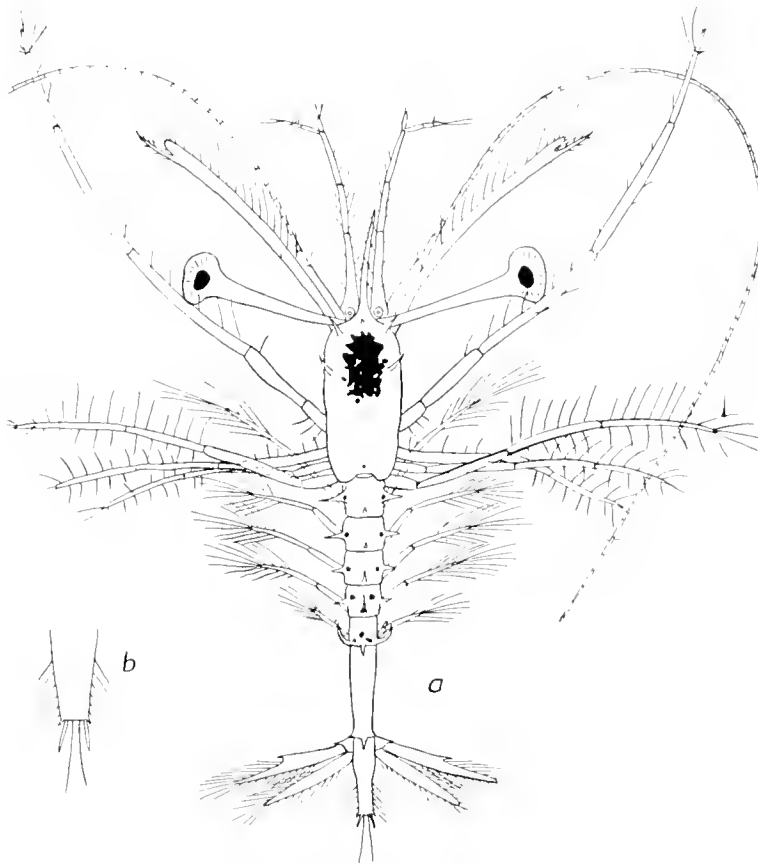


Fig. 9. *S. cornutus*. a, Mastigopus 1; b, telson.

Mandibular palp very small, unsegmented. Maxillipede 3 reaching far beyond antennules. Hansen has noted the great length of this appendage in young Mastigopus as compared with the adult, a feature which would, if its later development were not known, place it in Hansen's group II. Legs with small vestiges of exopods. Pleopods long, with small rudiment of endopod on pleopod 5 only. Uropod with bare part slightly longer than setose part (1.09 : 1).

Stage 2 (Fig. 10) differs very little from stage 1. The legs have no vestiges of exopods, and the pleural spines are reduced. In this specimen the dorsal spines of abdominal somites 1-3 were lost.

Two pairs of "luminous organs" (organs of Pesta) in the thorax were noted in specimens of 8 mm. upwards. At a size of 9 mm. the mandibular palp is of full size, but with relatively few setae. The form of the uropods is also changed to that of the adult. The antennule of the male takes the adult form in the last Mastigopus of 12 mm.

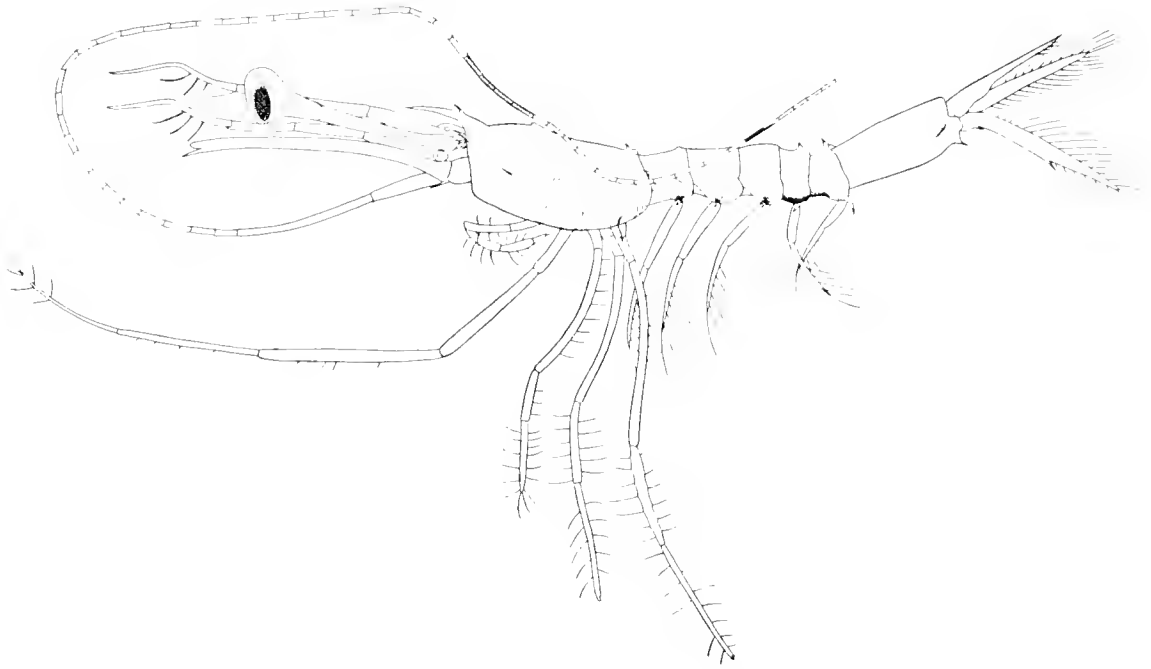


Fig. 10. *S. cornutus*. Mastigopus 2.

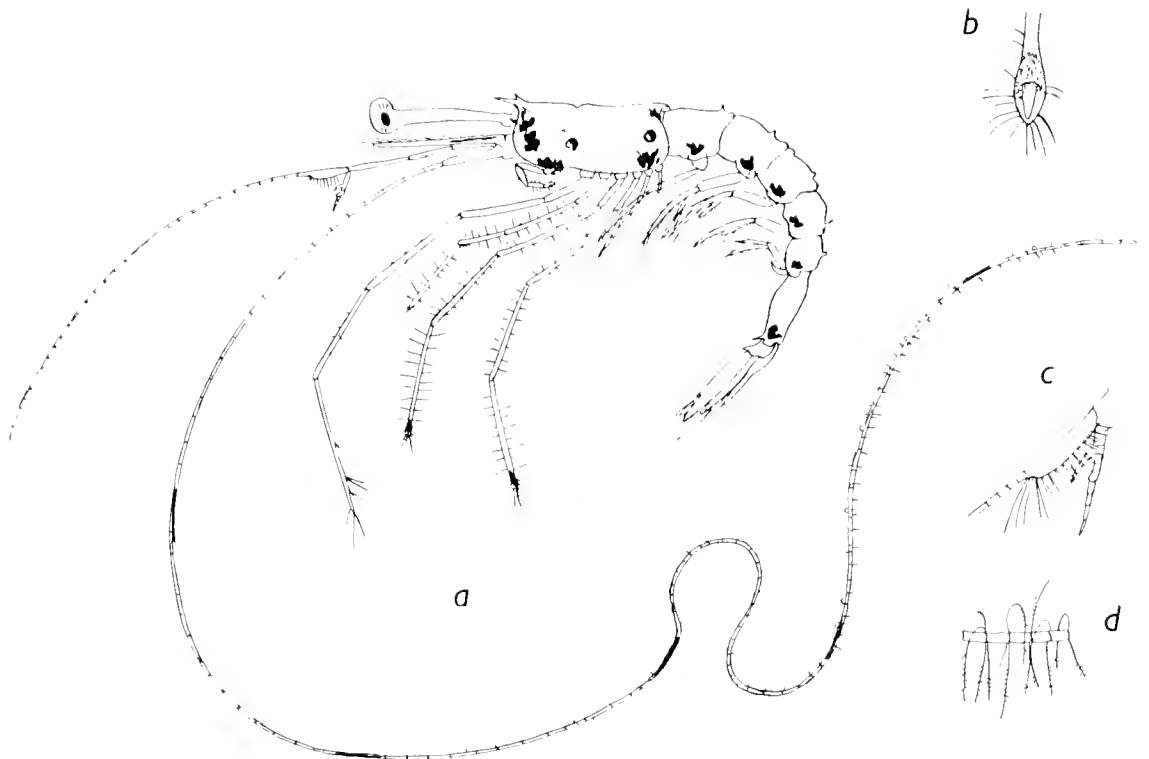


Fig. 11. *S. cornutus*. *a*, Mastigopus 12.5 mm.; *b*, end of leg 2; *c*, antennule; *d*, detail of antennal flagellum.

Hansen has noted that the sex is distinguishable at this stage by presence of a rudimentary petasma.

The dorsal spines of the abdomen may persist to the last Mastigopus stage (Fig. 11 *a-d*), and the pleural hook of somite 5 is also retained. The penultimate segment of maxillipede 3 in this stage is markedly dilated, and the propods of legs 2 and 3 have also a characteristically dilated form in all the later stages.

Colour. In the first and second mastigopus there is a large patch of vermilion in thorax (several patches in later stages). Somites 4 and 5 have 3 chromatophores, and in some cases these are expanded so that the whole of somite 4 is strikingly red. Antennal flagellum at first colourless, later banded with red. Tips of maxillipede 3 and legs 2 and 3 red, the colour sometimes absent in the first stage.

Sergestes arcticus Kröyer

Dohrn, 1870*c*, Pl. XVI, fig. 28, *Elaphocaris* 3.

Hansen, 1922, p. 68, Mastigopus; p. 70, *Acanthosoma*.

Illig, 1927, p. 308, Mastigopus.

The development from the first *Elaphocaris* has been thoroughly described by Wasserloos (1908), but we think it may be convenient to give some description of it here. The *Acanthosoma* figured by Illig differs greatly from *S. arcticus* in the form of the telson and length of the abdominal pleural spines. It appears to belong to *S. robustus*.

MATERIAL. This species was not found at Bermuda. We are indebted to Mr F. S. Russell for numerous specimens of all stages from *Elaphocaris* 2 taken in the Atlantic (49° 53' N, 11° 3' W). We have also specimens of the *Acanthosoma* and Mastigopus from Discovery Stations 100 (33° 21' S, 15° 18' E), 102 (35° 29' S, 18° 33' E), 278 (off Port Gentil, French Congo), and 714 (35° 09' S, 47° 00' W). An *Acanthosoma* from Terra Nova Station 251 (54° 2' S, 177° 0' W, New Zealand) seems to be indistinguishable from *S. arcticus*. Hansen (1903, p. 59) has identified *S. arcticus* in the Challenger collection from off Monte Video and south of Australia, while Stebbing has recorded it from the Cape. The distribution of the larvae is therefore in agreement with that of the adult.

DESCRIPTION. *Elaphocaris* 2 (Fig. 12 *a*). Length 1.2 mm. Rostrum 0.92 mm.

Rostrum with three pairs of lateral spines, which are smooth but with the ends split and brush-like. The spines of the lateral and posterior processes have also the same brush-like ending which is most characteristic of the species. Lateral process with eight spines. Posterior process with three pairs of lateral spines. Dorsal organ present, small. Eye small, pear-shaped, with small inner ventral papilla. Maxillipede 3 without setae.

Elaphocaris 3. Length 2.15 mm. Rostrum 1.34 mm.

Rostrum without lateral or ventral spines. Supraorbital process long and slender, with nine brush-ended spines. Posterior dorsal process with five pairs of similar spines. Abdominal somites with pleural points.

Telson arms very divergent, about twice as long as wide.

Acanthosoma 2 (Fig. 12 *b, c*). Length 4.8 mm. Rostrum 1.4 mm.

Rostrum with large basal spine. Supraorbital spine much shorter than eye. Hepatic, two pairs of lateral and posterior dorsal spines about equal. Dorsal organ small. Dorsal spines of abdominal somites 1 and 2 shorter than those of somites 3-5; lateral spines

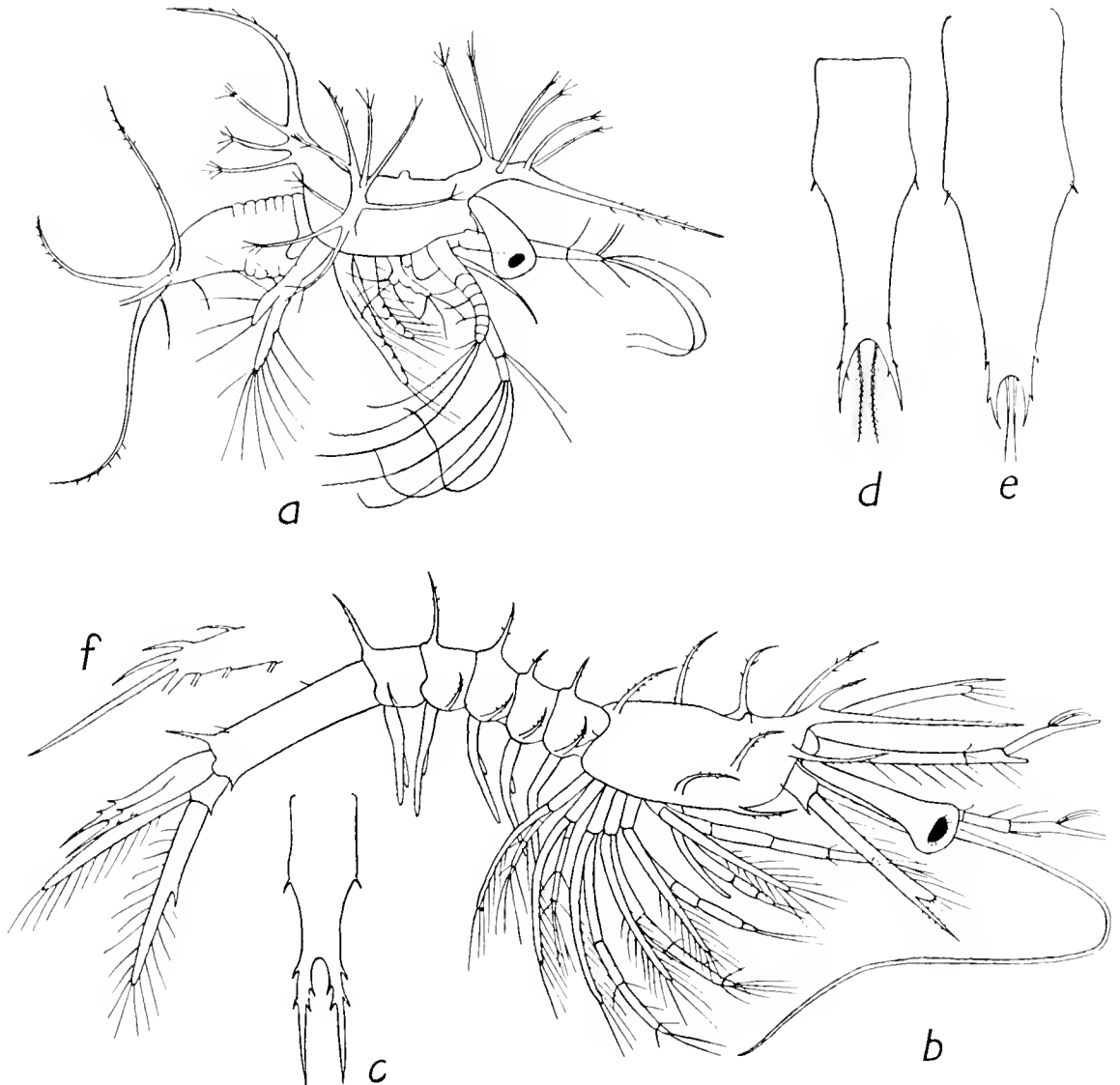


Fig. 12. *S. arcticus*. *a*, *Elaphocaris* 2; *b*, *Acanthosoma* 2; *c*, telson; *d, e*, telson of *Mastigopus* 5 and 7 mm.; *f*, antennal scale of *Acanthosoma* 1.

decreasing backwards, those of somite 5 small. Basal part of telson more than twice as long as wide, with small lateral spines; arms parallel, about three-quarters length of basal part, with two inner and two outer spines.

Eye about one-quarter length of body, the eyeball nearly round and less than one-third length of eye. There is a very small anterior papilla. Antennal scale very slender, with long apical spine; flagellum 5 mm. Mandibular palp present, unsegmented.

Pleopods 2-5 with rudiments of endopods. Uropod with bare part a little shorter than setose part, and ten times as long as wide.

Stage 1 differs only from stage 2 in size (3.6 mm.; rostrum 1.48 mm.), smallness of pleopods and form of antenna (fig. 12 *f*). The latter has a long flagellum (2.15 mm.) with a pair of very small spines near the base and another pair on the penultimate segment. A rudiment of the mandibular palp is present.

Mastigopus 1 (Fig. 12 *d, e*). Length 5.1 mm. Rostrum 0.99 mm.

Carapace with very small supraorbital and long hepatic spines. Posterior dorsal spine minute.

Abdominal somites with very minute dorsal spines on somites 1-3, those of 4-6 long and nearly equal. Pleura with small points. Telson $2\frac{1}{2}$ times as long as wide, with distal fork, each arm bearing a small inner and an outer spine; there is also a pair of small spines just in front of the fork.

Eye one-quarter length of body, of same shape as in *Acanthosoma*. Flagellum of antenna 16 mm., without kink and without curved setae. Mandibular palp small, two-segmented, with three apical setae. Legs with trace of exopods. Uropod seven times as long as wide, the bare part about equal to the setose part. Pleopods very long, 2-4 with small endopods without setae: endopod of pleopod 5 long, setose.

Sergestes tenuiremis Kröyer

Hansen, 1922, p. 86, Mastigopus; p. 89, *Acanthosoma*.

Gurney, 1924*c*, p. 88, fig. 2, *Elaphocaris* 2.

MATERIAL. This species was not common at Bermuda, and it has not been identified in the Discovery material. A moult was obtained from *Elaphocaris* 3 to *Acanthosoma*, but the cast skin was very fragmentary. It was, however, quite clear that the *Elaphocaris* was of the *hispida* type. We have no doubt that the two stages described belong to this species, partly by reason of the agreement in colour between them and the *Acanthosoma*, and partly because we have identified with reasonable certainty the only other forms of this type as belonging to *S. crassus* and *S. robustus*.

DESCRIPTION. *Elaphocaris* 2 (Fig. 13 *a*). Length 1.6 mm. Rostrum 1.12 mm.

Rostrum, lateral and dorsal processes simple, very long, and with numerous spinules, the lateral processes curving backwards. Telson arms long and slender. Eye short; eyeball large and asymmetrical.

Elaphocaris 3 (Fig. 13 *b*). Length 1.8 mm. Rostrum 1.12 mm.

Carapace with long supraorbital spines, and a pair of very small spines behind them and in front of the very small dorsal organ. Lateral processes very long, the spinules at their base in front longer than the rest, and recalling the "epaulette" found in *S. robustus*. Posterior process very long. Abdominal somites with small lateral spines. Telson arms long and slender.

Eyes on slender stalks, the eyeball large and asymmetrical, the greatest width nearly equal to total length of eye.

Colour. Body colourless in stage 2 except for a red spot at base of telson and in each arm of it. In stage 3 there is red in the antennular peduncle, in both branches of the antenna, and in the arms of the telson fork.

Acanthosoma 1 (Figs. 13 *c*, 14 *a*). Length 6.0 mm. Rostrum 1.4 mm.

Rostrum a little longer than the antennule, about equal to length of carapace. Of this stage we have only two specimens and in one of them the spine at the base of the rostrum is very long and spinulose (Fig. 13 *c*), whereas in the other it is minute (fig. 14 *a*), as it is shown in Hansen's figure of stage 2. Carapace about $1\frac{1}{2}$ times as long as wide.

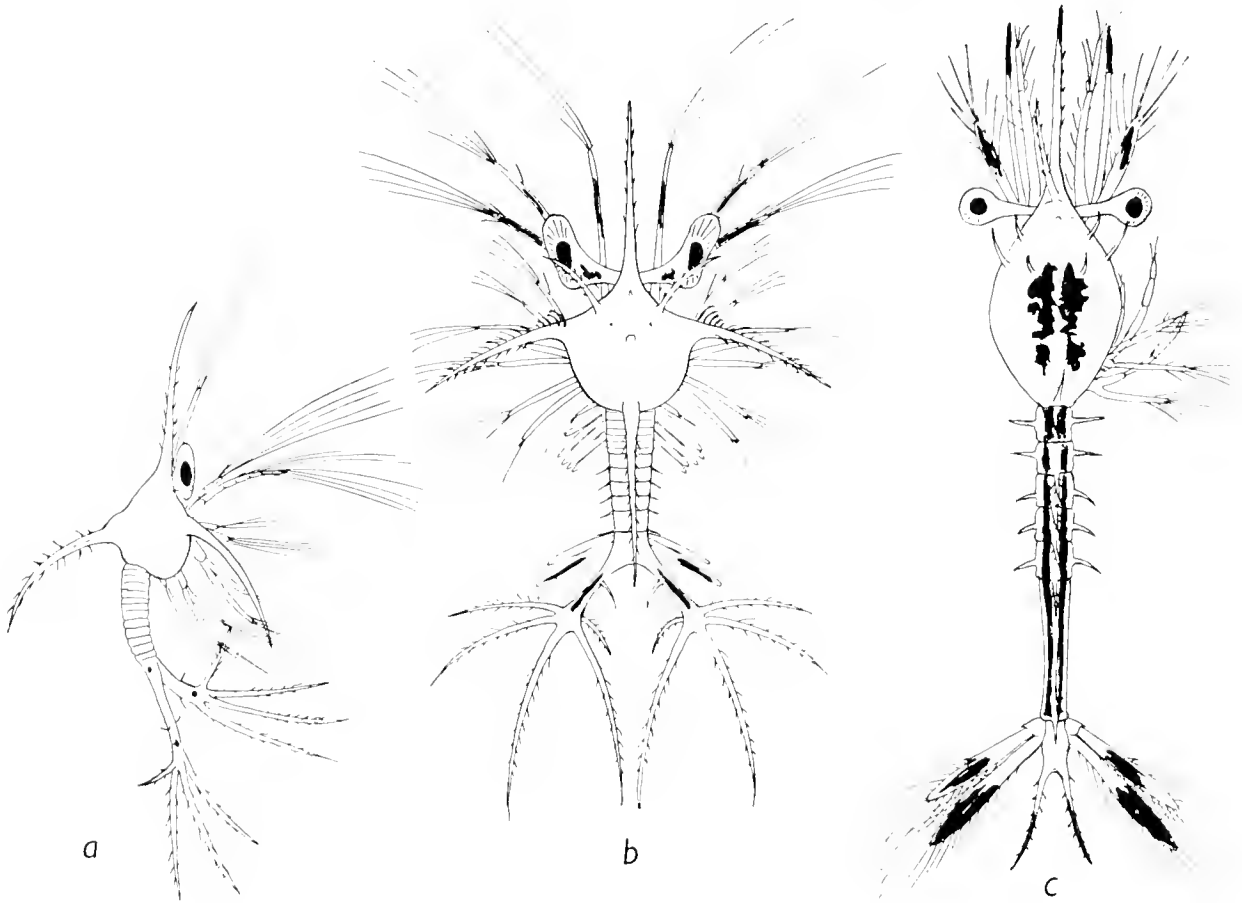


Fig. 13. *S. tenuiremis*. *a*, Elaphocaris 2; *b*, Elaphocaris 3; *c*, Acanthosoma 1.

One pair of short lateral spines with spinules; hepatic and dorsal spines small. Abdominal somites with dorsal spines rather small; spine of somite 1 smallest, smooth, 3-6 longer, with spinules. Lateral spines small, slender and smooth or nearly so. No median ventral spines. Telson $1\frac{1}{2}$ times as long as wide, without lateral spines; arms very long and slender, reaching beyond uropods, and with six outer and five inner spines.

Eye large, asymmetrical, the greatest width more than one-half total length, and total length nearly one-sixth length of body. Antennal scale six times as long as wide, with four apical and one outer seta; endopod longer than scale, with two very small inner spines. Labral spine very small. Pleopods minute. Endopod of uropod distinctly wider

and longer than exopod; exopod seven times as long as wide, the bare margin a little longer than setose part.

Colour. Bright red in thorax and throughout abdomen, and in arms of telson. Tips of rostrum, antennal scale, flagellum and uropods red. Setae of uropod yellow.

Acanthosoma 2. Length 5 mm. Rostrum 1.41 mm.

Mastigopus. The slender elongated form of the thorax is a very striking characteristic of this species and is shown in Bate's figures of *S. junceus* and *S. longicollus*, which are young Mastigopus stages.

We have only two specimens from Bermuda, of 6.5 and 7.8 mm. respectively, the former probably in stage 1. The latter was obtained by moult, but the moulted skin is too damaged to be of use in determining the stage, though it is believed to be stage 1.

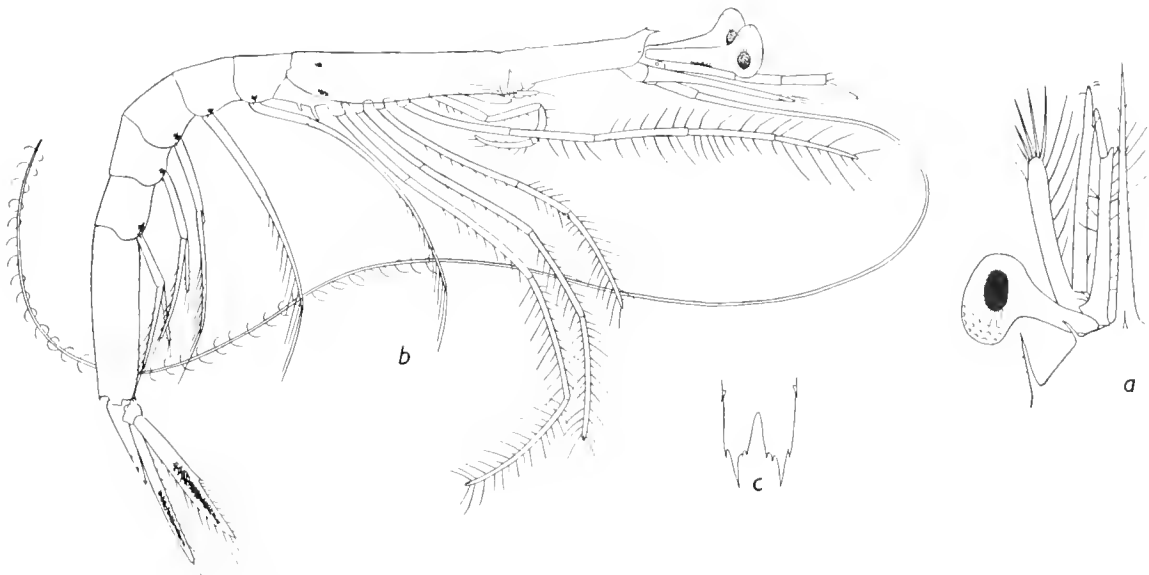


Fig. 14. *S. tenuiremis*. *a*, Acanthosoma 1, head of specimen moulted from *Elaphocaris*; *b*, Mastigopus 2 ? 7.8 mm.; *c*, telson.

Mastigopus 2 (?) (Fig. 14 *b*, *c*). Length 7.88 mm.

Rostrum very short, with strong basal tooth. Supraorbital spines present, but no hepatic. Abdomen without dorsal spines, but with small pleural points on each somite. Telson with deep median incision, each arm with one outer and two inner spines.

Eye less than one-seventh length of body (1 : 7.57), its length twice the greatest diameter of eyeball. There is a very small papilla on anterior face of stalk. Segments 2 and 3 of antennule equal. Antennal flagellum longer than body, without kink, but with curved setae in distal half. Mandibular palp present, unsegmented. Legs 4 and 5 very small, rudimentary. Pleopods long; 1 and 2 without endopod, 3 with non-setose endopod and 4 and 5 with setose endopods. Exopod of uropod six times as long as wide, the bare part considerably longer than the setose part (1 : 0.71).

The specimen of 6.5 mm. differs in having small dorsal spines on somites 4-6, the arms of the telson more slender, and the antennal flagellum shorter and without curved setae. In this specimen pleopods 2-5 each have endopods without setae.

Colour. Red patches as shown in Fig. 14 *b*.

Sergestes crassus Hansen

Hansen, 1922, p. 102, Mastigopus.

Gurney, 1924, p. 87, fig. 25, Elaphocaris 2; p. 94, fig. 32, Acanthosoma 2.

MATERIAL. This species is common at Bermuda. The first Elaphocaris was not identified, but the Acanthosoma was obtained twice by moulting from Elaphocaris 3,

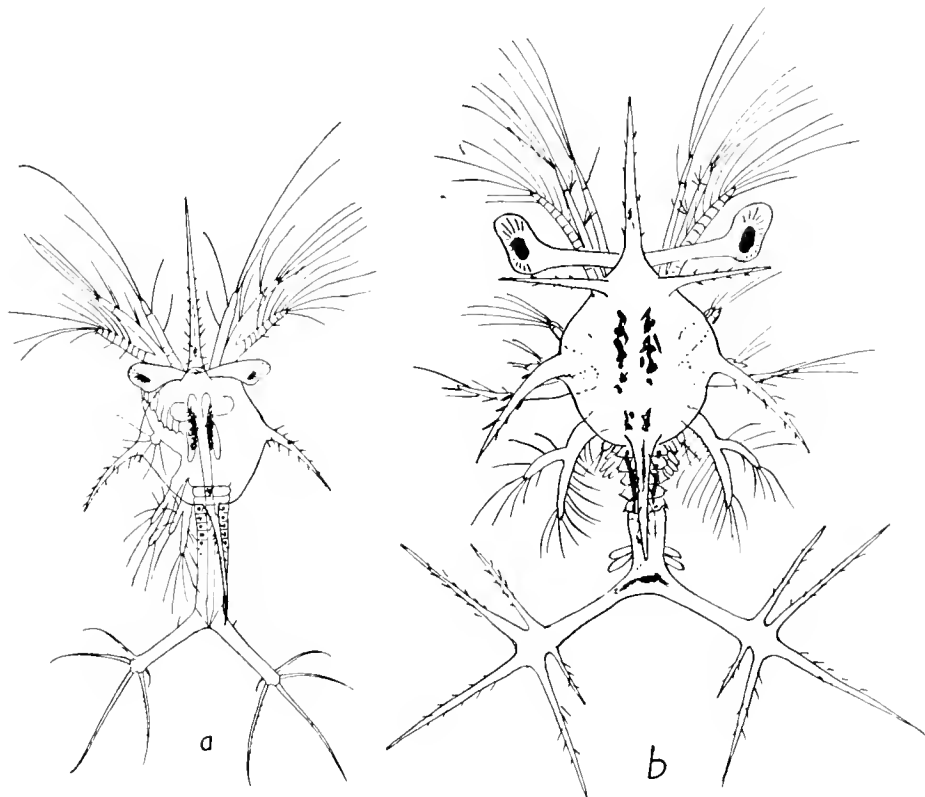


Fig. 15. *S. crassus*. *a*, Elaphocaris 2; *b*, Elaphocaris 3.

and Acanthosoma 1 moulted to Acanthosoma 2. The connexion of Acanthosoma with Mastigopus was not proved by moult, but the resemblance in form and colour is so close that we have no doubt of their identity.

DESCRIPTION. Elaphocaris 2 (Figs. 15 *a*, 16). Length 1.2 mm. Rostrum 0.91 mm.

Carapace as wide as long, with rather short, stout lateral processes and long posterior spine, reaching to end of body. Telson arms divergent, very slender, more than six times as long as wide; the spines comparatively short; spine 5 shorter than spine 4.

Eye rather pear-shaped, length a little more than half length of carapace. There is a minute ventral papilla on the eyestalk, and, in the specimen drawn, there was a pair of very small frontal organs. Labral spine very large.

Elaphocaris 3 (Fig. 15 *b*). Length 1.86. Rostrum 1.0 mm.

Rostrum much shorter in proportion than in stage 2, but about as long as carapace. Supraorbital, lateral and posterior processes very hispid. Supraorbital longer than eye. Telson as in stage 2. Abdominal somites with very small pleural spines, and with very small dorsal points.

Eye about three-quarters length of carapace, the eyeball asymmetrical. Papilla not seen in dorsal view.

Colour. Red in rostrum, and two lines down thorax and abdomen. In stage 3 there is also red in posterior dorsal process and at base of telson.

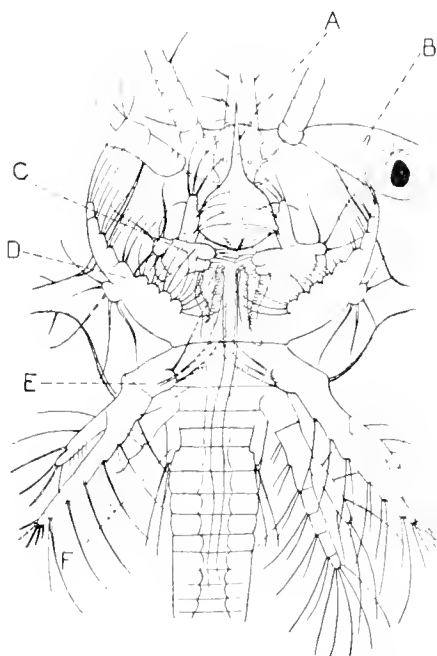


Fig. 16. *S. crassus*. Elaphocaris 2, ventral. *A*, frontal sensory papilla; *B*, ocular papilla; *C*, maxillule; *D*, maxilla; *E*, maxillipede 1; *F*, maxillipede 3.

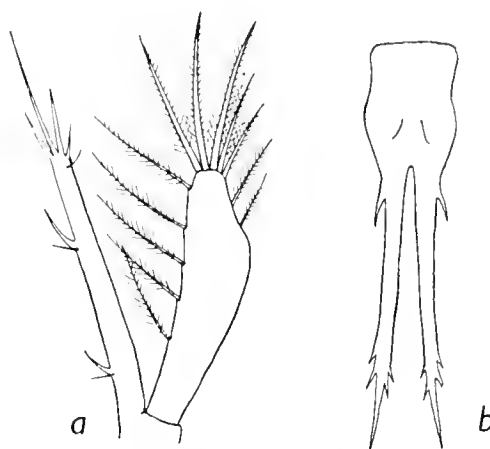


Fig. 17. *S. crassus*. Acanthosoma 1; *a*, antenna; *b*, telson.

Acanthosoma 1 (Fig. 17 *a, b*). Length 2.55 mm. Rostrum 0.85 mm.

Rostrum very spiny, with large basal spine. Supraorbital spines very small. One pair of small lateral spines. Margin of carapace with a row of spinules continuous with the spinules of the lateral spine. Dorsal organ very small. No posterior dorsal spine.

Abdominal somites with dorsal spines 1 and 2 smaller than 3-6, which are subequal. No ventral spines. Lateral spines short and prickly, decreasing backwards; that of somite 5 very small. Telson short, nearly as wide as long, but posterior fork with very long slender arms. These arms nearly parallel and reaching beyond the uropods, bearing two inner and two outer spines. The lateral spine of the telson is inserted just beyond the fork, on the arm itself.

Eye one-fifth length of body, the length not quite $1\frac{1}{2}$ times width of eyeball, which is slightly asymmetrical. No papilla seen on eyestalk. Antennal scale very broad near end, and of characteristic shape (Fig. 17 *a*); flagellum short, not much longer than scale,

unsegmented, with four small apical setae and two marginal spines. Labral spine large. Mandibular palp absent. Pleopods very small, simple. Uropods about seven times as long as wide; bare part slightly longer than setose (1 : 0.86).

Acanthosoma 2 (Fig. 18 *a*). Length 2.6 mm. Rostrum 0.74 mm.

Scarcely differing from stage 1. Antennal scale of same form, but with large denticulate spine. Flagellum not extending beyond rostrum. Mandible without palp. Pleopods very small, without endopods. Uropods unchanged.

Colour. Vermilion down sides of carapace, on legs, antennule, antennal scale, and distal part of exopod of uropod.

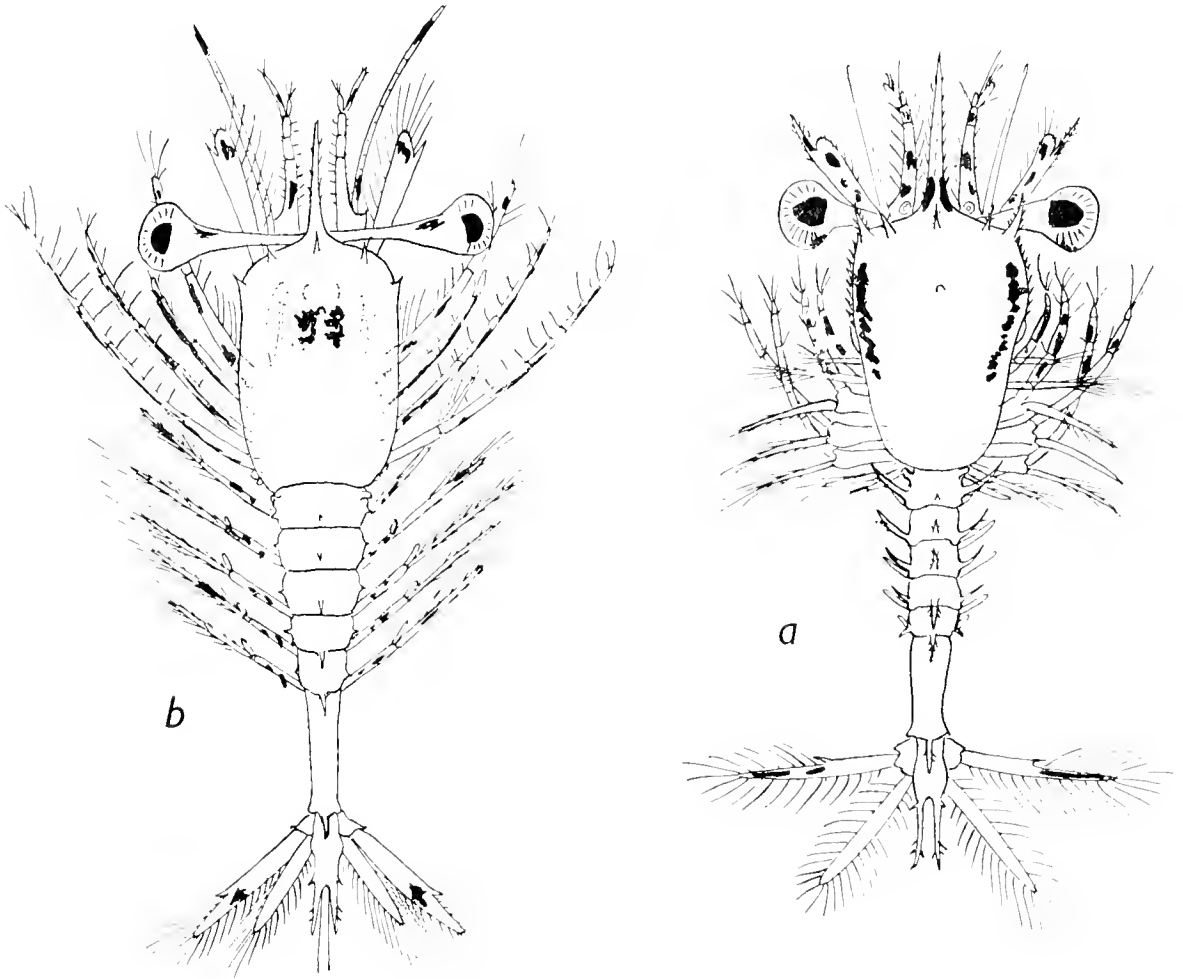


Fig. 18. *S. crassus*. *a*, *Acanthosoma* 2; *b*, *Mastigopus* 1.

Mastigopus 1 (Figs. 18 *b*, 19 *a-g*). Length 4.15 mm. Rostrum 0.75 mm.

Rostrum reaching end of peduncle of antennule; basal spine small. Carapace short, its length about $1\frac{1}{2}$ times the breadth. Supraorbital spine very small; marginal spine of *Acanthosoma* retained. Hepatic spine absent. Dorsal organ minute. Dorsal spines of abdominal somites 1-3 very small, those of 4-6 larger. Pleura rather expanded, with very small points. Telson twice as long as wide, with strong lateral spines; arms of

apical fork very slender, parallel, or even bending slightly inwards, not reaching end of uropods. Each arm with two outer spines and with or without one inner spine near apex.

Eye about one-seventh length of body, its length nearly twice the diameter of the eyeball, which is nearly round. Antennal scale widening towards the end, about five times as long as wide; flagellum about half length of body. Mandibular palp rudimentary, but with apical setae. Legs with vestiges of exopods. Pleopods very long, with rudiment of endopod on 2-5. Exopod of uropod with bare part a little longer than setose (1 : 0.8) and six times as long as wide.

The stout, broad body is characteristic of this species, and is retained in all stages. The dorsal spines of abdominal somites 4 and 5 remain up to a length of about 8 mm. The mandibular palp is still unsegmented in stage 2. At a length of about 7 mm. it is

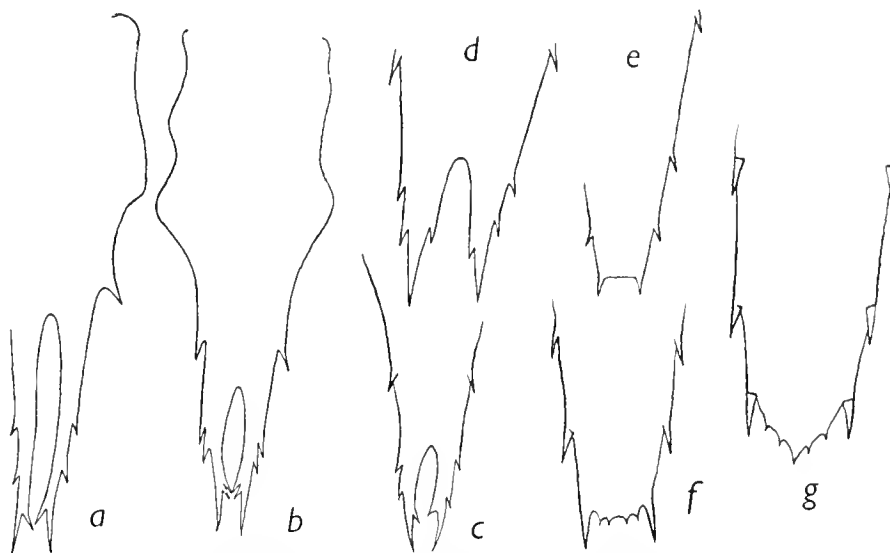


Fig. 19. *S. crassus*. Mastigopus telson. *a*, 4.2 mm.; *b*, 4.85 mm.; *c*, 4.68 mm.; *d*, 5.45 mm.; *e*, 6.95 mm.; *f*, 14 mm.; *g*, 15 mm.

large, two-segmented, and setose. The transformation of the telson is shown in Fig. 19. The largest Mastigopus is about 10 mm., and there is an immature phase, according to Hansen, up to about 20 mm., during which the petasma is formed.

Colour. Red in thorax, but abdomen colourless. Red patches in antennae and all limbs, and in exopod of uropods.

Sergestes robustus Smith

Lo Bianco, 1903, p. 182, Pl. vii, fig. 9, Acanthosoma 2.

Hansen, 1922, pp. 114, 117, Mastigopus and Acanthosoma.

Illig, 1927, fig. 62, Acanthosoma (as *S. arcticus*).

Cecchini, 1928*b*, p. 34, Mastigopus.

MATERIAL. Larvae of this species were taken but rarely at Bermuda, and only over very deep water, at depths of about 250 m. Moults were obtained of first to second Acanthosoma and of Acanthosoma to Mastigopus, but the identity of the Elaphocaris was not proved by moult.

A plankton sample from the north Atlantic ($49^{\circ} 53' N$, $11^{\circ} 3' W$) contains *Elaphocaris* of *hispid*a type and a number of specimens of *Acanthosoma* which, apart from a small difference in the uropods, agree with those of *S. robustus*. As this sample contains only larvae of this species and of *S. arcticus* we are satisfied that the *Elaphocaris* of *hispid*a form may be accepted with confidence as that of *S. robustus*. We have from Bermuda (1939) another form of *Elaphocaris* which is evidently closely related but differs markedly

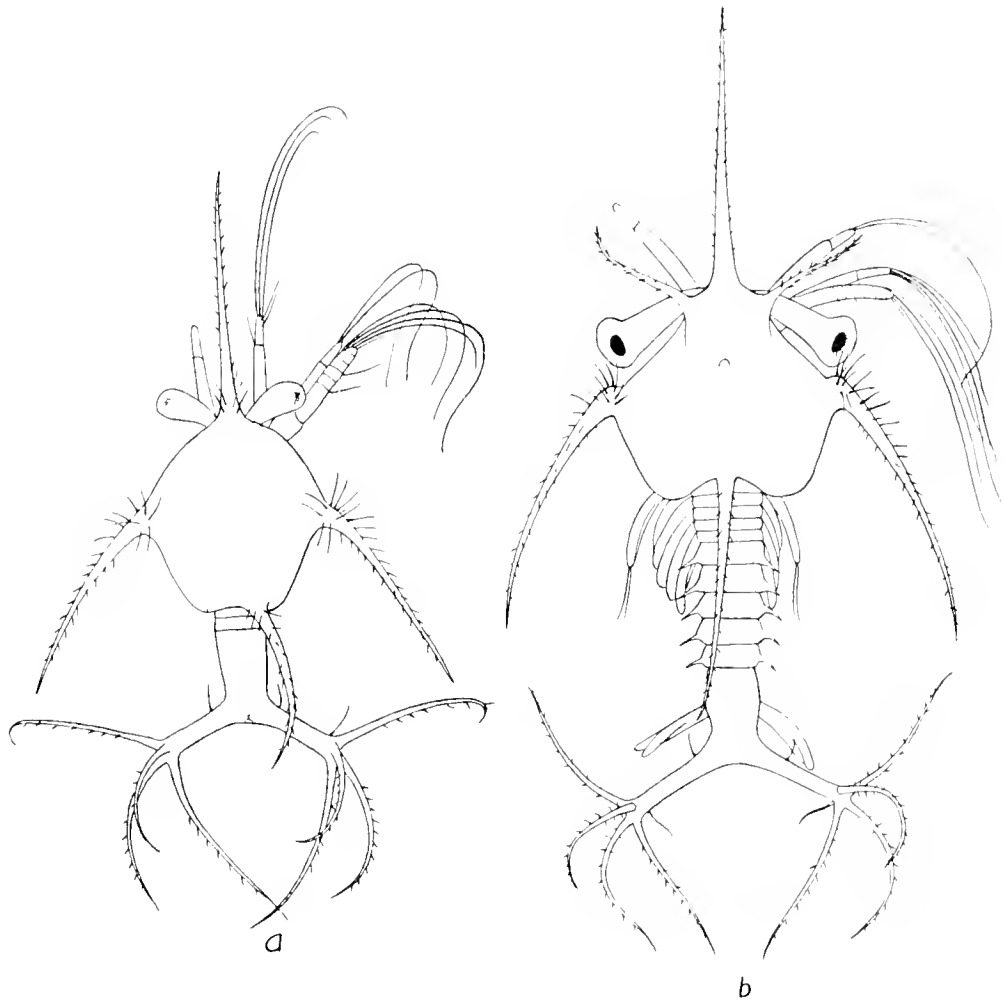


Fig. 20. *S. robustus*. a, *Elaphocaris* 2; b, *Elaphocaris* 3.

in the shortness of the telson branches. This no doubt belongs to one of the forms of *Acanthosoma* described below. As only one of these (Form D) was taken at Bermuda it may provisionally be attached to that species. The first *Elaphocaris* was, in this case, moulted to second, so that the sequence of stages is securely established.

DESCRIPTION. *Elaphocaris* 2 (Fig. 20 a). Length 1.17 mm. Rostrum 0.92 mm.

Rostrum with long spinules at base. Lateral process long, directed backwards at angle of about 50° with middle line, very prickly. There is a slight swelling at the base which bears a number of long spinules. Posterior process extending beyond end of body, with

a group of long spinules at base, but not swollen. Dorsal organ not seen. Telson arms almost at right angles to body line, long and slender.

Eye small, pear-shaped, with small anterior ventral papilla and without pigment (in formol).

Elaphocaris 3 (Fig. 20 *b*). Length 2.16 mm. Rostrum 1.28 mm.

Rostrum without long spinules at base. Supraorbital spine longer than eye. Lateral process as in stage 2, with swollen base. Posterior process not reaching end of body. Dorsal organ very small. Telson as in stage 2.

Eye large, about one-quarter length of body, the diameter of the eyeball about half length of eye.

Acanthosoma 1 (Fig. 21 *a-c*). Length 4.0–4.45 mm. Rostrum 1.5 mm.

Rostrum nearly as long as thorax. Carapace nearly twice as long as wide. Supraorbital spines shorter than eyes, with very small spinules. Hepatic spines large. Two pairs of lateral spines, of which the posterior is the smaller, with small spinules. Posterior dorsal spine short.

Abdominal somites with dorsal spines of somites 1 and 2 small, those of 3–6 larger; lateral spines very long, those of somite 5 the longest, and directed backwards at angle of 45° . Ventral spines absent. Telson twice as long as wide, with long lateral spines inserted at base of telson fork. The position of the lateral spine is somewhat variable, but it is always close to the fork. Arms of apical fork very long, slender, parallel at first and diverging towards end. Each branch has two inner and two outer marginal spines. Antennal scale of much the same shape as in *S. tenuiremis*, with five apical setae and one small outer seta; flagellum about $1\frac{1}{3}$ times as long as scale, with marginal spine at base and near end.

Eye very long and slender, about one-sixth length of body, the eyeball round, its diameter less than half length of eye. There is a small papilla on eyestalk. Mandible without palp. Pleopods small, without endopods. Uropods about seven times as long as wide, with very large outer spine; setose part of margin about equal to bare part.

Acanthosoma 2 (Fig. 22 *a-b*). Length 5.0 mm. Rostrum 2.0 mm.

General form as in stage 1. Antennal scale long and slender but widening distally, and with very long apical spine. Flagellum about half length of body. Branches of telson with two outer and two inner spines. There may also be a very small inner spine near base of arm. Exopod of uropod broad, about six times as long as wide, with strong marginal spine dividing outer margin into nearly equal portions. Pleopods long,



Fig. 21. *S. robustus*. *Acanthosoma* 1. *a, b*, flagellum and scale of antenna; *c*, eye, showing papilla.

apparently variable, either with rudimentary endopod on 2-5, or with rudiment only on pleopod 5.

Colour. The rich colour of the larva makes it very conspicuous. The carapace has a general faint pinkish hue, with a darker margin of brown or red-brown. Both branches of the uropod red-orange. Antennae, both scale and flagellum, red, and legs red and yellow.

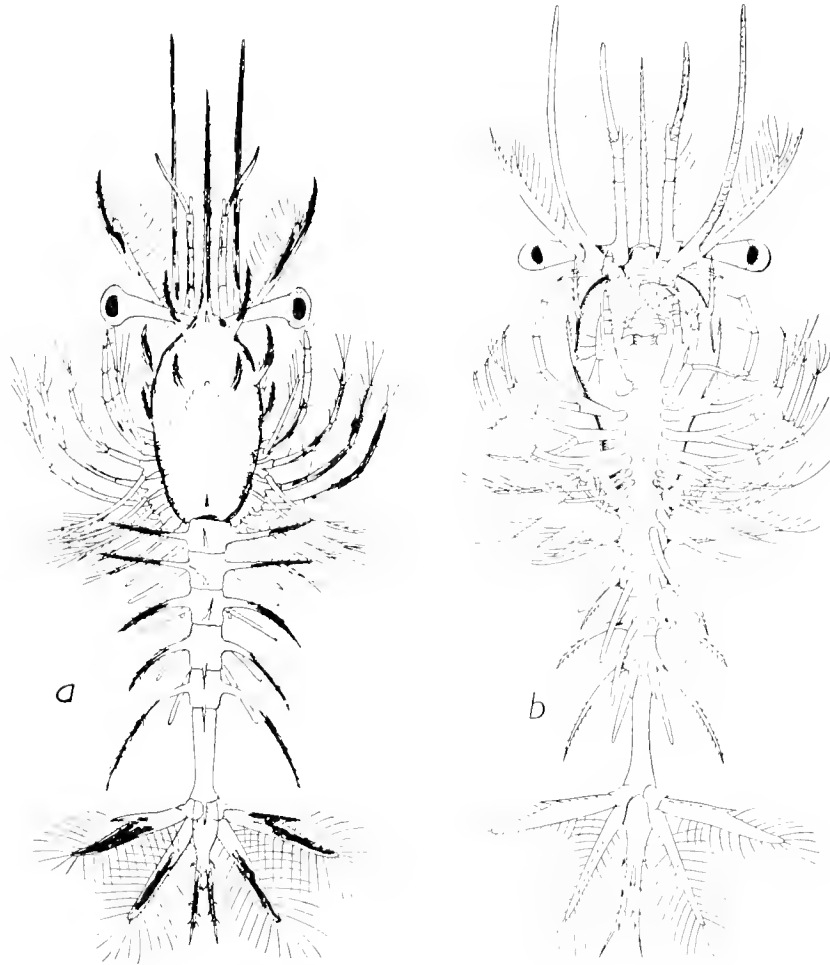


Fig. 22. *S. robustus*. Acanthosoma 2. a, dorsal; b, ventral.

Larvae in the Acanthosoma stage belonging to the *Elaphocaris* described above, from the north Atlantic, differ from Bermudan specimens in having the setose margin of the uropod about $1\frac{1}{2}$ times as long as the bare part in stage 1. In other respects the agreement is exact. A single specimen of Acanthosoma in stage 1 from Discovery Station 703 ($7^{\circ} 17' N$, $28^{\circ} 02' W$) has the same form of uropod, but differs in its small size (2.85 mm. without rostrum) and in having a longer eye, with the eyeball larger in proportion.

Mastigopus 1 (Figs. 23 and 24). Length 4.2 mm. Rostrum 0.72 mm.

Rostrum reaching to end of segment 2 of antennule; basal spine reduced to a small hair. Length of carapace more than twice the width. Supraorbital spine in the single

specimen observed represented by a pair of minute spines. Two pairs of lateral spines retained. Hepatic and posterior dorsal spines present, small.

Abdominal somites with small dorsal spines, that of somite 1 minute. Lateral spines of same form as in *Acanthosoma*, but reduced in length. Telson very little changed from *Acanthosoma*, $2\frac{1}{2}$ times as long as wide, with long lateral spines; apical fork slender, the arms parallel, with two outer and three inner spines. Antennal scale as in *Acanthosoma*, widening towards end, with very long apical spine; flagellum shorter than body.

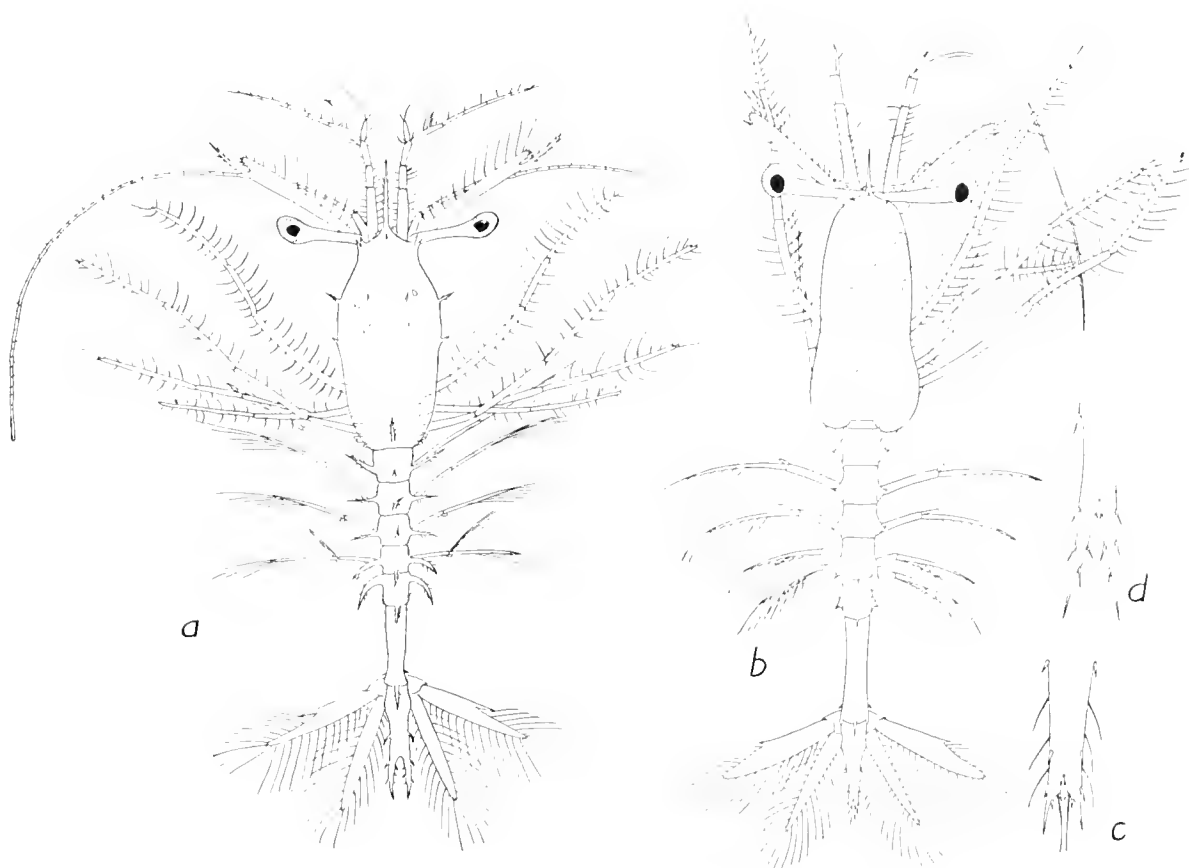


Fig. 23. *S. robustus*. *a*, Mastigopus 1; *b*, Mastigopus 2; *c*, telson; *d*, telson, stage 1.

Eye about one-sixth length of body, with small, nearly round, eyeball, and no anterior papilla. Labral spine absent. Mandible without palp. Legs with small vestiges of exopods. Pleopods very long; 1 and 2 without endopods; 3-5 with very small rudiments of endopods. Uropods nearly seven times as long as wide (6.7 : 1), the large outer spine in middle of margin.

In stage 2 (Fig. 23 *b*, *c*) the carapace has lost its dorsal and lateral spines, and the dorsal spines on abdominal somites 1-3, but the antennal flagellum is still short. The development of the telson is shown in Fig. 24.

The youngest stage figured by Hansen (7.6 mm.) is probably stage 2, since he does not mention the vestigial exopods on the legs; also the lateral spines on the abdomen

are greatly reduced. Stage 3 is probably represented in his figures 3 *f*, *g*, and we have a very similar stage of 9 mm. in which the telson has not yet lost the form characteristic of the *Acanthosoma*. The changes which take place in the telson are shown in Figs. 23, 24.

Colour as in the *Acanthosoma*.

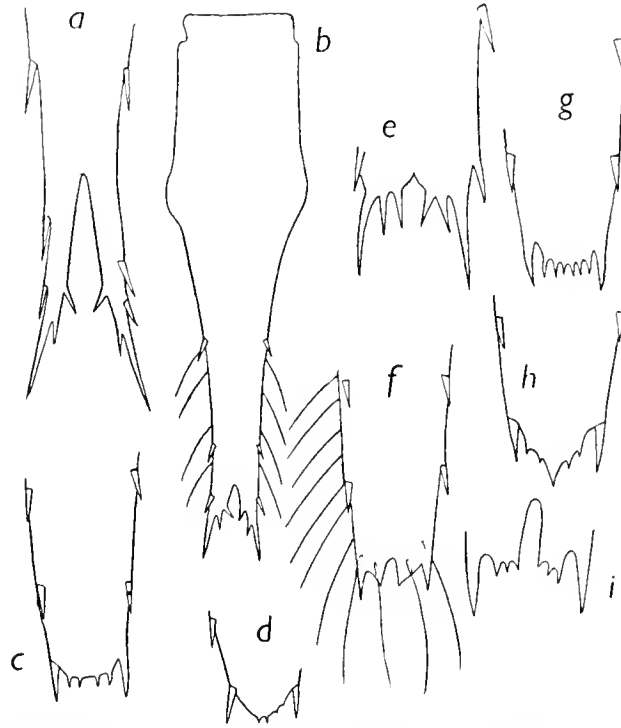


Fig. 24. *S. robustus*. Mastigopus telson. *a*, stage 1; *b*, stage 2; *c*, stage 4? 11 mm. moulted from form like *e*; *d*, stage 5? 12 mm.; *e*, stage 3, 6 mm.; *f*, stage 4, 10 mm.; *g*, *h*, moult and post-moult, 18 mm.; *i*, moult to stage 4 (*f*).

Sergestes prehensilis Bate

Syn. *S. gloriosus* Stebbing

(Gordon, 1935, J. Linn. Soc. xxxix, p. 314.)

Illig, 1927, fig. 125, *Acanthosoma* 2.

MATERIAL. Discovery Station 282 (1° 11' S, 5° 38' E). One specimen of *Acanthosoma* 2.

DESCRIPTION. *Acanthosoma* 2 (Fig. 25 *a-c*). Length 3.61 mm. Rostrum 1.42 mm.

Carapace a little longer than wide. Supraorbital spine shorter than eye; four pairs of marginal spines, of which the third is the longest; dorsal spine present. Dorsal organ small. Abdomen with dorsal spines on all somites, those of somites 1 and 2 not markedly smaller than the rest. Lateral spines very long, that of somite 5 as long as somite 6. Telson more than 2½ times as long as wide, with arms of distal fork slender, slightly divergent, with three inner and two outer spines. Lateral spines of telson far in front of fork.

Eye less than one-sixth length of body; eyeball nearly round, its diameter about one-third length of eye. Papilla present on stalk. Antennal scale slender, with long apical spine; flagellum twice as long as scale. Mandible with very small rudiment of palp.

Pleopods large, with very small rudiment of endopod on 4 and 5. Exopod of uropod with setose part a little longer than bare part, and eight times as long as wide.

REMARKS. The Acanthosoma described here agrees in all respects with that of *S. lucens* as described by Nakazawa (1916), except that in *S. lucens* there are dorsal spines on abdominal somites 2 and 4 only. There appear also to be differences in form of uropod and length of lateral abdominal spines.

The closely allied species *S. prehensilis* Bate (= *S. gloriosus* Stebbing) is recorded from the eastern coast of South Africa, and may be expected to have a larva like that of *S. lucens*. We regard it as most probable that the larva here described belongs to this species. The same larva has been described by Illig from off the coast of Sierra Leone, so that the range of *S. prehensilis* appears to extend up the west coast of Africa to north

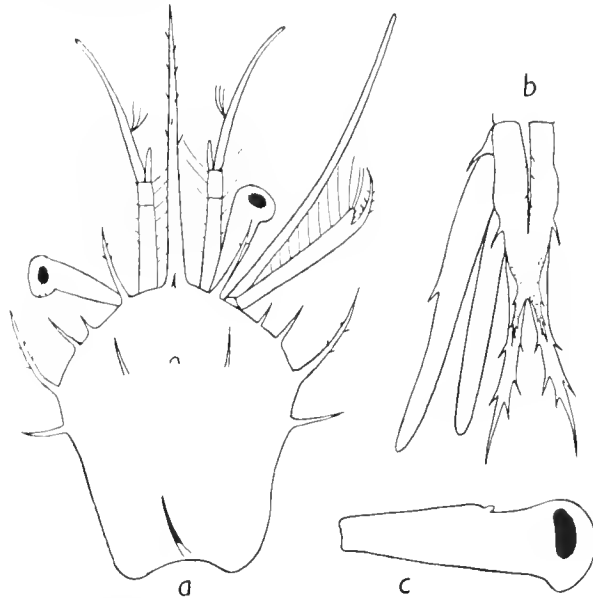


Fig. 25. *S. prehensilis*. Acanthosoma 2. a, thorax; b, telson; c, eye.

of the equator. Elaphocaris of the *hispidus* type resembling those of *S. lucens* were taken at Discovery Station 100 (Cape Town) and probably also belong to *S. prehensilis*.

Nakazawa refers his species to *S. prehensilis* Bate (or *S. phosphoreus* Kishinouye), but Hansen (1922, p. 35) has renamed the Japanese species *S. lucens* Hansen.

UNIDENTIFIED LARVAE OF THE *S. ROBUSTUS* GROUP

The Acanthosoma described above as that of *S. robustus* agrees with Hansen's description, and nearly all specimens taken at Bermuda belong to the same species. On the other hand, we have a number of specimens from the Discovery plankton, and one from Bermuda, which differ more or less from this type and may be the larvae of species hitherto not known as adults, or not recorded from the Atlantic. These may be described as forms A, B, C.

One of these may well be the larva of *S. regalis*, a species allied to *S. robustus*, which has recently been described by Dr I. Gordon (Ann. Mag. Nat. Hist. (11), iv, p. 498, 1939).

S. robustus Form A

Discovery Stations 99, 100, 102, 276, 715.

Stage 1. Length 4.45 mm. Rostrum 1.55 mm.

General form as in *S. robustus*, but carapace with three pairs of marginal spines. Telson with lateral spines in front of fork. Arms of telson with a series of five or six spines on the inner margin. Eye apparently without papilla. Setose margin of uropod about $1\frac{1}{2}$ times as long as bare part.

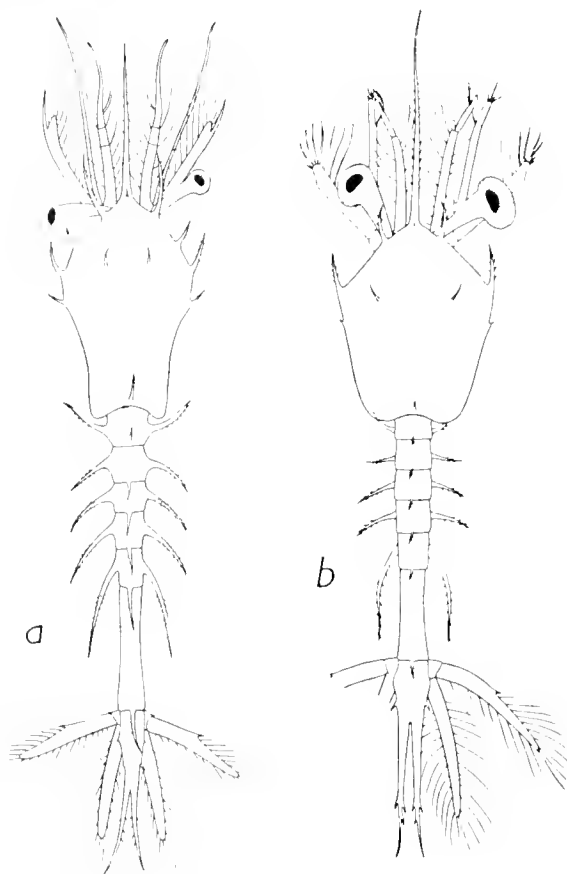


Fig. 26. *S. robustus* A. *a*, Acanthosoma 2; *b*, *S. robustus* B. Acanthosoma 1.

Stage 2 (Fig. 26 *a*). Length 5.9 mm. Rostrum 1.75 mm.

Pleopods with small rudiment of endopod on 2-5. Setose part of uropod about equal to bare part.

Mastigopus. The Mastigopus is scarcely distinguishable from *S. robustus*. The telson is shown in Fig. 27.

S. robustus Form B

Discovery Stations 708, 711.

Acanthosoma 1 (Fig. 26 *b*). Length 3.2 mm. Rostrum 1.2 mm.

Basal spine of rostrum minute. Carapace a little longer than wide (3.6:3.0) with two pairs of lateral spines, of which the posterior one is a mere point. Supraorbital and posterior dorsal spines very short. Lateral spines of somites 1-3 very much shorter

than in *S. robustus*, but those of somite 5 nearly as long as somite 6. Telson about $1\frac{1}{2}$ times as long as wide, the lateral spines well in front of fork. Arms of fork slender, parallel, with two outer and two inner spines, the two outer spines widely separated.

Eye about one-sixth length of body; length of eye $1\frac{1}{2}$ times width of eyeball; papilla present. Exopod about nine times as long as wide; setose part of margin slightly longer than bare part.

Stage 2. Length 3.95 mm. Rostrum 1.5 mm.

As stage 1, but scale with distal spine. Pleopods rather small, without endopods. Uropod a little broader, and setose part equal to bare part. Lateral spine of telson placed farther forward.

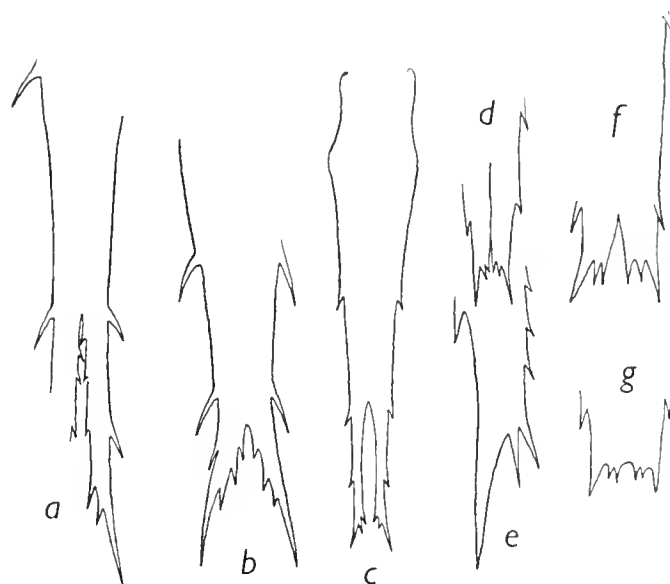


Fig. 27. *S. robustus* A. Mastigopus telson. a, 7.2 mm.; b, 5.7 mm.; c, 8 mm.; d, 9 mm.; e, the same, branch enlarged to show inner spines; f, 11.6 mm.; g, 15 mm.

We have no Mastigopus corresponding to the Acanthosoma of form B, but several which apparently belong to form A. Measurements of these have been made to compare with specimens from Bermuda which are presumed to be typical *S. robustus* but these do not reveal any differences which can be regarded as of specific value. The telson, however (Fig. 27), has the same differences as are seen in the Acanthosoma. It appears that form A is a species definitely recognizable as distinct in early larval stages but becoming indistinguishable from *S. robustus* in advanced Mastigopus stages.

S. robustus Form C

MATERIAL. One specimen of the Acanthosoma was taken in 1935 at Bermuda. The Elaphocaris stages described here were taken at Bermuda in 1939 and their reference to this *robustus* form is quite speculative. Stage 1 was connected with stage 2 by moult.

An Elaphocaris of the same form has already been described (Gurney, 1924, figs. 26, 28) from New Zealand.

Acanthosoma of the S. robustus group

Locality	Stage	Length without rostrum	Eye		Exopod of uropod		Ant. 2 scale	Lateral spines on carapace
			Length : body	Length : width	Setose : bare	Length : width	Length : width	
<i>S. robustus</i>								
Bermuda	2	4.70	6.00	2.50	1.00	6.70	11	2
"	2	4.20	6.10	2.26	1.20	6.80	11	2
North Atlantic	1	4.00	6.10	2.30	1.40	7.00	7	2
"	2	5.00	6.60	2.30	1.07	6.60	—	2
Disc. 99	1	4.15	7.20	2.30	1.10	7.00	9	2
" 701	2	4.00	5.30	2.20	1.04	6.00	—	2
" 276	1	4.25	7.08	1.77	1.43	7.90	7	2
<i>S. robustus</i> Form A								
Disc. 100	1	4.45	7.90	1.90	1.40	6.60	8	3
" 100	2	6.30	8.00	2.30	1.15	7.30	9	3
" 100	2	5.00	7.10	2.00	1.54	—	—	3
" 99	2	5.90	8.00	—	1.30	6.60	10	3
" 99	2	6.00	8.00	2.40	1.16	6.40	—	3
" 99	2	6.28	8.20	3.00	1.00	6.00	—	3
" 102	2	6.00	7.50	2.00	1.20	7.00	9.8	3
" 715	2	6.00	8.00	2.00	1.00	6.30	10	3
<i>S. prehensilis</i> (?)								
Disc. 282	2	3.61	6.60	2.70	1.00	6.00	9	4

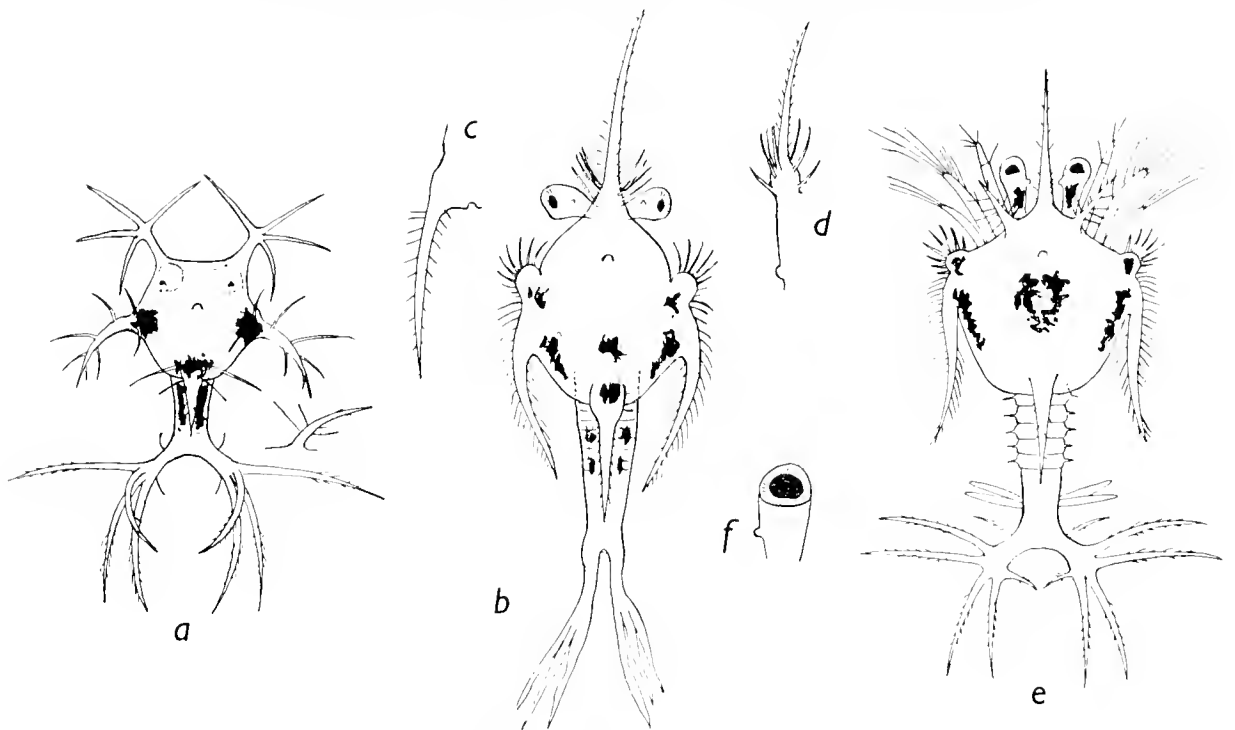


Fig. 28. *S. robustus* C. a, Elaphocaris 1; b, Elaphocaris 2; c, dorsal spine; d, rostral spine, side view; e, Elaphocaris 3; f, eye.

DESCRIPTION. *Elaphocaris* 1 (Fig. 28 *a*). Length 0.64 mm.

Anterior process quadrifid at end. Lateral process curving backwards, with seven spines. Posterior process with two pairs of spines. Dorsal organ present, small. Telson arms divergent, slender, spine 5 of same length as 4.

Elaphocaris 2 (Fig. 28 *b-d*). Length about 1 mm. Rostrum 0.64 mm.

Rostrum as long as carapace, swollen at base, where it bears four spines dorsally on either side. Lateral process long, hispid, directed backwards. The hispid margin is continued forwards into a rounded prominence, or "epaulette". Posterior process long, rather swollen at base, and hispid.

Eye rather short, pear-shaped, the eyeball not distinct from the stalk, which bears a small anterior papilla.

The only specimen seen is one moulted from stage 1, and the abdomen and telson are not fully formed.

Elaphocaris 3 (Fig. 28 *e, f*). Length 2.3 mm. Rostrum 1.12 mm.

Rostrum shorter than carapace and without the basal swelling of stage 2. Supra-orbital spines about as long as eyes, with long slender spinules. Lateral and posterior processes as in stage 2. Abdominal somites with small sharp pleural points. Telson arms divergent, slender, about twice as long as wide, the spines rather short. Eye slender, pear-shaped, as in stage 2, and with papilla.

Colour. In stages 1 and 2 there are patches of red in a ground of brownish orange at base of the lateral and posterior processes. In stage 3 the red colour is more pronounced and there is red in the eyestalk. The distribution of colour in the thorax is not quite the same, and there is no colour in the abdomen in the specimen described.

Acanthosoma 2 (Fig. 29). Length 5.3 mm. Rostrum 1.4 mm.

Carapace a little longer than wide, with two lateral spines of which the posterior pair is minute. Supra-orbital spine shorter than eye. Posterior dorsal and hepatic spines present. Dorsal organ very small.

Dorsal spines of abdominal somites 1 and 2 very small; those of 3-6 long, subequal. Lateral spines 1 and 5 the longest, the latter less than half length of somite 6. Telson nearly three times as long as wide, with large lateral spine inserted far in front of fork. Arms of fork rather divergent, much shorter than anterior part of telson, and with two outer and three or four inner spines.

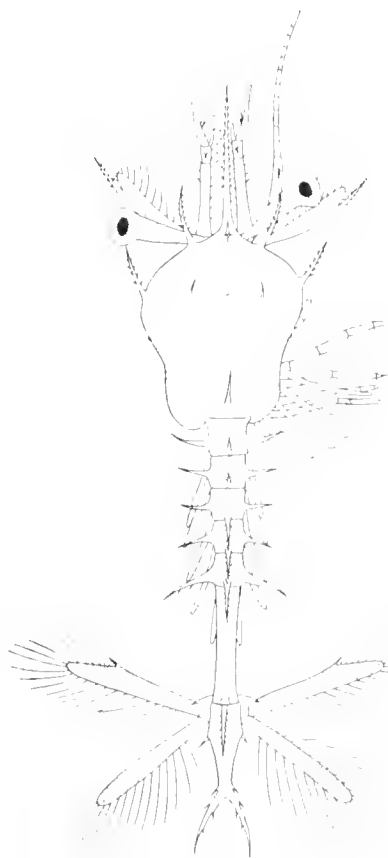


Fig. 29. *S. robustus* C. *Acanthosoma* 2.

Eye about one-seventh length of body; eyeball nearly round, its width nearly half length of eye. Antennal scale rather broad, with long apical spine; flagellum 2.1 mm. long. Mandible with rudimentary palp. Pleopods long, with small rudiments of endopods on 2-5. Exopod of uropod widening distally, its length about five times the width; bare margin 1.7 times as long as setose. The form of the exopod is not quite correctly shown in the figure—it should be broader at end.

Colour. Red round dorsal organ and in sides of thorax; down middle of abdomen; in eye, antennal scale and both branches of uropod.

Sergestes corniculum Kröyer

Hansen, 1922, pp. 134, 136, *Mastigopus* and *Acanthosoma*.

Gurney, 1924*c*, figs. 21, 22, 23 (?).

Cecchini, 1928*b*, p. 35, *Acanthosoma* and *Mastigopus*.

We are indebted to Mr M. D. Burkenroad for valuable information regarding this species. He informs us that *S. corniculum*, as described by Hansen, includes two species, and that there are at least three species of this group in the North Atlantic. In material from Bermuda which we have submitted to him he has recognized two distinct forms, but he is not at present able to give a final opinion or names for the species which he has distinguished. We had already found that there are two distinct larval forms at Bermuda. One of these, which we designate as form B, is identical with Hansen's *Acanthosoma*, and has been found also in several of the Discovery samples. The second, form A, was common in the summer of 1939, but was very rare in the spring of 1935, whereas form B was more common in 1935 and was taken rarely in early summer of 1938. The *Elaphocaris* was not moulted to *Acanthosoma*, but the colouring, general appearance and occurrence with the *Acanthosoma*, together with elimination of other species, make the identification with *S. corniculum s. lat.* practically certain. Two forms of *Elaphocaris* were taken in 1935, differing only in the number of spines on the carapace. Of these the form described as belonging to form A was the only one taken, with one exception in stage 2, in 1938-9. Since form A *Acanthosoma* was by far the more common in that period, it is assumed that the rarer form of 1935 belongs to form B.

Of form A the first *Elaphocaris* was moulted to stage 2, and *Acanthosoma* to *Mastigopus*. *Mastigopus* stage 2 was also obtained from stage 1. *Mastigopus* 1 was also obtained from the *Acanthosoma* in 1935.

A third form of *Acanthosoma*, which evidently belongs to the same superspecific group, is described below as *S. corniculum* C. This was not found at Bermuda, but at three of the Discovery Stations, two off the African coast and one near the coast of South America, all three near the equator.

Sergestes corniculum Form A

DESCRIPTION. Elaphocaris 1 (Fig. 30 *a*). Length 0.72 mm.

Anterior processes with four denticulate spines; lateral processes with six long basal spines; posterior process swollen at base with two pairs of spines. Dorsal organ conspicuous. Branches of telson short and broad, spine 5 much shorter than spine 4. A pair of small papillae on anterior margin represent the papillae of the eyestalk. Labral spine short.

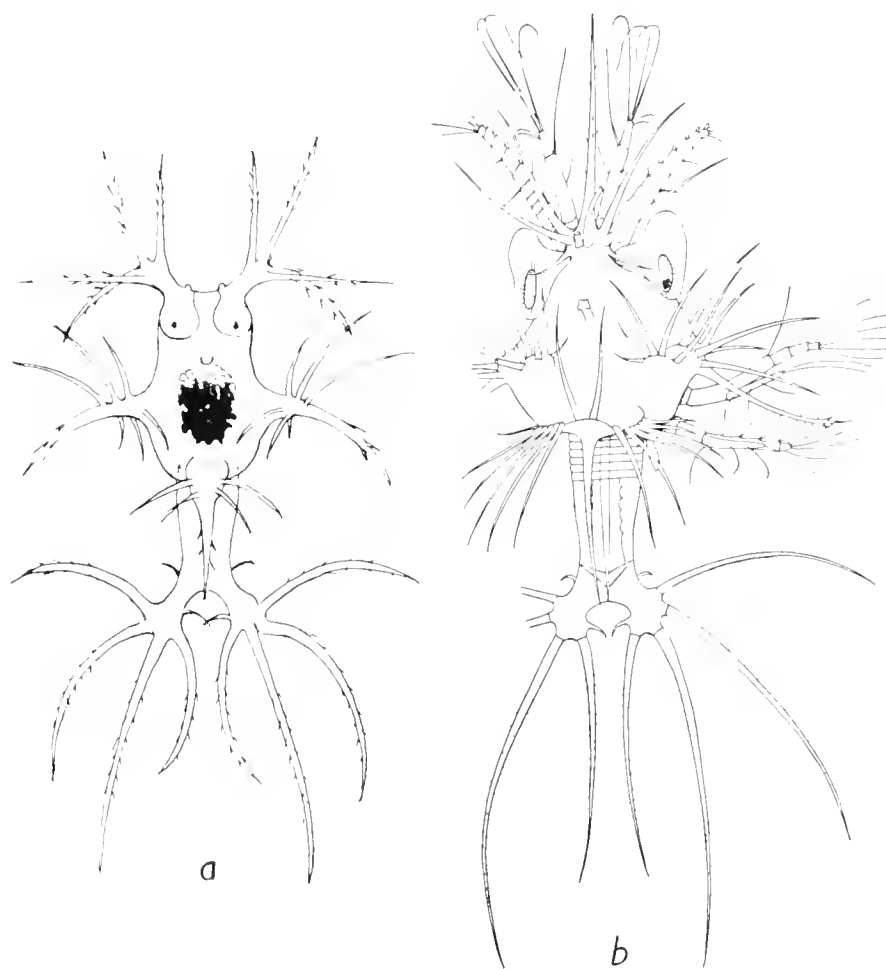


Fig. 30. *S. corniculum* A. *a*, Elaphocaris 1; *b*, Elaphocaris 2.

Elaphocaris 2 (Fig. 30 *b*). Length 1.3 mm. Rostrum 0.85 mm.

Rostrum simple, with four pairs of long spines at base. Carapace with a pair of long lateral spines and a group of about ten long spines springing from an elevation of the carapace at the base of the lateral spines. Posterior margin of carapace with a dorsal spine as long as the abdomen and a transverse row of 14 long spines. Dorsal organ very large. Telson arms very short, as wide as long, spine 5 considerably shorter than spine 4.

Eye very large, asymmetrical, width of eyeball greater than total length. Labral spine very long.

Elaphocaris 3. Length 1.5 mm. Rostrum 0.75 mm.

Rostrum without lateral or ventral spines. Supraorbital process large, curving inwards over the rostrum, with seven or eight spines. Lateral lappets of carapace bearing 12 or 13 spines. Posterior margin with a transverse row of 14 spines; posterior median spine as long as abdomen.

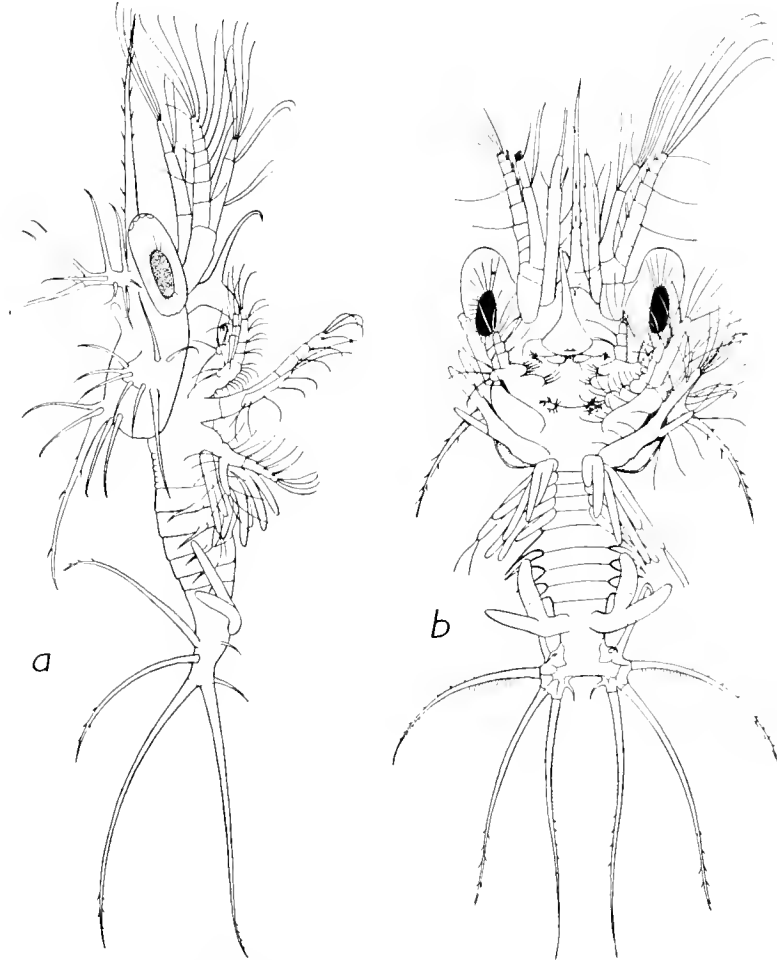


Fig. 31. *S. corniculum* B. *a*, *Elaphocaris* 3, lateral; *b*, ventral.

The *Elaphocaris* which is regarded as belonging to *Acanthosoma* form B (Fig. 31) differs in stage 3 from the form described above only in having fewer spines on the lateral and posterior parts of the carapace. The former group is of nine spines while there are only five on each side of the posterior median spine (Fig. 31 *a*).

Colour. A large bright red patch just behind centre of thorax; otherwise colourless.

Acanthosoma 1 (Fig. 32 *a*). Length 3.28 mm. Rostrum 1.1 mm.

Rostrum longer than antennule, with basal spine rather large. Supraorbital spine slender, longer than eye. Hepatic spine swollen at base and with long spinules at base; anterior lateral spine with a series of very long spinules at base; posterior lateral spine smaller, with two long spinules at base. Posterior dorsal spine absent. Dorsal organ a rather large blunt process.

Abdomen with long slender dorsal spines on all somites. Lateral spines long and stout, of about equal length. Each is armed with long spinules, the first on both sides and the others behind only; spine 5 has three of these long spinules. Telson deeply forked, with a pair of lateral spines, and two outer and two inner spines on each arm of the fork.

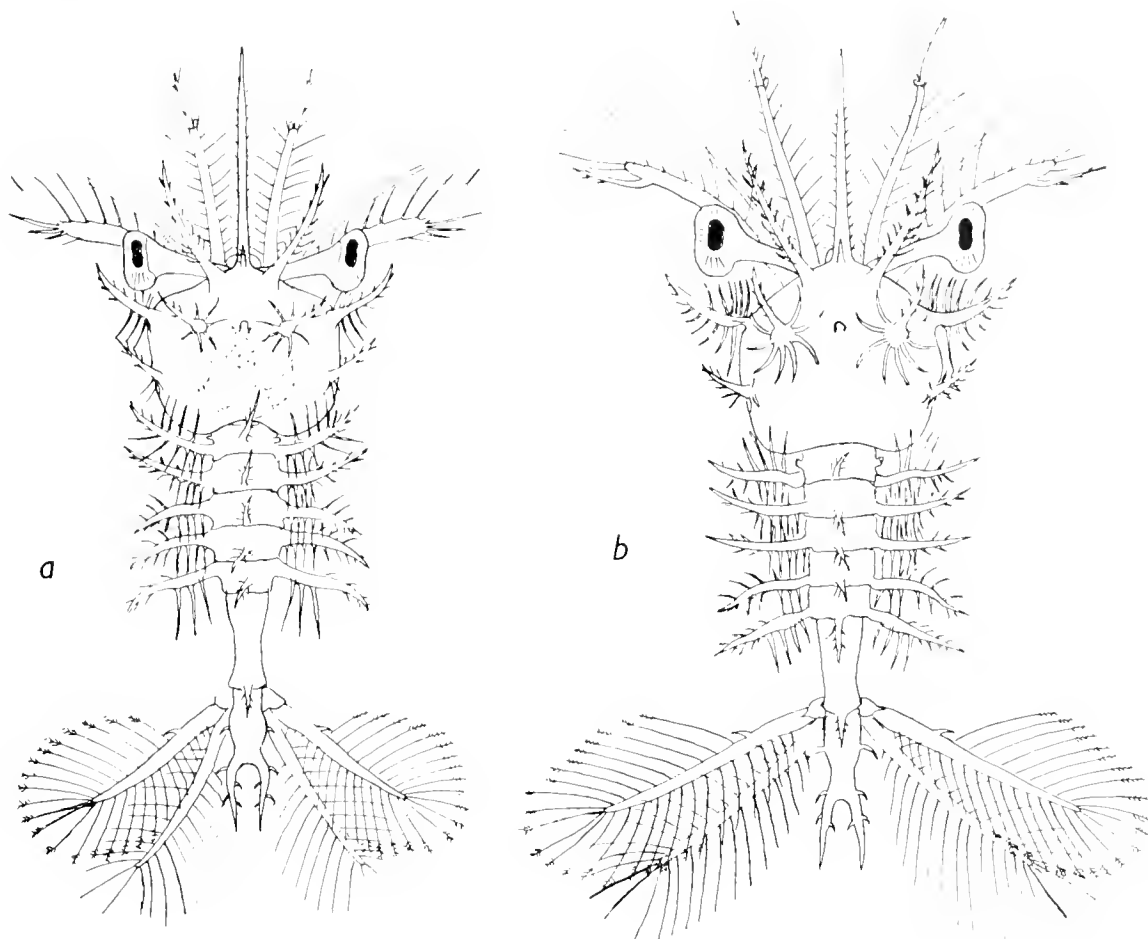


Fig. 32. *S. corniculum* A. *a*, Acanthosoma 1; *b*, Acanthosoma 2.

Eyes large, swollen behind, total length about one-fifth length of body. Width of eyeball half length of eye. Antennal scale with one outer seta, four stout terminal and seven inner marginal setae; flagellum much longer than scale. Pleopods small. Exopod of uropod with nine outer setae, this setose part twice as long as bare basal part.

Acanthosoma 2 (Figs. 32 *b*, 33 *b*). Length 3.6 mm. Rostrum 1.12 mm.

Rostrum shorter than antennule. Hepatic spine with nine long spinules at base. Lateral spines of abdomen longer, the last with four long posterior spinules. Antennal scale about 14 times as long as wide with long subapical spine. Pleopods long, with small endopods. Uropods about 13 times as long as wide: setose part 2.3 times as long as bare part. In both stages the setae are conspicuously feathered. Somite 6 with long setae on dorsal side.

Colour as in *Elaphocaris*.

Mastigopus 1 (Figs. 33 *a*, *c*, 34). Length 3.7 mm. Rostrum 0.85 mm.

Rostrum denticulate, with minute spine at base. Supraorbital, hepatic and anterior lateral spines present, much reduced. Dorsal organ small. Abdomen with conspicuous lateral spines on somites 1-5, dorsal spines reduced to minute points on somites 1 and 2, but rather long on somites 3-6. Telson with anterior lateral spine and small terminal fork; two or four setae within the fork.

Eye more than one-fifth length of body, the width of the eyeball more than half length of eye. Antennule with first segment of peduncle much the longest, the third slightly shorter than the second. Antennal flagellum longer than body. Mandibular palp of good

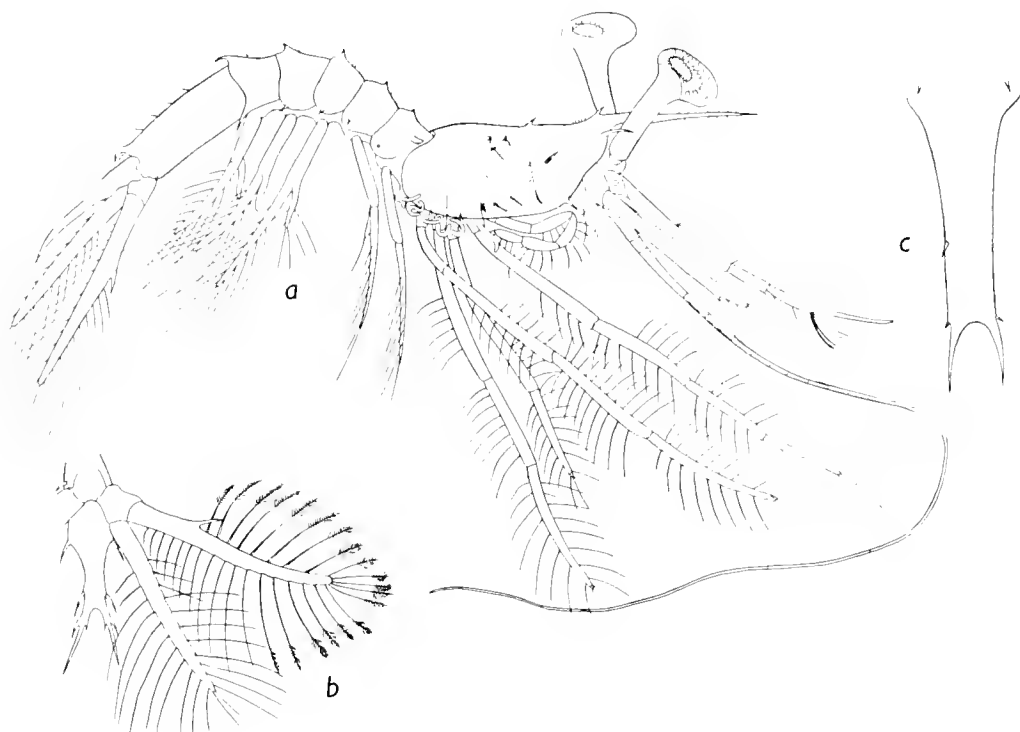


Fig. 33. *S. corniculum* A. *a*, Mastigopus 1 moulted from Acanthosoma; *b*, telson of Acanthosoma; *c*, telson of Mastigopus.

size but unsegmented. Maxillipede 3 and leg 3 nearly the same length. Legs 2 and 3 chelate. Legs with long twisted vestiges of exopods. Pleopods long; pleopods 3-5 with setose endopods, the fifth the longest; pleopod 2 with rudimentary, non-setose endopod. Uropods slender, about 11 times as long as wide; setose margin nearly, or quite, twice the bare part.

There is some variation in the number of setae on the telson and in degree of development of the pleopods. Also the vestiges of the exopods of the legs may be much reduced.

Colour. Red in thorax as in Acanthosoma. The legs may be colourless or with red distally. Later stages become more and more red, especially on the legs (Fig. 35).

Mastigopus 2 was obtained by moult from stage 1. Stage 2 differs very little from

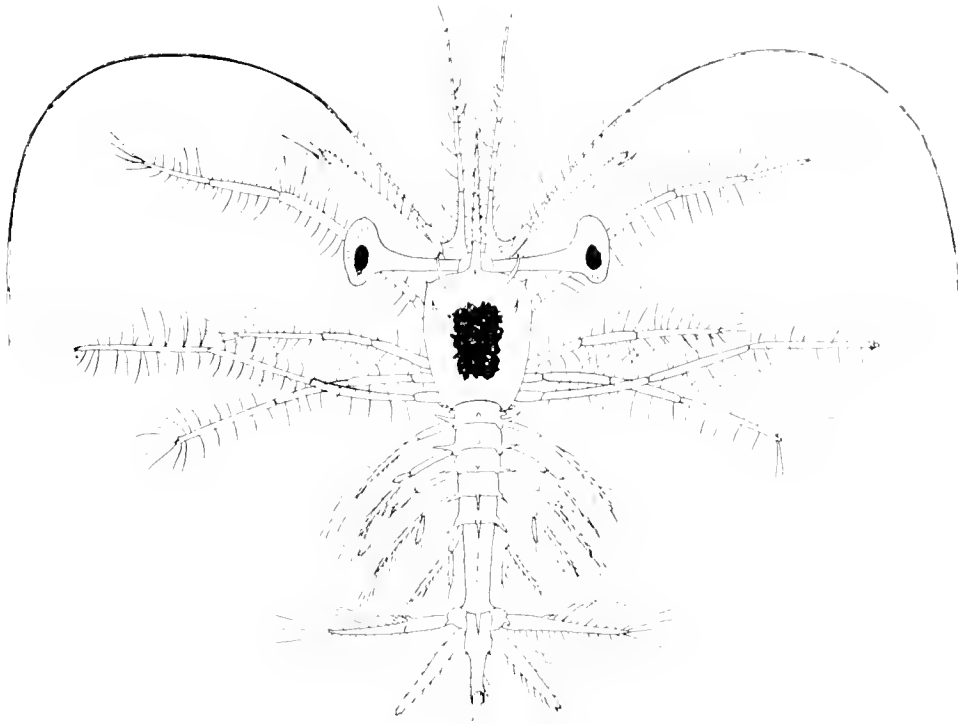


Fig. 34. *S. corniculum* A. Mastigopus 1, moulted from Acanthosoma, dorsal.

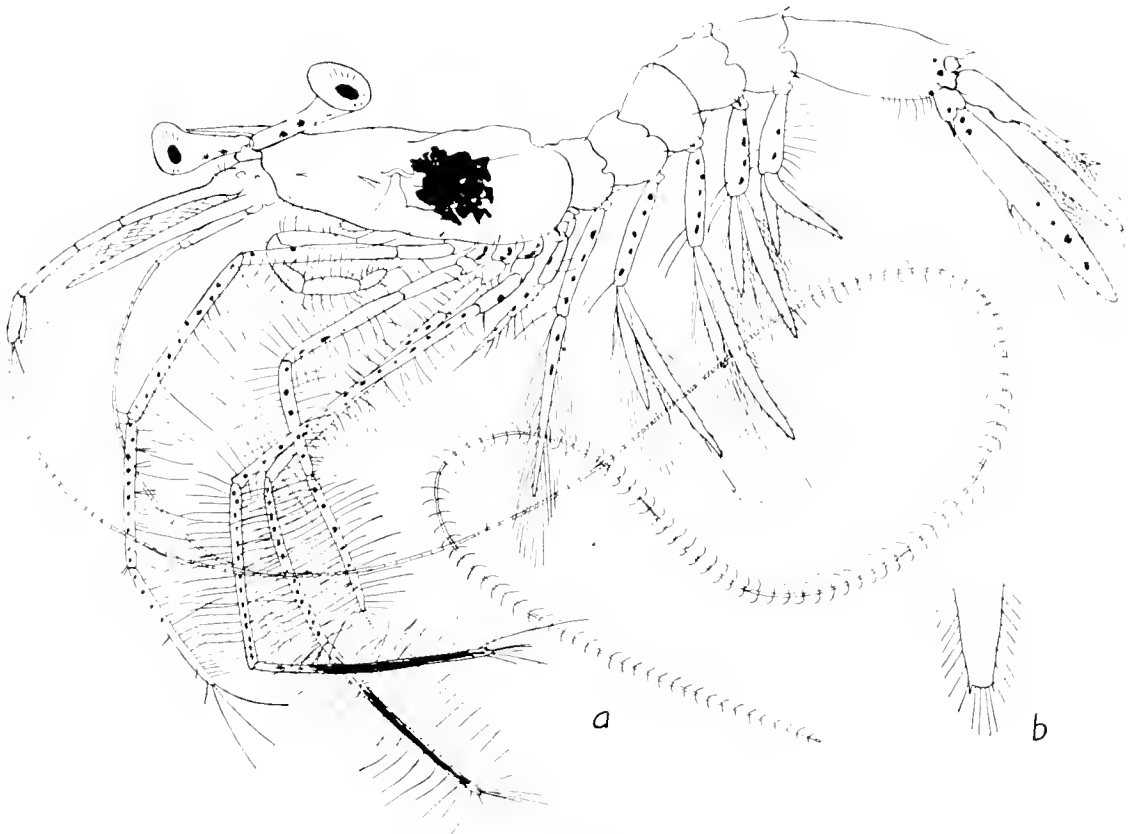


Fig. 35. *S. corniculum* A. Mastigopus 8.5 mm.; *b*, telson.

stage 1. The carapace retains in this, and even in later stages up to about 9 mm., a trace of the anterior marginal spine. Somites 1 and 2 have no dorsal spine, while those of somites 3-6 are very small, or even lost.

In the material submitted to Mr Burkenroad he has found one differing from the others in having neither hepatic nor supraorbital spine. In the material remaining, from 1935 and 1938-9, we have found none which lack this spine (37 specimens of 7 mm. and more). Measurements of the single specimen without hepatic spine as compared with others of about the same size show no significant differences except that the eye is shorter and the eyeball smaller. It is impossible, among the remaining specimens to detect any specific differences, though such differences might perhaps appear if a sufficiently large material could be measured.

Sergestes corniculum Form B

Acanthosoma 2 (Fig. 36 *a-c*). Length 2.62 mm. Rostrum 0.78 mm.

Rostrum longer than antennule. Carapace a little broader than long. Supraorbital spine longer than eye; hepatic spine slender, not swollen at base; anterior lateral spine with two long spinules only. Posterior dorsal spine absent. Dorsal organ a slender papilla. Dorsal spines of abdomen small on somites 1 and 2, longer on 3-6, that of somite 4 the longest. Lateral spines shorter than in species A and with few long spinules, that of somite 5 with one long spinule only.

Eye very large, with anterior papilla, its length about one-fifth length of body and not much greater than width of eyeball (1.23 : 1). Antennal scale very slender; flagellum 1.7 mm. Exopod of uropod with setose part nearly twice the bare part (1.8 : 1) and length eight times the width. Somite 6 with dorsal setae. Arms of telson fork with one inner, one outer, and one dorsal spine.

The description is from a specimen taken at Bermuda on 5 July 1938, which moulted from stage 1. Specimens of the same form, which appears to belong to the same species as was described by Hansen, have been examined from the following Discovery Stations:

—	8° 30' N, 17° 53' W,	701.	14° 39' N, 25° 51' W,
—	34° 33' N, 14° 32' W,	703.	7° 17' N, 28° 02' W,
281.	00° 46' S, 5° 49' E,	704.	3° 37' N, 29° 14' W.

At Station 281 *Elaphocaris* of type A were also taken. If these really belong to the *Acanthosoma* with which they were associated the *Elaphocaris* B described must represent a third species as yet unknown; but it is possible that the *Elaphocaris* of Station 281 belongs to the *Acanthosoma* described below as form C, from the adjacent Station 282.

Sergestes corniculum Form C

MATERIAL.

Discovery Stations: 278, off Port Gentil, French Congo; 282, 1° 11' S, 5° 38' E; 706, 3° 26' S, 32° 08' W.

DESCRIPTION. *Acanthosoma* 2 (Fig. 36 *d*). Length 3.39 mm. Rostrum 1.39 mm.

Rostrum much longer than antennule, with long basal spine. Carapace wider than long. Supraorbital spine longer than eye, nearly smooth. Hepatic spine large and stout, with a few long spinules at base, but not swollen at base. Anterior lateral spine with a number of long spinules. Posterior dorsal spine absent.

Dorsal spines of abdomen extremely long, that of somite 5 longer than somite 6.

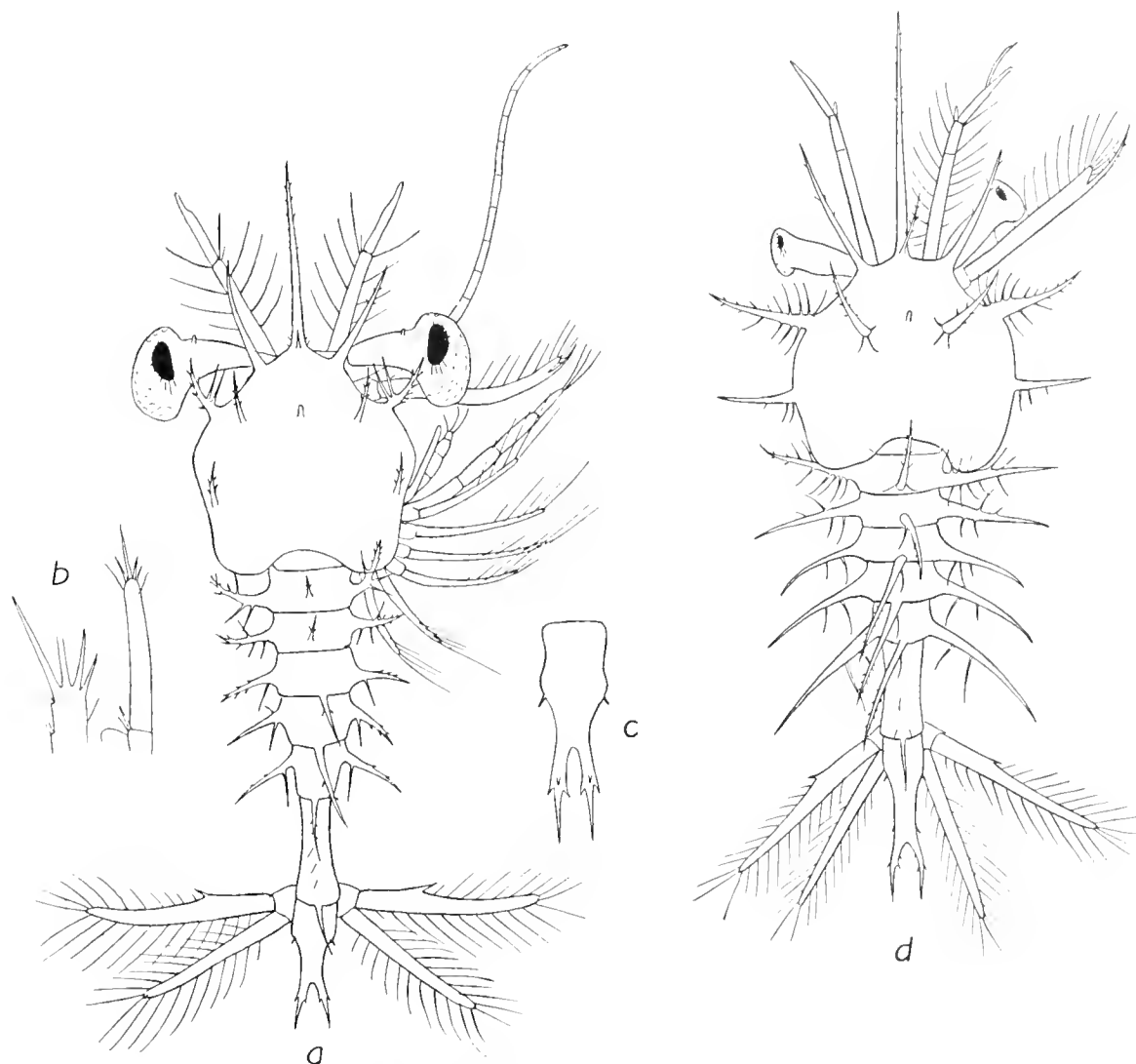


Fig. 36. *S. corniculum* B. a, Acanthosoma 2, moulted from stage 1; b, end of scale and endopod of antenna; c, telson; d, *S. corniculum* C, Acanthosoma 2.

Lateral spines very long, the fifth reaching beyond somite 6. Spine 1 with several long spinules at base; spine 5 with two only. Telson much narrowed behind the lateral spine and with slender fork. The arms of the fork bear two inner spines and one outer, the anterior outer spine being inserted in front of the fork. In stage 1 both outer spines are on the arm of the fork.

Eye rather slender, one-sixth length of body and twice width of eyeball. There is a

very small papilla. Antennal scale slender, with very long apical spine; flagellum long (broken). In stage 1 the scale has three stout apical setae and small spine and seta near end on outer side; flagellum unsegmented, twice length of scale. Pleopods long, with rudimentary endopod on 2-5. Uropod very slender, the setose margin twice length of bare part.

Mastigopus 1 (Fig. 37 *a, b*). Length 3.85 mm. Rostrum 0.6 mm.

Differs from *S. corniculum* A in shape of eye, which is relatively shorter and with smaller eyeball. The pleural point of somite 5 is shorter, and the setose part of the uropod more than twice the bare part. Otherwise the two forms are indistinguishable.

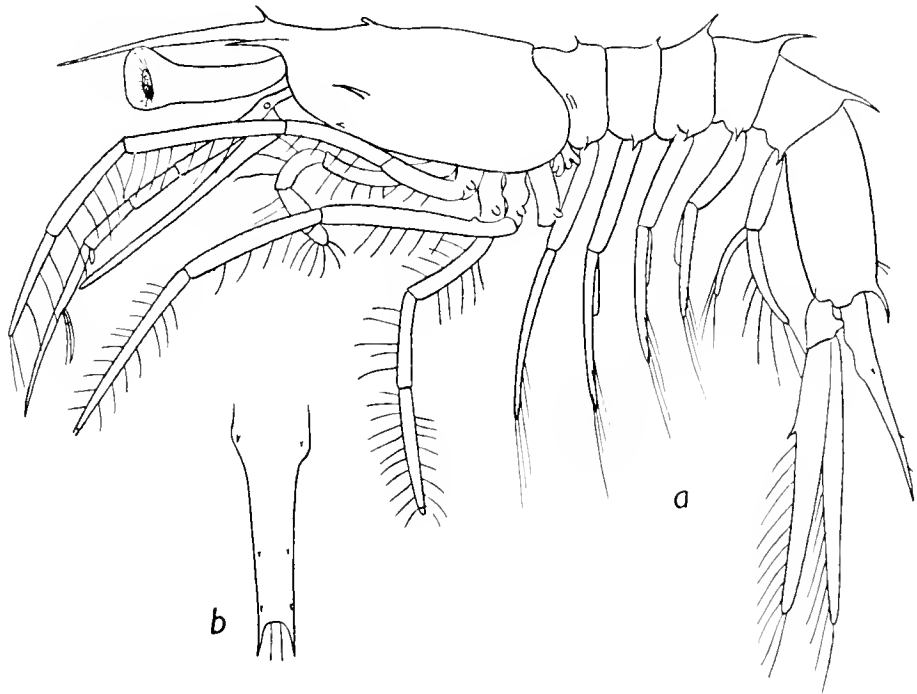


Fig. 37. *S. corniculum* C. *a*, *Mastigopus* 1; *b*, telson.

REMARKS. This Acanthosoma is very much like that of *S. corniculum* A, but differs in shape of eye and the great length of the dorsal spines of the abdomen. In the form of the eye it resembles the Acanthosoma attributed to *S. seminudus* Hansen (Hansen, 1919, p. 20), but that form has much shorter dorsal spines, and is not found in the Atlantic so far as is known.

GROUP II

Hansen's group II, with very large maxillipede 3, includes six Atlantic species. Of these *S. pectinatus* and *S. sargassi* seem to be so closely related that their larvae may be expected to be very similar. We know nothing certainly about the development of *S. sargassi*, but we have most of the stages of *S. pectinatus*, and its larvae differ distinctly in many respects from those of *S. vigilax*, for example. The larvae, in fact, support a division into two subgroups.

If all the Acanthosomas having a short, forked telson of the form known in *S. vigilax*

are separated out, it is found that they have a very close general similarity. They all agree in having the same form of eye, though differing in length of eyestalk; in having the uropod very slender and the setose part of the margin $1\frac{1}{2}$ or more times longer than the bare part; in having the lateral spine of somite 5 (and usually of 4 also) very short and simple, and in the presence of median ventral spines, or prominent papillae, on two or more of the abdominal somites.

Among the specimens of this group at our disposal four quite distinct species can be separated. One of these is *S. vigilax*; but the identity of the others is less certain.

We feel little doubt that we have correctly named the larvae of *S. edwardsi*, and the identification of *S. armatus*, though less secure, seems most probable, especially in view of the fact that Hansen mentions the presence of ventral spines on somites 1-3 of the Mastigopus.

If these species are accepted the fourth must belong to *S. diapontius*, but the identification by exclusion in this way is not very satisfactory, in view of the possibility that there may be other adult species still undescribed.

Sergestes pectinatus Sund

Hansen, 1822, p. 146, Mastigopus.

Cecchini, 1928*a*, fig. 3*a*; 1928*b*, pl. 2, fig. 4, Acanthosoma 2.

Illig, 1927, p. 319, *S. henseni*, Mastigopus, fig. 84 (?); p. 331, *S. nudus*, Mastigopus, fig. 104 (?).

MATERIAL. This is one of the commonest species at Bermuda, occurring as larva or Mastigopus in depths from surface to 300 metres. The Acanthosoma has been identified by moulting to Mastigopus, and the Elaphocaris is attributed to it by its resemblance to the Acanthosoma in colour, size and shape of eye.

DESCRIPTION. Elaphocaris 3 (Fig. 38 *a*). Length 1.12 mm. Rostrum 0.64 mm.

Rostrum denticulate. Supraorbital processes long and thin, branching into four spines, one thinner than the others. Lateral processes long, denticulate at tip, with a basal epaulette of eight spines. Dorsal process springing from a rounded base with four spines. Dorsal organ very small.

Abdominal somites with sharp lateral spines, the first three directed backwards. Telson with thick short branches and four long denticulate spines, and two very small spines. The first long spine directed forwards, the others backwards, very long and almost parallel.

Eye short, very large, the greatest width of eyeball exceeding length of eye.

Colour. Red at sides of carapace and abdomen and on eyestalks.

Acanthosoma 1 (Fig. 38 *b*). Length 2 mm. Rostrum 0.8 mm.

Rostrum much longer than antennule. Carapace broader than long, with a conspicuous angular prominence behind the anterior lateral spine. Supraorbital spine as long as eye. Hepatic spine small and simple. Anterior lateral spine very long and prickly; posterior lateral spine very small and springing from the dorsal surface. Posterior dorsal spine very small. Dorsal organ very large, conical.

Abdominal somites with small dorsal spines, that of somite 6 a little the longest. Lateral spines of somites 1-4 large, with coarse spinules; somite 5 with lateral spine small and simple. No median ventral spines. Telson about $1\frac{1}{2}$ times as long as wide, usually without lateral spine, and with narrow slender fork, the arms with two small outer and one inner spinule.

Eye large, asymmetrical, with short slender stalk. Total length of eye about one-fifth length of body, and greatest width of eyeball exceeding total length of eye. Antennal

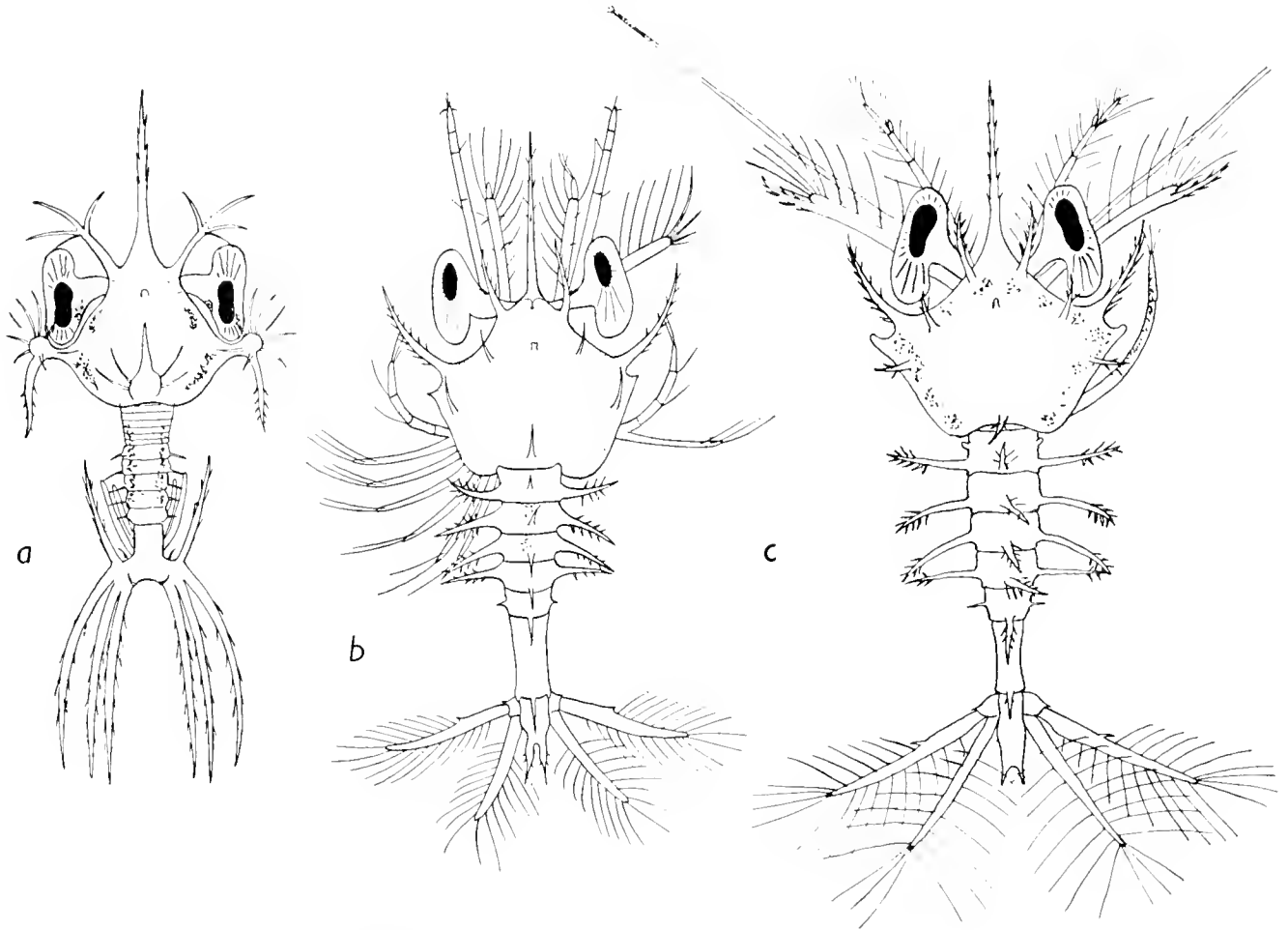


Fig. 38. *S. pectinatus*. a, Elaphocaris 3; b, Acanthosoma 1; c, Acanthosoma 2.

flagellum a little longer than rostrum; scale narrow, with four apical setae. Pleopods very small, bilobed. Exopod of uropod with setose margin $1\frac{1}{2}$ times as long as bare part.

Acanthosoma 2 (Fig. 38 c). Length 2.4 mm. Rostrum 0.8 mm.

Closely resembling stage 1. Supraorbital spine rather shorter. Telson tending to lose the posterior spines, but there is usually a fine spine on the outside where it is broadest. Antennal flagellum nearly twice as long as antennule; scale with long denticulate spine.

Colour. Carapace bright vermilion round margin. Red in eyestalk and tip of antennal flagellum. Abdomen colourless, or with red patch in somites 2 and 3.

Mastigopus 1 (Figs. 39 *a, b*, 40). Length 2.6 mm. Rostrum 0.6 mm.

Rostrum reaching beyond segment 1 of antennule. Supraorbital spines minute; hepatic, marginal and posterior dorsal spines absent.

Abdominal somites 1-3 without dorsal spines; somites 4 and 5 with large dorsal spines. All somites with rather large pleural points. No median ventral spines. Telson narrow, greatest width nearly one-third length, with small apical fork.

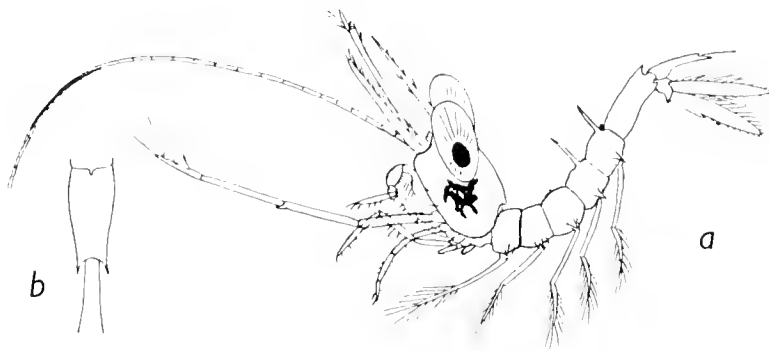


Fig. 39. *S. pectinatus*. *a*, Mastigopus 1; *b*, telson.

Eye very large, asymmetrical, with very short stalk, and turned backwards in characteristic manner. Antennal scale very long and slender (11:1); flagellum much longer than body, without conspicuous setae, the end segments slightly swollen. Legs without trace of exopods. Legs 4 and 5 remaining as rather large vestiges. Maxillipede 3 with spine at outer distal end of carpus. Pleopods without endopods. Exopod of uropod six times as long as wide; setose part twice as long as bare part.

Colour. Body colourless except for a vermilion patch in thorax. Antennal flagellum red at end and also, in later stages, with bands of red. In later stages the red in thorax extends to mouth region and base of eye, and red patches appear in somites 2-4 of abdomen.

In early stages the body is bent in a characteristic way as shown in Fig. 39.

The length of the antennal flagellum rapidly increases with age, as follows.

Mastigopus 1. Usually a little longer than body, but sometimes (Fig. 40) much longer, without kink, and with red at end, where it is slightly swollen.

Mastigopus 2 (moulted from 1). More than three times length of body, with several red portions at intervals, and with kink before first third. Dilated at end.

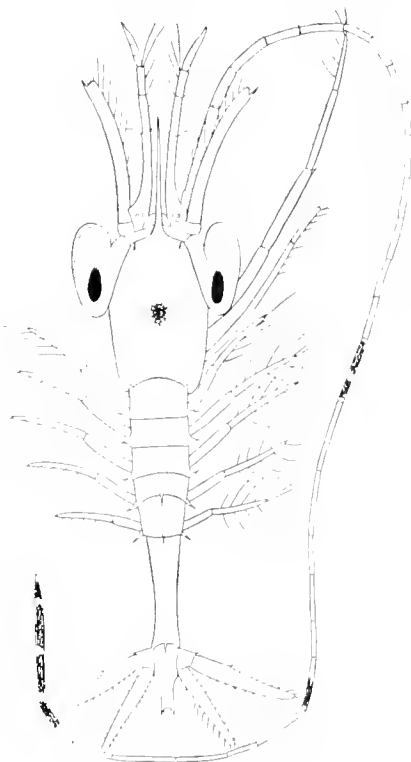


Fig. 40. *S. pectinatus*. Mastigopus 1.

Mastigopus ca. 5 mm. More than five times length of body. The kink in life is so situated that the flagellum is first directed backwards and then bent sharply at an acute angle. It can, however, be straightened out and held at angles to the body so that the kink hardly shows.

Mastigopus ca. 6 mm. (Fig. 41). Flagellum about six times as long as body. In the figure the kink is not visible.



Fig. 41. *S. pectinatus*. *a*, Mastigopus, 6 mm.; *b*, setae on flagellum.

Sergestes sargassi Ortm. Hansen

Hansen, 1922, p. 154, Mastigopus.

Illig, 1927, p. 330, *S. nudus*, Mastigopus (?), fig. 103.

Cecchini, 1928*b*, p. 38, Mastigopus (?).

Ortmann (1893, p. 69) mentions an Acanthosoma which he thought was that of *S. sargassi*, but without figure or adequate description.

MATERIAL. We have no larvae which can with certainty be referred to this species, and the Mastigopus is rare at Bermuda. The Acanthosoma described below, of which one specimen was taken in 1935 and one in 1938 at Bermuda, cannot be proved to belong to *S. sargassi*, but there is no other species to which it can be attached. Its colour and general resemblance to *S. pectinatus* support the identification.

DESCRIPTION. Acanthosoma 2 (Figs. 42, 43). Length 3.0 mm. Rostrum 0.96 mm.

Rostrum denticulate, longer than antennule, with long basal spine. Carapace as wide as long. Supraorbital spines denticulate, longer than eye; anterior lateral spines long and stout, with several long basal spinules; posterior lateral spines with long basal spinules. Hepatic spines long, slender, denticulate. Posterior dorsal spine very long, with spinules. Dorsal organ large.

Dorsal spines of abdomen long, with conspicuous spinules which are very long on spines 1-4. Lateral spines long and stout, that of somite 5 nearly as long as somite 6. Each spine with long spinules at base, but that of somite 5 with one or two only.

Abdominal somites without ventral spines. Telson with slender lateral spines and narrowed behind this point. Arms of distal fork slender, slightly divergent, with one inner and two outer spines.

Eye short, about one-sixth length of body, the greatest width of the eyeball nearly equal to length of eye. No papilla seen. Labral spine long. Antennal scale slender; flagellum about as long as abdomen. Pleopods without rudiments of endopods. Uropods slender, the bare part of the exopod less than half length of setose part.

Mastigopus. Hansen has described, but not figured, what is probably the first Mastigopus, measuring 4.1 mm. including rostrum. Our smallest specimen measures 4.35 mm. without rostrum, and is probably in stage 2.

Stage 2 (?). (Fig. 44). Length 4.35 mm. Rostrum 0.55 mm.

Rostrum not reaching end of segment 1 of antennule. Supraorbital and hepatic spines present, small. Dorsal organ absent.

Abdominal somites 1-4 without dorsal spines, but with small pleural points. Somites 5 and 6 with small dorsal spines, the former with pleural points large and directed backwards. Telson slender, without lateral spines and with small terminal fork.

Eye less than one-sixth length of body, the greatest width of the eyeball nearly equal to length of eye. Segment 1 of antennule longer than 2 and 3 combined, and segment 3 a little longer than 2. Antennal scale about seven times as long as wide; flagellum more than four times as long as body. Mandibular palp small, unsegmented. Legs 4 and 5 minute buds. Pleopods 2-5 with rudiments of endopods, without setae. Exopod of



Fig. 42. *S. sargassi*. Acanthosoma 2.



Fig. 43. *S. sargassi*. Acanthosoma 2, lateral.

uropod with outer spine large; setose margin one and a half times as long as the bare part.

Colour. Very red, mainly in abdominal somites 1-3 and 6.

At a body length of 5.6 mm. the rostrum is reduced to a minute point, though the supraorbital spines are of fair size. The endopods of the pleopods are setose.

In specimens of 6.78 mm. and 8 mm. there is no trace of the rostrum. The outer marginal spine of the uropod is retained at 8 mm.

REMARKS. The Mastigopus of *S. pectinatus* and *S. sargassi* can be readily distinguished in life by colour, the latter being deep crimson and pink all over, except for the telson, uropods and appendages, which are colourless. The flagellum seems to lack the red bands which are seen in *S. pectinatus*.

Structural differences are as follows:

(1) Terminal spinous process of carpus of maxillipede 3 in *S. pectinatus*.

(2) Much greater length of the setose part of the uropod in *S. pectinatus*, in which it is never less than twice the bare part, and may be three times as long; whereas it is not much more than $1\frac{1}{2}$ times in *S. sargassi*. The latter retains the marginal spine longer than *S. pectinatus*.

(3) The shape of the eye is distinctive, but difficult to describe. It may be said that the long diameter of the eyeball is markedly greater in *S. pectinatus*, whereas the eyestalk is distinctly shorter.

(4) *S. sargassi* is somewhat larger at equivalent stages.

The synonymy of this species seems to be rather obscure, and we have accepted Hansen's position. Illig's figures of the Mastigopus of *S. henseni* and *S. nudus* are not sufficiently complete for certain identification, but it may be suggested that Figs. 84 and 104 are of *S. pectinatus* and Fig. 103 of *S. sargassi*.

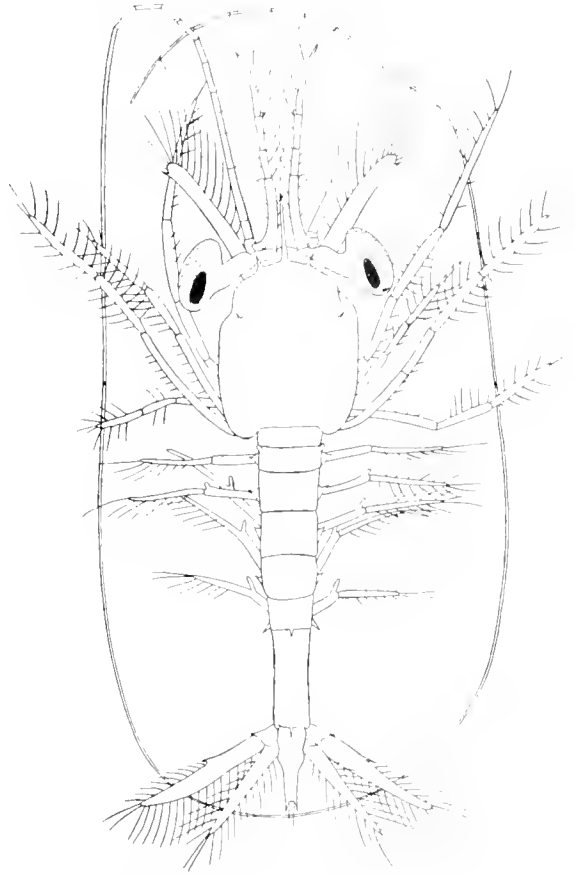


Fig. 44. *S. sargassi*. Mastigopus 2?

Sergestes vigilax Stimpson

Claus, 1863, Pl. XXVII, fig. 43, Acanthosoma; fig. 44, Mastigopus.

Claus, 1876, Pls. V, VI, Elaphocaris and Acanthosoma.

Hansen, 1922, p. 165, Mastigopus and Acanthosoma.

Gurney, 1924*c*, p. 80, fig. 17, Elaphocaris 2; p. 81, fig. 18, Elaphocaris 3 (?).

Illig, 1927, p. 344, fig. 127, Elaphocaris 3 (?).

Cecchini, 1928*b*, Acanthosoma 1 and 2 referred to.

MATERIAL. The species is common at Bermuda. Moults have been obtained of Elaphocaris 1 to stage 2; Elaphocaris 3 to Acanthosoma; Acanthosoma 1 to stage 2; Acanthosoma 2 to Mastigopus. In addition, several moults of the Mastigopus have been observed. The connection of Elaphocaris 2 to stage 3, which is the only gap in the sequence of moults, is established by general similarity in form and colour, and by capture in association with later stages in the Discovery material.

The larvae have been recognized in the material from the following Discovery Stations:

—	34° 33' N, 14° 32' W,	703.	7° 17' N, 28° 02' W,
100.	33° 20' S, 15° 18' E,	704.	3° 37' N, 29° 14' W,
701.	14° 39' N, 25° 51' W,	708.	10° 26' S, 34° 57' W,
702.	10° 59' N, 27° 04' W,	714.	35° 09' S, 47° 00' W.

Among the numerous specimens of the Acanthosoma examined from various stations in the Atlantic differences have been noted in the form of the pleural spines. These differences may point to the presence of distinct races or species within a *vigilax* group; but the material does not justify an attempt to define such races.

DESCRIPTION. Elaphocaris 1 (Fig. 45 *a*). Length 1.16 mm.

Anterior processes about as long as carapace, trifurcate, the median branch with denticles; base with four small spines. Lateral and posterior dorsal processes simple, with a few denticles, the lateral process a little longer than carapace. Telson branches short and stout, diverging, with four very long spines and two short ones; spine 5 much the longest, and exceeding length of whole body. Thorax containing numerous yolk globules.

Elaphocaris 2 (Fig. 45 *b*). Length 1.47–1.7 mm. Rostrum 1.0 mm.

Rostrum very broad at base over eye, with four pairs of lateral and two ventral spines. Lateral processes large and stout, with ten dorsal and lateral spines and one ventral. Posterior process with two pairs of lateral spines. Telson branches divergent, longer and more slender than in stage 1. Carapace with dorsal organ minute or absent. Eyeball not markedly asymmetrical, with slight indentation in centre, the diameter about half length of eye.

Elaphocaris 3 (Fig. 45 *c*). Length 2.6 mm. Rostrum 1.1 mm.

Rostrum as long as carapace, with one pair of lateral and two unpaired ventral spines (three seen in one specimen). Supraorbital spines large, with 15–17 spines. Lateral

process stout, with 15–18 spines. Posterior process with six pairs of spines. Eye large, asymmetrical, greatest diameter of eyeball more than half eye length. Somites of abdomen with sharp pleural spines.

Colour. These three stages are colourless, or with a yellowish tinge.

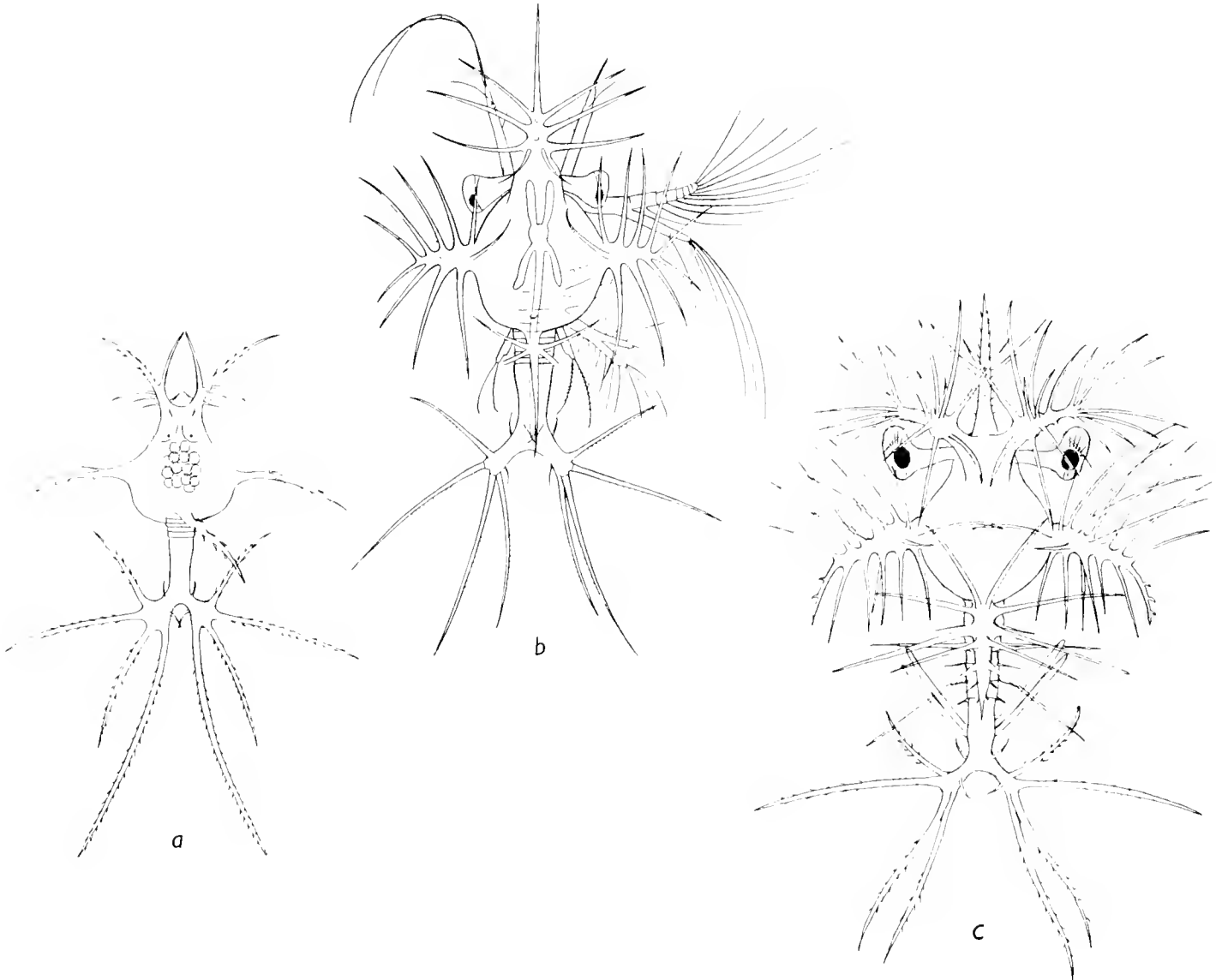


Fig. 45. *S. vigilax*. *a*, Elaphocaris 1; *b*, Elaphocaris 2; *c*, Elaphocaris 3.

Acanthosoma 1 (Fig. 46 *a*). Length 2.35 mm. Rostrum 0.6 mm.

Rostrum longer than antennules, with large basal spine. Supraorbital spines longer than eyes; hepatic spine rather large. Two pairs of lateral spines, of which the second is small and the first reaches about to end of eyes. Posterior dorsal spine small. Dorsal organ absent.

Abdominal somites 1 and 2 with small median ventral spines; lateral spines short, with small spinules, and a rather large backwardly directed basal spine, lateral spines

of somites 4 and 5 small and simple. Dorsal spines nearly equal, the third a little the largest. Telson parallel-sided, sharply constricted and with a simple fork at end. A pair of small lateral spines may or may not be present.

Eye large and asymmetrical, nearly one-fifth length of body, the eyeball two-thirds length of eye. The pigment is dark, usually with a small lighter-coloured area at one end. Labrum with large spine. Antennal scale very long and slender; flagellum nearly

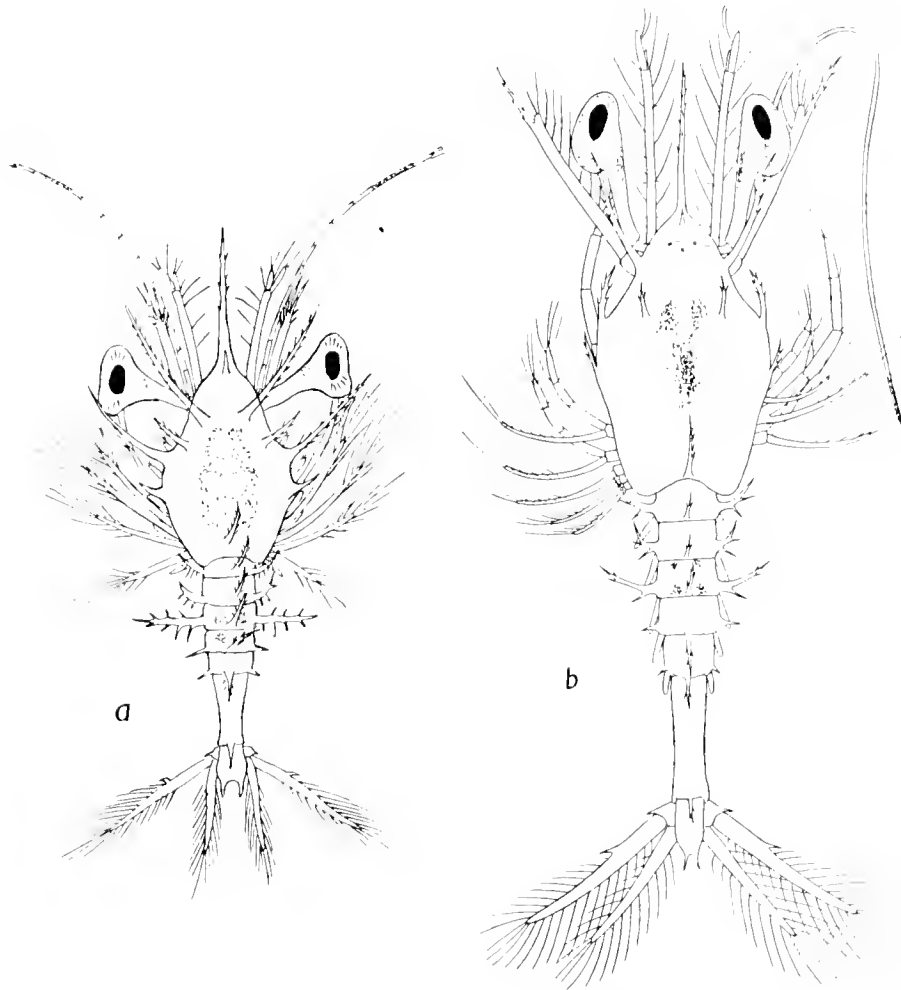


Fig. 46. *S. vigilax*. *a*, Acanthosoma 1; *b*, Acanthosoma 2.

as long as carapace with rostrum. Mandible without palp. Pleopods present as small buds. Exopod of uropod slender, bare part half length of setose part.

Colour. Red in thorax and abdominal somite 3. A little red in eyestalks and near end of flagellum.

Acanthosoma 2 (Figs. 46 *b*, 47). Length 3.2 mm. Rostrum 1.05 mm.

Generally as in stage 1 but supraorbital and lateral spines shorter. Eye somewhat larger, nearly one-quarter length of body, and greatest diameter of eyeball about half length of eye. Antennal scale very long and slender, with apical spine; flagellum 3.8 mm.

Maxillipede 3 very long, reaching beyond base of rostrum. Pleopods large, simple. Exopod of uropods about ten times as long as wide, the setose part 1.7 times as long as bare part. Mandibular palp absent.

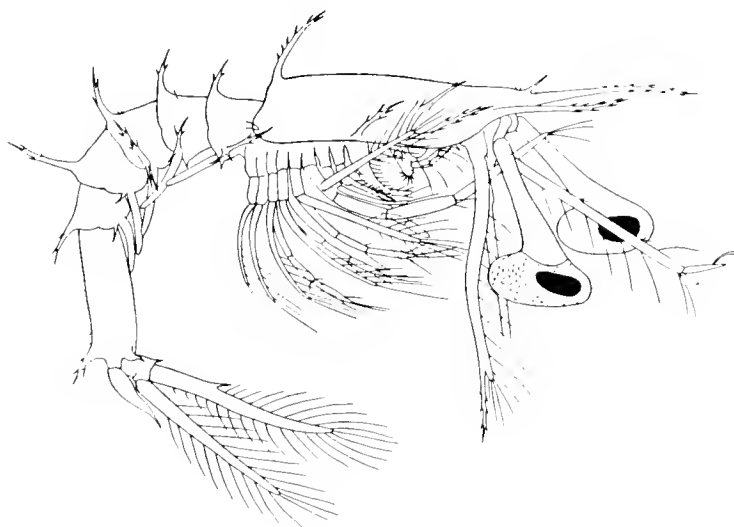


Fig. 47. *S. vigilax*. Acanthosoma 2.

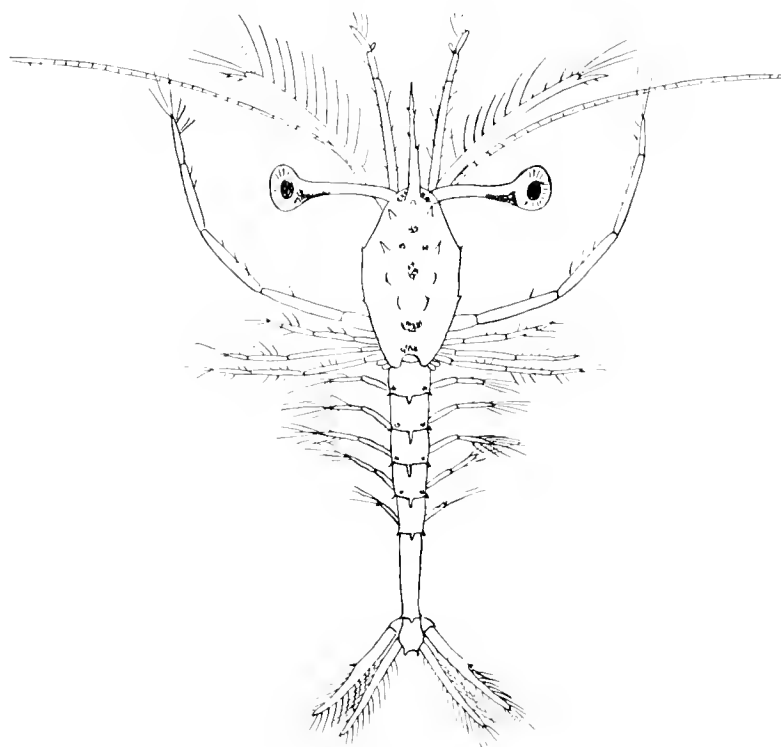


Fig. 48. *S. vigilax*. Mastigopus 1.

Mastigopus 1 (Fig. 48). Length 4.0 mm.

Rostrum as long as segment 1 of antennular peduncle. Carapace with small supra-orbital and hepatic spines. The lateral spines may be entirely lost, or represented by minute vestiges. Posterior dorsal spine rather large.

Abdominal somites with dorsal spines, the first two very small. Pleura with small points. Somites 1 and 2 with ventral spines. Telson not quite twice as long as wide, with very small distal fork.

Eye more than one-quarter length of body, and diameter of eyeball more than half length of eye. Labrum without spine. Antennal scale nearly 20 times as long as wide; flagellum 7.3 mm. long in a specimen of 3.2 mm. Mandibular palp absent.

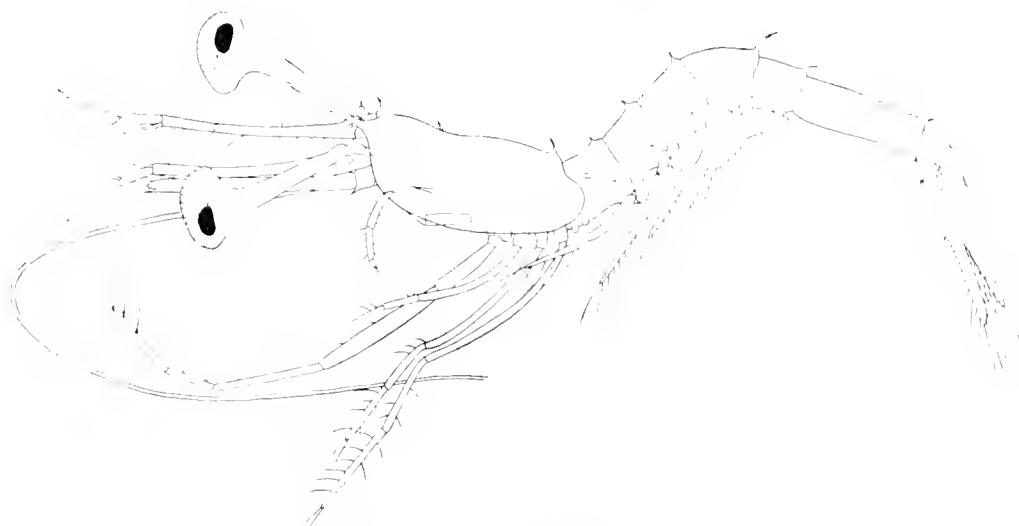


Fig. 49. *S. vigilax*. Mastigopus 2.

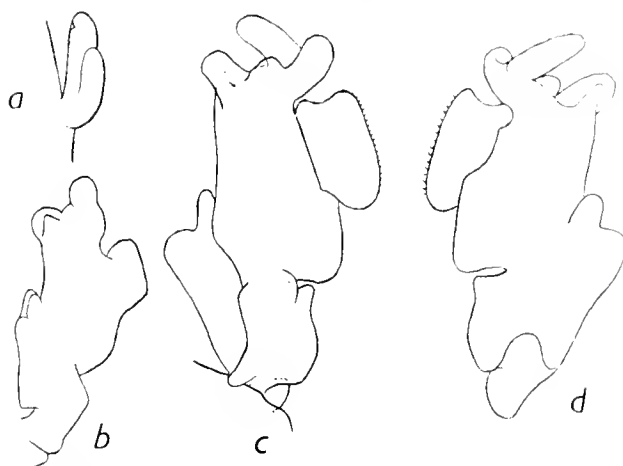


Fig. 50. *S. vigilax*. Petasma. *a*, specimen of 10.94 mm.; *b*, 14 mm.; *c*, 16.3 mm., left, from inside; *d*, the same, from outside.

Stage 2 retains all the spines of stage 1 almost without diminution.

There seems to be much variation in the degree to which the exopods of the legs are retained. Of three specimens moulted from the Acanthosoma one has no trace of exopods, one has minute vestiges, while the third has long exopods even on legs 4 and 5. Pleopods long, uniramous. Setose part of uropod rather more than half length of bare part.

Colour. Body largely colourless, but with bright red patches in eyestalk, at base of rostrum and in thorax.

As Hansen has shown, the Mastigopus phase with long stalked eyes persists up to about 16 mm., and the dorsal spines of the abdomen are retained to about 10 mm. These spines may be lost at 8 mm., but are generally to be found on somites 5 and 6, while the posterior dorsal spine of the thorax may be retained up to 9 mm. The smallest specimen in which we have seen the rudiment of the petasma (Fig. 50) is 10.9 mm., whereas Hansen found it in one of 9 mm. The mandibular palp develops very late, being absent up to about 6 mm. and not fully formed in a male of 11.8 mm. The endopods of the pleopods also develop late. We find in a specimen of 8 mm. the endopods very small, with few setae on 3-5 and no setae on 2.

Sergestes diapontius Bate

Hansen, 1922, p. 173, Mastigopus.

Illig, 1927, p. 338, fig. 117, Mastigopus; fig. 118, Acanthosoma.

MATERIAL. No specimens referable to this species were taken at Bermuda. The following descriptions are from specimens taken at Discovery Stations 282, 701, 702. The identification is somewhat doubtful (see p. 47).

DESCRIPTION. Acanthosoma 1 (Fig. 51 *b-d*). Length 3.0 mm. Rostrum 1.1 mm.

Rostrum much longer than antennule. Supraorbital spine longer than eye, not very spiny. Hepatic spine long and prickly; anterior lateral spine with very long spinules; posterior lateral spine thick, coarsely prickly. Dorsal spine large, prickly, nearly vertical. Dorsal organ minute.

Abdominal somites with dorsal spines long, the third the longest; lateral spines very long and prickly. Somites 1 and 2 with median ventral spines. Telson short, parallel-sided, with lateral spines and small fork, the branches of which are slender and nearly parallel.

Eye large, asymmetrical, less than one-fifth length of body, the eyeball about two-thirds total length. Labral spine minute. Antennal flagellum very long (no entire specimen seen). Mandibular palp absent. Maxillipede 3 not much larger than legs. Exopod of uropod with setose margin 2.7 times as long as bare part.

Acanthosoma 2 (Fig. 51 *a*). Length 3.5 mm. Rostrum 1.42 mm.

General form as in stage 1. Length of eye 1.7 times the greatest diameter of eyeball; total length of eye about one-sixth of body length. Pleopod 5 only with rudiment of endopod. Uropod unchanged.

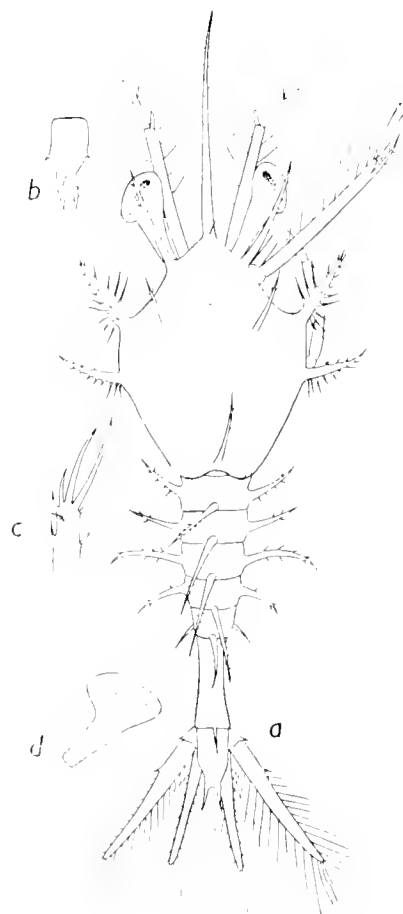


Fig. 51. *S. diapontius*. *a*, Acanthosoma 2; *b-d*, Acanthosoma 1, telson, antennal scale and eye.

There are differences in form of telson and uropod between these specimens and the figures given by Illig, and he does not mention ventral abdominal spines; but otherwise the agreement is close.

REMARKS. While of the same general form as the larva of *S. vigilax* the Acanthosoma described differs from it in nearly all details, particularly in the large size and long spinules of the lateral thoracic spines, and the longer dorsal spines of the abdomen. Both have ventral spines on abdominal somites 1 and 2. We have the authority of Hansen for regarding *S. penerinkii* Bate as the Mastigopus of *S. diapontius*, and he also confirms the presence of ventral spines on somites 1 and 2. We regard this particular feature as the strongest reason for reference of the Acanthosoma to *S. diapontius*.

We have not seen any Mastigopus which can be referred to this species. According to Hansen and Illig it resembles *S. vigilax* very closely. According to Hansen it differs from the latter in retaining the dorsal spines on abdominal somites 3-5 up to a length of 14 mm. The rostrum is said to be longer at equivalent stages, and the eyes shorter and with smaller eyeballs. These differences do not appear in Illig's figure of a Mastigopus of 5 mm. (Fig. 117) which lacks the ventral abdominal spines and has eyes as long and as large as *S. vigilax*.

Sergestes armatus Kröyer

Hansen, 1922, p. 179, Mastigopus.

Illig, 1927, fig. 126, Elaphocaris 2 (?).

Cecchini, 1928*b*, p. 41, Mastigopus.

MATERIAL. This appears to be a rare species at Bermuda. The characters of Elaphocaris 3 have been established by moult to Acanthosoma, but Elaphocaris 1 and 2 described below are referred to this species with some doubt since, though stage 1 was connected with stage 2 by moult, stage 2 was not so connected with stage 3. The difference in structure of the posterior process makes the identification doubtful, but the similarity in colour is very close, and it is difficult to suggest any other species to which these stages could belong. The first Mastigopus was obtained by moult from the Acanthosoma. The Acanthosoma was found also at Discovery Stations 701 and 703.

DESCRIPTION. Elaphocaris 1 (Fig. 52 *a*). Length 0.56 mm.

Anterior process with a pair of large lateral spines near base and a pair of smaller ones beyond. Lateral process almost at right angles to carapace and curving backwards at end, nearly smooth. Posterior process rather short, with two pairs of spines. Telson branches very long and slender; spine 5 not greatly longer than the others. Labral spine unusually long.

Elaphocaris 2 (Fig. 52 *b, c*). Length 0.7 mm. Rostrum 0.96 mm.

Rostrum very long and stout, with three pairs of lateral and two dorsal spines. Lateral process with four pairs of lateral spines. Posterior process swollen at base where it bears eight spines.

Colour. A large patch of crimson in gastric region. A fleck of red in the black pigment of the eye.

Elaphocaris 3 (Fig. 53 *a, b*). Length (approximate) 2.0 mm. Rostrum 0.9 mm.

Rostrum rather short, with one pair of lateral and two long ventral spines. Supra-orbital process very stout, with 18 spines. Lateral process stout, with 19 spines. Posterior process not reaching end of abdomen, with four pairs of lateral spines. In the specimen described there is an unpaired spine at the base directed forwards.

Abdominal somites with slender pleural spines. Arms of telson narrow, width less than half length; spine 5 the longest.

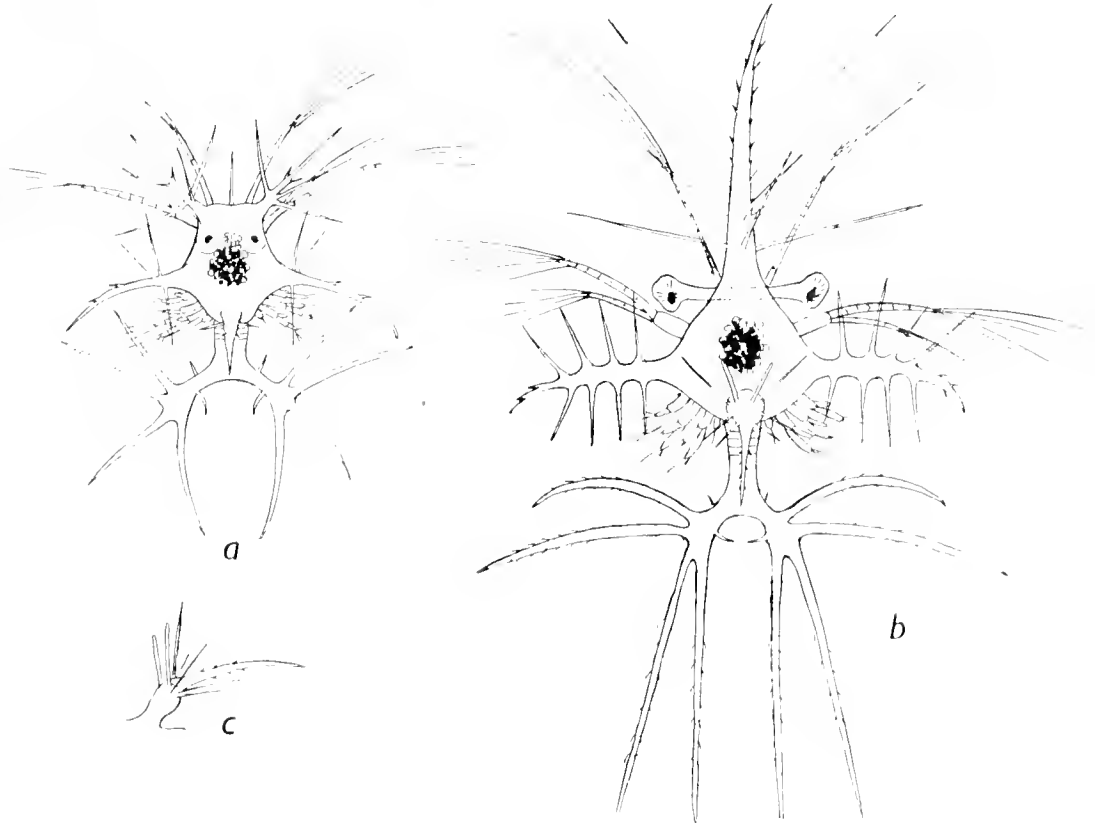


Fig. 52. *S. armatus*. *a*, *Elaphocaris* 1; *b*, *Elaphocaris* 2; *c*, dorsal spine, side view.

The description and figure are taken from a moulted skin, since no others were taken at Bermuda. A damaged specimen from Discovery Station 701 which appears to belong to this species has a minute dorsal organ, and the eye is short and pear-shaped, the width of eyeball three-quarters length of eye.

Acanthosoma 1 (Fig. 54). Length 3.1 mm. Rostrum 0.9 mm.

Rostrum a little longer than antennule, with small basal spine. Supraorbital spines reaching end of segment 1 of antennule. Hepatic spine very small. Two pairs of stout lateral spines. Posterior dorsal spine rather small. Dorsal organ very small.

Abdominal somites with dorsal spines nearly equal, the third a little the longest. Lateral spines 1-3 very stout and spiny; 4 and 5 small, smooth, or with a few spinules. Telson about $1\frac{1}{2}$ times as long as wide, with small distal fork and no lateral spines. Somites 1-3 with blunt ventral spines.

Eye about one-fifth length of body; eyeball asymmetrical, the greatest width nearly equal to total length, without papilla. Labral spine present. Antennal scale eight times as long as wide; flagellum more than twice length of antennule. Mandible without palp. Exopod of uropod narrow, seven times as long as wide, the setose margin more than $1\frac{1}{2}$ times length of bare part.

Acanthosoma 2. The only specimen of this stage taken moulted to Mastigopus, and the cast skin is not sufficiently complete for description. The telson differs from the



Fig. 53. *S. armatus*. a, Elaphocaris 3, cast skin; b, telson.



Fig. 54. *S. armatus*. Acanthosoma 1.

specimen of stage 1 described in having a pair of very small dorso-lateral spines, and the arms of the fork smooth. Exopod of uropod setose part of margin 1.8 times as long as bare part.

Colour (stage 1). Antennules dark grey at end. Flagellum of antenna orange red at end. Thorax and eye with red markings as shown in Fig. 54. Abdomen colourless.

Mastigopus 1. Length 3.2 mm. Rostrum 0.38 mm.

Carapace with small hepatic and posterior dorsal spines but no trace of lateral spines. Abdominal somites with dorsal spines, very small on somites 1 and 2, longest on 4.

Minute pleural spines on each somite. Somites 1-3 with sharp median ventral spines. Telson short, with small sharp-pointed fork and no lateral spines.

Eye nearly one-quarter length of body; eyeball asymmetrical, greatest width a little more than half total length. Legs with long vestiges of exopods. Pleopods without endopods. Exopod of uropod slender, about ten times as long as wide, the bare part little more than half length of setose margin.

We have specimens of the *Mastigopus* of 5.9, 9.5 and 12 mm. (Fig. 55). At 9.5 mm. the abdominal somites retain the pleural spines, but they are lost at 12 mm. The dorsal spines are all retained up to 12 mm., and on all but somite 1 in a specimen of 19 mm. figured by Hansen.

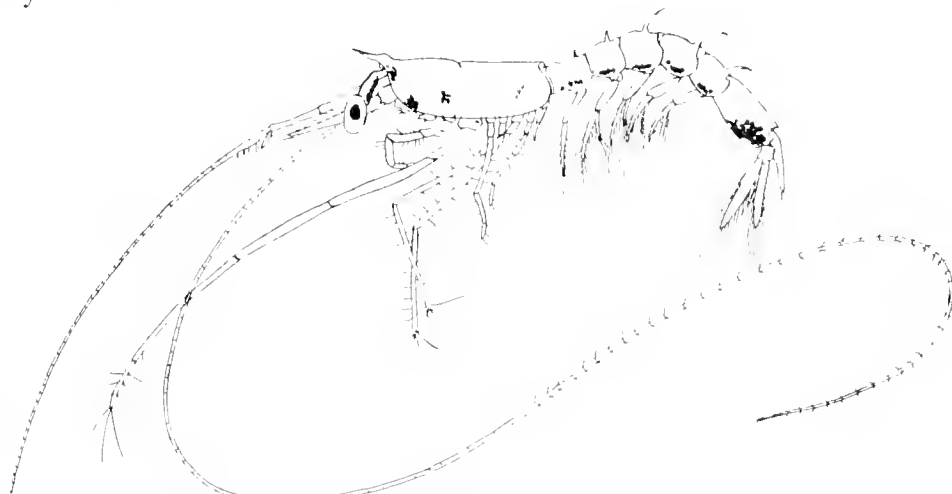


Fig. 55. *S. armatus*. *Mastigopus*, 12 mm.

Sergestes edwardsi Kröyer

Hansen, 1922, p. 185, *Mastigopus*.

Illig, 1927, p. 324, *Mastigopus* and *Acanthosoma* 2.

MATERIAL. This species was not taken at Bermuda. The following descriptions are from specimens taken at Discovery Stations 701, 702, 703, 704, 705, 706, 708, from $14^{\circ} 39' N$, $25^{\circ} 57' W$ to $10^{\circ} 26' S$, $34^{\circ} 57' W$.

DESCRIPTION. *Elaphocaris* (Fig. 56 *a, b*). An *Elaphocaris* in stage 2 taken at Station 704 probably belongs to this species. It very closely resembles *S. vigilax*. Length 1.00 mm. Rostrum broken.

Rostrum with two median ventral and four pairs of lateral spines at base. Lateral process with ten spines including the main terminal spine. Posterior process with two pairs of lateral spines. Telson arms about twice as long as wide. Dorsal organ rather large.

Eye short, the greatest width nearly equal to the length, without papilla. Labral spine not very long.

Acanthosoma 1 (Fig. 56 *d-f*). Length 2.0-2.41 mm. Rostrum 0.75-0.85 mm.

Rostrum shorter than antennule. Supraorbital spine longer than eye. Two lateral spines large, with small spinules. Posterior dorsal spine very long, bent forwards and

reaching nearly to hepatic spine. Dorsal organ very small. Dorsal spines of abdomen decreasing from in front backwards. Lateral spine of somite 1 very much longer than the rest, turned forwards. Lateral spines of somites 2-5 small, simple, 2-4 with small basal accessory spine. Somites 1-5 with median ventral spines. Telson short, parallel-sided, with small lateral spines and small simple apical fork, the arms of which are nearly parallel.

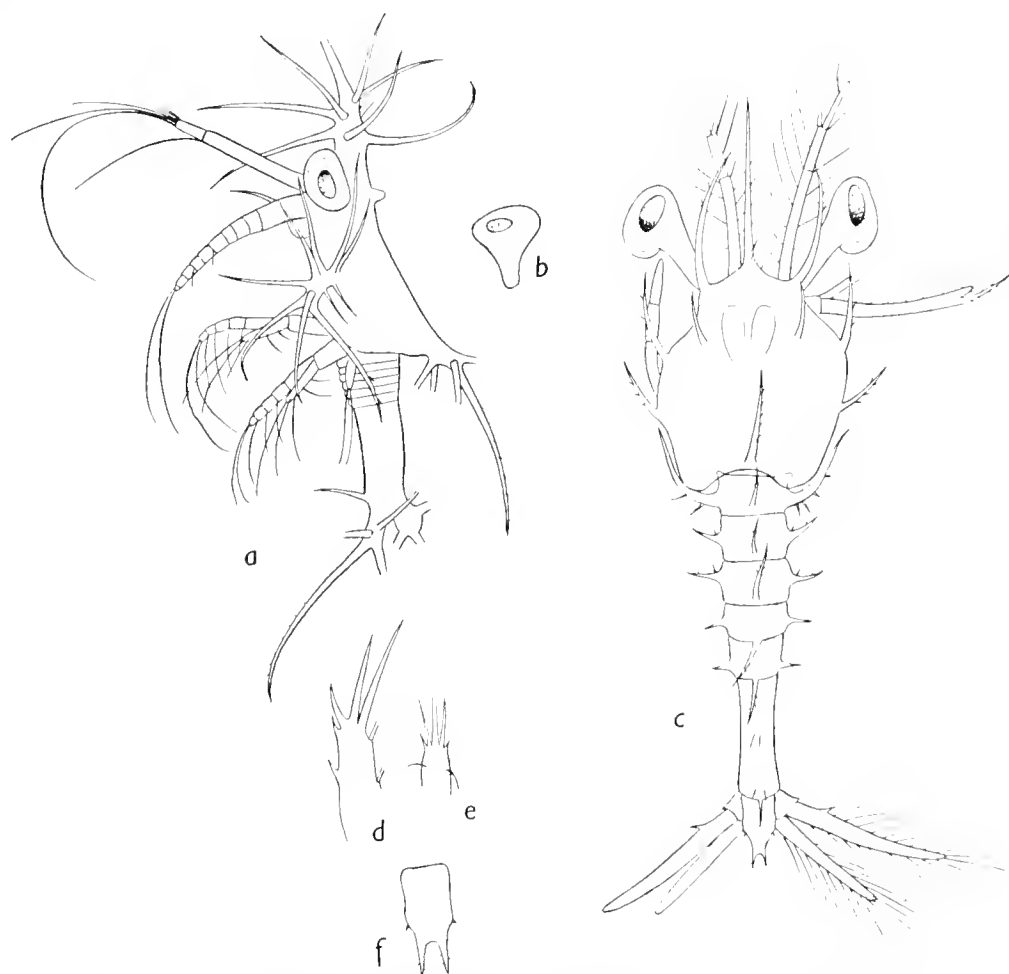


Fig. 56. *S. edwardsi*. *a*, Elaphocaris 2; *b*, eye; *c*, Acanthosoma 2; *d-f*, Acanthosoma 1, antennal scale, end of antennal endopod and telson.

Eye large, asymmetrical, about one-fifth length of body, without papilla. Greatest diameter of eyeball more than half length of eye. In preserved specimens the pigment is pale, with a darker area at one end. Antennal scale short, with two small spines on outer margin near end, and three stout apical setae; flagellum very long (2.48 mm.) with a pair of small spines near base and one on antepenultimate segment. Mandible without palp. Exopod of uropod about seven times as long as wide, the setose part three times as long as the bare part.

Acanthosoma 2 (Fig. 56 *c*). Length 2.7 mm. Rostrum 0.75 mm.

Mandible without palp. Maxillipede 3 much larger than legs. Pleopods small, without endopods.

Mastigopus 1. Length 3.15 mm. Rostrum 0.55 mm.

Supraorbital, hepatic and posterior dorsal spines present, but no marginal. Dorsal organ very small.

Abdomen with minute dorsal spines on somites 1-3, those of 4 and 5 larger; spine on somite 6 minute. Minute pleural points on somite 4 and larger on somite 5; none on somites 1-3. Median ventral spines on somites 1-4. Telson short, as in *S. vigilax*.

Eye of same form as in *Acanthosoma*, with same dark area in the pigmented part. Mandible without palp. Legs without trace of exopods. Legs 4 and 5 vestigial. Pleopods without endopods. Exopod of uropods, setose part five times as long as bare part and about seven times as long as wide.

REMARKS. Hansen has described (1919, p. 25) the *Acanthosoma* of *S. orientalis* which is very closely allied to *S. edwardsi* and seems to replace it in the Pacific. So far as can be seen from his figures and description the *Acanthosoma* is almost identical with that of *S. edwardsi*. He does not, however, mention the median ventral abdominal spines.

TABLES OF MEASUREMENTS

The following tables of measurements show clearly some of the differences between species in shape of eye and its length in proportion to the body, and in the proportion the setose part of the outer margin of the uropod bears to the bare part. Where sufficient specimens are available the changes which take place with growth are shown. These measurements reveal much individual variation, and it must be confessed that they are open to the objection that the proportion of eye to body cannot be entirely accurate owing to the difficulty of measuring the body correctly when, as is generally the case, it is bent nearly double.

The specimens of *S. corniculum* measured include more than one species, but we have been unable to separate them with certainty. Those marked * and ** have been examined by Mr Burkenroad and are regarded by him as probably representing two different species.

Measurements of Mastigopus

Length without rostrum	Eye		Exopod of uropod	
	Length : body	Length : width	Setose : bare	Length : width
<i>S. atlanticus</i>				
3.40	3.86	1.76	1.25	18.00
3.91	3.90	2.27	1.16	11.40
5.20	4.70	2.00	0.90	8.40
5.35	4.60	1.70	0.80	9.00
6.00	5.00	2.00	0.70	8.00
7.10	5.20	2.00	0.60	—
8.35	6.00	—	0.55	6.20
9.90	7.60	2.10	0.50	4.50
10.35	7.70	—	0.50	6.00

Measurements of Mastigopus (continued)

Length without rostrum	Eye		Exopod of uropod	
	Length : body	Length : width	Setose : bare	Length : width
<i>S. cornutus</i>				
4.80	3.40	2.80	1.00	9.00
5.30	4.00	2.90	1.17	8.40
5.40	4.00	3.90	1.12	9.00
9.00	3.00	4.30	0.50	4.50
<i>S. arcticus</i>				
5.10	4.20	3.20	1.04	7.20
6.68	4.70	3.50	1.02	7.90
7.20	5.80	3.50	1.25	6.00
10.00	6.20	3.90	1.30	7.30
<i>S. crassus</i>				
4.15	6.90	1.70	1.30	6.10
4.20	7.50	1.80	1.25	4.30
4.68	6.10	—	1.30	4.20
4.85	5.00	2.00	1.50	5.70
6.00	8.00	1.50	1.70	4.40
6.95	8.30	2.00	2.00	4.00
7.30	8.00	2.20	1.80	4.30
15.00	10.80	—	2.40	4.50
<i>S. robustus</i> (Bermuda)				
5.10	6.00	2.60	0.82	5.40
6.60	6.60	2.70	0.76	5.00
7.50	7.10	2.50	0.67	4.20
9.00	7.50	2.24	0.50	5.40
10.00	7.60	2.24	0.40	5.30
11.00	7.70	2.60	0.49	5.00
13.00	9.20	2.70	0.49	4.80
18.80	12.60	3.30	0.41	4.50
<i>S. robustus</i> Form A				
7.20	8.40	2.50	0.80	7.00
7.35	8.30	2.00	0.73	7.40
9.00	8.10	3.10	0.77	6.00
12.75	9.80	2.40	0.55	5.70
15.00	7.50	—	0.55	4.00
<i>S. corniculum</i> (Bermuda)				
**3.20	4.40	1.60	1.68	9.50
3.80	4.80	1.80	2.00	10.00
3.88	4.70	1.80	1.60	9.00
4.00	4.60	1.70	1.57	8.10
5.00	5.00	1.70	1.47	8.00
6.00	6.00	1.70	1.46	7.00
6.00	5.00	1.65	1.40	6.40
6.70	7.10	1.58	1.60	6.70
8.20	7.10	1.70	1.50	6.70
*8.20	6.30	1.80	1.50	6.60
8.50	7.00	1.80	1.50	7.00
8.80	6.90	1.80	1.70	8.50

Measurements of Mastigopus (continued)

Length without rostrum	Eye		Exopod of uropod	
	Length : body	Length : width	Setose : bare	Length : width
<i>S. corniculum</i> (Bermuda) (continued)				
* 9.50	8.70	2.20	1.70	6.20
10.00	7.10	—	1.54	6.40
11.60	8.60	1.60	1.50	—
12.00	8.00	2.10	1.66	6.70
12.15	9.20	2.00	1.34	6.50
* 13.00	8.60	1.60	1.80	—
17.20	11.30	2.10	1.54	6.20
<i>S. pectinatus</i> (Bermuda)				
2.50	5.00	0.94	2.00	—
4.10	7.00	0.86	2.25	—
6.00	6.60	0.95	2.70	—
6.13	6.80	0.95	2.10	—
8.60	5.20	1.00	3.30	—
<i>S. sargassi</i> (Bermuda)				
4.35	6.80	1.14	1.60	6.90
5.60	7.50	1.10	1.60	6.05
6.30	8.30	1.00	1.80	6.77
6.78	8.00	1.00	1.64	5.60
8.20	8.60	1.20	1.90	6.50
10.25	10.70	1.20	1.70	6.23
<i>S. vigilax</i>				
4.20	4.00	2.00	2.17	9.50
5.05	3.80	2.00	2.06	9.00
5.15	3.70	2.60	2.20	7.00
5.20	4.00	2.00	2.00	—
5.40	4.00	2.00	1.52	—
5.70	4.13	2.30	2.17	6.00
5.69	4.70	—	1.80	6.00
6.20	4.70	2.00	—	—
8.00	4.00	2.45	2.90	5.00
8.00	4.00	2.10	2.35	—
9.00	4.40	2.50	3.50	6.00
♂ 10.94	5.20	2.50	4.00	—
♂ 11.65	5.00	2.50	4.00	6.00
♂ 11.80	4.80	2.70	3.40	4.60
♂ 12.25	4.70	—	3.30	—
♂ 14.00	5.50	2.80	3.90	5.30
♂ 16.30	6.15	2.50	3.00	—
<i>S. armatus</i>				
3.20	4.00	1.80	2.00	10.30
5.90	5.00	1.60	1.70	9.87
9.50	6.60	2.37	1.72	8.16
<i>S. edwardsi</i>				
3.15	7.88	1.47	5.00	7.50

LITERATURE

A very full list of literature is given by Hansen (1922) and all papers referred to in this report will be found in Gurney, *Bibliography of the larvae of Decapod Crustacea* (Ray Society, London, 1939). The only papers mentioned which are not included in this bibliography are:

- BURKENROAD, M. D., 1937. The Templeton Crocker Expedition. XII. *Sergestidae from the lower Californian region, with descriptions of two new species and some remarks on the organs of Pesta in Sergestes*. Zoologica, New York, xxii, pp. 315-29.
- GORDON, I., 1935. *On new or imperfectly known species of Crustacea Macrura*. J. Linn. Soc. Lond. Zool. xxxix, pp. 307-51.

[*Discovery Reports. Vol. XX, pp. 69-306, Plates I-XXIII, November 1940.*]

ASTEROIDEA

BY

WALTER K. FISHER

Director, Hopkins Marine Station of Stanford University

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ASTEROIDEA

By Walter K. Fisher

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(Plates I–XXIII; Text-figs. A–M)

INTRODUCTION

THIS report deals with the sea stars collected by the 'Discovery', the 'Discovery II', and the 'William Scoresby' during the years 1925–36 in sub-Antarctic and Antarctic seas from the Falkland Island region to South Georgia, South Sandwich Group, South Orkneys, Antarctic Archipelago, and Ross Sea. A few hauls were made off Tristan da Cunha, Gough Island, Bouvet Island, and Marion Island. Certain species from Africa and elsewhere, which do not pertain to the Antarctic and sub-Antarctic faunas, have been listed separately.

Our knowledge of the Asteroid fauna of the sub-Antarctic and Antarctic seas is chiefly derived from the work of Koehler, based on the collections of the 'Scotia', the 'Nimrod', the 'Pourquoi-Pas?', the Australasian Antarctic Expedition, and the Swedish Antarctic Expedition. But much earlier the 'Challenger' occupied a number of stations between Prince Edward Islands and the Magellanic region, which included Kerguelen, Heard, and two stations (153, 156) near the Antarctic Circle at longitude $79\frac{1}{2}^{\circ}$ and $95\frac{1}{2}^{\circ}$ E. In the Challenger Report Sladen described numerous now familiar sub-Antarctic species and also the following Antarctic forms:

<i>Hyphalaster planus</i>	<i>P. stellifer</i>
<i>Lonchotaster forcipifer</i>	<i>Hymenaster nobilis</i>
<i>Mimastrella cognata</i> (olim <i>Mimaster</i>)	<i>H. formosus</i>
<i>Bathybiaster loripes obesus</i>	<i>H. sacculatus</i>
<i>Benthoptecten antarcticus</i> (olim <i>Pararchaster</i>)	<i>H. caelatus</i>
<i>Acodontaster elongatus</i> (olim <i>Guathaster</i>)	<i>H. crucifer</i>
<i>Chitonaster cataphractus</i>	<i>H. latebrosus</i>
<i>Perknaster fuscus</i>	<i>Freyella fragilissima</i>
<i>P. densus</i>	<i>Pedicellaster hypernotius</i>
<i>Porania antarctica glabra</i>	<i>Labidiaster annulatus</i>
<i>Solaster regularis subarcuatus</i>	<i>Smilasterias triremis</i>
<i>Pteraster rugatus</i>	

As these comprise around 20 per cent of the entire list of Antarctic sea stars, it will be seen that the 'Challenger' was in every sense a real pioneer.

Another important contribution is Perrier's (1891) report on the collections made in 1882–3 by the 'Mission Scientifique du Cap Horn'. This paper furnished a number of new sub-Antarctic species, still valid, and not a few nomenclatorial tangles. Only two of Perrier's species, *Perknaster sladeni* and *Pteraster lebruni*, extend into Antarctic waters.

The Belgica collection reported by Hubert Ludwig (1903) added eleven new Antarctic species, of which three are synonymous with Challenger species.

The new species in the Discovery collection, some from regions already partly explored, indicate that we are yet a long way from having a complete picture of the Antarctic fauna. The following is a list of new forms, the exclusively sub-Antarctic being marked with an asterisk:

<i>Acodontaster elongatus granuliferus</i> forma <i>ceramoideus</i> *	<i>L. densus</i>
<i>Notioceramus anomalus</i>	<i>Paralophaster godefroyi meseres</i>
<i>Pergamaster synaptorus</i>	<i>Odinella nutrix</i>
<i>Cladaster analogus</i> *	<i>Antelaster australis</i>
<i>Hippasteria falklandica</i> *	<i>Lethasterias australis</i> *
<i>Perknaster sladeni georgianus</i>	<i>Notasterias stolophora</i>
<i>Anseropoda antarctica</i>	<i>Psalidaster mordax</i> *
<i>Mirastrella biradialis</i>	<i>Lysasterias homiora</i>
<i>Rhopiella koehleri</i>	<i>L. heteractis</i>
<i>Lophaster marionis</i> *	<i>Luidia heterozona</i> (Africa)

Notioceramus, *Mirastrella*, *Odinella*, and *Psalidaster* are new generic types, based upon new species, while *Rhopiella*, *Paralophaster*, and *Myoraster* are based upon species already known. A new subgenus *Apterodon* is instituted for a natural section of *Pteraster*, and *Euretaster* is a new name for the old genus *Retaster*, which by one of the accidents of nomenclature was really without a name. *Spoladaster* is a new generic name for *Cryaster brachyactis* H. L. Clark, which is not a *Cryaster* (i.e. *Perknaster*) but is related to *Tylaster* (Asteropidae).

It is still premature to analyse in detail the distribution of Antarctic species. The Discovery collection has materially enlarged, sometimes radically, the previously known range of included species. Some forms now believed to have a limited distribution are undoubtedly wide ranging. Certain characteristics of the Antarctic fauna may be noted.

There are no families strictly confined to the southern hemisphere, although the Ganeriidae are southern with two possible exceptions,¹ and the Odontasteridae are more numerous in genera and species in sub-Antarctic and Antarctic regions.

The following genera are Antarctic† or sub-Antarctic*:

ASTROPECTINIDAE	GANERIIDAE
<i>Mimastrella</i> †*	<i>Scotiaster</i> †
ODONTASTERIDAE	<i>Ganeria</i> †*
<i>Asterodon</i> *	<i>Cycethra</i> †*
<i>Acodontaster</i> †*	<i>Perknaster</i> †*
GONIASTERIDAE	ASTERINIDAE
<i>Notioceramus</i> †	<i>Kampylaster</i> †
<i>Pergamaster</i> †	<i>Mirastrella</i> †
<i>Chitonaster</i> †	

¹ *Lcilaster* A. H. Clark, 1938, p. 1, pl. 1, figs. 1, 2. *Alentiaster* A. H. Clark, *Proc. U.S. National Museum*, vol. LXXXVI, 1939, p. 497, pl. 57.

ECHINASTERIDAE	<i>Psolidaster</i> *
<i>Rhopiella</i> †	<i>Anasterias</i> *
SOLASTERIDAE	<i>Lysasterias</i> †
<i>Paralophaster</i> †	<i>Diplasterias</i> *†
<i>Myoraster</i> †	<i>Adelasterias</i> †
<i>Cuenotaster</i> †	<i>Cryptasterias</i> †*
BRISINGIDAE	<i>Saliasterias</i> †
<i>Odinella</i> †	<i>Neosmilaster</i> †*
<i>Belgicella</i> †	<i>Smilasterias</i> †*
ASTERIIDAE	<i>Eremasterias</i> *
<i>Labidiaster</i> †*	<i>Cosmasterias</i> *†
<i>Notasterias</i> †	<i>Granaster</i> †
	<i>Calvasterias</i> *

The species which give “character” to the Antarctic fauna either by their surpassing size* or frequency† of occurrence are the following:

<i>Leptychaster accrescens</i> *	<i>Perknaster fuscus antarcticus</i> *†
<i>L. flexuosus</i> *	<i>P. charcoti</i> *
<i>L. magnificus</i> *	<i>P. aurorae</i> *
<i>Bathybiaster loripes obesus</i> *†	<i>Porania antarctica glabra</i> †
<i>Psilaster charcoti</i> *†	<i>Myoraster antarcticus</i> *†
<i>Luidiaster gerlachei</i> *	<i>Cuenotaster involutus</i>
<i>Odontaster meridionalis</i> †	<i>Labidiaster annulatus</i> *†
<i>O. validus</i> †	<i>Lysasterias perrieri</i> *†
<i>Acodontaster elongatus</i> *	<i>Diplasterias brucei</i> *†
<i>A. conspicuus</i> *	<i>Granaster nutrix</i> †
<i>A. hodgsoni</i> *	

This list of course omits many species which are equally characteristic or unusual but which do not bulk large in collections. Such are the other species of genera peculiar to the Antarctic listed above, as well as the rare *Notioceramus*, *Pergamaster*, *Chitonaster*, *Kampylaster*, *Mirastrella*, *Rhopiella*, *Paralophaster* and *Odinella*.

The last is a very unusual new type of Brisingidae, a family not well represented in southern seas. It has “evolved” an entirely new type of marsupium for the care of developing eggs—the only known case of “brooding” in the family.

The brooding or paedophoric habit of certain sea stars of the cold waters of both northern and southern hemispheres has long been known. Ludwig in 1903 (p. 56) published a list of references to eleven Antarctic and sub-Antarctic species.

It is likely that all species of *Pteraster*, *Euretaster*, *Diplopteraster* and *Hymenaster* brood their young in the supradorsal chamber. The habit is probably widespread in *Leptychaster* and *Henricia*, as well as in all genera having large eggs and gonoducts which open ventrally. Eggs, embryos, or young have been observed in the brood cavity of the following southern genera: *Kampylaster*, *Rhopiella*, *Odinella*, *Anasterias*, *Lysasterias*, *Diplasterias*, *Cryptasterias*,¹ *Neosmilaster*, *Granaster*. The following genera are probably

¹ Koehler (1906, p. 21) states that several specimens “sont fixés dans l'attitude incubatrice, le disque relevé et la base des bras rapprochée; mais aucun d'eux n'est en gestation”. The eggs of *C. turqueti* are few and unusually large.

paedophoric: *Mirastrella*, *Anteliaster*, *Psalidaster*; but they have not as yet been observed carrying embryos or young.

Koehler published in 1912 (pp. 252-5) a most useful list of Antarctic and sub-Antarctic sea stars in which sixty-seven species are cited. In the following revised list there are 114 species, even though fifteen names of Koehler's table do not appear in my list. This is reduced to ten, however, by the inclusion of five of Koehler's sub-Antarctic species in my list. Numerous new species, of course, were added by Koehler subsequent to 1912.

LIST OF ANTARCTIC SEA STARS WITH BATHYMETRIC RANGE.
SPECIES PRECEDED BY ASTERISK ARE ALSO SUB-ANTARCTIC

- Hyphalaster scotiae* Koehler, 2580 m.
H. planus Sladen, 3568 m.
Lonchotaster forcipifer Sladen, 2568-3615 m.
Leptychaster kerguelensis Smith, 18-384 m.
L. flexuosus Koehler, 351-581 m.
L. accrescens Koehler, 97-608 m.
L. magnificus (Koehler), 5-203 m.
 **Mimastrella cognata* (Sladen), 450-2424 m.
Bathybiaster loripes obesus Sladen, 18-420 m.
Psilaster charcoti (Koehler), 0-2424 m.
Dytaster felix Koehler, 2580 m.
Luidiaster gurlachei (Ludwig), 160-810 m.
L. antarcticus (Koehler), 3238 m. (*Marcelaster antarcticus*)
Benthopecten antarcticus (Sladen), 3065 m.
Odontaster meridionalis (Smith), 0-647 m.
O. validus Koehler, 0-653 m.
Acodontaster elongatus (Sladen), 108-647 m.
 **A. conspicuus* (Koehler), 24-647 m.
A. marginatus (Koehler), 250 m.
A. waiti (Koehler), 160-647 m.
A. hodgsoni (Bell), 3-204 m.
Notioceramus anomalus Fisher, 342 m.
Pergamaster incertus (Bell), 96-3111 m.
P. synaptorus Fisher, 342 m.
Chitonaster cataphractus Sladen, 3614 m.
C. johannae Koehler, 3248 m.
Scotiaster inornatus Koehler, 3848 m.
Ganeria attenuata Koehler, 3248 m.
 **Cycethra verrucosa* (Philippi), 60-342 m.
 **Perknaster fuscus* Sladen, 46-138 m.
P. fuscus antarcticus (Koehler), 11-335 m.
 **P. densus* Sladen, 101-233 m.
 **P. sladeni* (Perrier), 199-500 m.
P. sladeni georgianus Fisher, 120-204 m.
P. charcoti (Koehler), 0-235 m.
P. aurorae (Koehler), 18-310 m.
P. aurantiacus Koehler, 92-254 m.
Anseropoda antarctica Fisher, 342 m.
Kampylaster incurvatus Koehler, 93-351 m.
Mirastrella biradialis Fisher, 177-342 m.
Porania antarctica glabra Sladen, 15-567 m.
 **Echinaster spinulifer* E. A. Smith,¹ 0-91 m.
Rhopiella koehleri Fisher, 93-335 m.
R. hirsuta (Koehler), 276-647 m.
R. pterasteroides (Koehler), 655 m.
R. smilax (Koehler), 191-581 m.
R. smithi (Ludwig), 450 m.
 **Henricia pagenstecheri* (Studer), 18-250 m.
H. pagenstecheri parva (Koehler), 191-610 m.
 **H. diffidens* (Koehler), 75-463 m.
 **Lophaster stellans* Sladen, 450 m.²
L. gaini Koehler, 191-732 m.
L. densus Fisher, 200-610 m.
Paralophaster godefroyi (Koehler), 250-400 m.
P. godefroyi meseres Fisher, 567 m.
P. asperatus Koehler, 191 m.
P. lorioli Koehler, 4575 m.
Solaster regularis subarcuatus Sladen, 183-500 m.
Myroaster antarcticus (Koehler), 99-750 m.
M.? *tenuis*³ (Koehler), 191 m.
Cucnotaster involutus (Koehler), 60-700 m.
Remaster gourdoni Koehler, 10-342 m.
Peribolaster macleani Koehler, 191-581 m.
 **Pteraster lebruni* Perrier, 74-450 m.
P. aculeatus Koehler, 614 m.
P. rugatus Sladen, 274 m.
 **P. stellifer* Sladen, 79-655 m.
Hymenaster nobilis Sladen,¹ 3294 m.
H. formosus Sladen,⁴ 3294 m.

¹ A Kerguelen species recorded from South Georgia, 91 m., by G. A. Smith, 1923, p. 368.

² The Antarctic specimens recorded by Ludwig (1903, p. 27). The species is typically sub-Antarctic.

³ May belong in *Lophaster*.

⁴ Challenger St. 158, 50° 1' S, 123° 4' E, bottom temperature 33.5° F.

- H. sacculatus* Sladen,¹ 3294 m.
H. caelatus Sladen,¹ 3294 m.
H. crucifer Sladen,¹ 3294 m.
H. latebrosus Sladen,² 3568 m.
H. perspicuus Ludwig, 450 m.
H. campanulatus Koehler, 2580 m.
H. edax Koehler, 3248 m.
H. fucatus Koehler, 2580 m.
H. densus Koehler, 4794 m.
Odinella nutrix Fisher, 120–545 m.
Belgicella racovitzana Ludwig, 2580–2800 m.
Freyella fragilissima Sladen, 2515–3615 m.
F. giardi Koehler, 4575 m.
 **Pedicellaster hypernotius* Sladen, 93–450 m.
P. formatus Koehler, 219 m.
Antelaster australis Fisher, 177–260 m.
Labidiaster annulatus Sladen, 93–440 m.
Sclerasterias candicans (Ludwig), 450–560 m.
Notasterias armata Koehler, 30–647 m.
N. stolophora Fisher, 247 m.
N. bongraini (Koehler), 109–830 m.
N. pedicellaris (Koehler), 2580 m.
N. haswelli Koehler, 109–647 m.
Lysasterias perrieri (Studer), 0–647 m.
L. heteractis Fisher, 342 m.
L. adeliae (Koehler), 22–335 m.
L. joffrei (Koehler), 351–810 m.
L. chirophora (Ludwig), 450–560 m.
L. hemiora Fisher, 70 m.
L. lactea (Ludwig), 450 m.
L. belgicae (Ludwig), 560 m.
Adelasterias papillosa (Koehler), 0–6 m.
 **Diplasterias brandti* (Bell), 50–300 m.
 **D. meridionalis* (Perrier), 0–234 m.
D. brucei (Koehler), 0–581 m.
D. fochi (Koehler), 109–732 m.
D. octoradiata (Studer),³ 8–55 m.
D. radiata (Koehler),⁴ 160–177 m.
Cryptasterias turqueti (Koehler), 0–36 m.
Saliasterias brachiata Koehler, 647 m.
Neosmilaster georgianus (Studer), 0–335 m.
 **Neosmilaster steineni* (Studer), 99–160 m.
Smilasterias triremis Sladen, 93–335 m.
 **Cosmasterias lurida* (Philippi), 0–636 m.
Grammaster nutrix (Studer), 0–250 m.

The Discovery collection has afforded an opportunity to revise certain groups, notably the Odontasteridae and *Perkuaster*, with the result that the status of a number of genera and of two higher groups is altered. I am unable to see the utility of retaining the following:

- | | |
|-----------------------------------------------------------|------------------------------------------------------------------|
| <i>Priamaster</i> Koehler = <i>Leptychaster</i> Smith | <i>Autasterias</i> Koehler = <i>Notasterias</i> Koehler |
| Priamasterinae Fisher | Notasteriinae Fisher = Cosinasteriinae pars |
| <i>Ripaster</i> Koehler = <i>Psilaster</i> Sladen | <i>Sporasterias</i> Perrier = <i>Anasterias</i> Perrier |
| <i>Marcelaster</i> Koehler = <i>Luidiaster</i> Studer | <i>Parastichaster</i> Koehler = <i>Anasterias</i> Perrier |
| <i>Heuresaster</i> Bell = <i>Acodontaster</i> Verrill | <i>Kalyptasterias</i> Koehler = <i>Anasterias</i> Perrier |
| <i>Pseudontaster</i> Koehler = <i>Acodontaster</i> | <i>Anasterias</i> Ludwig nec Perrier = <i>Lysasterias</i> Fisher |
| <i>Tridontaster</i> Koehler = <i>Acodontaster</i> | <i>Paedasterias</i> Verrill = <i>Lysasterias</i> |
| <i>Metadontaster</i> Koehler = <i>Acodontaster</i> | <i>Podasterias</i> Perrier = <i>Diplasterias</i> Perrier |
| <i>Peridontaster</i> Koehler = <i>Odontaster</i> Verrill | <i>Kochleraster</i> Fisher = <i>Diplasterias</i> |
| <i>Epidontaster</i> Koehler = <i>Odontaster</i> | <i>Bathyasterias</i> Fisher (subgenus) = <i>Diplasterias</i> |
| <i>Glabraster</i> A. H. Clark = <i>Porania</i> Gray | <i>Ctenasterias</i> Koehler nec Verrill = <i>Neosmilaster</i> |
| <i>Cryaster</i> Koehler = <i>Perkuaster</i> Sladen | Fisher |
| Cryasteridae Fisher = Ganeriidae pars. | <i>Hemiasterias</i> Verrill = <i>Granaster</i> Perrier |
| <i>Labidiastrella</i> Verrill = <i>Labidiaster</i> Lütken | <i>Parasterina</i> Fisher = <i>Nepanthia</i> Gray |

¹ Challenger St. 158, 50° 1' S, 123° 4' E, bottom temperature 33.5° F.
² Challenger St. 157, 53° 55' S, 108° 35' E, bottom temperature 32.1° F.
³ South Georgia only.
⁴ Shag Rocks (South Georgia) only.

ASTEROIDEA

Family GONIOPECTINIDAE Verrill, emended¹Genus *Ctenodiscus* Müller & Troschel*Ctenodiscus australis* Lütken

Ctenodiscus australis Lütken, *Vidensk. Medd. naturh. Foren. i. Kjobenhavn*, 1871, p. 288.—Sladen, 1889, p. 172, pl. 30, figs. 1-6.—Perrier, 1891, p. 142.

- St. WS 73. 51° 01' S, 58° 54' W, 121 m., fine dark sand, 8 specimens.
 St. WS 75. 51° 01' 30" S, 60° 31' W, 72 m., 1 specimen.
 St. WS 79. 51° 01' 30" S, 64° 59' 30" W, 131-132 m., fine dark sand, 1 specimen.
 St. WS 80. 50° 57' S, 63° 37' 30" W, 152-156, fine dark sand, 1 specimen.
 St. WS 81. 8 miles north-west of North Island, West Falkland Island, 81-82 m., sand, 3 specimens.
 St. WS 82. 51° 30' S, 61° 15' W, 140-144 m., 1 specimen.
 St. WS 92. 51° 58' 30" S, 65° 01' W, 145-143 m., 9 specimens.
 St. WS 94. 50° 11' 15" S, 64° 57' 45" S, 110-116 m., 1 specimen.
 St. WS 98. 49° 54' 15" S, 60° 35' 30" W, 171-173 m., 12 specimens.
 St. WS 108. East of Punta Mendanosa, Argentina, 48° 30' 45" S, 63° 33' 45" W, 118-120 m., 1 specimen.
 St. WS 109. 50° 18' 48" S, 58° 28' 30" W, 145 m., fine dark sand, 1 specimen.
 St. WS 210. 50° 17' S, 60° 06' W, 161 m., green sand, 8 specimens.
 St. WS 211. 50° 17' S, 60° 06' W, 174 m., 2 specimens.
 St. WS 212. 49° 22' S, 60° 10' W, 242-249 m., 1 specimen.
 St. WS 214. 48° 25' S, 60° 40' W, 208 m., 14 specimens.
 St. WS 216. East of Golfo San Jorge, Argentina, 47° 37' S, 60° 50' W, 219-133 m., find sand, 1 specimen.
 St. WS 233. 49° 25' S, 59° 45' W, 185-175 m., fine green sand, 2 specimens.
 St. WS 234. 48° 52' S, 60° 25' W, 195-207 m., 2 specimens.
 St. WS 236. East of Golfo San Jorge, Argentina, 46° 55' S, 60° 40' W, 272-300 m., 1 specimen.
 St. WS 243. 51° 06' S, 64° 30' W, 144-141 m., coarse dark sand, 9 specimens.
 St. WS 244. 52° S, 62° 40' W, 253-247 m., fine dark sand and mud, 2 specimens.
 St. WS 245. 52° 36' S, 63° 40' W, 304-290 m., 1 specimen.
 St. WS 249. 52° 10' S, 57° 30' W, 166 m., fine brown and green sand, shells, stone, 9 specimens.
 St. WS 756. 50° 54' 39" S, 59° 58' W, 118 m., 1 specimen.
 St. WS 764 B. Off Argentina, 44° 38' S, 61° 58' W, 106 m., 2 specimens.
 St. WS 766. Off Argentina, 44° 58' S, 60° 05' W, 545 m., 1 specimen.
 St. WS 773. East of Golfo San Jorge, Argentina, 47° 28' S, 60° 51' W, 291 m., 2 specimens.
 St. WS 774. 47° 08' S, 62° 02' W, 139 m., dark green sand and mud, 3 specimens.
 St. WS 775. 46° 44' 45" S, 63° 33' W, 115-110 m., gravel, fine grey sand, 2 specimens.
 St. WS 782 A. 50° 29½' S, 58° 23¾' W, 141-146 m., 19 specimens.
 St. WS 783. 50° 03' S, 60° 10' W, 155-159 m., 2 specimens.
 St. WS 784. 49° 48' S, 61° 05' W, 164-170 m., dark green sand, 2 specimens.
 St. WS 785 C. 49° 23' 45" S, 62° 41' 15" W, 150-146 m., dark green sand, 1 specimen.
 St. WS 790 B. Off Golfo San Jorge, Argentina, 45° 31' 30" S, 63° 31' W, 99-101 m., green grey sand, 3 specimens.

¹ See Fisher (1919, p. 43) for discussion of relationships of *Ctenodiscus*.

- St. WS 791. $45^{\circ} 38' S$, $62^{\circ} 57' W$, 97-96 m., 1 specimen.
 St. WS 792. $45^{\circ} 49' 30'' S$, $62^{\circ} 20' 15'' W$, 102-106 m., dark green sand, 1 specimen.
 St. WS 793. $45^{\circ} 53' S$, $61^{\circ} 35' W$, 108-111 m., 2 specimens.
 St. WS 795. $46^{\circ} 14' S$, $60^{\circ} 24' W$, 157-161 m., 1 specimen.
 St. WS 796. $47^{\circ} 49' 37'' S$, $63^{\circ} 42\frac{1}{2}' W$, 106-113 m., 1 specimen.
 St. WS 797. $47^{\circ} 45' 18'' S$, $64^{\circ} 10' 30'' W$, 115-112 m., stones, 2 specimens.
 St. WS 801. $48^{\circ} 26\frac{1}{4}' S$, $61^{\circ} 28' W$, 165 m., 3 specimens.
 St. WS 805. $50^{\circ} 10\frac{1}{4}' S$, $63^{\circ} 29' W$, 148 m., 2 specimens.
 St. WS 809. East of Porto Santa Cruz, Argentina, $49^{\circ} 28\frac{1}{4}' S$, $66^{\circ} 29' W$, 107-104 m., 1 specimen.
 St. WS 817. $52^{\circ} 23' S$, $64^{\circ} 19' W$, 191-202 m., 3 specimens.
 St. WS 818A. $52^{\circ} 31\frac{1}{4}' S$, $63^{\circ} 25' W$, 272-278 m., 1 specimen.
 St. WS 819A. $52^{\circ} 41' 52'' S$, $62^{\circ} 39' 30'' W$, 312-329 m., 1 specimen.
 St. WS 839. $53^{\circ} 30' S$, $63^{\circ} 29' W$, 403-434 m., 1 specimen.

In the considerable series of specimens of all sizes there is much more uniformity of structure than I found in north Pacific examples of *C. crispatus*,¹ of which I had 883 specimens. Owing to the great variability among these, and perhaps somewhat influenced by Perrier's remarks,² I questioned the validity of *C. australis*, of which I had no adequate material. It now seems to me possible that Perrier was not dealing with typical *australis* but with variants arising from a mingling of *australis* and *procurator*, as his specimens were taken, with the exception of one locality off Argentina, in the Magellan-Cape Horn region (Beagle Canal, Franklin Canal, Murray Narrows). There is no great difficulty in distinguishing typical *australis* from north Atlantic material.

As Sladen (1889) has already pointed out, *australis* can be distinguished from *procurator* by its constantly larger paxillae and fewer marginal plates. I have only two specimens of *procurator*, from 122 fathoms off Chile: R is 22 mm. and there are 17 and 18 marginal plates, while in comparable examples of *australis* there are 12 and 13. The largest paxillae of the Chilean specimens have 6 or 7 spinelets (none in centre) and are therefore similar to the type of *procurator*. In *australis* the largest paxillae (in interradial triangles) commonly have 9-11 peripheral and upward of 5-8 central spinelets, all longer and stouter than in *procurator*. Naturally there is a big contrast in the size of the paxillae.

While *australis* looks more like *crispatus* than either, one resembles *procurator*. I believe the first two are nevertheless distinct in the sense that any two nearly related species of sea stars are distinct. Why two recognizable species of *Ctenodiscus* occupy the two sides of southern South America is a puzzle. *Ctenodiscus* is very widely distributed in the north and eastern Pacific, namely, from the Sea of Japan to the Bering Sea and the Arctic Ocean, south along the American coast to central California, Gulf of California, and Gulf of Panama. There are no records south of Panama until the home of *procurator*, off Chile, is reached.

However, it may be recalled that *Ceramaster patagonicus* is found on the Alaskan coast and in the southern Bering Sea. *Odontaster crassus* of California is closely similar to *O. grayi* of the Falkland-Magellan region. The relatively gigantic *Pedicellaster magister*

¹ Fisher, 1911, p. 32.

² Perrier, 1891, pp. 143, 144.

Fisher¹ of Alaska is more nearly like *P. hypernotius* Sladen of the Antarctic than it is like *P. typicus* of the north Atlantic and adjacent Arctic.

It seems to me probable that a *Ctenodiscus* species similar to *procurator* was formerly common to southern South America and Alaska, that later *C. crispatus* invaded Bering Sea from the Arctic and extended its range southward, as it has done on the Atlantic coast; that there has been a commingling of two originally distinct forms in the north Pacific, resulting in the highly unstable *Ctenodiscus* found there to-day.

C. australis would be the south Atlantic equivalent of a relatively more stable north Atlantic stock. It is worth noting that *C. crispatus* is a true high Arctic species which extends into boreal waters, whereas neither *C. australis* nor *C. procurator* has been taken in Antarctic waters.

The largest specimens of *australis* have R 26 mm., r 14 mm., and 13 marginal plates in each series. The largest north Pacific example of *crispatus* has R 40 mm. and 17-18 marginal plates; but specimens nearly as large (R 29-35 mm.) have only 11-13 marginals.

YOUNG. At St. WS 212 a series of 9 young was taken. The 5 smallest, 1.7 mm. in diameter, are pentagonal, with relatively enormous terminal plates which occupy most of the periphery. Each plate carries a dorsal spike-like sharp spine, nearly as long as the minor radius, and 2 or 3 shorter terminal ones. There are 2 short marginal pairs of plates and 3 rather rudimentary cribriform organs. The median is interradiar and the others are between the border of terminal plate and each marginal plate. These marginals encroach upon the paxillar area about $\frac{1}{2}$ r; and centre of disk is raised into a low cone. The close-set rudimentary abactinal plates have 1-3 tiny spinelets. There are 3 pairs of relatively large tube feet on which the tip is no better developed than in the adult. Each mouth angle has a prominent pair of plates with 4 or 5 short spinelets on the furrow border (sometimes 1 occupies apex of mouth angle), and 1 prominent suboral on outer part of plate. Adambulacral plates 2, the inner with 2, the outer with 1 spinelet.

The largest specimen of the series has R 2.3 mm. and r 1.7 mm., a stellate contour, and 5 cribriform organs on each side (2 supero- and 2 inferomarginals to each ray). The largest paxillae have 4 or 5 short spinelets, while the madreporite is covered with 14 spinelets and looks like a large paxilla. Tube feet, 5 pairs; adambulacrals 4, the first with 4, the others with 3 short sharp spinelets; 2 actinal interradiar plates on each interradius.

FOOD. *Ctenodiscus* evidently lives nearly covered by the soft mud or muddy sand of its characteristic habitat, the conical elevation of centre of disk rising above the surface as in the case of *Astropecten*. The cribriform channels of the marginal and actinal surfaces are contrivances for maintenance of currents of water to and from the actinal surface by means of the ectodermal cilia.

If food is conveyed to the mouth by these cilia, it is not the principal source, since mud is ingested in large quantities along with whatever contained objects are small enough to pass through the mouth. Sometimes the abactinal surface is convex from an overstuffed stomach, as in the case of a specimen from St. WS 805. In the fine sand and muddy debris, in which simple sponge spicules are numerous, are 3 pebbles, the largest

¹ Fisher, 1928, pp. 35, 36.

6 mm. in diameter, fragments of an encrusting bryozoan, a gastropod shell, delicate membranous worm tubes, and a sea-urchin spine, possibly *Austrocidaris canaliculata* (A. Agassiz). Treatment of the mud with sodium hypochlorite indicates a large percentage of organic material.

Family ASTROPECTINIDAE Gray

Genus *Leptychaster* Smith

Leptychaster Smith, *Ann. Mag. Nat. Hist.*, Ser. 4, xvii, 1876, p. 110. Type *L. kerguelenensis* Smith.
Leptoptychaster Smith, *Philos. Trans. Roy. Soc.*, Zool. Kerguelen Island, CLXVIII, 1879, p. 278.

Emendation of *Leptychaster*.

Parastropecten Ludwig, *Mem. Mus. Comp. Zool.*, xxxii, 1905, p. 76. Type *P. inermis* Ludwig.

Glyphaster Verrill, *Amer. Nat.*, XLIII, 1909, p. 553. Type *Leptychaster anomalus* Fisher.—1914, p. 327.

Priamaster Koehler, 1912, p. 92. Type *P. magnificus* Koehler.

Trophodiscus Fisher, 1917, p. 367. Type *T. almus* Fisher.

New information on the structure of *Leptychaster kerguelenensis* makes it desirable to review the north Pacific species referred to *Leptychaster*. These are *L. arcticus* (found also in the north Atlantic), *L. pacificus* Fisher, *L. propinquus* Fisher, *L. anomalus* Fisher.¹ When the accounts of these species were written no information was available on the distribution of the gonads in the type of the genus, nor had I seen a specimen of *kerguelenensis*. In the description of *Trophodiscus almus*, the distribution of gonads in 4 species of *Leptychaster* is stated as follows (Fisher, 1917*a*, p. 371): "In four species of the genus *Leptychaster* which I have been able to examine, the testes differ in distribution from the ovaries. In *L. arcticus*, *L. pacificus*, *L. propinquus* and *L. anomalus* (the last three being North Pacific species) the ovaries are in a single tuft close to the inter-radial septum—a pair, thus, in each interbrachium. In some specimens the branches may extend far along the ray, but they are attached in only one place, as stated above. In the male the gonads form a series of independent tufts of tubules, parallel with the margin, and distributed for a third to nearly a half the length of ray, according to the size of the specimen. The distribution of the testes in the above species of *Leptychaster* is therefore similar to the distribution of both ovaries and testes in *Trophodiscus*, *Dipsacaster*, *Ctenopleura*, *Tethyaster*, *Thrissacanthias*, and other genera. This condition of the gonads is apparently characteristic of the genus *Leptychaster*, although of course it will doubtless be found to be true of other genera. The reason I did not discover this when working up my North Pacific Asteroidea, Part I, was the fact that I dissected then only a single example of each species, which happened in each case to be a female. Recently, at the United States Museum, I found 'serial gonads' in a specimen of *L. arcticus* from station 21, Cashes Ledge. A specimen from station 4779 (North Pacific) has serial gonads and is a *male*, while a *female* from station 5047 has strictly interradial, non-serial, gonads.

¹ These species are described and figured in Fisher (1911), where a definition of *Leptychaster* is given, based on the northern species only. The statement in regard to distribution of gonads is erroneous, as explained below.

"This arrangement of the gonads holds true in all specimens examined, namely:

"*Leptychaster propinquus*, 2 males and 3 females; station 4788.

"*L. anomalus*, 1 male, station 4233; 1 female, station 4280.

"*L. pacificus*, 1 male, station 3223; 2 females, station 2862."

I have ascertained that in *L. kerguelensis* the ovaries are not as in the northern species, but are serially arranged close to the marginal plates; and that *L. magnificus* and *L. accrescens* also have both ovaries and testes in series (although not close to marginal plates).

The northern forms have not been observed to brood their young. They differ also in having somewhat longer, less compressed adambulacral plates with a curved furrow margin, rather than the sharply angular one of *kerguelensis*, *accrescens*, and *magnificus*. The furrow armature of these three southern species is composed of 3 spines which generally stand upright in a co-ordinated group. In the northern forms, even in *arcticus*, it is a comb of spines (3-6 in different species, usually 3 or 4) followed by 3 longiseries of 3-5 similar spines (Fisher, 1911, pl. 5, figs. 1, 2). The southern forms have relatively larger tube feet.

In the specimen of *L. kerguelensis* the papulae are confined to the margin of the abactinal area, where the plates have very short lobes. Elsewhere the plates are roundish. But in *accrescens* and *magnificus* the papulae extend completely across ray and all the plates are stellate or strongly 6- or 5-lobed (in *magnificus* reduced to 4 near margin of area).

I have discussed (1911, pp. 52, 53) the difficulty of distributing the north Pacific species between *Glyphaster* Verrill (= *Parastropecten* Ludwig) and *Leptychaster*. Verrill (1914, p. 327) did this, but his diagnosis of *Glyphaster* is not correct. He states that "the inferomarginal plates are convex, not carinated". As a matter of fact they are strongly carinated, especially on the lateral face. The deep, narrow, superomarginal and inferomarginal fascioles are lined with very fine spinelets. In Verrill's system, *Leptychaster propinquus* would fall in *Glyphaster*, yet the inferomarginals are as short and oblique as in *Leptychaster pacificus* and the superomarginals are small. Since the marginals are short, the disparity between the number of inferomarginals and adambulacrals is not so great as is emphasized by Verrill for the type *anomalus*. In an adult specimen of *anomalus* there are 16 superomarginals to 29 adambulacrals; in *propinquus* there are 22 superomarginals to 29 adambulacrals; in *pacificus* (*Leptychaster* in Verrill's system) there are 25 superomarginals to 29 adambulacrals.

The curious difference in the male and female gonads, common to the 4 species, is further evidence that they are very closely related. The diversity in body form is no greater than that found in *Odontaster penicillatus*.

On the other hand, the 4 species differ from the southern forms in the distribution of the gonads and in having the less compressed adambulacrals with a rounded instead of sharply angular furrow margin. The inner end of the marginal series of mouth spines lacks the conspicuous decurrent angle found in *Leptychaster accrescens* and *flexuosus*, and less prominently in *magnificus* and *kerguelensis*. After observing the amplitude of

variation in *Odontaster*, I am strongly inclined to follow a middle course and to leave these four species in *Leptychaster*, to which I would add *Trophodiscus*. In order to emphasize what seem to be valid sections I would institute subgenera based upon anatomical characters, the value of which must be determined by experience.

Genus *Leptychaster* Smith

Subgenus *Leptychaster*. Type *L. kerguelensis*. Form stellate; adambulacrals short, with very angular furrow margin; gonads of both sexes in several to many tufts extending along dorsal wall of ray; marginal mouth spines forming a decurrent angle near inner end of plates.

- a*¹. Papulae confined to rather narrow marginal area, where plates have short lobes; elsewhere roundish.
- b*¹. Series of gonads near margin of abactinal area; paedophoric. *L. kerguelensis* Smith.
- b*². Series of gonads well spaced from margin: rays very long; probably not paedophoric. *L. flexuosus* Koehler.
- a*². Papulae distributed all over abactinal surface; all abactinal plates, except in young of *accrescens*, strongly lobed; species probably not paedophoric. *L. magnificus* (Koehler).
L. accrescens Koehler.

Subgenus *Parastropecten* Ludwig. Type *P. inermis* Ludwig (*Glyphaster* Verrill, type *Leptychaster anomalus* Fisher). Form stellate to arcuate stellato-pentagonal; adambulacral plates with rounded furrow margin bearing a comb of 3–6 spines; gonads of male in a series, those of female in a strictly interradial tuft; abactinal plates lobed except for rather narrow radial area free from papulae; marginal mouth spines *not* forming an evident decurrent angle near inner end of plate; probably not paedophoric.

L. inermis Ludwig.¹

L. anomalus Fisher.

L. propinquus Fisher.

L. pacificus Fisher.

L. arcticus (Sars).

Subgenus *Trophodiscus* Fisher. Type *T. almus* Fisher (1917*a*, p. 367, pls. 28–30). Stellate-pentagonal; marginal plates conspicuous, granular; adambulacral armature pectinate; first adambulacral plate compressed; both male and female gonads serially arranged; abactinal plates of papular area with short lobes; papulae absent from centre of disk and narrow midradial band; marginal mouth spines not forming a decurrent angle.

L. almus Fisher.

In the diagnosis of *Trophodiscus* (*loc. cit.*) is the following: "Near to *Leptychaster* Smith, but differing in having both ovaries and testes serially arranged along each side of the proximal half of ray." This error is due to the circumstance that comparison was made with *L. anomalus*, *L. pacificus* and *L. arcticus*, in which the ovaries are interradial

¹ The type is immature. The species greatly resembles *L. anomalus*. If it happens that the gonads are different from those of *anomalus*, then *Glyphaster* will be available for *anomalus*, *propinquus* and *arcticus*.

and testes in series (subgenus *Parastropecten*, above). In *Trophodiscus* the gonads are as in *Leptychaster*, sensu stricto, and, moreover, the species is *paedophoric*.

It must be freely admitted that there is a wide difference in appearance between *L. kerguelenensis* and *Trophodiscus almus*, which has broad marginals superficially covered with granuliform spinelets. These mask the deep fascicles between the transverse elevated ridges of the plates. One can scarcely believe in the existence of these deep grooves until the plates are cleaned. The first adambulacral plate is of a different form from the others, being compressed, as in *Parastropecten* and *Leptychaster* s.s. In the latter all the plates are normally so short that the slight disparity in the first plate is not so apparent as in *Parastropecten*.

REMARKS ON *PRIAMASTER*. A detailed comparison of "*Priamaster*" *magnificus* and *Leptychaster accrescens* reveals so many points in common that one is forced to conclude that they are closely related species. If *accrescens* is a *Leptychaster*, then *magnificus* falls in the same genus.

Priamaster, of which *magnificus* is the only known species, is eliminated, as is also *Priamasterinae* Fisher,¹ a subfamily of the Radiasteridae for *Priamaster* and *Gephyreaster*. This subfamily was based upon a misconception of *Priamaster*, especially as regards the structure of the tube feet. The distribution of the gonads was not given in the original description. The podia of *Gephyreaster* have well-developed flattish sucking disks, broader than the column of the podium. In *Priamaster*, as in other species of *Leptychaster*, the terminal knob is of a low acorn shape or hemispherical form without a sucking disk, and much narrower than the column of the podium.

In the foregoing synopsis of *Leptychaster* I have indicated two divisions of the subgenus *Leptychaster*. A subgenus *Priamaster* might be justified for the second on the basis of the differences mentioned. However, in young specimens of *accrescens* the distribution of the papulae is interrupted on the ray by a longitudinal band midway between radial line and margin. Between these two bands there is a radial area of papulae. In general facies and in possessing short, angulated adambulacrals the southern species form a fairly homogeneous group. But it is improbable that the *accrescens-magnificus* group is *paedophoric*.

REMARKS ON *MIMASTRELLA*.² Sladen³ has described and figured *Mimaster cognatus*, while Ludwig⁴ added a description and figures of the characteristic spinelets which he compared with those of *Luidia*. These 4-pronged spinelets are equally like those of *Lophaster*, as Koehler⁵ pointed out, but with a vast difference in size.

Mimastrella cognata bears a very close superficial resemblance to *Leptychaster*⁶ in respect to the small pailliform superomarginals, adambulacral armature, tube feet,

¹ *Ann. Mag. Nat. Hist.*, ser. 8, xx, 1917, p. 172. Also 1919, p. 216.

² Fisher, "Notes on the Systematic Position of Certain Genera and Higher Groups of Starfishes", *Proc. Biol. Soc. Washington*, xxix, 1916, p. 5. Type *Mimaster cognatus* Sladen.

³ Sladen, 1889, p. 336, pl. 47, figs. 3, 4; pl. 62, figs. 4, 5.

⁴ Ludwig, 1903, p. 6, pl. 2, figs. 11-17.

⁵ Koehler, 1920, p. 257.

⁶ Fisher, 1911, pp. 53, 175.

carinated, paxilliform actinal plates, serial gonads. The lateral abactinal plates are 4-lobed and regularly imbricated. The extreme lateral abactinal plates of *L. magnificus* are also 4-lobed and imbricated, while the others are 5- or 6-lobed. Superambulacral plates are present. In *Mimastrella cognata* there is an odd interradian series of actinal intermediate plates extending from mouth plates a third of the distance to margin. If of no great importance, this series is significant since it is found in most species of *Leptychaster*.

In diagnosing *Mimastrella* (*loc. cit.* 1916) I contrasted it with *Radiaster* (olim *Mimaster*), and stated that the tube feet have small sucking disks. They are not functional sucking disks, but are mammiform, and narrower than the podium, as in *Leptychaster*, and allied genera.

No *Leptychaster* which I have examined has the 3- or 4-pronged terminally flaring spinelets¹ of *Mimastrella*. Whether this character, and the somewhat reduced, more paxilliform, inferomarginals are of superspecific value, only other species of *Mimastrella* will demonstrate.

M. cognata may be described as a *Leptychaster* with narrow inferomarginals, and highly characteristic (mostly) 4-pronged spinelets. Whether such an aberrant species should be given generic rank or relegated to a subgenus is a matter of opinion. Were it not for the spinelets I would hardly hesitate to include it in *Leptychaster*. As matters stand it is probably best to maintain a genus *Mimastrella*.

Leptychaster kerguelensis Smith

Leptychaster kerguelensis Smith, *Ann. Mag. Nat. Hist.*, ser. 4, xvii, 1876, p. 110.

Leptotychoaster kerguelensis Smith, *Philos. Trans. Roy. Soc.*, Zool. Kerguelen Island, CLXVIII, p. 278, pl. 17, fig. 2.—Sladen, 1889, p. 184, pl. 31, figs. 1, 2; pl. 32, figs. 1, 2.

Leptotychoaster kerguelensis, Koehler, 1917, p. 52, pl. 6, figs. 1, 2, 7, 12.

St. 1562. Vicinity of Marion Island, 46° 53' S, 37° 55' E, 97–104 m., 3 specimens.

St. 1563. Vicinity of Marion Island, 46° 48.4' S, 37° 49.2' E, 101–106 m., 1 specimen.

The specimen from St. 1563 measures R 53 mm., r 13 mm., br 15–16 mm.; the largest of the three from St. 1562 has R 23 mm., r 7 mm.

Both Sladen (1889) and Koehler (1917) have described and figured this species. Their largest specimens measured R 66 and 65 mm., r 13 mm. The specimen from St. 1563 agrees well with Koehler's figures (1917, pl. 6, figs. 1, 2). His fig. 1 shows the considerable disparity in size between the small paxillae of centre of disk and radial region of ray and the obviously large ones of the lateral part of the abactinal area. Sladen's figure does not bring this out.

Koehler has also discussed *Leptychaster antarcticus* which Bell (1908, p. 9) recorded as the young of *kerguelensis*, although the type has a different oral armature and more numerous adambulacral spines, differently disposed. Bell's large specimens of

¹ Koehler (1920) figures spinelets of *accrescens*, pl. 74, fig. 1; *magnificus*, fig. 2; *flexuosus*, pl. 75, fig. 3; *arcticus*, fig. 4; *kerguelensis*, fig. 6. I have found that spinelets of *anomalous*, *propinquus* and *pacificus* are of the general type of *arcticus*.

"*kerguelenensis*" from Victoria Land are either *L. accrescens* or *magnificus*, or both. Whether his records from the Cape of Good Hope really refer to this species can only be determined by an examination of his specimens. Mortensen (1933) omits the species from his revised list of sea stars of South African seas.

TYPE LOCALITY. Kerguelen Island.

DISTRIBUTION. Kerguelen Island and Marion Island regions, shore to 384 m.

Leptychaster kerguelenensis mendosus Koehler

Leptotychoaster mendosus Koehler, 1923, p. 98, pl. 12, figs. 3-5.

St. WS 86, Falkland Islands, 53° 53' S, 60° 34' 30" W, 151-147 m., sand, shells, stones, 1 specimen.

Koehler's only specimen measured R 40 mm., r 11 mm. The details of plates and spines are closely similar to those of *kerguelenensis*. In *mendosus* the ray has a slightly different contour, being broader and tapering from a less arcuate interbrachium. There is less disparity in size between the mesial and lateral abactinal paxillae.

It seems obvious that this form is very close to *kerguelenensis*, at best a race of that species, for which reason I have employed a trinomial designation.

TYPE LOCALITY. East of Tierra del Fuego, 54° 43' S, 64° 8' W, 86 m.

Leptychaster flexuosus Koehler

Leptotychoaster flexuosus Koehler, 1920, p. 252, pl. 51, figs. 1-4; pl. 75, fig. 3.

St. 1660. Ross Sea, 74° 46' 4" S, 178° 23' 4" E, 351 m., 2 specimens.

This remarkable species has been fully described and figured by Koehler, whose only specimen measured R 130-135 mm., r 26 mm. The larger Discovery specimen measures R 340-345 mm., r 36 mm., br 36 mm., breadth of ray half way to tip 13 mm. At this point the inferomarginal plates are 2 mm. broad by 1 mm. long; the superomarginal paxillae are 0.5-0.75 mm. broad. There are 358 inferomarginals in one series from interbrachial angle to tip of the ray.

There is a conspicuous band along the middle of the abactinal area of ray free from papulae. The abactinal plates are roundish, except a narrow band adjacent to superomarginals. Here 4 or 5 plates of each oblique transverse row have short lobes.

The functional gonads (male) are in tufts hanging from the genital stolon which is well spaced from the superomarginals. They extend along ray from interbrachial angle a distance equal to the minor radius. The genital stolon with very small undeveloped gonads can be traced about the same distance beyond the functional gonads. But, with such long rays, the point is only at about the end of basal fifth of ray.

In this species, the angular series of marginal mouth spinelets which extends downward to the peristome is well developed and rather more accentuated than in *accrescens* and *magnificus*. It is also more sharply angular than in the small specimens of *kerguelenensis* available for study.

On the inner side of the base of the tube feet are numerous papilliform outgrowths which, when podia are contracted, touch the radial nerve and those of opposite podia.

Although this species is sharply differentiated from all others of the subgenus *Leptychaster*, I think it is closer to *kerguelenensis* than to *accrescens*.

It would be a matter of great interest to know the behaviour of this species and the part played by the extraordinary rays.

TYPE LOCALITY. Lat. $66^{\circ} 55' S$, long. $145^{\circ} 21' E$, 318 fathoms (just within Antarctic Circle, north-east of Ross Sea proper).

DISTRIBUTION. Known only from type locality and St. 1660, Ross Sea.

Leptychaster accrescens Koehler

Leptychaster kerguelensis Bell (nec Smith), 1908, p. 9.

Leptychaster accrescens Koehler, 1920, p. 246, pl. 52, fig. 5; pl. 53, figs. 1-3; pl. 54, figs. 2-9; pl. 55, fig. 1; pl. 74, fig. 1.—1923, p. 98, pl. 13, fig. 3.

St. 42. Off mouth of Cumberland Bay, South Georgia, 120-204 m., 3 specimens, largest R 110 mm.

St. 140. Stromness Harbour to Larsen Point, South Georgia, 122-135 m., green mud, stones, 1 specimen.

St. 148. Off Cape Saunders, South Georgia, 132-146 m., grey mud and stones, 2 specimens, 1 very large, R 235 mm.

St. 474. One mile west of Shag Rocks, South Georgia, 199 m., 1 very young specimen.

St. 1660, Ross Sea, $74^{\circ} 46.4' S$, $178^{\circ} 23.4' E$, 351 m., 3 specimens.

St. 2467. Near Bouvet Island, $54^{\circ} 24.1' S$, $3^{\circ} 15.2' E$, 124-119 m., 3 specimens.

St. 2563. Near Bouvet Island, $54^{\circ} 23.8' S$, $3^{\circ} 28.4' E$, 97 m., 1 specimen.

Koehler has fully described and figured this species and listed the external features which differ from those of *Leptychaster kerguelensis*. It is in reality far removed from that species. Examples of *accrescens* of the size of adult *kerguelenensis* (i.e. R 45 mm.) are quite immature, the gonads being scarcely discernible. Indeed, in a specimen as large as R 110 mm. the gonads which extend for two-thirds the length of ray are very small (1 April 1926); while in the largest example from the same region (9 January 1927) the large ovaries contain fully formed eggs (R 235 mm.).

Bell's large specimens, presumably from Victoria Land, are certainly not *L. kerguelensis*. They are either this species or *L. magnificus*.

In the largest specimen, St. 148, R = 235-240 mm., r = 80 mm., R = 3r; br = 90 mm. This is an imposing sea star. The 4-ranked tube feet are bulky, even in the contracted condition being 15-20 mm. long, 7-8 mm. thick, and terminated by a convex or hemispherical nipple, 2 mm. in diameter. If the power of extension is equal to that of young specimens the tube feet can easily reach 45 mm. One tube foot is bifurcate with two terminal knobs.

The adambulacral plates are distorted by the external row of tube feet so that two or sometimes three angular furrow margins intervene between two external podia (and correspond to the alternate, inner podium). Directly across ray from such a double furrow margin is an interval; that is, an external podium. This distortion is indicated in a specimen as small as R 62 mm., and is well marked in the specimen with R 110 mm. It is also characteristic of *L. magnificus*.

The adambulacral armature of *accrescens* and *magnificus* is also similar. Both have the

short furrow spinelet on the angular margin of plate, followed by 5-7 longer subambulacral spines in 3 longitudinal series of 2 each; or 2 series with an odd spine behind furrow spine, or on outer margin of plate. The plates are characteristically shorter than broad and are distorted in adult specimens as indicated above.

The rays of *magnificus* are more arched, the paxillae slightly larger, and the marginal plates less numerous. In *accrescens* with R 110 mm. there are 90 inferomarginals, and in *magnificus* with R 117 mm. there are 67. This difference is evident from Koehler's figures. At interbranchial angle the width of the combined marginal plates is about the same in the two species, but in *magnificus* the superomarginals are a little larger. The slight disparity in size between the upper and lower marginal plates of Koehler's figure is not constant; in our specimen of *magnificus* there is a marked disparity. Both species have an equally high narrow keel to the marginal plates, separating very deep marginal fasciolar furrows. I am at a loss to understand Koehler's statement that they are shallower in *magnificus*. He uses this as a differential character of *Priamaster*. The gonads are distributed precisely alike in the two species. In the two comparable specimens there is so little difference in the extent of the actinal intermediate areas that it is rather futile to contrast them. In our specimens there are slightly more spinelets on the actinal paxillae of *accrescens*.

The abactinal plates are stellate, with 5 or 6 rather slender lobes, on the radial as well as on lateral parts of the abactinal area. In mature specimens there is no median radial area free from papulae. In young examples, however, this continuity is interrupted by two adradial bands, free from papulae. There are thus on the rays two marginal and a radial area of papulae.

The colour in life is pale yellow with interradial bars of chocolate brown extending nearly to centre of disk and a cross-bar of brown near end of ray (R 110 mm.). In the very large specimen only the latter markings are present; and in four small examples only the interradial bars are present. The examples from Ross Sea lack the brown markings. The largest specimen from St. 2467 was bright orange, tube feet dark orange.

After the completion of this report, Dr N. A. Mackintosh sent photographs of a large specimen and records of others. Three specimens from St. 2467 measure respectively R 260, 260, 230 mm., r 85, 80, 80 mm., breadth of ray at base in all three 90 mm. The specimen from St. 2563 measures R 230 mm., r 65 mm., br 80 mm.

TYPE LOCALITY. Not indicated. Probably $65^{\circ} 42' S$, $92^{\circ} 10' E$, 60 fathoms.

DISTRIBUTION. The species is evidently circumpolar. It was taken by the Australasian Antarctic Expedition between $64^{\circ} 32'$ and $66^{\circ} 50' S$, and $92^{\circ} 10'$ and $142^{\circ} 6' E$, 60-354 fathoms. Probably at least some of Bell's specimens from Victoria Land are referable to *accrescens*. Koehler has already reported it from South Georgia (1923, p. 98).

Leptychaster magnificus (Koehler)

Asterias longstaffi Bell? 1908, p. 7. In any event the name is a *nomen nudum*, since the printed matter which follows it is misleading, and in no wise describes the specimen. I have seen the type.

Priamaster magnificus Koehler, 1912, p. 92, pl. 8, figs. 1, 3, 8.—1920, p. 255.

St. 599. Off Loubet Land, east of Adelaide Island, 67° 08' S, 69° 06½' W, 203 m., 1 specimen.

The specimen measures R 117 mm., r 25 mm.; R=3.3 r; breadth of ray at interradial line, 41 mm. It is therefore smaller than Koehler's type which measured R 192 mm., r 63 mm., br 70 mm.

Koehler (1912) has given a detailed description and excellent figure. Later (1920) he recognized the close similarity between his *Priamaster* and *Leptychaster* but could not come to the point of abandoning *Priamaster*. Character by character *Priamaster* is a *Leptychaster*. I have ascertained that the gonads have a distribution very similar to those of *L. kerguelenensis*, a specimen of which I have examined. This is one of the examples mentioned by Sladen (1889, p. 186) from Marion Island, R 38 mm., r 11 mm. In typical *Leptychaster*, both male and female, the gonads form a series of tufts or lobes, slightly spaced, depending from the genital stolon and extending far along the ray. In *L. kerguelenensis* the ovaries form a series close to the inner edge of superomarginal plates for half the length of the ray. In the giant specimen of *L. accrescens* the ovaries are far removed from the margin (a little nearer radial line than margin) and the long, divided lobes form rather voluminous, spaced, tufts extending for two-thirds the length of ray. A male specimen (St. 42) having R 110 mm. has a similar distribution of the gonads. In *L. magnificus* the gonads are distributed precisely as in *accrescens*.

The two large species differ from the small *kerguelenensis* in having the genital stolon, and its dependent gonads, far removed from the margin of abactinal area. If *Priamaster* is a valid genus, then *accrescens* is also a *Priamaster*.

The large, 4-ranked tube feet are characteristic of both *magnificus* and *accrescens*. In young *accrescens* (R 64 mm.) the crowded, imperfectly 4-ranked condition is characteristic of only the proximal half of furrow. In a specimen with R 110 mm. the crowding occupies about two-thirds length of furrow—rather more than in the slightly larger specimen of *magnificus*. Koehler's type of *magnificus* (R 193 mm.) with a more extensive development of the 4-ranked condition compares with the large *accrescens*, from St. 148, in which R is 235 mm. and the tube feet are 4-ranked to within 25–50 mm. of tip of ray.

The characters which Koehler invokes in support of a separate genus *Priamaster* are: (1) different form of body; (2) reduced actinal interradial areas; (3) nearly equal size of upper and lower marginal plates; (4) superomarginals not visible when one views the specimen from above; (5) the inferomarginal plates at beginning of series do not have a salient keel as in true *Leptychaster*; (6) the madreporic plate is visible; (7) the ambulacral furrow is much wider than in *L. accrescens*.

In rebuttal it may be stated, seriatim: (1) not of generic significance; (2) not more reduced than in *L. kerguelenensis*; (3) a varietal character since our specimen has infero-

marginals nearly twice as broad as superomarginals; (4) varietal character; in our specimen visible except in interradial arc; (5) there is a high keel and this is indicated in Kochler's fig. 1 in the two interradia on right; (6) covered as much as in an equal-sized specimen of *L. accrescens*, in which centre of plate is visible; (7) extremely variable; specimen of *L. accrescens* (R 110 mm.) has wider furrows than *L. magnificus* (R 117 mm.); see second paragraph above.

TYPE LOCALITY. Petermann Island, south of Palmer Archipelago, 40-70 m., mud and pebbles. Co-type from Jenny Island, southern end of Adelaide Island, 5 m., pebbles.

DISTRIBUTION. Vicinity of Adelaide Island and Petermann Island (McMurdo Strait, Victoria Land, if "*Asterias longstaffi*" is this species).

Genus *Bathybiaster* Danielssen & Koren

Bathybiaster Danielssen & Koren, *Nyt Mag. for Naturvidensk.*, xxvii, part 4, 1883, p. 285. Type *Astropecten pallidus* D. & K. 1877 = *Archaster vexillifer* Wyville Thomson, 1873.

Ilyaster Danielssen & Koren, *Nyt Mag. for Naturvidensk.*, xxviii, part 1, p. 4. Type *Ilyaster mirabilis* D. & K.

Phoxaster Sladen, *Narr. Chall. Exp.*, 1, 1885, p. 611 (no species); 1889, p. 234. Type *Phoxaster pumilis* Sladen.

The north Atlantic *Bathybiaster vexillifer* (Wyville Thompson, 1873), *B. pallidus* (Danielssen & Koren, 1877), and *B. robustus* (Verrill, 1884), are forms of the same species, which takes the oldest name, *vexillifer*.

The circumpolar Antarctic *B. loripes obesus* and its warmer water race *B. loripes* are very similar to *B. vexillifer* and are subject to a corresponding range of variation. If the southern forms are compared side by side with equal-sized *B. vexillifer* and *vexillifer robustus*, it is at once seen that the southern forms have shorter, hence more numerous, marginal plates. Three specimens with R 107 mm. are as follows: *B. vexillifer robustus* 63 marginals. [In typical *vexillifer* (or *pallidus*, for which see Danielssen & Koren, 1884, pl. 14, fig. 1), the marginals are 63 in a specimen with R 107 mm.] *B. loripes*, 70 marginals; *B. loripes obesus*, 127 marginals. Another specimen of *obesus* from the same station (167) with R 140 mm. likewise has 127 marginal plates.

Probably it is obvious enough that *Bathybiaster* and *Psilaster* are very closely related and actually difficult to separate on the basis of the adambulacral armature and the fleshy covering of the actinal intermediate spinelets. The armature of the marginal plates is of no value. In *Bathybiaster*, however, the abactinal paxillae of the papular area (which excludes a narrow strip along radius) have a 6-lobed or stellate base. The plates imbricate strongly by means of these lobes. The plates of the radial strip are not lobed and are in close contact. In typical *Psilaster* the abactinal plates do not imbricate nor are they in contact even along the non-papulated radial area of ray; nor are they lobed, but are circular, polygonal, or elliptical. In the aberrant *Psilaster charcoti* (least *Bathybiaster*-like of any *Psilaster*) the lateral 5 or 6 plates of a transverse series have about 6 slight lobes, of which that on the outer (marginal side) is the largest and touches the

next external plate. But the plates of central portion of abactinal surface are roundish, and are not in contact. It is only the lateral-most part of the papular areas that have the lobed plates, whereas in *Bathybiaster* all the papular area is provided with stellate, imbricating plates. Furthermore, in *Psilaster charcoti* the non-papulated radial area has very distinctly separated plates as in typical *Psilaster*.

Bathybiaster loripes Sladen

Bathybiaster loripes Sladen, 1889, p. 240, pl. 36, figs. 1, 2; pl. 42, figs. 1, 2.

Goniopecten Fleuriasi Perrier, 1891, p. 140, pl. 12, figs. 2a, 2b; p. 190.

Bathybiaster spinulatus Koehler, 1917, p. 55, pl. 6, figs. 13, 14, 16, 17. Kerguelen, shallow water.

St. WS 98. Falkland Plateau, 49° 54' 15" S, 60° 35' 30" W, 171-173 m., 3 specimens.

St. WS 216. Falkland Plateau, 47° 37' S, 60° 50' W, 219-133 m., fine sand, 1 specimen.

St. WS 773. Falkland Plateau, 47° 28' S, 60° 51' W, 291 m., 1 specimen.

St. WS 819B. Falkland Plateau, 52° 45' S, 62° 27½' W, 329-342 m., 8 specimens.

A study of the extensive series of specimens of *loripes* and *obesus* indicates that *obesus* is a circumpolar species, of which *loripes* is a northern, warmer water, race. It is unfortunate that the priority of *loripes* necessitates its use for the species in its widest sense. It would be better biology to call the Falkland form *Bathybiaster obesus loripes*.

The type of *loripes* from the western coast of South America, near the entrance to the Strait of Magellan (245 fathoms) is only medium sized as compared with specimens from the Falkland plateau, the largest of which has R 110 mm.

Sladen's figure depicts the spines as standing out from the rays, whereas in the specimens under observation the inferomarginal spines are closely appressed and very inconspicuous. This somewhat vivacious interpretation by the artist is of psychological importance, since it may easily have influenced Koehler to believe that his *B. liouvillei* (i.e. *obesus*) is more trenchantly different from *loripes* than really is the case. Some specimens of *loripes* have inferomarginal spines as short as they are in *obesus* (Palmer Archipelago), but the latter lack the superomarginal spines of *loripes*. These superomarginal spines of *loripes* are sometimes very inconspicuous. As an extreme variation, they may be lacking altogether, as in one example from St. WS 98; whereas two others have small, broad, squamiform spines.

Bathybiaster spinulatus Koehler, from shallow water, Kerguelen Island, was based on only one specimen having R 90 mm., the description and figures of which leave nothing to be desired. The spinulation of the marginal plates is the principal feature in which *spinulatus* is believed to differ from *loripes*, its obviously nearest relative. It is evident that Koehler relied solely upon Sladen's description and figures of *loripes*. In his rather involved summary of differences, Koehler has invoked the shape, number, and position of the marginal spinules, but his conclusions are untenable since specimens of *loripes* may have as many spines as *spinulatus*, and in precisely the same position! For one item, the upper of the 2 or 3 inferomarginal spines is not always at the extreme upper end of the plate, as Koehler believed, but in large specimens tends to drop a slight but inconstant distance below, forming a somewhat irregular longiseries precisely as

indicated by Koehler's photographic figures of *spiculatus*. The supposed difference in the shape of the furrow spines does not exist.

A priori there is nothing surprising in the occurrence of *loripes* at Kerguelen in shallow water, as temperature is probably the important factor for its survival at any sub-Antarctic locality. Although the race has not been recorded from Macquarie Island it probably occurs there in appropriate surroundings, since a common Falkland species, *Anasterias antarctica*, has been taken. The latter species is the more surprising because it carries its eggs and young and lacks the advantage of pelagic larvae. *Bathybiaster* probably has pelagic larvae.

B. loripes more closely resembles *B. vexillifer* than does *obesus*. *Vexillifer* varies considerably in respect to the spinulation of the marginal plates, so that comparison of this character is unsatisfactory. *Vexillifer* appears to have consistently longer, hence fewer, marginal plates, as noted under *Bathybiaster*, above.

Goniopecten fleuriasi Perrier, from Beagle Canal, south coast of Tierra del Fuego, is clearly *B. loripes*. Bottom temperatures recorded: 198 m., 8.1° C.; 270 m., 7.7° C.

TYPE LOCALITY. Challenger St. 311, off the western coast of South America, near the entrance to the Strait of Magellan, opposite Port Churruca, 245 fathoms, blue mud, bottom temperature 46° F.

DISTRIBUTION. Strait of Magellan and western entrance, 198–490 m. (Sladen, Perrier); plateau of the Falkland Islands, 219–342 m. ('Discovery'); Kerguelen Island, shallow (Koehler).

Bathybiaster loripes obesus Sladen

Bathybiaster loripes var. *obesa* Sladen, 1889, p. 242.

Bathybiaster liouvillei Koehler, 1912, p. 96, pl. 6, figs. 2, 3, 4, 12; pl. 8, figs. 5, 6; 1920, p. 263, pl. 73, fig. 1; 1923, p. 100.

- St. 30. West Cumberland Bay, South Georgia, 251 m., 2 specimens.
- St. 39. East Cumberland Bay, South Georgia, 179–235 m., grey mud, 1 specimen.
- St. 42. Off mouth of Cumberland Bay, South Georgia, 120–204 m., 10 specimens.
- St. 45. 2.7 miles S, 85° E of Jason Light, South Georgia, 238–270 m., grey mud, 17 specimens.
- St. 123. Off mouth of Cumberland Bay, South Georgia, 230–250 m., grey mud, 5 specimens.
- St. 148. Off Cape Saunders, South Georgia, 132–148 m., grey mud, stones, 1 specimen.
- St. 160. Near Shag Rocks, 177 m., grey mud, stones, 1 specimen.
- St. 167. Off Signy Island, South Orkneys, 244–344 m., green mud, 2 specimens.
- St. 181. Schollaert Channel, Palmer Archipelago, 160–335 m., mud, 6 specimens.
- St. 182. Schollaert Channel, Palmer Archipelago, 278–500 m., 2 specimens.
- St. 187. Neumayr Channel, Palmer Archipelago, 259 m., mud, 1 specimen.
- St. 458. 7 miles S, 50° W of Cape Circumcision, Bouvet Island, 357–377 m., 2 specimens.
- St. WS 27. South Georgia, 53° 55' S, 38° 0' W, 106–109 m., gravel, 1 specimen.
- St. WS 32. Mouth of Drygalski Fjord, South Georgia, 91–225 m., 3 specimens.
- St. MS 68. East Cumberland Bay, South Georgia, 220–247 m., 1 specimen.
- St. 1660. Ross Sea, 74° 46.4' S, 178° 23.4' E, 351 m., 11 specimens.
- St. 1952. Between Penguin Island and Lion's Rump, King George Island, South Shetlands, 367–383 m., 1 specimen.

This form has been fully described and figured by Koehler. It is regrettable that his name, *liouvillei*, is untenable. It is apparent from Sladen's description that his Kerguelen

specimens from 127 fathoms are referable to the Antarctic form, and I have confirmed this by an examination of an example from the type locality, Challenger St. 149H. Although this specimen is small (R 47 mm.) it shows the characteristics of the Antarctic form rather than of *loripes*.

Since both forms are variable in the robustness of ray and the rather confusing matter of marginal spinules, the most constant difference seems to be the greater number of marginal plates in *obesus*. In two specimens, each having R 107 mm., *obesus* has 127 marginal plates while *loripes* has 70. These short marginal plates are well brought out in Koehler's figures. In general, Sladen's observations hold good. He says, p. 243:

"The rays are rather more distinctly cylindrical, the union of the abactinal and lateral areas being less angular and less conspicuous. The abactinal area is habitually much more inflated which gives the variety a conspicuously puffed up appearance. The small isolated spinelets or enlarged squamules on the marginal plates are smaller and less developed; and in young examples may be absent altogether from the inferomarginal plates and represented on the summit of the superomarginal plates by a squamule only very slightly greater than those forming the rest of the covering of the plates."

The specimens from St. 458, Bouvet Island, 357-377 m., are clearly *obesus*, as are those from South Georgia. Large specimens from South Georgia, the Palmer Islands, and South Orkneys have a very small superomarginal spinule at the upper end of the plate and also a second at about the middle; while the inferomarginals carry, proximally 3 or 4 small appressed sharp spines in a vertical series and distally 2 or 3. Two very large specimens, from St. 1660, Ross Sea, have R 204 mm. and 175 mm., r 32 mm., and are comparable to Koehler's largest example from Adélie Land, in which R is 170 mm., r 35 mm. (Koehler, 1920, p. 263). There are usually 3 sharp superomarginal spinules and 3 or 4 inferomarginal, very closely appressed to the plates but obviously larger than the rounded squamules covering the plates. A large specimen from St. WS 27, South Georgia, 106-109 m., gravel, has R 160 mm., r 25 mm., and 3 superomarginal spinules in a vertical series, easily distinguished from the broad, rounded squamules covering the plate by their slightly greater length and sharp points. The proximal inferomarginals have usually 4, and the distal inferomarginals 3, similar enlarged spinules.

For purposes of recognition the following points may be stressed. The rays of *obesus* have more rounded sides, and there is a less evident angle of demarcation between the lateral and abactinal surface of the ray, which (especially in the high Antarctic specimens) is inflated or "puffed up". But the rays are not broader at the base in medium-sized and large specimens. All the marginal spinules are smaller in *obesus*, the uppermost superomarginal spinule being very small, or absent. The abactinal paxillae of *obesus* "run" slightly smaller than in *loripes*, but are not invariably so, for in a specimen from St. 167, South Orkneys, with R 140 mm., they measure very close to the paxillae of *loripes* from St. WS 819. The number of marginal plates is a very tangible character when there are specimens of *loripes* for comparison.

TYPE LOCALITY. Challenger St. 149H. Off Cumberland Bay, Kerguelen Island, 127 fathoms, volcanic mud.

DISTRIBUTION. Antarctic, circumpolar. Kerguelen, 127 fathoms, volcanic mud (Sladen). South Shetlands, 18–420 m., mud; Adélie Land, 151 fathoms; Shag Rock Bank, 160 m., gravel, sand; South Georgia, 250–310 m., clay (Koehler).

South Georgia, 91–270 m.; South Orkneys, 244–344 m.; Palmer Islands, 160–500 m.; Bouvet Island, 357–377 m.; Ross Sea, 351 m. ('Discovery').

Genus *Psilaster* Sladen

Psilaster Sladen, *Narr. Chall. Exp.*, 1, 1885, p. 611. Type *Astropecten andromeda* M. & T.

Ripaster Koehler, 1906, p. 4. Type *R. charcoti* Koehler.

Phidiaster Koehler, 1909, p. 28. Type *Ph. agassizi* Koehler.

REMARKS ON *RIPASTER*. There are enough young specimens to give a hint as to the relationship of the genus *Ripaster* since they are more "generalized" than the adults. The smallest has R 5.5 mm., r 2.5 mm. Up to a size where R is 16–20 mm., and R equal to about 3 r, they resemble a *Leptychaster* with a vertical comb of 3 or 4 appressed inferomarginal spines. The superomarginal spines are just beginning to differentiate from the other spinelets of the plate and would not be significant if we did not know the end result. No *Leptychaster*, of course, has specialized marginal spines. As a consequence such a sea star would probably be allocated to *Psilaster*, rather than to *Persephonaster* especially if the mouth and adambulacral plates were carefully examined.

Koehler compared *Ripaster* with *Dytaster*. It has nothing to do with that rather specialized and easily recognized genus. *Ripaster* in general appearance closely resembles a *Persephonaster* of the broad-rayed type, such as *P. euryactis* of the Philippines. This resemblance concerns especially the form of ray, its attenuation at extremity and the bristling marginal armature. Like *Persephonaster*, *Ripaster* has the gonads confined to the interradial region and lacks, in the actinal interradial area, an unpaired series of plates extending from the outer end of the mouth-plates nearly or quite to the inferomarginals. Such an unpaired series, more or less well developed, is present in *Leptychaster*, *Blakiaster* and *Astromesites*.

The adambulacral and mouth-plates of *Ripaster* are like those of *Psilaster* rather than *Persephonaster*. The first adambulacral is strongly compressed as in *Psilaster* and *Bathybiaster*, with 2 closely appressed transverse rows of spines, 2 or 3 of which may be allocated to the narrow, angular, furrow margin. Similarly, each mouth-plate carries 2 closely appressed rows of spines extending from outer to inner end of each plate, as in *Psilaster* and *Bathybiaster*. In *Persephonaster* the first adambulacral is nearly or quite like the others, with a furrow comb of 5 or more spines. In *Ripaster*, *Psilaster* and *Bathybiaster* the second adambulacral is also compressed, and even the third shows some distortion in *Bathybiaster* and *Psilaster*. The mouth-plates of *Persephonaster* have a more extensive actinal surface, with numerous intermediate suboral spines. There is a definite marginal comb bordering on the abulacral furrow (not differentiated in *Ripaster*, *Psilaster*, *Bathybiaster*). In *Persephonaster* there is a very characteristic angular group or tuft of small spines at the inner end of each mouth-plate, above the tooth and the obvious marginal spines. These spines¹ are adjacent to the first tube foot, and the upper spinelets

¹ Fisher, 1919, pl. 38, fig. 1.

of the group may be in contact with the peristomial membrane. There is no sign of these in *Ripaster*, *Psilaster*, or *Bathybiaster*.

Koehler makes some point of the structure of the marginal plates. I can find no difference between *Ripaster* and *Psilaster*, except that in *Ripaster* the vertical fasciolar grooves of the marginal plates are a trifle shallower. These are the grooves, lined with ciliary spinelets, which intervene (on the dorsoventral suture line) between the ridge-like tabula of the marginal plates. Each ridge passes unbroken from supero- to infero-marginal plate, and is homologous to the tabulum of the abactinal paxillae.

Whether the more numerous superomarginal spines of *Ripaster* constitute a feature of generic value must remain a matter of opinion. In *Persephonaster* (as in *Astropecten*) superomarginal spines may be absent (*Persephonaster cingulatus* Fisher) or there may be a vertical comb of them (*P. luzonicus* Fisher). The adults of all described species of *Psilaster* have at least one superomarginal spine.

My feeling is that *charcoti* is a rather aberrant Antarctic outpost of the cosmopolitan *Psilaster*.

Psilaster charcoti (Koehler)

- Ripaster charcoti* Koehler, 1906, p. 4, pl. 3, figs. 20, 21, 31, 32; 1908, p. 540; 1912, p. 101, pl. 8, fig. 2; 1920, p. 258, pl. 51, fig. 5; pl. 52, fig. 1; pl. 72, fig. 1.
Ripaster longispinus Koehler, 1920, pl. 51, figs. 5-8; pl. 52, figs. 2-4; pl. 72, fig. 2; 1928, p. 95, pl. 12, figs. 6-8.
- St. 27. West Cumberland Bay, South Georgia, 110 m., 2 specimens.
 St. 30. West Cumberland Bay, South Georgia, 251 m., 2 specimens.
 St. 39. East Cumberland Bay, South Georgia, 179-235 m., grey mud, 5 specimens.
 St. 45. 2.7 miles S, 85° E of Jason Light, South Georgia, 238-270 m., grey mud, 4 specimens.
 St. 123. Off mouth of Cumberland Bay, South Georgia, 230-250 m., grey mud, 2 specimens.
 St. 140. Stromness Harbour to Larsen Point, South Georgia, 122-136 m., green mud, stones, 2 specimens.
 St. 148. Off Cape Saunders, South Georgia, 132-148 m., grey mud, stones, 2 specimens.
 St. 170. Off Cape Bowles, Clarence Island, 61° 25' 30" S, 53° 46' W, 242 m., rock, 1 specimen.
 St. 181. Schollaert Channel, Palmer Archipelago, 160-335 m., mud, 4 specimens.
 St. 182. Neumayr Channel, Palmer Archipelago, 259 m., mud, 1 specimen.
 St. 187. Neumayr Channel, Palmer Archipelago, 259 m., 2 specimens.
 St. 366. Four cables south of Cook Island, South Sandwich Islands, 77-152 m., 1 specimen.
 St. 371. One mile east of Montagu Island, South Sandwich Islands, 99-161 m., 4 specimens.
 St. 458. Seven miles S, 50° W of Cape Circumcision, Bouvet Island, 357-377 m., 1 very young specimen.
 St. WS 27. South Georgia, 53° 55' S, 38° 01' W, 106-109 m., gravel, 2 specimens.
 St. WS 32. Mouth of Drygalski Fjord, South Georgia, 91-225 m., 3 specimens.
 St. WS 865. 50° 03' S, 64° 14' W, 126 m., 3 specimens.
 St. MS 68. East Cumberland Bay, South Georgia, 220-247 m., 3 specimens.
 St. 356. Terra Nova (loaned by British Museum, register 1914.8.12.17-18; labelled "*Asterias longstaffi*" by Prof. F. J. Bell; an example of forma *longispinus*).
 St. 1660. Ross Sea, 74° 46.4' S, 178° 23.4' E, 351 m., 10 specimens (forma *longispinus*).
 St. 1952. Between Penguin Island and Lion's Rump, King George Island, South Shetlands, 367-383 m., 1 specimen, R 163 mm., r 42 mm. (forma *longispinus*).
 St. 1957. Off south side of Clarence Island, South Shetlands, 2 specimens (forma *longispinus*).

This species has been minutely described and elaborately figured by Koehler, who separated the extremes of variation under two specific names. The anomalies of distribution apparently raised no question since he recorded the two "species" from the same dredge haul.

It is perfectly apparent from the fine series under observation that we have an Antarctic species which has practically the same geographic distribution as *Bathybiaster loripes obesus*. Specimens with shorter superomarginal spines and referable to forma *charcoti* are found at South Georgia where the long-spined form also occurs. The latter also occurs in the high Antarctic localities, such as the Palmer Archipelago, Ross Sea, and latitude $65^{\circ} 06'$ to $66^{\circ} 55'$ S, longitude 96° to 145° E (type series of *longispinus*). At one of the stations in this area, together with *longispinus*, *charcoti* was dredged.

While the extremes are as Koehler has described them, there are intermediates which are with difficulty assigned to either forma. Perhaps this is another way of saying that both formae are variable. For instance, there is as much latitude of variation between figs. 6 and 8, pl. 12 (Koehler, 1920) representing *longispinus* as there is between the same fig. 6, and fig. 2, pl. 8 (Koehler, 1912) representing *charcoti*. Also, the contrasting figures given by Koehler (1920, pl. 51, fig. 5, *charcoti* and fig. 6, *longispinus*; pl. 52, fig. 1, *charcoti* and fig. 2, *longispinus*) represent the very extremes of difference. In the Discovery collection are examples connecting these two extremes. No sharp line of distinction can be drawn separating two species, or even two formae of the same species.

COLOUR NOTES. St. 1952, large specimen, bright pink above, yellow below. St. 1957, abactinal surface pale delicate pink, inclining to delicate purple towards and at centre.

TYPE LOCALITY. Booth-Wandel Island, south of Palmer Archipelago. Paratypes from Wincke Islands and Briscoe Islands.

DISTRIBUTION. Circumpolar. In the western hemisphere: Briscoe Islands, Wandel Island, Palmer Archipelago, South Shetlands 30–75 m., mud, pebbles, rocks, grey mud (Koehler); 160–335 m. ('Discovery'). Clarence Island 242 m., rock ('Discovery'). South of South Orkneys, 1775 fathoms (Koehler). South Sandwich Islands ('Discovery'). South Georgia, 75–310 m., stones, clay (Koehler); 91–270 m., grey mud, stones ('Discovery').

Eastern hemisphere: Area comprising $92^{\circ} 10'$ to $145^{\circ} 21'$ E and $65^{\circ} 06'$ to $66^{\circ} 55'$ S, 60–325 fathoms (Koehler). Bouvet Island, 357–377 m.; Ross Sea, 351 m. ('Discovery').

Family BENTHOPECTINIDAE Verrill

Genus *Pontaster* Sladen

Pontaster Sladen, *Narr. Challenger Exp.*, 1, 1885, p. 610; 1889, p. 23. Type *Astropecten tenuispinus* Düben & Koren.—Ludwig, 1910, p. 447.

Pontaster planeta Sladen

Pontaster planeta Sladen, 1889, p. 30, pl. 10, figs. 1, 2; pl. 13, figs. 1, 2.—Ludwig, 1910, p. 447.

St. WS 821. South of West Island, Falkland Islands, $52^{\circ} 55\frac{3}{4}'$ S, $60^{\circ} 55'$ W, 351–367 m., 1 specimen.

The type measures R 37 mm., r 6.5 mm., R:r 5.5 r. The present specimen measures R 100 mm., r 20 mm., R:r 5 r. Its large size is therefore remarkable. Comparison of this specimen has been made with one from the type locality and there are no differences which cannot be attributed to the disparity of size.

The central enlarged spinule of paxillae is present all over the abactinal area. Some plates of disk have 3 or 4 of these. Of the smaller secondary spinelets, there may be 20 co-ordinated in a convex group on larger plates of disk while much smaller interpolated secondary plates have only 5 or 6, and no enlarged spinule. The superomarginal plates carry a single, sharp, subconical spine 3 mm. long at base of ray. Proximal inferomarginals with a similar, lateral, spine 4.5 mm. long; and on actinal surface of plate, 3 or 2 successively smaller spines in a transverse series. Distally these accessory marginals are usually 2, then 1. The secondary spinelets are very slender, spaced, and lengthened adjacent to the principal spines.

Similar, slender, spaced, spinelets cover the actinal interradial area, the plates of which form about 4 chevrons with some extra plates adjacent to first inferomarginals. Plates of innermost row extend to fourth inferomarginal. Most of actinal plates with 1 or 2 enlarged central spinules.

Adambulacral plates with a prominent furrow margin as described and figured by Sladen. Six or seven spinelets can be assigned to this angular margin, but the same series is continued along the adoral transverse edge of plate by 4-6 additional, similar spinelets. The actinal surface is occupied by the broadened bases of the subambulacrals, which vary from 2 to 4, are robust, about 3 mm. long, slightly tapered beyond the base, and are bluntly pointed; or, in the case of the second from furrow, subclavate with compressed, subtruncate tip.

The *combined* mouth-plates form a broad subtruncate projection nearly as broad as the length of interradial dimension. On the broad actinostomial margin are 6 stout, tapered, flattened spines (3 to each plate), the central pair about 3 mm. long. On the furrow margin, continuing this series, are 4 much smaller spines. The actinal surface is occupied by about 8 or 9 prominent tapered acute spines.

The papularium of each ray is perfectly flat, for which reason its extent is not easy to determine from the outside. It is strongly bilobed distally. Total length about 12 mm.; breadth 6.5 mm.; length of each lobe 8 mm. Papulae small, well spaced.

The dorsal muscle bands are well developed, about 4 mm. broad, slightly spaced from one another. The inner, truncate end is attached to abactinal wall opposite ninth ambulacral ossicle. From the outer corner of this inner end a *rudimentary* tendon connects with a thin specialized dorsal crest of eighth ambulacral ossicle. This ridge is perceptibly higher than that of seventh or ninth plates. In this respect *Pontaster* is more nearly like *Cheiraster* than *Pectinaster*. In the latter the tendon is better developed.

Pedicellariae are not present.

COLOUR NOTE. Disk and base of arms pale warm pink.

TYPE LOCALITY. Challenger St. 311, off western coast of South America, near the

entrance to the Straits of Magellan, opposite Port Churruca, 245 fathoms, blue mud; bottom temperature 46° F.

DISTRIBUTION. Slopes of Falkland-Cape Horn Plateau, 350-500 m.

Genus *Luidiaster* Studer

Luidiaster Studer, *Sitzungsber. naturforsch. Freunde, Berlin*, 16 Oct. 1883, p. 131. Type *L. hirsutus* Studer.—Ludwig, 1910, p. 451.—Fisher, 1911, p. 127.—Verrill, 1914, p. 311.
Acantharchaster Verrill, *Proc. U.S. Nat. Mus.*, xvii, 1894, p. 268. Type *Archaster dawsoni* Verrill.

Luidiaster gerlachei (Ludwig)

Cheiraster gerlachei Ludwig, 1903, p. 9, pl. 1, figs. 1-8; pl. 2, figs. 9, 10.

Luidiaster gerlachei Ludwig, 1910, pp. 252, 253.—Fisher, 1911, p. 127.—Koehler, 1920, p. 244, pl. 55, figs. 2-5; pl. 65, fig. 8.

St. 181. Schollaert Channel, Palmer Archipelago, 160-335 m., mud, 5 specimens.

St. 1660. Ross Sea, 74° 46'4" S, 178° 23'4" E, 351 m., 18 specimens, R 20 to R 76 mm.

St. 1957. Off south side of Clarence Island, South Shetlands, 785-810 m., 11 specimens.

The largest specimen (St. 181) has R 110 mm., r 18 mm., R = 6.1 r; br at interradius 20 mm., at fifth superomarginal, 15 mm. Ludwig's largest specimen had R 78 mm., while Koehler's measured R 54 mm.

Ludwig has described this species in great detail. Koehler has supplied notes on variations as well as very useful photographic figures.

In his second paper, Ludwig (1910, p. 453) contrasts *gerlachei* with the much older *hirsutus* of Studer, of which he had two specimens. According to this synopsis *hirsutus* has a double cirlet of smaller spinelets surrounding the central spine of the paxillae, unequal ventrolateral spinelets, and pedicellariae on the ventrolateral plates only. *Gerlachei* has a single cirlet of paxillar spinelets, equal ventrolateral spinelets, and pedicellariae on the ventrolateral as well as on other plates.

In the Discovery specimens the first character holds fairly well, but some of the larger plates of disk of biggest specimen have a second circle, or extra spinelets within the single circle. This specimen has *unequal* actinal intermediate (ventrolateral) spines. To be more precise an elongate central spine is surrounded by smaller, unequal secondary spinules. This disparity is exhibited by the smallest specimen, R 20 mm., St. 1660. In the largest specimen there are numerous large pectinate pedicellariae on actinal interradial areas, especially adjacent to adambulacrals, which are continued far along ray between the inferomarginals; but in three other examples (R 33 to R 55 mm.) the pedicellariae are confined to actinal interradian areas (sometimes only one pedicellaria to an area).

Ludwig states in the same synopsis, that both *hirsutus* and *gerlachei* differ from *teres* in having one inferomarginal spine while *teres* has two. The largest specimen (R 110 mm.) has regularly 2 inferomarginal spines, the longer of which near base of ray, measures 8 mm., and the shorter 4 or 5 mm. Two other specimens also have the second spine developed.

The very angular furrow margin of the adambulacral plates carries 8 or 9 spines and 3-5 others along the adoral border; subambulacral spines 2, slender, slightly curved, the longer about 6 mm. at base of ray; on disk they are a little shorter, subcylindrical, blunt.

The dorsal muscle bands meet along the median line. In the specimen examined, the short tendon from the inner end of band passes over the inner face of marginal plates (to which it is attached) and fastens to a specialized crest of the seventh ambulacral ossicle, on one side of ray, and to eighth on the other side.

Ludwig planned a much fuller treatment of the *Notomyota* than the frankly preliminary account of 1910. Unfortunately this work was never realized. No detailed description and no figures of *L. hirsutus* have been published. It will not be surprising if eventually *hirsutus* and *gerlachei* are found to represent two races of a single circumpolar species. The two examples of *hirsutus* studied by Ludwig were taken by the 'Valdivia' at Bouvet Island (03° 30' E, 54° 30' S). The records of *L. gerlachei* are from much further south (64° to 70°).

In 1911 (Fisher, 1911, p. 127) I raised the question whether *Luidiaster dawsoni* is congeneric with *gerlachei*. I have compared specimens and believe that they are. But as shown by Ludwig's key (1910, p. 453) *dawsoni* stands apart by the extraordinary development of its spines, especially those of inferomarginal plates.

TYPE LOCALITY. Southern Bellinghausen Sea, near Ice Barrier, west of Charcot Island.

DISTRIBUTION. Circumpolar, Antarctic, between latitudes 70° and 64° S. Recorded by Ludwig (1903) between 80° 48' and 84° 06' W, 70° and 70° 23' S, 450-560 m. Koehler's specimens were taken by the Australasian Antarctic Expedition between 96° 13' and 145° 31' E, 64° 44' and 66° 55' S, 230-358 fathoms.

Family ODONTASTERIDAE Verrill

Gnathasterinae (pars) Perrier, 1894, pp. 244, 251.—Meissner, 1896, p. 92.

Gnathasteridées Koehler, 1920, p. 179.

Odontasteridae Verrill, 1899, p. 201.—Ludwig, 1903, p. 19.—Fisher, 1905, p. 302; 1911, p. 153, diagnosis—Farquhar, *Trans. New Zealand Inst.*, XLV, 1913, p. 212.

KEY TO THE GENERA OF ODONTASTERIDAE

*a*¹. A recurved, glassy tipped spine on each mouth-plate—two side by side, at each mouth angle.

*b*¹. Marginal plates decreasing regularly in size from base to extremity of rays.

Asterodon Perrier.

*b*². Marginal plates at first increasing in size; rays dilated.

Diplodontias Fisher.

*a*². At each mouth angle a strongly recurved spine (common to the two plates), the tip of which is normally glassy. On either side of this, a suboral spine sometimes is enlarged and recurved and may have a short glassy tip.

*b*¹. Marginal increasing in size toward extremity of rays.

Eurygonias Farquhar.

*b*². Marginals decreasing in size toward extremity of rays.

- c*¹. Abactinal plates with a distinct tabulum crowned with short to fairly long spinelets; marginal plates small, to well-developed, more or less tabulate, spinulose; actinal area densely spinulose. *Odontaster* Verrill.
- c*². Abactinal plates without a distinct tabulum, but slightly convex. They are crowned with low granules, sometimes involved in a thin integument, which, however, in no way hides them. Marginal plates prominent to small, granulose, not tabulate; actinal areas covered with granules which, in some species, are gradually transformed to spinelets as oral angle is approached. *Acodontaster* Verrill.

From the above synopsis it will be seen that five genera are recognized, whereas Koehler (1920, p. 190) admitted eleven. *Heuresaster* Bell was overlooked, but it is obviously the same as Koehler's *Tridontaster*.

I regret the necessity for departing so widely from the results obtained by Koehler; but it is inevitable since in certain cases he adduced to distinguish his genera characters of only specific, or even less than specific, significance.

It would be useful to separate *Odontaster* from *Gnathaster*, but it cannot be done. For one thing the marginal plates of *Gnathaster* vary widely, if we include such diverse species as *Odontaster validus*, where they are paxilliform, and *O. penicillatus* forma *grayi*, where they are block-like and covered by elongate granules or short spinelets. But *Gnathaster* must include the widely variable *penicillatus*, which bridges the gap to a restricted *Odontaster*.

Unfortunately Koehler made *O. penicillatus* forma *grayi* (i.e. *O. grayi* Bell) the type of *Peridontaster*. *Grayi* intergrades perfectly with *Odontaster penicillatus* (*O. pilulatus* Sladen) which in turn is closely related to *O. meridionalis* (Smith), the type of *Gnathaster*. Such differences as *Odontaster grayi* shows to *O. meridionalis* are therefore not generic. In another direction, *O. grayi* (apart from its pentagonal shape) obviously resembles *O. hispidus*, the type of *Odontaster*! *Odontaster*, *Gnathaster* and *Peridontaster* cannot be separated on the basis of characters now known.

I believe that the small type of *Epidontaster* is the young of *Odontaster meridionalis* having accessory teeth—not an uncommon variation in that species. Only one specimen is cited.

The character of the plates and their armature is the same in *Acodontaster*, *Pseudontaster*, *Metadontaster*, and *Tridontaster* (*Heuresaster* Bell). *Pseudontaster* simply has somewhat smaller marginal plates than has *Acodontaster*. *Pseudontaster moderatus* Koehler and *Ps. stellatus* Koehler, in my opinion, are variants of the circumpolar *Acodontaster elongatus* (Sladen), type of *Acodontaster*. For some curious reason Koehler never recognized *elongatus* (see *Odontaster cremeus* Ludwig, 1903; Koehler, 1912; *Acodontaster cremeus* Koehler, 1920).

In view of the obviously close relationship of *Tridontaster laseroni* to *Acodontaster conspicuus* and the occasional presence of accessory teeth in the latter, I cannot take seriously the use of accessory teeth alone as the criterion of a new genus.

Metadontaster contains a single species *M. waitei*, which is so close to *Acodontaster conspicuus* that I am uncertain whether to call it a species or a form of *conspicuus*.

There follows a list of the *Odontasteridae* of the southern hemisphere as given in

Koehler's revision of 1920 with the addition of two new species added in 1923. With each is the interpretation given in the present paper:

Koehler	Fisher
<i>Acodontaster elongatus</i> (Sladen) name only	<i>A. elongatus</i>
<i>A. elongatus</i> var <i>abbreviatus</i>	<i>A. conspicuus</i>
<i>A. cremeus</i> (Ludwig)	<i>A. elongatus</i>
<i>A. capitatus</i> (Koehler)	<i>A. elongatus</i> forma <i>capitatus</i>
<i>A. granuliferus</i> (Koehler)	<i>A. elongatus granuliferus</i> forma <i>granuliferus</i>
<i>Pseudontaster marginatus</i> Koehler	<i>A. marginatus</i>
<i>Ps. stellatus</i> Koehler	<i>A. elongatus</i>
<i>Ps. conspicuus</i> Koehler	<i>A. conspicuus</i>
<i>Ps. moderatus</i> Koehler	<i>A. elongatus</i>
<i>Tridontaster laseroni</i> Koehler	<i>A. hodgsoni</i> (Bell)
<i>Metadontaster waitei</i> Koehler	<i>A. waitei</i>
<i>Gnathaster meridionalis</i> (Smith) name only	<i>Odontaster meridionalis</i>
<i>G. penicillatus</i> (Philippi)	<i>O. penicillatus</i> forma <i>penicillatus</i>
<i>G. validus</i> (Koehler)	<i>O. validus</i>
<i>G. tenuis</i> (Koehler)	<i>O. validus</i> forma <i>tenuis</i>
<i>G. elegans</i> (Koehler)	<i>O. meridionalis</i> (Smith)
<i>Peridontaster grayi</i> (Bell)	<i>O. penicillatus</i> forma <i>grayi</i>
<i>P. pusillus</i> (Koehler)	<i>O. pusillus</i>
<i>Epidontaster pentagonalis</i> Koehler	<i>O. meridionalis</i> juv.
<i>Asterodon singularis</i> (M. & T.)	<i>A. singularis</i> forma <i>singularis</i>

Genus *Odontaster* Verrill

Odontaster Verrill, *Amer. J. Sci.*, xx, 1880, p. 402. Type *O. hispidus* Verrill.
Gnathaster Sladen, 1889, p. 205. Type *G. meridionalis* (Smith).—Perrier, 1894, first reviser.
Gnathodon Verrill, 1899, p. 203 (error).
Epidontaster Koehler, 1920, pp. 191, 195. Type *E. pentagonalis* Koehler = *Odontaster meridionalis* (Smith).
Peridontaster Koehler, 1920, pp. 192, 194. Type *Odontaster grayi* Bell = *O. penicillatus* Philippi, var.
Gymnognathaster Döderlein, 1928, p. 297. Type *G. gaussae* Döderlein (perhaps a young *O. meridionalis*, R 7 mm.).

Odontaster meridionalis (Smith)

Astrogonium meridionale Smith, 1876, p. 109.
Pentagonaster meridionalis Smith, 1879, p. 276, pl. 16, figs. 6, 6a.
Gnathaster meridionalis Sladen, 1889, p. 287, pl. 47, figs. 1, 2; pl. 48, figs. 5, 6; pl. 49, figs. 11, 12.
Odontaster elegans Koehler, 1912, p. 72, pl. 7, figs. 5-11.
Gnathaster elegans Koehler, 1920, p. 227, pl. 41, figs. 7, 8; pl. 71, fig. 4.—1923, p. 85.—Döderlein, 1928, p. 297.
Epidontaster pentagonalis Koehler, 1920, p. 235, pl. 39, figs. 3, 4, 8; pl. 41, figs. 9-11.
 St. 160. Near Shag Rocks, 53° 43' 40" S, 40° 57' W, 177 m., grey mud, rocks, 1 specimen.
 St. 164. East end of Normanna Strait, South Orkneys, near Cape Hansen, Coronation Island, 24-36 m., 3 specimens.
 St. 170. Off Cape Bowles, Clarence Island, 61° 20' 30" S, 53° 46' W, 342 m., rocks, 3 young specimens.
 St. 190. Bismarck Strait, Palmer Archipelago, 93-130 m., rock or stones and mud, 3 young specimens.
 St. 371. One mile east of Montagu Island, South Sandwich Islands, 99-161 m., 2 large specimens.

- St. 474. One mile west of Shag Rocks, 199 m., 1 specimen.
 St. 1562. Marion Island, 46° 53' S, 37° 55' E, 97 m., 4 specimens.
 St. 1563. Marion Island, 46° 48.4' S, 47° 49.2' E, 101-106 m., 4 young specimens.
 St. 1564. Marion Island, 46° 36.5' S, 38° 02.3' E, 108-113 m., 1 specimen.

This is one of the most handsome sea stars of the Antarctic. The paxillae are well developed with numerous spinelets, of which those occupying the centre of tabulum are characteristically clavate, heavier than the marginal spinelets, and in large specimens quite crowded. The marginal plates can hardly be called paxillae. Rather they are conspicuous squarish blocks with a low broad tabulum crowned by many crowded spinelets, essentially like the abactinal but larger. The largest specimen (R 91 mm., St. 371) has paxillae and marginals with more numerous spinelets than Koehler's fig. 7, pl. 7 (1912). The smallest specimen (St. 190) has R 5 mm. The characteristic thorny tips of the spinelets are described and figured by Koehler.

In the two large specimens (St. 371) each median "tooth" is accompanied on either side by an accessory tooth, actually an enlarged suboral spine (sometimes upright, sometimes bent slightly away from the mouth angle), the tip of which is hyaline. These accessory teeth are developed in a specimen (St. 164) having R 48 mm., but the membrane has not yet retracted from the tip.

For a comparison of this species with *Odontaster validus*, see the table of variations under the latter.

This is an Antarctic species. It is therefore not surprising that the young and medium-sized specimens from Marion Island vary slightly from the Antarctic form. For instance, there is an obvious lack of the slender spinelets which occur on the margin of the paxillae of typical large specimens and which are indicated in Sladen's fig. 1, pl. 47.

Koehler states that his specimens of *elegans* from the region between longitudes 92° and 145° E (64° 32' and 66° 55' S) are in no way different from the types which were collected by the second Charcot Expedition in the Antarctic Archipelago. It is difficult to understand why Koehler overlooked *meridionalis* and compared his *elegans* only with *validus*. There can be no doubt that *meridionalis* and *elegans* are the same species.

Epidontaster pentagonalis Koehler was dredged at St. 8, Australasian Antarctic Expedition, 66° 8' S, 94° 17' E, 120 fathoms, at which *Odontaster meridionalis* was taken. The genus and species is based upon one young specimen having R 17 mm., r 10 mm., characterized by having an accessory "tooth" on either side of the usual median tooth. Otherwise it is a short-rayed *O. meridionalis* very similar to a young specimen (R 8.5 mm.) from St. 170. This small specimen, which has the proportions of Koehler's, shows an incipient accessory tooth on either side of the median. As noted above the two largest specimens, from St. 371, each have the accessory teeth, the extreme hyaline tip of which shows beyond the membranous envelope. In the larger of these two specimens R is 63 mm.; in the other R is 58 mm. It follows therefore that the accessory teeth here, as elsewhere in the *Odontasteridae*, are not of generic significance.

COLOUR NOTE. St. 164, orange yellow, Ridgway scale 170 y.c.

TYPE LOCALITY. Kerguelen Island.

DISTRIBUTION. As far south as Alexander Land (68° 35' S, 72° 40' W, 297 m.); off Adelaide Island; Petermann Island; Palmer Archipelago; South Orkneys; South Sandwich Islands; South Georgia. East Antarctica from 88° to 145° 21' E and 64° 32' to 66° 55' S. Heard Kerguelen and Marion Islands. The greatest depth appears to be 354 fathoms at 66° 51' S, 142° 06' E.

The species is evidently circumpolar, Marion, Kerguelen and South Georgia being its northern outposts.

Odontaster validus Koehler

Odontaster validus Koehler, 1906, p. 6, pl. 3, figs. 22-26.—1908, p. 12.—1911, p. 27.—1912, p. 68, pl. 7, figs. 1-4, 12.

Odontaster tenuis Koehler, 1906, p. 8, pl. 4, figs. 33-38.—1920, p. 232, pl. 40, figs. 1-3, 6; pl. 41, figs. 3, 4; pl. 72, fig. 4.

Cycethra verrucosa Bell, 1908, p. 10, pl. 5, fig. 1*b*.—1917, pl. 1, figs. 1-6 (fide Koehler).

Gnathaster validus Koehler, 1920, p. 228, pl. 34, fig. 10; pl. 40, figs. 4, 5, 7; pl. 41, figs. 2, 5; pl. 72, fig. 3.—1923, p. 84 (Shag Rocks, South Georgia).

St. 145. Stromness Harbour, South Georgia, 26-35 m., 2 specimens.

St. 163. Paul Harbour, Signy Island, South Orkneys, 18-27 m., 18 specimens.

St. 164. East end of Normanna Strait, South Orkneys, near Cape Hansen, Coronation Island, 24-36 m., 97 specimens.

St. 173. Port Foster, Deception Island, South Shetlands, 24 specimens.

St. 368. Douglas Strait, Southern Thule, South Sandwich Islands, 653 m., 2 forma *validus*, 1 forma *tenuis*.

St. 370. Two miles north-east of Bristol Island, South Sandwich Islands, 18-80 m., 8 specimens

St. 456. One mile east of Bouvet Island, 40-45 m., 3 specimens.

St. 1941. Leith Harbour, South Georgia, 55-22 m., 2 specimens.

St. 1959. Scotia Bay, South Orkneys, 5 m., 14 specimens (taken in fish trap).

St. WS 25. Undine Harbour (North), South Georgia, 18-27 m., sand, 6 specimens.

St. WS 62. Wilson Harbour, South Georgia, 15-45 m., 2 specimens.

St. MS 6. East Cumberland Bay, South Georgia, 27 m., 10 specimens.

St. MS 10. Same as MS 6, 27 m., 17 specimens.

St. MS 12. Same as MS 6, 25-53 m., 2 specimens.

St. MS 63. Same as MS 6, 23 m., 8 specimens.

St. MS 71. Same as MS 6, 120-60 m., 1 specimen.

St. MS 74. Same as MS 6, 22-40 m., 3 specimens.

Cumberland Bay, South Georgia, November 1929, 2 specimens.

Koehler has elaborately described and figured this species, which Bell recorded and figured as *Cycethra verrucosa* (1908, p. 10, pl. 5, fig. 1). The British Museum has kindly forwarded one of Bell's specimens from the Discovery Winter Quarters. It is an example of *Odontaster validus* forma *validus* with rather attenuate rays, R 44 mm., r 18.5 mm.

Since there are 97 specimens from St. 164 it seems desirable to analyse the variations found at this station and to include also variants from other localities. These are given in synoptical form and *O. meridionalis* is introduced to indicate its position with reference to the varieties of *validus*. *O. tenuis* intergrades perfectly with the typical form. Of

the latter I have one of the type series, namely, one of the two specimens recorded by Koehler (1906, p. 6) from Booth-Wandel Island.

In the following synopsis to save space I have abbreviated references to Koehler's excellent photographic figures, as follows: VII is pl. 7, Koehler, 1912; XL and XLI are pl. 40 and 41, Koehler, 1920. The numerals following any of these refer to the figures on that particular plate.

The Booth-Wandel specimen has long actinal spines, about the same as in VII, 12, or XL, 5 (left side) but not so long as the extremes included under A^1C^3 below; nor as short as those of A^2 , B^1C^1 ; it lies between these two. On the whole, specimens with actinal spines shorter than the subambulacral (either slightly or decidedly) are more numerous than those having the two sets of spines subequal.

SYNOPSIS OF VARIATIONS OF *ODONTASTER VALIDUS*

- A^1 . Actinal intermediate spines as long as, or nearly as long as, the subambulacral spines. They give the actinal intermediate area a *shaggy* appearance. The outer plates carry only 2 or 3 spines although those near the mouth-plates may have 4-7 (XL, 1, 2, 5).
- B^1 . Marginal, especially the superomarginal plates, small, *spaced*, paxilliform, especially in interradial region, but increasing in size on ray, although still spaced and paxilliform; superomarginal plates of interbrachial region with about 12 (6-15) spines; paxillae small, spaced (VII, 1, 3; XL, 6, 7; XLI, 4, 5).
- C^1 . Abactinal and marginal spines longer; paxillae with longer, slenderer pedicels; with the spinelets they resemble little brushes; rays longer and slenderer (XL, 3). St. 368; forma *tenuis* Koehler.
- C^2 . Rays as in C^1 and abactinal and marginal paxillae still well spaced, but with shorter spinelets; St. 368, 173, intermediate forms.
- C^3 . Rays of moderate length and not especially attenuate distally; abactinal paxillae with lower pedicels (as compared to C^1) and shorter spinelets; marginal plates virtually without pedicels, their spinelets radiating (the plates as a consequence appearing less widely spaced) or compressed into a brushlike group by reason of which the marginal paxillae appear to be more distantly spaced. There are often 1 or 2 small actinal 2- or 3-valved pedicellariae, much shorter than spinelets, near mouth-plates (VII, 1, 3, 4; XL, 7). St. 164, 23 specimens; St. 173, *et al.*
forma *validus*.
- B^2 . Superomarginal plates larger, broader than long, obviously larger than adjacent abactinal paxillae. The spines (15-25) are usually co-ordinated in 3 or 4 transverse series (as in XL, 7, but with more spines, as contrasted with VII, 3). St. 370, St. 456, St. MS 6, *et al.*
forma *validus*.
- A^2 . Actinal intermediate spines distinctly *shorter* than the subambulacral spines, which, as a consequence, form a differentiated *cheval-de-frise* along the border of the ambulacral furrow (VII, 2, 8, 11; 12 is intermediate with A^1); rays usually as in A^1C^3 , but variable; sometimes as long as in forma *tenuis*.
- B^1 . Actinal intermediate spines 1-3 per plate on marginal parts of area and 3-6 near mouth-plates (VII, 2).
- C^1 . As in A^1 , B^1 , C^3 ; paxillae small, well spaced; superomarginals of interbrachium small, paxilliform, with 6-15 spinelets; 1-3 small 2- or 3-valved pedicellariae on actinal plates near mouth-plates (e.g. St. MS 6); 58 specimens St. 140; St. 173; St. 368; St. 370, *et al.*
forma *validus*.

- C^2 . Abactinal paxillae small, as in C^1 , but superomarginal plates larger, bearing, in interbrachium, 20 or more spinelets in a compact group wider than long. St. 370; St. MS 74, *et al.* forma *validus*.
- C^3 . Superomarginal plates paxilliform, with slightly more obvious tabulum than in C^1 , and in interbrachial area with more (18–25) spinelets. The central spinelets are slender and nearly as long as the peripheral. The abactinal paxillae have 10–15 peripheral spinelets and 5–10 similar slender central ones (where typical *validus* has usually 1–4 central and 5–9 peripheral spinelets). Central paxillar spinelets not clavate as in *meridionalis*. This variation intergrades perfectly with typical *validus*. It resembles superficially a variant of *meridionalis* but can be recognized by the fewer actinal spines and slender central paxillar spines. 7 specimens, St. 164. forma *validus*.
- B^2 . Actinal intermediate spines many to a plate, the central usually subclavate and more robust than the peripheral of the group. They form a dense covering for the actinal surface and are usually bent toward the margin. Marginal plates larger than in *validus*, with numerous spines, which form a very compact group, of which the central are more robust and characteristically clavate. Abactinal paxillae large, with numerous central clavate spinelets surrounded by slender peripheral ones. Spines ending in sharp points or awns (VII, 5–11). *O. meridionalis*.

On account of the isolated position of Bouvet Island the three specimens from St. 456, 40–45 m., have been examined with great care since there was naturally some expectation of finding *Odontaster meridionalis*. The specimens are referable to section A^1 of the above synopsis. One conforms to B^2 , while two fall under B^1C^2 , which contains everything not referable to *tenuis*, but having somewhat longer abactinal and marginal spinelets than are found in the general run of forma *validus* with long actinal spines (A^1)—about as in Koehler VII 1, where the spinelets are obviously longer than XL 7 and shorter than XL 6 (*tenuis*).

The three specimens from St. 368 (363 m.) are of interest since one of them is the only example of forma *tenuis* in the collection; another is conceivably an intergrade; while the third is certainly not *tenuis* since it falls under A^2 of the synopsis, yet has longer, slenderer rays than the typical form of *validus*. There is great variation in the size of the madreporite in all phases of *validus*. The figure of *tenuis* given by Koehler (1920, pl. 40, fig. 3) shows a large plate. In the Bouvet Island specimen it is about one-half this size. A few specimens of undoubted forma *validus* have the madreporite as large as in this figure of *tenuis*.

Our largest specimens are from St. 370, South Sandwich Island. Of these the largest has R 70 mm., r 25 mm., br 25–28 mm., breadth of madreporite 11 mm. The rays are rather slender and obviously long, the rays being longer in proportion to disk than in Koehler's figures of *tenuis*, which this specimen clearly is not. The smallest from St. 370 has R 49 mm., r 22 mm., br 26 mm., breadth of madreporite, 3.5 mm. This specimen is a typical forma *validus* with swollen disk, small, well-spaced paxillae, the superomarginals of interbrachial region having about 12 spinelets. The mouth angles are worthy of close attention, for *each* has 3 "teeth", the normal recurved median, and a shorter one on either side, such as characterize Koehler's "*Epidontaster*" and

"*Tridontaster*". Not all the lateral teeth have a hyaline tip protruding through the sheath.

In *Odontaster validus* there is much variation in the armature of the mouth-plates as regards the size of the unpaired hyaline spine and of the *innermost* of the 2 or 3 suborals which stand on either side of this hyaline tooth.

(1) The unpaired spine may be missing (St. MS 6) and the "bud" of a new one appears in its place. This suggests a strenuous use for the teeth during which they are occasionally broken. The laterals have not superseded it.

(2) In one angle (St. 164) there are 2 subequal sharp, glassy tipped teeth, as in the genus *Asterodon*; the same variation occurs in *Odontaster penicillatus* forma *grayi*. From its position I would say that one is the true unpaired tooth and the other a suboral spine.

(3) In one angle there are 2 enlarged teeth which are certainly the innermost suboral spines. The median tooth appears to have been broken and never to have regenerated. The 2 teeth are blunt, recurved, and hardly hyaline at tip. The other 4 normal mouth angles have only the tip of unpaired tooth emerging from its sheath, while in 2 of these mouth angles the inner suborals are conspicuously enlarged and needed only a little time to become "hyaline" (St. WS 62).

(4) This last feature is not so important as it would seem since a considerable number of specimens (St. 164, St. MS 10) have the sacculus persisting at the end of some, or all, of the 5 normal teeth which thus have no exposed hyaline tip (see Koehler's genus "*Metadontaster*").

(5) Finally, there is great diversity in the size and shape of the unpaired tooth. They may be thick, broad, and only half as long as the median suture separating mouth-plates; or short and slender; or slender, and of various lengths to a trifle more than three-fourths that of median suture. The truncate base of spine is at the inner end of mouth-plates (M 71) or spaced from the end. These variations in the size and shape of teeth may occur at the same station (164).

It is obvious from the foregoing paragraphs that there is considerable latitude of variation. In spite of Koehler's resuscitation of his *O. tenuis* (1920, p. 232) I believe he was correct in his earlier view (1912, p. 68) when he reduced it to a variety of *validus*.

COLOUR NOTES (Ridgway's nomenclature). St. 164, Bordeaux purple (apparently no distinction between specimens of A^1 and A^2 of synopsis). St. 173, 22 specimens, pansy purple; 2 specimens, apricot orange. Of these two exceptions one belongs in A^1C^3 , the other in A^1B^2 of synopsis. St. 1959, very dark brown, almost black, with whitish spinelets dorsally and yellowish white ventrally.

TYPE LOCALITY. Antwerp Island, Palmer Archipelago (First Charcot Expedition).

DISTRIBUTION. Circumpolar, north to South Georgia (including Shag Rocks) and Bouvet Island; shore to 653 m.

Koehler in his several memoirs lists numerous stations, including (1908, p. 540) "iles Falkland, 5-20 brasses". I believe this to be due to a misplaced label. The locality is unlikely. The extensive work of R.S.S. 'William Scoresby' on the Falkland Plateau has failed to provide a single specimen of *validus*, but numerous examples of other species of *Odontaster*.

Odontaster penicillatus (Philippi)

- Goniodiscus penicillatus* Philippi, 1870, p. 268.
Calliderma grayi Bell, 1881, p. 95, pl. 8, fig. 5.
Pentagonaster paxillosus Bell, 1881, p. 95.
Gnathaster pilulatus Sladen, 1889, p. 292, pl. 57, figs. 5-7.—Verrill, 1899, p. 205.
Gnathaster grayi Sladen, 1889, p. 286.—Verrill, 1899, p. 205.
Asterodon pedicellaris Perrier, 1891, p. 135, pl. 8, figs. 1a, 1b.
Odontaster grayi Bell, *Proc. Zool. Soc. Lond.*, 1893, p. 261.—Ludwig, 1905, p. 48, pl. 5, figs. 6-9.—Fisher, 1911, pp. 154, 158.
Odontaster pedicellaris Bell, 1893, p. 262.
Gnathaster pedicellaris Perrier, 1894, pp. 2, 244.—Verrill, 1899, p. 205.
Odontaster meridionalis Leipoldt, 1895, p. 620, pl. 31, fig. 8f, pl. 32, fig. 8a-e, g.—Meissner, 1896, p. 93.
Odontaster penicillatus Meissner, *Zool. Anzeiger*, XXI, 1898, p. 394.—Ludwig, 1905, p. 46, pl. 5, figs. 4, 5.
Gnathaster penicillatus Koehler, 1920, p. 194.
Peridontaster grayi Koehler, 1920, p. 194, pl. 39, figs. 5, 6.—1923, p. 86, pl. 11, figs. 1-4; pl. 12, figs. 9, 10.
- St. 652. Burdwood Bank, 169-171 m., 1 specimen.
 All the following stations 'William Scoresby'.
73. Falkland Islands, 51° 01' S, 58° 54' W, 121 m., fine dark sand, 1 f. *penicillatus*.
 81. 8 miles north-west of North Island, West Falkland Island, 81-82 m., sand, 4 f. *penicillatus*, 1 f. *grayi*.
 83. 14 miles south-west of George Island, East Falkland Island, 137-129 m., fine green sand and shell, 17 f. *grayi*.
 84. 7½ miles south-west of Sea Lion Island, East Falkland Island, 75-74 m., shells and stones, 4 f. *penicillatus*.
 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., and shells, 6 f. *penicillatus*, 2 f. *grayi*.
 86. Falkland Islands, 53° 53' 30" S, 60° 34' 30" W, 151-147 m., shell and stones, 16 f. *grayi*, 4 intergrades.
 93. West Falkland Island, 51° 51' S, 61° 30' W, 133-130 m., grey sand, 1 f. *grayi*, 1 intergrade.
 97. Falkland Islands, 49° 00' 30" S, 61° 58' W, 146-145 m., 1 intergrade.
 98. Falkland Islands, 49° 54' 15" S, 60° 35' 30" W, 171-173 m., 1 f. *penicillatus*.
 99. Falkland Islands, 49° 42' S, 59° 14' 30" W, 251-255 m., fine dark sand, 2 f. *grayi*.
 225. Falkland Islands, 50° 20' S, 62° 30' W, 162-161 m., green sand, shells, pebbles, 3 f. *grayi*.
 244. Falkland Islands, 52° S, 62° 42' W, 253-247 m., sand and mud, 1 intergrade.
 246. Falkland Islands, 52° 25' S, 61° W, 267-208 m., coarse green sand and pebbles, 3 f. *grayi*.
 248. Falkland Islands, 52° 40' S, 58° 30' W, 210-242 m., fine green sand, pebbles, shells, 1 f. *penicillatus*, 1 intergrade.
 756. Falkland Islands, 50° 54' 39" S, 59° 58' W, 118-104 m., 1 f. *penicillatus*.
 765. Off Cape Dos Bahias 45° 07' S, 60° 28¼' W, 113-118 m., 1 f. *grayi*.
 776. Off Golfo San Jorge, 46° 18½' S, 65° 02½' W, 107-99 m., 1 f. *penicillatus*.
 804A. Falkland Plateau, 50° 22¾' S, 62° 49' W, 150-143 m., 1 f. *grayi*.
 804B. Near 804A, 143-150 m., 1 f. *grayi*.
 805. Falkland Plateau, 50° 10¼' S, 63° 29' W, 148 m., 1 f. *penicillatus*.
 824. Falkland Islands, 52° 29¼' S, 58° 27¼' W, 146-137 m., 4 f. *grayi*.
 825. Falkland Islands, 50° 50' S, 57° 15' W, 135 m., 3 f. *grayi*.
 841. Falkland Islands, 54° 11¾' S, 60° 21½' W, 109-120 m., 1 f. *grayi*.
 848. Falkland Plateau, 50° 37½' S, 66° 24' W, 115-117 m., 1 f. *penicillatus*.
 871. 53° 16' S, 64° 12' W, 336-341 m., 1 f. *penicillatus*, 1 f. *grayi*.

As detailed under "Remarks", *Odontaster penicillatus* appears to be a composite of several formae. The problem is complicated by the absence of figures of Philippi's type specimen whereby the type form may be identified. In the absence of this information, the type form is assumed to be that described and figured by Sladen as *Gnathaster pilulatus*. As a matter of fact it may well be one of three others analysed in the sub-joined key. Similarly, the type form of *Odontaster grayi* is assumed to be that with narrower superomarginals, as figured by Koehler, 1912, pl. 11, figs. 1, 2.

The following synopsis may be of aid in distinguishing the principal varieties, though this will not be easy without an extensive series of specimens for comparison.

- a*¹. Forma *penicillatus*. Form stellate, the breadth of ray at base equal to or less than the length measured along side; marginal plates 11–21 according to size of specimen; see "Remarks".
- b*¹. Central spinelets of paxillae conspicuously larger than marginal spinelets; paxillae distinctly spaced.
- c*¹. Superomarginal plates narrow (Sladen's figure of *pilulatus*). St. WS 84.
- c*². Superomarginal plates patently heavier and broader than in Sladen's figure of *pilulatus*. St. WS 776.
- b*². Central spinelets of paxillae not conspicuously larger than median spinelets, usually slender; paxillae not spaced.
- c*¹. Superomarginal plates slightly narrower to slightly broader than in Sladen's figure of *pilulatus*; breadth of proximal plates equal to length of $1\frac{1}{4}$ – $1\frac{3}{4}$ plates. St. WS 98, WS 756A.
- c*². Superomarginal plates broader and encroaching more upon paxillar area; breadth equal to length of 2– $2\frac{1}{4}$ plates. St. WS 848. Here also would go 8 specimens with broad, rather coarsely granulate, superomarginals; form stellate; superomarginals 13–15. They are more stellate than the general run of *grayi*, yet appear more closely allied to that form on account of the low number of marginals. The body form is that of *penicillatus*. In the register of specimens they are entered as "intergrades".
- a*². Forma *grayi*. Form pentagonal to stellate-pentagonal; rays broader at base than length along the side; marginal plates upward of 17; see "Remarks".
- b*¹. Superomarginal plates narrow (Koehler, 1912, pl. 11, fig. 2) to medium broad. These intergrade with *b*²; usually but not invariably larger specimens. St. WS 83, WS 86.
- b*². Superomarginal plates broad (Koehler, 1912, pl. 12, fig. 9).
- c*¹. Superomarginal and to a less extent paxillar spinelets granuliform in appearance; actinal spinelets coarser; specimens usually small, although the largest specimen of *f. grayi* (R 42 mm., St. WS 765) falls here.
- c*². Superomarginal spinelets slender, close-set three times as long as thick; paxillae small, widely spaced, with slender delicate spinelets; actinal spinelets long and slender. One specimen, arcuately stellate-pentagonal, R 42 mm., 15 superomarginals, St. WS 825. This specimen has 3 teeth to each mouth angle and falls in Koehler's *Epidontaster* but appears to be a variant of forma *grayi*.

REMARKS. The extensive series of specimens has revealed a very considerable range of variation. Some of these specimens satisfactorily bridge the gap supposed to exist between *Odontaster penicillatus* Philippi (*O. pilulatus* Sladen) and *O. grayi* Bell. In the species known as *grayi* the body shape ranges from pentagonal, usually slightly to decidedly "arcuate" (Koehler, XI, 2¹), to broadly stellato-pentagonal, there being,

¹ These references are to Koehler, 1912, pls. 11 and 12; Koehler, 1920, pl. 39; Sladen, 1889, pl. 57.

sometimes an angle instead of a curve at the interradial plate (Koehler, XII, 9 and 10). The superomarginal plates run as high as 17 and are conspicuously broad, or only slightly broader than long. The best figure of *penicillatus* is that of Sladen (LVII, 5) in which the shape is broadly stellate and the superomarginals rather narrow. Ludwig's (1905, pl. 5, fig. 4) figure of *penicillatus* is of a very young specimen (R 4 mm.) and useless for estimating the appearance of the adult. His figures of *grayi* (pl. 5, figs. 6-9) represent the two varieties illustrated by Koehler, but at a younger stage.

There are other major variations not illustrated. On the assumption that *grayi* is represented by the pentagonal specimens with fewer superomarginals, and *penicillatus* by examples of a stellate shape with more numerous superomarginals, the following analytical table was made of all except very young examples. The columns are to be read from top to bottom. The specimens are arranged in columns A-G in groups according to the number of superomarginals to a ray (excluding interradial plate). The third, fourth, fifth transverse columns attempt to differentiate form of body. Stellato-pentagonal indicates that there is a broad angle at the interradius as in Koehler's fig. XI, 9, while the side of the ray is fairly straight. The breadth of the ray at interradius must be *greater* than its length measured along the side. In stellate specimens (transverse column 5) the two dimensions are equal or the length is the greater (Sladen, LVII, 5).

Column ...	A	B	C	D	E	F	G
1. No. of superomarginal plates	10	11-12	13	14	15	16-17	20-21
2. Range in length of R in mm.	10-22	13-36	14-49	24-38	25-42	24-46	42-50
3. No. of specimens pentagonal or arcuate pentagonal	8	13	5	2	0	0	0
4. No. of specimens stellato-pentagonal	2	7	6 ³	1	5 ⁶	3 ⁷	0
5. No. of specimens stellate	0	3 ¹	2	7 ¹	2	6	2
6. No. with broad marginals	9	16	6	4 ⁵	5	5 ⁸	1 ¹⁰
7. No. with narrow or medium superomarginals	1	7 ²	7	6	2	4 ⁹	1 ¹¹
Total no.	10	23	13	10	7	9	2

¹ Three young *penicillatus*, R 13-14 mm., Sts. WS 81, 871.

² Largest arcuate pentagonal, R 23 mm., St. WS 85; 3 forma *penicillatus*, 4 f. *grayi*.

³ See notes; contains intermediate forms.

⁴ Four forma *penicillatus* and 3 broad-margined intergrades or stellate f. *grayi*.

⁵ One forma *grayi* and 2 intergrades or stellate f. *grayi*.

⁶ None of these is typical *grayi*; 1 (St. WS 248) is the heavy margined substellate form of *grayi*. The largest, R 42 mm., has 3 teeth.

⁷ Sts. WS 225, 248; not typical *grayi*.

⁸ Includes the 3 not typical *grayi*; 1 forma *penicillatus*, 1 intermediate.

⁹ Three similar to *pilulatus* of Sladen; 1 aberrant.

¹⁰ St. WS 848, R 50 mm., r 25 mm., R = 2r, forma *penicillatus*.

¹¹ St. WS 98, R 42 mm., r 22 mm.; superomarginals about as broad as in Sladen's figure of *pilulatus*.

With exception of 6 specimens in 4C there is no great difficulty in assigning to forma *grayi* all specimens in columns 3 and 4 and A-F. These range in size from R 10 to R 46 mm., and have 10-17 superomarginal plates. These specimens include the 2 (intergrading) subformae illustrated by Koehler (XI, 2 and XII, 9, 10), the extremes having narrow and broad superomarginal plates. The contour of these specimens varies from slightly arcuate pentagonal to deeply arcuate pentagonal and stellato-pentagonal, the last having, in all cases, broad superomarginals.

At the other extreme, the 2 specimens in 5G (one with broad, one with medium superomarginals) represent 2 of the 3 recognizable varieties of forma *penicillatus*. The third variety is represented by the type of "*Gnathaster pilulatus*".

Twenty-six remaining specimens are included in column 5, B-F, and in 4C. The 3 small specimens in 5B are young forma *penicillatus*. Two in 5C are just within the category of stellate and are forma *penicillatus*, the central paxillar spinelets being slenderer than in Sladen's figure (LVII, 5); Sts. WS 81, 84.

The 6 specimens in C4 (stellato-pentagonal, with 13 superomarginals) are of 3 sorts. One specimen (St. WS 85, R 19 mm.) is evidently "*pilulatus*" in spite of its few marginals. Two (St. WS 86, R 23 and 27 mm.) have the breadth of ray at base only a trifle greater than length on side. The marginals are broader, the pseudopaxillae more closely placed, and their central spinelets slenderer than in *pilulatus*. These specimens, captured with typical *grayi*, may be considered another forma or intermediates. (Three similar specimens with 14 superomarginals are listed in 5D.) Finally (in 4C) are 3 specimens (Sts. WS 83, 804, 652; R 20-32 mm.) with very heavy marginals and a more stellate contour than Koehler's fig. XII, 9. These may be considered a substellate phase of *grayi*, but are not at all typical of the form.

Of the 7 specimens in 5D (14 superomarginals) 4 are similar to Sladen's *pilulatus* (R 24-34 mm., Sts. WS 73, 84, 85). Three have broad superomarginals and are the same as the intermediates mentioned in the preceding paragraph.

The 2 specimens in 5E are similar to Sladen's *pilulatus* (Sts. WS 81, 85).

The 6 specimens falling in 5F include 4 forms: 3 specimens (R 24-46 mm., Sts. WS 84, 85, 776) are close to Sladen's *pilulatus*, although 2 have somewhat broader superomarginals; 1 (R 32 mm., St. WS 805) has broad superomarginals, slender pseudopaxillar spinelets and is similar to the broader margined example of *penicillatus* in 5G; 1 of the two remaining specimens (R 35 mm., St. WS 756A) has coarse, granuliform spinelets, narrow marginals and large paxillae. It is possibly a variant of *pilulatus*. The other (R 34 mm., St. WS 244) has broad superomarginals with coarse granules and smaller, spaced pseudopaxillae, the short spinelets of which are noticeably less in diameter than the superomarginal granules. It is perhaps another of the problematical intermediates.

Ludwig's idea that *penicillatus* is a deeper water species than *grayi* is not borne out by the present material. Forma *grayi* was taken alone at 10 stations ranging in depth from 109 to 255 m. Forma *penicillatus* alone was taken at 6 stations ranging in depth from 74 to 148 m. They were taken together in hauls ranging in depth from 79 to 82 m.

Forma *penicillatus* and a problematical intergrade were taken as deep as 242 m. There is probably no effective difference in the bathymetrical distribution of the two forms.

Koehler (1920, pp. 191, 195) has based a new genus *Epidontaster* upon *E. pentagonalis* (*loc. cit.* p. 235, pl. 39, figs. 3, 4, 8; pl. 41, figs. 9-11) a new species, which is probably a variant of *Odontaster meridionalis* characterized by having 3 hyaline teeth to each mouth angle. The presence of a smaller hyaline tooth on either side of the median tooth is a normal variation in *Odontaster*. The innermost suboral spine on either side of the median tooth varies considerably in size. When it reaches a certain length it tends to bend away from the mouth angle and in extreme cases to acquire a blunt or pointed hyaline tip. I have noted 3 hyaline teeth in 8 specimens of forma *grayi*, ranging in size from R 14 mm. to R 42 mm., from Sts. WS 83, 84, 86, 246, 824, 825. Numerous others have the lateral inner suboral spine simply enlarged. In forma *penicillatus* 5 specimens from Sts. WS 73, 85, 756A have such enlarged laterals, which can scarcely be called hyaline.

Odontaster crassus Fisher (1911, p. 54, pl. 29, figs. 1-4; pl. 56, fig. 6), coast of California, 43-284 fathoms, resembles a stellate forma *grayi*. The marginal plates are fewer and much more massive than in the heaviest margined specimens of *grayi*. In *crassus* the superomarginals are 7 or 8, while in a comparable specimen of *grayi* they are 10-12. In *crassus* the primary interradiial plates are conspicuously larger than the other abactinal plates which is not the case in *grayi*. In *crassus* the actinal spines are much coarser than in any of the numerous examples of *grayi*.

Genus *Acodontaster* Verrill

Gnathaster pars, Sladen, 1889, p. 285.

Acodontaster Verrill, 1899, p. 204. Type *Gnathaster elongatus* Sladen.

Heuresaster Bell, 1908, p. 8. Type *H. hodgsoni* Bell.

Pseudontaster Koehler, 1912, p. 85. Type *Ps. marginatus* Koehler.

Metadontaster Koehler, 1920, pp. 191, 193. Type *M. waitei* Koehler.

Tridontaster Koehler, 1920, pp. 191, 193. Type *T. laseroni* Koehler.

Odontaster pars, authors.

Acodontaster elongatus (Sladen)

Gnathaster elongatus Sladen, 1889, p. 288, pl. 19, figs. 5, 6; pl. 48, figs. 1-4; pl. 49, figs. 5-10.

Acondontaster elongatus Verrill, 1899, p. 204.

Odontaster cremeus Ludwig, 1903, p. 21.—Koehler, 1912, pp. 81, 198, pl. 3, figs. 1, 3.

Acodontaster cremeus Koehler, 1920, p. 199, pl. 45, figs. 1-4, 7-12; pl. 47, figs. 1, 3, 4; pl. 69, figs. 3, 4.

Pseudontaster stellatus Koehler, 1920, p. 210, pl. 50, figs. 1-7; pl. 70, fig. 2 (forma).

Pseudontaster moderatus Koehler, 1923, p. 89, pl. 11, figs. 6, 7 (Shag Rocks).

St. 123. Off mouth of Cumberland Bay, South Georgia, 230-250 m., grey mud, 1 specimen.

St. 148. Off Cape Saunders, South Georgia, 132-148 m., grey mud and stones, 1 specimen.

St. 149. Mouth of East Cumberland Bay, South Georgia, 220-234 m., mud, 1 specimen (R 104 mm., r 36 mm.).

St. 170. Off Cape Bowles, Clarence Island, 63° 17' 20" S, 59° 48' 15" W, 200 m., mud, stones, gravel, 3 young specimens.

St. 181. Schollaert Channel, Palmer Archipelago, 160-330 m., mud and stones, 1 specimen.

St. 1564. Marion Island, 46° 36.5' S, 38° 02.3' E, 108-113 m., 1 specimen.

The largest specimen, St. 123, has R 95 mm., r 34 mm., br 40 mm. In shape it is intermediate between Sladen's figs. 1 and 2, pl. 48, and considerably larger than fig. 1 which has R 66 mm. The specimen from St. 181 has R 70 mm., r 27 mm., br 28-29 mm., and is like fig. 1 except that the abactinal surface is much inflated and the pseudopaxillae more widely spaced. The example from Marion Island (R 49 mm., r 20 mm.) is closely similar to Sladen's fig. 3, pl. 48.

It is difficult to ascertain whether *Acodontaster cremeus* Koehler is Ludwig's species, for the latter was based upon an obviously immature and inadequate specimen (R 18.5 mm.) collected by the 'Belgica' in 450 m., 71° 18' S and 88° 02' W. It is figured by Koehler, 1912, pl. 3, figs. 1 and 3, and 1920, pl. 47, fig. 1.

Koehler's *cremeus*, ranging in size from R 14 to 23 mm., is probably the young or a depauperate form of *elongatus*. In his description of *Acodontaster granuliferus*, Koehler emphasizes its similarity to *cremeus*. Now, as detailed below, *granuliferus* seems to be one of the manifestations of a race of *elongatus* which lives on the Falkland Plateau. The similarity of *cremeus* and *granuliferus* is explicable on the assumption that they are corresponding formae of two races of *elongatus*.

Pseudontaster stellatus Koehler from 64° 32' S, 97° 20' E, 110 fathoms, was collected in the same haul as one of the specimens of *Acodontaster cremeus*. The species is based upon a single specimen having R 56 mm. The description of the species is therefore only a description of a specimen, which I believe to be the adult of Koehler's *cremeus*, and a form of *elongatus* with slightly narrower than typical marginal plates and somewhat shorter rays. The importance which Koehler places upon the inflation of the disk is difficult to explain since such variations are of no greater significance than a full stomach, swollen gonads, or an artefact of preservation. For instance, it may be produced by immersing a living specimen in fresh water. The Discovery specimen from St. 181 has an inflated disk. Koehler makes no mention of *Acodontaster elongatus* in his description of *stellatus*, since he was convinced that *Pseudontaster* constituted a natural group. Therefore the type of *Acodontaster* was naturally not in competition with *stellatus*.

The type of *Acodontaster capitatus* (Koehler), having R 20 mm., was taken in 254 m. near Adelaide Island (67° 43' S, 70° 45' 42'' W), while 6 other specimens were dredged in 354 and 318 fathoms, at 66° 50' S, 142° 6' E and at 66° 55' S, 145° 21' E (off Adélie Land). The largest of these has R 55 mm., r 16 mm. It is rather obviously near *A. elongatus*, the principal differences being that *capitatus* has slightly slenderer and longer rays, narrower superomarginal plates, and coarser granules than the typical form. It is probably a high antarctic forma of *elongatus*. See Koehler, 1912, p. 82, pl. 6, figs. 5, 8, 9, 11; 1920, p. 195, pl. 44, figs. 1-10; pl. 45, figs. 5, 6.

TYPE LOCALITY. Not indicated by Sladen. Probably off Cumberland Bay, Kerguelen Island, 127 fathoms, greenish volcanic mud.

DISTRIBUTION. Circumpolar, Antarctic, north to Kerguelen, Heard, Marion Islands, and South Georgia.

Acodontaster elongatus granuliferus (Koehler)
(Plate I, figs. 1-6)

Asterodon Grayi, Perrier, 1891, p. 138.

Odontaster granuliferus Koehler, 1912, p. 77, pl. 6, figs. 7, 10.

Odontaster propinquus A. H. Clark, 1917, p. 7.

Acodontaster granuliferus Koehler, 1920, p. 192.

Odontaster glaber Barattini, 1938, p. 22.

DIAGNOSIS. Differing from typical *elongatus* in having shorter rays, broader disk, fewer marginal plates, the superomarginals sometimes thick, broad, and convex. Form stellate to arcuate stellato-pentagonal.

In the following list of localities *c* and *g* after the number of specimens signifies forma *ceramoideus* and forma *granuliferus*.

St. 652. Burwood Bank, 171-169 m., 1 *c*.

St. WS 80. Falkland Islands, 50° 57' S, 63° 37' 30" W, 152-156 m., fine dark sand, 2 *g*.

St. WS 81. 8 miles N 11° W of North Island, West Falkland Island, 81-82 m., sand, 1 *g*.

St. WS 83. 14 miles S 64° W of George Island, East Falkland Island, 137-129 m., fine green sand and shell, 2 *c*, 1 intergrade.

St. WS 84. 7½ miles S 9° W of Sea Lion Island, East Falkland Island, 75-74 m., shells and stones, 1 *g*.

St. WS 85. Falkland Islands, 52° 09' S, 58° 18' W, 79 m., sand and shells, 2 *g*.

St. WS 93. West Falkland Island, 51° 51' S, 61° 30' W, 133-130 m., fine dark sand and stones, 2 *g*, 2 *c*.

St. WS 98. 49° 54' 15" S, 60° 35' 30" W, 171 m., 2 *g*.

St. WS 246. Falkland Islands, 52° 25' S, 61° 00' W, 267-208 m., coarse green sand and pebbles,

1 *c*.

St. WS 248. Falkland Islands, 52° 40' S, 58° 30' W, 210-242 m., fine green sand, pebbles, 2 *c*.

St. WS 793. 45° 53' S, 61° 35' W, 108-111 m., 1 *c*.

St. WS 796B. 47° 53½' S, 63° 32½' W, 108-112 m., 1 *g*.

St. WS 799A. 48° 04½' S, 62° 48' 07" W, 141-137 m., 1 *c*.

St. WS 804. 50° 22¾' S, 62° 49' W, 150-143 m., 1 *g*.

St. WS 807. 49° 50½' S, 65° 03' W, 125-126 m., 1 *c*.

St. WS 815. 51° 51¾' S, 65° 44' W, 132-162 m., 1 *g*.

St. WS 823. 52° 14½' S, 60° 01' W, 80-95 m., 1 *g*.

St. WS 824. 52° 29¼' S, 53° 27¼' W, 146-137 m., 1 *g*.

St. WS 825. 50° 50' S, 57° 15¼' W, 135 m., 1 *g*, 1 *c*.

St. WS 871. 53° 16' S, 64° 12' W, 336-841 m., 1 *g*.

Acodontaster elongatus, in a fairly typical form, ranges to South Georgia, but on the Falkland Plateau is represented by a race which occurs in two formae. The extremes of variation might well be considered to represent distinct species if they were not connected by numerous intergrading specimens. This variation closely parallels that noted under *O. penicillatus*, in which occurs the same transition from a stellate form with narrower, more numerous marginals (e.g. *Odontaster penicillatus* forma *penicillatus*) to one arcuately pentagonal with short rays and broader, convex, fewer marginal plates (e.g. forma *grayi*).

Koehler details the history of the type of his *granuliferus*, which was identified by Perrier with Bell's *Calliderma grayi*, and which is now in the Museum d'Histoire Naturelle. It is clearly the form designated below as forma *granuliferus* and is nearest typical *elongatus*. In the extreme form, such as the type illustrated by Koehler, the granular abactinal surface passes without any very perceptible change to that of the superomarginals which form a rounded bevel to the margin and are not thick when viewed from the side. The abactinal plates have practically no tabulum—only a convex surface covered by round-topped to subtruncate, crowded, 4- or 5-sided granules (e.g. specimens A, B, C of table). Then the superomarginals become more convex, are generally broader than in A, B and C, and the margin of ray is thicker (D, E, F of table). These specimens have 21 or 22 superomarginals in contrast to 26 in A and B (C is a smaller specimen). A to F have been grouped under forma *granuliferus*.

Then with no hiatus and still with broad superomarginals, the rays gradually shorten and the marginals become fewer (G to K of table). The large specimen G with R 59 mm. has 19 superomarginals while B, with R 55 mm., has 26. Specimen K is the most extreme, with 13 broad convex superomarginals. This is the type of forma *ceramoideus*. A comparable specimen of forma *granuliferus* has 20 superomarginals, about half as wide.

Specimen	St. WS	R mm.	r mm.	Superomarginal plates
A	81	69	32	26
B	823	55	25	26
C	85	39	18	20
D	804	54	27	21, 22
E	796B	52	27	22
F	825	57	27	22
G	799A	59	34	19
H	83	42	24	16
I	248	36	21	15
J	652	37	23	15
K	246	33.5	20	13

The photographic figures, in connection with two of the type (Koehler, 1912), must suffice to elucidate the two formae which are here formally noticed in order to emphasize the interesting parallel with *Odontaster penicillatus*.

Forma *granuliferus* Koehler (Plate I, figs. 1, 2).

DIAGNOSIS. Near *elongatus* but with shorter rays, broader disk, fewer and shorter marginal plates; superomarginal plates wider than long with plane abactinal surface, the series forming a rounded bevel to margin of body, or else slightly convex, forming a convex border; form stellate.

Odontaster propinquus Clark belongs to this forma. The type, which I have examined, was taken at Albatross St. 2771, 51° 34' N, 68° W, 50.5 fathoms, grey sand, bottom temperature, 49.4 F.

Forma *ceramoideus* nov. (Plate I, figs. 3, 5, 6).

DIAGNOSIS. Differing from extreme examples of forma *granuliferus* in the arcuate, stellate-pentagonal shape, and in having fewer, generally broader superomarginal plates, which are always more or less convex and constitute, with the similar inferomarginals, a thick frame enclosing the body.

Type St WS 246.

REMARKS. The smallest specimen of forma *granuliferus* has R 12.5 mm. and about the same form as the adult. It would probably be difficult to distinguish from the young of typical *elongatus*. There are 13 superomarginals, the same as in specimen K having R 33.5 mm. The smallest specimen of *ceramoideus* has R 8.5 mm., 8 superomarginals and a stellato-pentagonal form. It was taken at St. WS 825 along with specimen F, which is something of an intergrade as regards the fewer, thick marginals (but is stellate in form).

Forma *ceramoideus* is easy to confuse with *O. penicillatus* forma *grayi* with which it is sometimes associated. In *ceramoideus* (and *granuliferus*) the actinal spinelets of the oral angles are gradually transformed into polygonal *granules* toward the inferomarginal plates so that the actinal plates, for some distance back from the inferomarginals, are armed with granules similar to those of the inferomarginals. In *grayi* all the actinal plates are spinulose, and the inferomarginal armature is spinulose rather than granulose; the abactinal plates are distinctly tabulate and are, in fact, low paxillae.

TYPE LOCALITY OF *ACODONTASTER ELONGATUS GRANULIFERUS*. 53° 13' S, 68° 31' W (east coast of Tierra del Fuego), 97 m. (Mission Scientifique du Cap Horn, 1882-3).

DISTRIBUTION. Falkland Plateau; Cape region; north to Uruguay where *A. glaber* (Barattini) may constitute a recognizable race.

Acodontaster conspicuus (Koehler)

Pseudontaster conspicuus Koehler, 1920, p. 202, pl. 42, figs. 1-7; pl. 43, figs. 1-10; pl. 70, fig. 1.—1923, p. 88, pl. 13, figs. 4-6.

Acodontaster elongatus var. *abbreviatus* Koehler, 1923, p. 81, pl. 10, figs. 1-3 (South Georgia, 24-52 m.).

St. 42. Off mouth of Cumberland Bay, South Georgia, 120-204 m., 2 specimens.

St. 123. Off mouth of Cumberland Bay, South Georgia, 230-250 m., grey mud, 1 specimen.

St. 148. Off Cape Saunders, South Georgia, 132-148 m., grey mud and stones, 1 specimen.

St. 149. Mouth of East Cumberland Bay, South Georgia, 200-234 m., mud, 1 specimen, R 70 mm., r 30 mm.

St. WS 865. 50° 03' S, 64° 14' W, 126 m., 1 specimen, R 82 mm., r 36 mm.

This species has been figured and described in detail by Koehler. It is characterized by curious pedicellariae composed of 3 or 4 enlarged, flat-topped granules, which do not protrude beyond the other granules, except on the actinal plates near the oral angle. Here the actinal granules gradually lengthen into spinelets and the valves of the pedicellariae likewise lengthen. They sometimes form a conical fascicle of 3 or 4 pointed thickened spinelets; or retain their characteristic shape, with longer valves (Koehler, 1920, pl. 43, fig. 9).

Acodontaster waitei also has these pedicellariae and so closely resembles *conspicuus* in most respects that the two forms may easily be confused. Whether they are 2 species, or forms of one, will require more material to determine. *A. conspicuus* is characterized by a large unpaired tooth with a well-developed hyaline tip; while in *waitei* the unpaired tooth is inconspicuous, compressed, the hyaline point only slightly or not at all apparent.

It seems to me to be probable that the two specimens (G, H) which Koehler names variety *inarmata* (1920, p. 210, pl. 43, figs. 6, 7) may well be the young of some forma of *A. elongatus*.

Acodontaster elongatus var. *abbreviatus* Koehler, from Cumberland Bay, South Georgia, 24-52 m., was based upon a single immature specimen (R 22 mm.), in which the rays are relatively shorter than in the adult. Pedicellariae characteristic of *A. conspicuus* are present on the abactinal, superomarginal, and inferomarginal plates, while there is a conical fasciculate pedicellaria, composed of 4 spines, at the oral angle of each actinal area. A specimen with R 36 mm. from St. 42 has an identical distribution of the same kinds of pedicellariae, there being 2 or 3 fasciculate pedicellariae near the oral angle. Their valves are about twice as broad as the adjacent spines. As the animal grows the valves of all the pedicellariae increase in breadth more rapidly than do the surrounding granules, so that they are relatively larger in old specimens.

TYPE LOCALITY. St. 1 (Australasian Antarctic Exp.) 66° 50' S, 142° 06' E, 354 fathoms.

DISTRIBUTION. Off Adélie Land, 25-354 fathoms; off Graham Land, 150 m.; South Georgia, 24-250 m. If the specimen from St. WS 865 is correctly labelled, Falkland Plateau is the northern limit.

Acodontaster waitei (Koehler)

Metadontaster waitei Koehler, 1920, p. 219, pl. 46, figs. 1-6; pl. 47, figs. 5, 6; pl. 48, fig. 8; pl. 49, figs. 1-3, 19; pl. 71, figs. 1, 2.

St. 181. Schollaert Channel, Palmer Archipelago, 64° 20' S, 63° 01' W, 160-335 m., mud, 1 specimen (R 75 mm., r 29 mm.).

This is probably a form of *A. conspicuus*, which it closely resembles in all characters except that of the specialized oral spine and in having spinose conical fasciculate pedicellariae on the first few adambulacral plates. The tooth is smaller, and narrower at the base, than in *conspicuus*. It is compressed, and instead of lying close along the median oral suture, stands erect. The tip is covered by the integument or else only a very small hyaline portion protrudes. The actinal pedicellariae are in no wise different from those of *conspicuus*, as may be seen from Koehler's figure (1920, pl. 46, fig. 2); but they are more numerous in our example since the series adjacent to the adambulacral plate extends for a third to half the length of the furrow (10-20 pedicellariae). In addition, smaller pedicellariae occur on the proximal inferomarginal plates (absent in Koehler's specimens) but there are none on the abactinal surface. These inferomarginal pedicellariae are identical in form with those of *conspicuus*.

To make this form the type of a new genus on the strength of its small tooth is to ignore the sum total of the other characters. The highly special pedicellariae in particular are almost signboards to declare the close kinship of *conspicuus* and *waitei*. This is further supported by the skeletal structure and integumentary armature.

Koehler's type was taken in the same haul with *A. conspicuus*.

TYPE LOCALITY. St. 1, Australasian Antarctic Exp., 66° 50' S, 142° 06' E, 354 fathoms.

DISTRIBUTION. Adélie Land, and Antarctic Archipelago, to 354 fathoms. Note: the specimen recorded by Koehler from 110 fathoms off Queen Mary's Land (1920, p. 225, pl. 49, figs. 1-3) is perhaps a definitely distinct forma.

Acodontaster hodgsoni (Bell)

Heuresaster hodgsoni Bell, 1908, p. 8, pl. 3.

Tridontaster laseroni Koehler, 1920, p. 214, pl. 47, figs. 7-10; pl. 48, figs. 1-7; pl. 69, fig. 5.

St. 42. Off mouth of Cumberland Bay, South Georgia, 120-204 m., 1 specimen (R 74 mm., r 31 mm.).

Koehler has described and figured this species in great detail. It is regrettable that his name must be replaced by that of Bell who has furnished a figure of the actinal aspect. Otherwise the species could not be identified by Bell's vague description, which is also misleading, since he refers *Heuresaster* to the Poraniidae!

In addition to the Discovery specimen I have examined a slightly larger one from the British Museum labelled St. 316, Terra Nova, 353-55. Both agree in detail with Koehler's description, even to the actinal fasciculate pedicellariae (Koehler, 1920, p. 217, pl. 47, figs. 7, 9).

Other than having accessory "teeth", this species is an *Acodontaster* with small marginal plates of the type of *A. conspicuus*. In the Discovery specimen there are 2 subequal accessory spines on either side of the median tooth and these have little or no hyaline point. In the Terra Nova example three mouth angles have also this second accessory spine without a hyaline tip, while in the first accessory a little of the hyaline point is exposed.

Now *A. conspicuus* from St. 42 (as well as from Sts. 149 and WS 865) may have 1 or 2 accessory teeth or spines, without a hyaline tip. As *A. hodgsoni* was taken along with this specimen of *A. conspicuus* from St. 42, it was at first believed to be a forma of *conspicuus*. But it lacks the characteristic pedicellariae. An example of *A. elongatus* from St. 181 has 2 (in one case 3) accessory teeth with a short hyaline tip.

The possession of 3 teeth is a normal variation in *Odontaster validus* and *O. penicillatus*. It is apparently of no greater value here, since there may also be 5 teeth to a mouth angle as readily as 3.

TYPE LOCALITY. McMurdo Sound, South Victoria Land, 2 fathoms.

DISTRIBUTION. Circumpolar. Koehler's specimens were taken off Queen Mary Land (92° to 97° E) 60-110 fathoms, and off Adélie Land, 25 fathoms.

Genus *Asterodon* Perrier

Asterodon Perrier, *Comptes rendus*, CVI, 1888, p. 765.—1891, p. 129. Type *A. singularis* (Müller & Troschel).—Verrill, 1899, p. 203.

Asterodon singularis (Müller & Troschel)

Goniodiscus singularis Müller & Troschel, *Arch. für Naturgesch.*, IX, 1843, p. 116.

Asterodon granulatus Perrier, 1891, p. 132, pl. 11, figs. 4a, 4b.

Asterodon singularis Perrier, 1891, p. 134, pl. 13, figs. 3a, 3b.—Ludwig, 1903, p. 19.—1905, p. 40, pl. 5, figs. 1–3.—Kochler, 1923, p. 84.

Odontaster singularis Bell, *Proc. Zool. Soc. Lond.*, 1893, p. 262.—Leipoldt, 1895, p. 614 (list of references).—Meissner, 1896, p. 92, pl. 6, figs. 5, 5a (type), 6.—1904, p. 19.—Clark, 1910, p. 332, pl. 2, fig. 4.

St. WS 583. 53° 39' S, 70° 54½' W (Strait of Magellan), 14–78 m., 1 specimen, forma *granulosus*.

It is evident that there are two intergrading formae, paralleling those found in *Odontaster penicillatus* and *Acodontaster elongatus granuliferus*.

Forma *singularis*.

Form stellate, with well-developed rays. Marginal plates more numerous (upward of 18), not encroaching widely upon the abactinal and actinal surfaces. Granuliform pedicellariae present or absent.

Müller and Troschel's type has been figured by Meissner, 1896, pl. 6, figs. 5, 5a. Other figures are Perrier, 1891, pl. 13, figs. 3a, 3b; Ludwig, 1905, pl. 5, fig. 1; Leipoldt, 1895, pl. 31, fig. 7a–c; Clark 1910, pl. 2, fig. 4.

Forma *granulosus*.

Asterodon granulatus Perrier, 1891, p. 132, pl. 11, figs. 4a, 4b (Punta Arenas).

Form arcuately pentagonal, with short rays, marginals of both series fewer (upward of 12) and heavier, forming a broad margin to body. Pedicellariae present.

Both the specimen figured by Perrier and that by Ludwig (1905, pl. 5, figs. 2, 3) are young. The specimen from St. WS 583 has R 35.5 mm., r 21.5 mm. It is notable for the broad marginals, 12 to a ray (in addition to interradial marginal). The first 2–5 ambulacral plates have 2 furrow spines, the rest 1. The abactinal, marginal, and actinal plates carry (in the aggregate) numerous pedicellariae with 2–4 granuliform valves which do not rise above the general surface of the granules.

If this specimen is compared with the published figures of *singularis*, the supero-marginals appear to be at least twice as broad, while the ray is broader, shorter, and more obtuse.

TYPE LOCALITY. Chile. Type no. 754, Berlin Museum, *vide* Meissner, 1896.

DISTRIBUTION. Coasts of Tierra del Fuego, north along the west coast of South America to 20° S latitude; low tide to 80 m.

Family GONIASTERIDAE Verrill

Genus *Pseudarchaster* Sladen*Pseudarchaster discus* Sladen

Pseudarchaster discus Sladen, 1889, p. 110, pl. 19, figs. 1, 2; pl. 42, figs. 3, 4.

Astrogonium patagonicum Perrier, 1891, p. 125, pl. 13, figs. 2a, 2b (Beagle Canal).

St. WS 781. $50^{\circ} 30' S$, $58^{\circ} 50' W$, 148 m., 1 specimen.

St. WS 782A. $50^{\circ} 29\frac{1}{4}' S$, $58^{\circ} 23\frac{3}{4}' W$, 141-146 m., 1 specimen.

St. WS 805. $50^{\circ} 10\frac{1}{4}' S$, $63^{\circ} 29' W$, 148 m., 2 specimens.

St. WS 850. $51^{\circ} 18\frac{3}{4}' S$, $63^{\circ} 30\frac{1}{4}' W$, 57-166 m., 1 specimen.

The specimens are large compared to the type, R ranging from 55 to 60 mm., whereas the type has R 30 mm. The post-adambulacral fascioles described by Sladen are present. Along the *transverse* margins of the actinal plates adjacent to adambulacrals, the spinelets, which are smaller than those of the rest of surface, bend over the sutural groove and touch similar spinelets of adjacent plate, forming a crude pectinate pedicellaria. These are most apparent or best differentiated near the mouth plates, where each comb has about 7 spinelets. There is an unpaired pedicellaria at outer end of mouth-plates; and a similar co-operation is apparent between the outer marginal adambulacral spinelets and adjacent actinal intermediate spinelets, although these combs are not so regular as the transverse ones.

As in other species of *Pseudarchaster* of which a series is known, specimens may be divided into two groups. In the one the rays are shorter and the marginal plates are shorter and broader than in the other, but there is no significant difference in the number of marginal plates (34-35).

Astrogonium patagonicum Perrier seems to me to be specifically the same as *discus* and to be referable to the slender-rayed variety. On the right side of Perrier's fig. 2b one can see, with a lens, an indication of the pectinate pedicellariae. In his list of sub-Antarctic echinoderms, Koehler (1912, p. 211) lists both *Astrogonium patagonicum* and *Pseudarchaster discus* as peculiar to the Magellan fauna, although he was certainly aware that the generic names are synonymous.

The persistent misuse of *Astrogonium* in France is a curious case of misguided loyalty to Perrier who started the vogue by appropriating a name, which never had any status, for a group of species (*Pseudarchaster* and *Aphroditaster*) none of which was listed in the original description of *Astrogonium* (Müller & Troschel, 1842, p. 52) for the obvious reason that none was known in 1842. Yet in 1894, five years after *Pseudarchaster* was published with figures, Perrier substituted *Astrogonium*.

Müller and Troschel in their *System der Asteriden*, 1842, established *Astrogonium*, without type, for 4 described genera, now in current use, namely *Hippasteria*, *Goniaster*, *Pentagonaster*, *Tosia*. If one adopts the first species as type, then *Astrogonium* was a synonym of *Hippasteria* Gray, 1840; if the oldest generic name included in the group, then *Astrogonium* is a synonym of *Goniaster* Agassiz, 1835. As stated above, no species of

Pseudarchaster was known at this time. Hence it would seem fantastic even to consider *Astrogonium* in connection with *Pseudarchaster*. Perrier by the same logic transferred Gray's *Dorigona* to Sladen's *Nymphaster*; yet no species of *Nymphaster* was included in Gray's genus, and none was known until many years after *Dorigona* was described.

Two species obviously related to *discus* are *Ps. pectinifer* Ludwig, Galapagos Islands, 812 fathoms, and *Ps. dissonus* Fisher, Bering Sea to Oregon, 859–1064 fathoms. Both are large species, *dissonus* reaching R 170 mm. In *dissonus* the post-adambulacral fascioles have become true valvate pedicellariae of a definite specialized form (Fisher, 1911, p. 192, pl. 34, figs. 1–3; pl. 57, figs. 7, 7a). In *pectinifer* these pedicellariae are as in *discus*, but more developed on account of the larger size of the specimens. *Ps. pectinifer* lives in a temperature of 38.5° while *dissonus* has a known range of 35.8 to 37.3° F., far colder than the water at moderate depth in the Magellan region where typical *discus* is found.

TYPE LOCALITY. Challenger St. 307, Messier Channel, between the western coast of Chile and Wellington Island, 140 fathoms, blue mud.

DISTRIBUTION. Magellanic and Falkland region, 140–283 m.

Genus *Ceramaster* Verrill

Ceramaster patagonicus (Sladen)

Pentagonaster patagonicus Sladen, 1889, p. 269, pl. 46, figs. 3, 4; pl. 49, figs. 3, 4.

Ceramaster patagonicus Fisher, 1911, p. 214, pl. 37, fig. 4; pl. 38, figs. 1, 2; pl. 60, fig. 3.—Koehler, 1923, p. 94.

St. WS 76. 51° 01' S, 66° 31' 30" W, 110–113 mm., coarse dark sand, 1 specimen.

St. WS 80. 50° 51' S, 63° 37' 30" W, 152–156 m., fine dark sand, 10 specimens.

St. WS 225. 50° 20' S, 62° 30' W, 162 m., 1 specimen.

St. WS 243. 51° 06' S, 64° 30' W, 144–141 m., coarse dark sand, 2 specimens.

St. WS 801. 48° 26¼' S, 61° 28' W, 165 m., 1 specimen.

St. WS 804. 50° 22¾' S, 62° 49' W, 150–143 m., 1 specimen.

St. WS 805. 50° 10¼' S, 63° 29' W, 148 m., 1 specimen.

St. WS 813. 51° 35¼' S, 67° 16¼' W, 106–92 m., 1 specimen.

St. WS 848. 50° 37½' S, 66° 24' W, 115–117 m., 1 specimen.

St. WS 850. 51° 18¾' S, 63° 30¼' W, 1 specimen.

This very widely distributed species has been figured and described by Sladen and the writer. After examining the Discovery collection I am convinced that the specimens from the north Pacific are *patagonicus*. Some of the small differences which I noted between these specimens and Sladen's excellent figures disappear with a series of southern specimens in hand. The latter are about as variable as the north Pacific specimens. The largest example has R 63 mm., r 45 mm.

It is possible that Perrier's *Pentagonaster austrogranularis* (1891, p. 127, pl. 12, figs. 3a, 3b) may prove to be a small *patagonicus*. All specimens of *granularis* attributed to the north Pacific have turned out to be *patagonicus*. Perrier's 2 specimens came from New Year Sound, 340 m., well within the range of *patagonicus*.

TYPE LOCALITY. Challenger St. 313, near the Atlantic entrance to the Strait of Magellan, 55 fathoms, sand; bottom temperature 47·8° F.

DISTRIBUTION. Falkland Plateau, Burdwood Bank; Gulf of California; southern Alaska to southern part of Bering Sea; 55–245 fathoms.

Notioceramus gen.nov.

DIAGNOSIS. Resembling *Peltaster* Verrill in having the entire surface covered with granules and the abactinal plates of radial papular areas without an elevated tabulum; differing from *Peltaster* in having short adambulacral plates with 2 (1–3) coarse furrow spines and a shorter but heavier subambulacral spine, followed by 1 or 2 smaller tubercles; pedicellariae primitive, composed of 3 flattened granules.

Type *Notioceramus anomalus*.

REMARKS. The type species is represented by only one specimen. Its abactinal surface resembles that of *Peltaster micropeltus*¹ (Fisher), but there the resemblance ends, for in *micropeltus* the adambulacral plates are longer than broad, with a furrow series of 5 or 6 small spines (rather like those of *Ceramaster*) and 2 long series of small granules (3 or 4 in first series, 5 or 6 in the outermost). Abactinally there are rather numerous small upright two-jawed spoon-shaped pedicellariae about the size of the granules. The jaws are often curved.

The adambulacral armature of *Peltaster* is of the type of *Ceramaster*, in which there is typically a gradation in length from the furrow spines through 2 or 3 series of successively shorter granules to the actinal granulation. In *Notioceramus* the armature can more appropriately be compared to that of *Cladaster* and *Hippasteria*. In fact, the armature is similar to that of certain plates of *H. falklandica*, at about mid R, even to the form of the subambulacral spines, except that in the latter species unequal granules occupy the transverse and outer margins of the plates.

In *Progoniaster* Döderlein,² in which all the plates are granulated, the adambulacral armature is similar to that of *Peltaster*. The only specimen of *P. atavus* is probably immature.

Notioceramus anomalus sp.nov.

(Fig. D, 1–1e; Plate II, fig. 4; Plate IV, fig. 5)

DIAGNOSIS. General form pentagonal, produced into short slender rays; disk low, scarcely inflated, but rays convex dorsally; margins bevelled and rounded; entire animal covered with rather coarse, close-set granules; abactinal plates rather small, not tabulate, with 6–8 granules on plates of radial series, diminishing as to size, regularity, and number of granules toward margin; marginal plates 17; adambulacrals with 2 (proximally sometimes 3, distally usually 1) coarse furrow spines, a still heavier subambulacral,

¹ *Tosia* (*Ceramaster*) *micropelta* Fisher, 1906a, p. 1054, pl. 21, fig. 2; pl. 26, figs. 4, 4a; 313–800 fathoms, off Bird Island, Hawaiian Islands. This species was later assigned to *Peltaster* (Fisher, 1911, p. 205) but it is not typical, although it has numerous furrow spines and subambulacral granules.

² Döderlein, *Die Asteriden der Liboga-Expedition, Pentagonasteridae*, 1924, p. 61, pl. 17, figs. 3–3c.

and 1 or 2 tubercular granules on outer end of plate. R 35 mm., r 19 mm., br at inter-radius 21–22 mm., at middle of ray 10 mm.

DESCRIPTION. Abactinal plates not tabulate, though the radial and adradial have a convex surface, which gradually flattens on interradial region, where surface of plates is flush with integument—if not distorted by drying. The midradial plates are superficially wider than long, not very regular, nor particularly neat and uniform in size. This series reaches terminal plate. The plates of either adradial series are even less regular, are irregularly oblong or squarish and the series ceases 1–3 superomarginals distant from end of ray. The other plates are quite irregular and do not form well-defined series. Midradial plates with 5–8 coarse, subspherical granules (the larger 0.4–0.5 mm. diameter) those of distal plates often in 2 transverse series; other plates with 3–6 granules, according to distance from margin; primary interradials and central with about 15 or 16 granules. Madreporic plate 2.5 mm. in diameter, its inner margin $\frac{1}{3}$ r from centre of disk.

The abactinal plates are irregular in outline and imbricate as indicated in the figure of the coelomic surface of proximal radial area. The carinal plates are slightly smaller than the adradials of the 2 series at either side. Beyond these 2 series the plates become very rapidly smaller and more closely imbricated as there are no papulae. On the narrow part of the ray the carinals are larger than the adradials and are accompanied at either side by a single series of small papulae. Proximally there are 4 irregular series of small papulae.

The granulation of abactinal surface decreases gradually in size from the radial line to margin of area. Superomarginal and inferomarginal granules successively slightly larger than the peripheral abactinal, while the actinal granules are still larger and more distinctly spaced. A thin skin envelops the granules.

Superomarginal plates 17, generally a little wider than long, forming a slightly rounded bevelled border to abactinal area, as do the inferomarginals to the actinal. These plates are not tabulate but are individually slightly convex. Distally there is no trace of central tubercles on either series.

Adambulacral plates about as wide as length of furrow margin. Furrow spines 2, coarse, compressed, prismatic, 1.5 plates long measured on furrow margin. Back of these is a single, subequal, broad, round-tipped spine often occupying entire length of plate and with its broad side to furrow. Outer margin with 1 or 2 compressed or prismatic tubercles intermediate in size between the large tubercle and actinal granules. The distal plates usually have a transverse series of 3 coarse spines, the median the thickest. The first 2 plates sometimes have 3 furrow spines.

Mouth-plates not convex; with long furrow margin carrying 5 spines like the adambulacral; a curved series of 4 suborals rather like the outermost adambulacral tubercle.

Two 3-valved pedicellariae are present, one on outer part of a first adambulacral plate, the other adjacent to outer end of a second plate (Fig. D, 1*e*). As the jaws are only slightly modified granules, flattened and somewhat excavated on the innerface, the pedicellariae are very primitive.

TYPE LOCALITY. St. 170. Off Cape Bowles, Clarence Island, 342 m., rock, 1 specimen.

Genus *Pergamaster* Koehler

Pergamaster Koehler, 1920, p. 237. Type *P. tessellatus* Koehler.

Koehler has made the curious error of describing the peripheral *granules* of the abactinal and marginal plates as small *plates*. He says, "Les plaques dorsales du disque, qui sont absolument nues, sont plates, assez grandes et sont séparées par *des plaques très petites* ordinairement disposées sur deux rangs. Des plaques semblables et toujours de très petite taille, séparent les plaques marginales dorsales et ventrales successives, et séparent également chaque rangée l'une de l'autre." These, of course, are not secondary plates as the description implies but the flat granules such as are found on the periphery of abactinal, marginal, and sometimes actinal plates of several genera of Goniasteridae, e.g. *Iconaster*, *Astroceramus*, *Lithosoma*, *Plinthaster*, *Calliaster*.

Koehler compares *Pergamaster* with *Plinthaster* but its 2 or 3 coarse furrow spines and subambulacral tubercle are reminiscent of *Astroceramus*. It seems to me that *Lithosoma* and *Iconaster* (especially its subgenus *Glyphodiscus*¹) are also related, but more distantly perhaps than *Astroceramus* and *Plinthaster*. Pedicellariae aid in establishing relationships but these are not present in *Pergamaster*.

Pergamaster incertus (Bell)

(Plate II, figs. 1, 2)

Pentagonaster incertus Bell, 1908, p. 9.

? *Pergamaster tessellatus* Koehler, 1920, p. 238, pl. 49, figs. 5-17.

St. 1872. East of Joinville Island, Antarctic Archipelago, 63° 29.6' S, 54° 03.1' W, 247 m., 1 small specimen.

The specimen measures R 13.5 mm., r 8 mm., br at interradius 8 mm. It differs from the type of *incertus* in having the actinal plates surrounded by only a single series of granules as in the smaller specimen of *synaptorus*. If the latter species shows this variation, probably due to age, it is likely that *incertus* does also. The specimen has been identified as *incertus* because the radial abactinal plates extend to the terminal plate, and the abactinal plates and granules are less plane than in *synaptorus* and thereby resemble more nearly those of *incertus*. Superomarginals 6 or 7, furrow spines 2 or 3; the distal granule of inner subambulacral series enlarged to a clavate tubercle thicker than furrow spines and of about the same length.

Mr D. Dilwyn John had made two photographs of the type of *incertus*, of which R is 26-27 mm., and r 14 mm., and which are reproduced herewith. Bell's vague remarks in lieu of a description, though perhaps technically sufficient to establish the species, are quite valueless for purposes of identification. The photographs show that the furrow spines are generally 2 and that the subambulacral tubercle is essentially as in the small specimen listed above. The actinal interradii areas are completely covered with granules as in the type of *synaptorus*.

¹ Fisher, 1919, p. 306; *G. perierctus* Fisher, *loc. cit.* pl. 79, fig. 4; pl. 81, fig. 3; pl. 83, figs. 2, 3; pl. 93, figs. 1, 1a.

It seems likely that Koehler's *Pergamaster tessellatus* is at best only a form of *incertus*. His 3 specimens were all larger, R being 43, 40 and 35-36 mm. Koehler does not mention the prominent subambulacral tubercle which appears to be absent on the proximal plates but can be seen with a lens on the distal plates in figs. 6 and 8, pl. 49 (Koehler, 1920). In the type of *synaptorus* this tubercle is sporadic on the proximal plates but regularly occurs in the paratype. Koehler's specimens (1920, p. 238, pl. 49, figs. 5-17) were taken at 2 stations: 64° 34' S, 127° 17' E, 1700 fathoms and 64° 32' S, 97° 20' E, 110 fathoms.

TYPE LOCALITY. McMurdo Sound, south-west corner of Ross Sea, about 77° S, 96-120 fathoms.

Pergamaster synaptorus sp.nov.

(Plate II, fig. 3; Plate III, fig. 1)

DIAGNOSIS. Differing from *Pergamaster incertus* (Bell) and *P. tessellatus* Koehler in having the distal 5-7 pairs of superomarginals joined medially, excluding abactinal plates from terminal part of ray. R 45 mm., r 27 mm., br at interradius 28 mm.; paratype measures R 33 mm., r 13.5 mm., br 13.5 mm.

DESCRIPTION. The precise form and arrangement of the abactinal plates can be determined from the figures. The exposed surface of the plate is flat and is in reality a very low tabulum surrounded by a single series of unequal flat granules, flush with the surface. Koehler uses the misleading term "little plates" for the granules. The adradial row of plates extends to the middle of the fourth superomarginal of type (and to middle of third of paratype) while the radial series continues to middle of eighth superomarginal (sixth of paratype). Beyond this point 5-7 superomarginals meet in the midradial line, those of opposite side, but are usually not accurately paired. Papulae inconspicuous, occupying a broad petaloid radial area. Madreporite variable, small to large, situated at mid r.

The marginals are bare except for the peripheral series of elongate or squarish granules flush with surface. The plates of the 2 series sometimes correspond, sometimes do not. Superomarginals 13-14 (11-12 in paratype) block-like, broader than long, and forming a rounded border to ray and disk. The second plate is conspicuously larger than first, and thence they decrease very gradually in size along ray.

The inferomarginals form a more abruptly rounded margin and, from the fourth plate on, are in contact with adambulacrals (fifth in paratype).

The actinal plates of type are completely covered with coarse close-set polygonal granules, but those of paratype have only a peripheral series leaving the centre of plate bare. There are 3 chevrons of these plates to each interradiation. The series adjacent to adambulacrals extends to proximal border of fourth inferomarginal of type (one-half to one plate farther in paratype).

Adambulacral plates proximally a little broader than long and narrowing on ray proper until the two dimensions are about equal. Furrow spines 2 or 3, subequal, heavy, blunt, sometimes slightly compressed, and about as long as width of plate. Back of these

are 4 or 5 coarse granules in 2 longiseries. The aboral granule of inner series is often enlarged into a tubercle one-half or two-thirds length of furrow spine. In the paratype this tubercle is present on nearly all the plates, is thicker than furrow spines, and increases in length so that on ray proper it is as long as and much heavier than the furrow spines. In the type its occurrence is very irregular.

The combined mouth-plates are lozenge-shaped actinally, the furrow margin being about as long as the first adambulacral suture. Marginal spines 4 or 5, similar to proximal adambulacral furrow spines but a little longer and gradually lengthening to the oral angle where the 2 "teeth" are the longest spines on the body. Each plate normally has one suboral adjacent to distal marginal spine while the outer half of combined plates is covered with low coarse granules.

TYPE LOCALITY. St. 170. Off Cape Bowles, Clarence Island, 342 m., rock, 2 specimens.

REMARKS. This species differs from *P. incertus* as indicated in the diagnosis. In all the specimens of *P. tessellatus* Koehler, of which the largest has R 43 mm., the midradial series of abactinal plates reaches the terminal plate, thereby separating the distal superomarginals; while the adjacent adradials reach the ninth or tenth superomarginals, which is farther than the *radial* series reaches in *P. synaptorus*. In the much smaller type of *incertus* the adradials reach to the sixth superomarginal (11 in all) or to about one-third R from end of ray. In *P. synaptorus* the adradials extend along ray two-fifths R (or to three-fifths R from end of ray).

Genus *Cladaster* Verrill

Cladaster analogus sp.nov.

(Fig. D, 2; Plate IV, figs. 1-3)

DIAGNOSIS. Closely related to *Cladaster validus* Fisher; stellato-pentagonal with short rays, thick disk, block-like marginals and unequal, spaced granulation on surface of plates; madreporite larger than any abactinal plate; pedicellariae very broadly spatulate with flat jaws, arising from a pit on the plate but without a differentiated depression for the opened jaws; superomarginals 11; adambulacrals with 2, sometimes 3, heavy, compressed round-tipped furrow spines; one major subambulacral and a secondary smaller one on outer end of plate independent of the small marginal granules. R 57 mm., r 34 mm., br (interradius) 35-37 mm.

DESCRIPTION. The abactinal plates are fairly regularly arranged on the radial areas in series parallel to the midradial, in which the largest plates are situated about one-third R from the conspicuous subcircular central plate. Across the ray from interradius to interradius and passing the midradial series at about mid R are 13 plates. The radial plates are subcircular to subhexagonal, the others mostly subcircular. They are separated by a shallow furrow covered normally by the close-set, peripheral granules which are superficially 4-sided, round-tipped, convex, and deciduous. The exposed surface really constitutes a very low tabulum and is nearly plane. It normally carries, spaced unequal,

deciduous subspherical granules, the largest of which are slightly larger than the peripheral, the smallest (more round-tipped cylindrical to thimble-form) decidedly smaller than the peripheral. A majority of these granules have been rubbed off the plates. Here and there is a small tongs-shaped pedicellaria arising from a depression of the plate. The jaws are spatulate, constricted at middle, and about 0.5 mm. wide by 0.5 mm. high. The large flat madreporite is one-third r from centre; diameter 5 mm. Papulae very small, apparently about 6, around plates of radial area.

The marginal plates are block-like, wider than long, convex, and form a thick, rounded border. Both series regularly diminish in size distally. Superomarginals 11, the last plate of one series meeting 1 or 2 of opposite side of ray medially. The plates are bordered by squarish granules similar to the abactinal while the surface is covered with very deciduous, slightly spaced, subspherical granules which increase in size to small tubercles in centre of plate, especially toward end of ray. The inferomarginals are similarly provided with granules which are slightly more uniform in size.

A single row of actinal plates extends the length of 5 or 5½ inferomarginals; the next row, 2½ or 3; the third, 2; the fourth, 1½; while the remaining 2 chevrons are in the span of the interradiial pair of plates. The actinal plates are rather ornate with 1-3 central granules; or, on inner 3 series, a central broadly spatulate pedicellaria, with jaws about twice the height and breadth of the abactinal. The peripheral granules are regularly much larger on the side toward margin and end of ray.

The adambulacral armature is essentially that of *Hippasteria*, consisting of 2, sometimes 3, heavy, compressed, round-tipped furrow spines about as long as width of plate. On centre of plate is a much heavier subcylindrical round-tipped tubercle (with a smaller adoral companion on first 4 or 5 plates). Near outer end of plate is a tapered tubercular spine about half as long, or sometimes 2, side by side. The margin of plate (except the furrow) is occupied by prismatic granules like those of adjacent actinals, which elongate into coarse prismatic spinelets toward furrow. I find only one subambulacral spatulate pedicellaria. Marginal oral spines 6, coarse, compressed and prismatic; suborals crowded, about 6 to an oral angle.

TYPE LOCALITY. St. WS 86. Falkland Islands, 53° 53' 30" S, 60° 34' 30" W, 151-147 m., shell and stones, 1 specimen.

REMARKS. This species is very closely related to *C. validus* Fisher¹ from Amukta Pass, Aleutian Islands, 52° 06' N, 171° 45' W, 283 fathoms, rocks, black sand, hydrocorals. The only known specimen of *validus* has R 17 mm., r 10 mm., and is probably young. It differs from *analogus* in minor details such as a definite tumid naked area on the superomarginals. Although most of the superomarginals of *analogus* have lost their granules, the scars are discernible and there appears to be nothing like a specialized area. In *analogus* the madreporite is larger than any abactinal plate; in *validus* it is distinctly smaller than the radials, although this may well be associated with immaturity. In *validus* the pedicellariae are abactinally a trifle larger (relative to size of plate) than in *analogus* and the jaws have more distinctly incurved ends. The actinal pedicellariae of

¹ Fisher, 1911, p. 222, pl. 41, figs. 1, 2.

analogus have broader jaws. Considering the difference in size of the two specimens, the adambulacral armature is remarkably alike. In *validus* the second or outer subambulacral tubercle (distinct from the marginal series of granules) is not developed, although on the margin of plate there are 1 or 2 granules larger than the immediately adjacent actinal granules. In *analogus* these outer marginal granules are subequal to the adjacent actinals.

The disparity in size of the peripheral granules of actinal plates occurs also in *validus*.

In *Cladaster rudis* Verrill¹ the only example has R 25 mm., r 12 mm., and 4 distal superomarginals in contact medially. The pedicellariae have narrower jaws of a different form to those of *validus* and *analogus*. In *rudis* there is no specialized naked area on the superomarginals, the granules being scattered. The dark spots shown in Verrill's fig. 2 (which might be interpreted as specialized areas) I was unable to observe with a strong lens. The adambulacral armature of *rudis* lacks the second subambulacral spine, there being, as in *validus*, 2 enlarged marginal granules just external to the subambulacral spine.

In *C. macrobrachius* Clark² from Cape of Good Hope (R 40 mm., r 16 mm.) the 5 distal pairs of superomarginals meet medially, and in spite of its smaller size most of the adambulacrals have 3 furrow spines, while the subambulacrals are generally in 3 longi-series of 3 spines each, the aboral of the first series and the median of the outer being really spines—the rest scarcely more than granules.

Hippasteria imperialis Goto,³ a large species from 640 m. off Misaki, Japan, is possibly a *Cladaster* but hardly a *Hippasteria*.

Genus *Hippasteria* Gray

Döderlein⁴ has shown that *Hippasteria* is not closely related to *Anthenea*, with which it was formerly associated in a special family by Perrier, but is a typical Goniasterid near to *Calliaster*, while *Anthenea* is an Oreasterid. Verrill⁵ segregated *Hippasteria* from *Anthenea* in 1899 making of it and *Cladaster* a subfamily Hippasteriinae. Döderlein could have strengthened his case by citing *Cladaster*, which is obviously a typical Goniasterid yet very closely related to *Hippasteria*. Likewise, *Hippasteria imperialis* Goto,⁶ possibly a *Cladaster* or else a new genus, bridges completely any hiatus which may have existed between *Hippasteria* and thoroughly typical Goniasteridae. It follows therefore that the subfamily Hippasteriinae is superfluous.

Hippasteria falklandica sp.nov.

(Plate III, fig. 2; Plate IV, fig. 4)

DIAGNOSIS. Resembling *Hippasteria heathi* Fisher of Alaska, but lacking the prominent abactinal and marginal spines of that species and differing in minor details of adambulacral armature and in granulation of marginal plates. Differing from *H. phrygiaua* (and presumably also *H. hyadesi*) in the different form of the abactinal plates

¹ Verrill, 1899, p. 176, pl. 28, figs. 2-2c.

³ Goto, 1914, p. 338, pl. 12, figs. 178-193.

⁵ Verrill, 1899, p. 174.

² Clark, 1923, p. 268, pl. 13, figs. 1, 2.

⁴ Döderlein, 1922, p. 47.

⁶ Goto, 1914, p. 338.

and their indistinctness; in the large number of abactinal and marginal pedicellariae; in the irregularity of the marginal plates, wholly covered with granules and lacking characteristic tubercles. R 129 mm., r 43 mm., R=3r; br 52 mm. (least distorted ray).

DESCRIPTION. Perriers' description of *H. hyadesi* (Straits of Magellan, 326 m.) is limited to a short comparison of the type with *H. phrygiana*.¹ No figures were published and so far as I am aware no second specimen has been taken. Perrier states, in effect, that the only difference between *hyadesi* and *phrygiana* lies in the wider ambulacral furrow of the former. In the adambulacral armature he finds slight differences but some of these are covered by variations of *phrygiana*. I have therefore assumed that the characters of abactinal plates and marginal plates in respect to form, armature, and occurrence of pedicellariae seemed to Perrier to be almost indetical in the two species. As these features are radically different in *H. falklandica* I have considered it safe to use for comparison a specimen of *H. phrygiana* (R 105 mm.) from 75 fathoms off Martha's Vineyard, Massachusetts, which closely resembles Mortensen's figure² of a Skagerrak example.

The following account of *falklandica* is largely in the form of a comparison with *heathi* and *phrygiana*. It is hoped that the photographs may supply information on details omitted or too summarily treated.

Abactinal surface. The outlines of the plates are rather obscure and difficult to distinguish on account of the crowded, unequal granulation, except in the case of numerous oblong-elliptical primary plates. Almost the entire surface of these is occupied by a long, low, bivalved (or trivalved) pedicellaria. On the border of these plates are unequal low granules, very unequally spaced, or no granules at all. Smaller secondary and tertiary plates usually carry a central globose prominent tubercle, occupying most of the surface. Interspersed among these, as may be seen in the photograph, are 3 or 4 sizes of small tubercles and granules none of which clearly outline subcircular or irregular secondary and tertiary plates as in *phrygiana*. In *phrygiana* the subcircular primary plates generally carry a central thimble-shaped tubercle, the length of which seldom exceeds the width of plate (but greatly exceeds it in *H. spinosa* Verrill of the north Pacific). The rest of the surface is bare and periphery is bordered neatly by close-set, small granules. In *falklandica* none of the plates show a bare surface, and therefore greatly resemble *H. heathi* Fisher³ from 206 fathoms, Clarence Straits, Alaska, which I am inclined to regard as a much closer relative than is *phrygiana*. Some of the abactinal plates of *heathi*, however, carry prominent upright tubercular spines like those of *H. spinosa*.

MARGINAL PLATES. These are covered with unequal coarse granules and irregularly placed short subglobose or acorn-shaped tubercles, with often a large bivalved pedicellaria. Superomarginals 22 or 23, longer than wide except toward tip of ray where they are wider than long and where a few plates have a bare surface. They are distinctly smaller than in *phrygiana* and *heathi* and, partly due to granulation, are not sharply differentiated from the abactinals. The (larger) specimen of *phrygiana* has only 16

¹ Perrier, 1891, p. 128.

² Mortensen, 1933, pl. 11, fig. 2.

³ Fisher, 1911, p. 231, pl. 44, figs. 1, 2; pl. 58, figs. 5, 5a; pl. 60, fig. 6.

superomarginals which very gradually decrease in size toward the end of ray, whereas in *falklandica* the terminal 4 or 5 plates increase in size. The plates vary greatly in the number (1-5), size, and position of the tubercles and pedicellariae.

Except at tip of ray, the inferomarginals are distinctly larger than the superomarginals and are irregularly 4- to 6-sided. Owing to the covering of granules and tubercles they are not at all clearly marked off from the actinal plates. The usually 4 or 5 unequal tubercles are very irregularly distributed, while the valves of the large pedicellariae are sometimes subdivided into 2 or 3 to allow for a slight curvature.

The marginals are entirely different from those of *phrygiana*, in which the superomarginals carry 1 or 2 central thimble-shaped tubercles and the inferomarginals, 1-5, and only exceptionally a pedicellaria. In *H. heathi* the marginal spines (usually several to a plate) are much more prominent even than in *phrygiana*, but the proximal superomarginals and nearly all the inferomarginals carry, in addition, a bivalved pedicellaria, as in *falklandica*. Instead of the neat peripheral series of granules of *phrygiana*, *heathi* approaches *falklandica* in having stout unequal conical granules in 1 or 2 interrupted series. But most of the surface is taken up by the stout spines and pedicellariae.

ACTINAL INTERMEDIATE AREAS. Nearly all the plates are occupied by exceptionally long low bivalved pedicellariae (lower and longer than in my specimen of *phrygiana*), and are bordered by a series of very unequal, coarse, often squarish or prismatic granules. Interspersed smaller plates, especially near margin of area, carry 1 or 2 subspherical tubercles slightly smaller than the largest abactinal ones. In *heathi* these tubercles are short thick spines, shorter than the prominent marginal spines.

ADAMBULACRAL ARMATURE. Furrow spines more often 2 than 3, coarse, compressed, round-tipped. Behind these are 3 subambulacral tubercles, the inner shorter but broader than the furrow spines, round-tipped, broad side to furrow; the next is about half as long, but wide, often ovate in shape; the outer or third is usually an enlarged granule of a group which occupies the outer end of plate and extends along either transverse margin part way to inner end of plate. On the first plate (and in one series on the second and third) the subambulacral tubercles are replaced by a large bivalved pedicellaria. Orals 5 or 6, suborals 1 or 2, similar to but heavier than corresponding adambulacrals.

TYPE LOCALITY. St. WS 99. Falkland Islands, 49° 42' S, 59° 14' 30" W, 251-225 m., fine dark sand, 1 specimen.

Family GANERIIDAE Perrier

Genus *Ganeria* Gray

Ganeria Gray, *Proc. Zool. Soc. Lond.*, 1847, part 15, p. 83.

Ganeria falklandica Gray

Ganeria falklandica Gray, *Proc. Zool. Soc. Lond.*, 1847, part 15, p. 83.—Sladen, 1889, p. 383, pl. 60,

figs. 1, 2; pl. 62, figs. 6, 7.—Meissner, *Arch. Naturgesch.*, 1896, p. 94.—Kochler, 1923, p. 71.

Ganeria hahni Perrier, 1891, p. 118, pl. 11, figs. 3*a*, 3*b*.—Kochler, 1923, p. 72, pl. 9, figs. 3, 4.

Ganeria robusta Perrier, 1891, p. 119, pl. 11, figs. 1*a*, 1*b*.

Ganeria papillosa Perrier, 1891, p. 121, pl. 12, figs. 1*a*, 1*b*.

St. 55. Entrance to Port Stanley, East Falkland Island, 10–16 m., 1 specimen.

St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shell, 1 forma *falklandica*, 1 forma *hahni*.

St. WS 92. Between Falkland Islands and Strait of Magellan, 51° 58' 30" S, 65° 01' W, 145–143 m., 1 specimen, intermediate between forma *falklandica* and forma *hahni*.

St. WS 776. South-east of Cape Tres Puntas, Argentina, 47° 49' 37" S, 63° 42½' W, 106–113 m., 1 specimen.

St. WS 798. Off Cape Tres Puntas, Argentina, 47° 32' S, 65° 02' W, 49–66 m., 1 specimen.

St. WS 807. East of Porto Santa Cruz, Argentina, 49° 50½' S, 65° 03' W, 125–126 m., 1 specimen.

St. WS 847A. East of Porto Santa Cruz, Argentina, 50° 15¾' S, 67° 57' W, 51–56 m., 3 specimens.

St. WS 847B. East of Porto Santa Cruz, Argentina, 50° 18¾' S, 67° 44' W, 56–84 m., 3 specimens.

St. WS 849. Falkland Plateau, 50° 56¾' S, 60° 58' W, 137 m., 1 specimen.

Ganeria robusta Perrier is apparently typical *G. falklandica*, while *G. papillosa*, founded on a single specimen, may well represent an individual variant of forma *falklandica*. *G. hahni* is distinguished particularly by its slender rays, rather than by peculiarities in number and disposition of spines, since the latter characters are repeated in certain broad rayed specimens referable to forma *falklandica*. The type of *G. hahni* is probably *sui generis* rather than the representative of a natural forma, although I have used the name in the record of specimens.

G. falklandica is decidedly variable but the amplitude seems to be less than in *Cycethra verrucosa*. Among the specimens of the latter from St. 55 is a curious variant discussed in connection with examples believed to represent Perrier's *Lebrunaster*. This specimen has the proportions of forma *hahni*, the rays being narrow. The actinal surface is clearly that of *Ganeria*. The marginal plates are small; the tabulae are well spaced one from another, and carry 7 or 8 spines in the equivalent of 2 series after the manner of some variants of *Ganeria*. Some of the proximal marginals are more paxilliform and not very different from those of *Cycethra*, having very small marginals. But the abactinal skeleton is more like that of *Cycethra* than *Ganeria*. The surface is uniformly covered with spaced, small, fasciculate groups consisting of 3 or 4 cylindrical, blunt, upright spinelets. One may safely say the animal is rather more than half *Ganeria*.

TYPE LOCALITY. Falkland Islands.

DISTRIBUTION. Falkland Plateau and the region of the Strait of Magellan; shallow water to 137 m.

Genus *Cycethra* Bell

Cycethra Bell, *Proc. Zool. Soc. Lond.*, 1881, p. 96. Type *C. simplex* Bell.

Lebrunaster Perrier, 1891, p. 116. Type *L. paxillosus* Perrier.

Under *Cycethra verrucosa* will be found notes on several aberrant specimens from Sts. 55 and WS 85 which are considered to represent Perrier's *Lebrunaster*, known only by the type specimen. These specimens combine certain characters of both *Cycethra* and *Ganeria* in such an unstable manner as to suggest that they may be hybrids.

Antarctic specimens of *Cycethra verrucosa* are peculiar and probably constitute a distinct race which shows close similarity to *Perknaster densus* as well as to typical *Perknaster*, such as *P. fuscus*.

Cycethra verrucosa (Philippi)

(Fig. C, 4a-4g)

- Goniodiscus verrucosus* Philippi, *Arch. Naturgesch.*, 1857, p. 130.
- Cycethra simplex* Bell, *Proc. Zool. Soc. Lond.*, 1881, p. 96, pl. 9, figs. 5, 6.—Perrier, 1891, pp. 122, 170 (varieties *elongata*, *media*, *asterina*, *subelectilis*, *calva*, *regularis*, *asteriscus*).—Meissner, 1896, p. 95.—Bell, 1902, p. 215.
- Cycethra electilis* Sladen, 1889, p. 377, pl. 60, figs. 3, 4; pl. 62, figs. 2, 3.
- Cycethra nitida* Sladen, 1889, p. 379, pl. 61, figs. 3, 4; pl. 62, figs. 10, 11.
- Cycethra pinguis* Sladen, 1889, p. 380, pl. 61, figs. 1, 2; pl. 62, figs. 8, 9.
- Lebrunaster paxillosus* Perrier, 1891, p. 116, pl. 9, figs. 4a-4c.
- Cycethra verrucosa* Meissner, *Zool. Anz.*, 1898, p. 394.—1904, p. 14.—Ludwig, 1905, p. 53, pl. 6, figs. 2, 3.—Koehler, 1908, p. 557.—1912, p. 64.—1923, p. 60, pl. 7, figs. 5, 11, 12, 13; pl. 8, figs. 3-9.—Döderlein, 1928, p. 296 (Kerguelen).
- St. 51. Off Eddystone Rock, East Falkland Island, 105-115 m., fine sand, 1 *nitida*, juv.
- St. 55. Entrance to Port Stanley, East Falkland Island, 10-16 m., 1 *electilis*, 3 *Lebrunaster*.
- St. 58. Port Stanley, East Falkland Island, 1-2 m., 1 *electilis*.
- St. WS 83. 14 miles S, 64° W of George Island, East Falkland Island, 137-129 m., fine green sand and shell, 1 *electilis*.
- St. WS 84. 7½ miles S, 9° W of Sea Lion Island, East Falkland Island, 75-74 m., coarse sand, shells and stones, 2 *pinguis*, 2 *electilis*.
- St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shell, 3 *electilis*, 2 *electilis-pinguis*.
- St. WS 86. Falkland Islands, 53° 53' 30" S, 60° 34' 30" W, 151-147 m., sand, shell, stones, 1 *electilis*.
- St. WS 90. 13 miles N, 83° E of Cape Virgin's Light, Argentina, 81-82 m., fine dark sand, 1 *electilis*.
- St. WS 93. West Falkland Island, 133-130 m., grey sand, 2 *pinguis*, 1 *electilis-pinguis*, 1 *nitida*.
- St. WS 211. Falkland Islands, 50° 17' S, 60° 06' W, 174 m., 1 *pinguis*.
- St. WS 246. Falkland Islands, 52° 25' S, 61° W, 267-208 m., coarse green sand, pebbles, 1 *pinguis*.
- St. WS 248. Falkland Islands, 52° 40' S, 58° 30' W, 210-242 m., green sand, pebbles, shells, 2 *pinguis*.
- St. WS 755. 51° 39' S, 57° 39' W, 75 m., 5 *pinguis*, juv.
- St. WS 756A. Falkland Islands, 50° 54' 39" S, 59° 58' W, 118-90 m., 1 *electilis*.
- St. WS 776. Off Cape Tres Puntas, Argentina 46° 18¼' S, 65° 02½' W, 107-99 m., 1 *nitida*.
- St. WS 791. North-east of Cape Tres Puntas, Argentina, 45° 41¼' S, 62° 45' W, 96-101 m., 1 *pinguis*.
- St. WS 796. South-east of Cape Tres Puntas, Argentina, 47° 49' 37" S, 63° 42½' W, 106-113 m., 1 *pinguis*.
- St. WS 797. 47° 45' 18" S, 64° 10' 30" W, 117 m., stones, 1 *pinguis*.
- St. WS 809. East of Santa Cruz, Argentina, 49° 28¼' S, 66° 29' W, 107-104 m., 1 *nitida*.
- St. WS 811B. Off R. Gallegas, Argentina, 51° 24½' S, 67° 53' W, 96-98 m., 2 *nitida*.
- St. WS 836. South-east of Atlantic entrance to Strait of Magellan, 53° 05½' S, 67° 38' W, 64 m., 1 *nitida*.
- St. WS 847A. Off Porto Santa Cruz, Argentina, 50° 15¾' S, 67° 57' W, 51-56 m., 1 *pinguis*, 1 *nitida*.
- St. WS 847B. Off Porto Santa Cruz, Argentina, 56-84 m., 1 *pinguis*.
- St. WS 852. 44° 12' 30" S, 64° 13' W, 84 m., 4 *nitida*.

Antarctic localities

- St. 123. Off mouth of Cumberland Bay, South Georgia, 230-250 m., grey mud; 1 specimen.
 St. 140. Stromness Harbour to Larsen Point, South Georgia, 122-136 m., 1 specimen.
 St. 149. Mouth of Cumberland Bay, South Georgia, 200-234 m., 1 specimen.
 St. 160. Near Shag Rocks, 177 m., grey mud, stones, 1 specimen.
 St. 167. Off Signy Island, South Orkneys, 244-207 m., green mud, 2 specimens.
 St. 170. Off Cape Bowles, Clarence Island, South Shetlands, 342 m., 5 specimens.
 St. MS 68. East Cumberland Bay, South Georgia, 220-247 m., 1 specimen.
 St. MS 71. East Cumberland Bay, South Georgia, 110-60 m., 6 specimens.

REMARKS ON SPECIMENS FROM FALKLAND PLATEAU. Probably no known sea star is more variable than *Cycethra verrucosa*, which is scarcely a species in the accepted sense of the term. Rather it is a complex of a considerable number of intergrading small species and formae, which may be likened to an asymmetrical net. Some of the more conspicuous nodes have received names. But other names apply to single specimens, as in the case of certain variations described by Perrier (1891). We cannot now determine whether these illustrate actual recognizable formae, or are simply "individual variations".

An obstacle to the establishment of named formae is the difficulty of ascertaining recognition characters which hold good for different ages. Practically all signs fail in *Cycethra*. Least stable is the breadth of ray and the size of the disk, though, generally speaking, the narrower the ray the smaller the disk.

The species, or formae, so ably described and illustrated by Sladen, are recognizable in individuals with narrow, medium, and broad rays. There is a very slender-rayed forma *electilis* which may represent a valid forma distinct from *electilis*. Similarly, *nitida* occurs in a broad-rayed form, quite different from Sladen's figure. There are large specimens combining the characters of *pinguis* and *nitida*.

Koehler (1923, p. 61) gives an extended discussion and his figures are a contribution. Yet little real progress will be made until one person can assemble and compare all available material with the type specimens. Koehler has illustrated a slender-rayed forma *nitida* (1923, pl. 7, figs. 5, 11) which is (to the extent of the figures) closely similar to a specimen from St. 55, having R 65, r 18 mm. (R more than 3r). The actinal surface of our specimen is clearly not that of *nitida*, but of *electilis*. The adambulacral armature is also that of *electilis*. Three other examples from this station are similar to Perrier's *Lebrunmaster paxillosus* (*vide infra*).

Before any final assignment of names can be made it will be necessary to determine the type forma, namely, forma *verrucosa*; whether this includes forma *simplex* Bell; whether *simplex* includes, possibly, forma *electilis* Sladen, or any of the seven new formae described by Perrier in 1891.

In the list of localities I have assigned most of the specimens to the "nearest" of Sladen's three categories—*pinguis*, *electilis*, *nitida*, using adambulacral armature, actinal plates, and abactinal plates, but not proportions which, as stated above, are apparently

not significant. The marginal plates are very variable in size and armature. In forma *electilis* (in its broadest sense) they may be small and similar in form and armature to those of *Ganeria*.

The mystery of *Lebrunaster paxillosus* Perrier appears to be solved by three specimens from St. 55. The type and only known specimen of *Lebrunaster* was collected at Santa Cruz, Argentina, where both *Cycethra* and *Ganeria* occur. Our two largest specimens have R 22 mm., r 9 mm. and have small spaced marginals, like those of *Ganeria*, which carry 2 transverse series or in some cases only 1 series of spinelets. The actinal plates carry 2 or 3 rather short spines, about the size of the marginal spines. Lines run from margin to ambulacral furrow across the actinal area. The abactinal plates are those of *Cycethra* and carry in one specimen 3-6 spinelets in a fasciculate group; but in the other specimen there are only 2 or 3 spinelets; groups well spaced. Two other specimens (St. WS 84, R 26 mm., St. WS 85, R 25 mm.) are also "*Lebrunaster*" but the small marginals are less carinate, more typically *Cycethra*, and the adambulacral armature is like that of Perrier's fig. 4c (1891, pl. 9) which of course is typical of *Cycethra*. The actinal plates carry 3 or 4 short spinelets. The abactinal surface of the specimen from St. WS 85 shows, slightly, the irregularity of the plates of the radial area characteristic of *Ganeria*. But the actinal surface of both specimens is that of *Cycethra*, whereas in the three specimens from St. 55 the actinal surface (but not abactinal) would pass for that of an aberrant *Ganeria* with short spines, especially as the marginal plates are those of *Ganeria*. It was probably the *Ganeria*-like marginal plates which led Perrier at the end of his description of *Lebrunaster paxillosus* to say "voisine de *Ganeria*".

In a fourth specimen, from St. 55 (R 39 mm.), the armature of the adambulacral and actinal plates is that of *Ganeria*. The marginal plates have well-spaced tabula bearing the equivalent of 2 transverse rows of spines (7 or 8 in all) but in a few cases the spinelets form a fasciculate group with one in the centre. The abactinal surface carries small, uniformly spaced, fasciculate groups of 4 or 5 spinelets, without any irregularity of plates on the radial region. It is therefore *Cycethra*. These curious specimens, exhibiting in different degrees the characters of *Ganeria* and *Cycethra*, may be hybrids and suggest a possible explanation of *Lebrunaster*. No typical *Ganeria falklandica* was taken at St. 55; but at St. WS 85 a small specimen of forma *falklandica* and a large one of forma *hahni* were dredged, along with *Cycethra* and that example of "*Lebrunaster*" having a slight distortion of the radial abactinal plates.

These aberrant *Cycethra* (except the specimen from St. 55 which is most *Ganeria*-like) would fall in forma *electilis*. Sladen's figures (1889, pl. 60, figs. 3, 4) of the type are not very different from Perrier's figures of *Lebrunaster*. The marginal armature is spaced.

Whatever the cause of these curious variations, I believe that the type of *Lebrunaster* is an example of them and does not represent a valid genus, or species.

REMARKS ON ANTARCTIC SPECIMENS. There are 7 specimens ranging in size R 25 mm. to R 75 mm. Thirteen young vary from R 6.5 mm. to R 14 mm. A specimen of the first group from East Cumberland Bay (St. MS 68) resembles in a general way a slender-

rayed form from Stanley Harbour, Falkland Islands (St. 55) which is similar to the specimen from the same locality figured by Koehler (1923, pl. 7, fig. 5). This South Georgia specimen has very small marginals.

The other 6 specimens are somewhat peculiar and suggest *Perknaster* (e.g. *P. densus*). The rays are more pointed than in northern forms and although narrow for the genus are characteristically inflated at the base. The marginals are very small and in 2 specimens from St. 170 they cannot be distinguished from the other plates. Yet these specimens are not separable from two taken at St. 167, South Orkneys, in which the marginals, though only slightly larger than adjacent abactinal plates and not larger than plates of radial region, can be distinguished by their contrast to the actinals.

Mr D. Dilwyn John kindly compared one of the specimens from St. 170 with the type of *Perknaster densus*. In *densus*, briefly, the abactinal and lateral surfaces are more densely covered with spine groups, the groups and spines being more closely packed. While in *densus* the actinal spines and groups are close enough together to obscure the arrangement of the plates, this is not true of the South Shetlands specimen where the groups are slightly spaced. The adambulacral armature is essentially the same in both forms. Fundamentally there are 2 furrow spinelets, slightly longer in the Discovery specimens. Mr John points out that the adambulacral spines of *densus* are less uniform than shown by Sladen's figures and description. Proximally the furrow pair form a somewhat oblique series and the distal member is more prominent into the furrow. Then in the middle part of the ray the spines are as in Sladen's figure (1889, pl. 98, fig. 12), but distally there is only *one* furrow spine. This is true of the Discovery specimens. In one specimen from St. 167, the furrow series remains slightly oblique all along the ray, with the slightly larger distal spine more advanced into furrow, until on the outer fifth of ray it, alone, stands on the margin and the other one diagonally behind it, precisely as Mr John has sketched it for *densus*. In *densus* he shows a group of four other subequal spinelets behind the second spine. In the Discovery specimens there may be a group of 3, or all 5 may form a fairly regular transverse series on the plate. In either case the arrangement is that of typical *Perknaster*.

The series of 13 young in the absence of adult specimens would probably be classified as *Perknaster* rather than *Cycethra*. The skeleton is well knit as may be expected in the young of *Perknaster*. As compared to *P. antarcticus* the abactinal spinelets are more numerous (3-8 per plate) and the skin thinner. But the spinelets are very much like those of *Perknaster* as the figures will show. Only the first few plates have two adambulacral furrow spines. Over most of the ray there is but one. Back of this spine there are three or four variously disposed, sometimes making an oblique transverse series of four with a fifth aborad to the third or fourth spine (or the interval between them). This is the typical arrangement in *Perknaster*.

Five of these young and the smallest adult were taken at St. MS 71. A spine of this adult (R 25 mm.) is figured (fig. 4a) for comparison with the abactinal spines of *P. aurorae* from St. MS 71 (figs. 3, 3a). In the latter specimen the abactinal paxillar pedicels are higher than in *Cycethra*.

I believe these young are especially valuable in indicating the close relationship between *Cycethra* and *Perknaster*.

DISTRIBUTION. Characteristic of the Falkland-Magellan fauna; north to 45° 20' S on the Pacific Coast of South America, and to 40° 40' S on the Atlantic coast; to 55° S on the coast of Tierra del Fuego. Low water to 267 m.

Shag Rocks; South Georgia; South Orkneys; South Shetlands; south to Marguerite Bay, 67° 43' S (Koehler, 1912).

Döderlein has recorded a very young specimen from Observation Bay, Kerguelen, near the type locality of *Perknaster densus*.

Genus *Perknaster* Sladen

Perknaster Sladen, 1889, p. 550. Type *P. fuscus* Sladen.

Cribraster Perrier, *Comptes Rendus*, CVI, no. 11, 1888, p. 675 (*nomen nudum*).—1891, p. 104. Type *C. sladeni* Perrier.

Cryaster Koehler, 1906, p. 24. Type *C. antarcticus* Koehler.

Cribellopsis Koehler, 1917, p. 36. Type *C. rallieri* Koehler.

The sea stars of this characteristic Antarctic and sub-Antarctic group are closely allied to *Cycethra* despite the decidedly peculiar and specialized structure of fully grown specimens. With increasing age the body wall thickens, while in varying degree the abactinal skeleton degenerates. In extreme cases the plates and even spinelets disappear. The glandular skin proper is thick, pulpy, and thrown into a myriad of tiny folds and pustules (at least in alcoholic specimens). Immersed in this maze of wrinkles and papillae are numerous small papulae and the small paxillae. In alcoholic specimens the latter are often difficult to distinguish, since their sacculate investment closely resembles the skin pustules and may not rise above the general level.

In 1906 Koehler described the first of the three species upon which he founded the genus *Cryaster* and the family Cryasteridae. In subsequent monographs he further elaborated *Cryaster antarcticus* and described *C. charcoti* and *C. aurorae*, as well as *Perknaster aurantiacus*. Examination of an authentic specimen of *Perknaster fuscus* Sladen, type of the genus, clearly demonstrates that all of Koehler's species of *Cryaster* are typical *Perknaster*, which obviously has priority. It will be necessary to examine the detailed structure of *P. aurantiacus* to determine whether it is distinct from *P. sladeni* (Perrier).

In the Discovery collection is a fairly representative example of the latter species which Perrier described as *Cribraster sladeni*, from a single specimen taken near the Falkland Islands. It is obviously of the same genus as *fuscus* and *antarcticus*, from which it differs *inter alia* in having tall, slender paxillae. It penetrates to high latitudes and is found along with *antarcticus* in the Palmer Archipelago. It cannot therefore be regarded simply as a northern outpost race of *antarcticus*.

Perknaster contains the following nominal species in order of naming:

fuscus Sladen 1889.
densus Sladen 1889.
sladeni (Perrier) 1891.
antarcticus (Koehler) 1906.

charcoti (Koehler) 1912.
aurantiacus Koehler 1912.
aurorae (Koehler) 1920.
georgianus nov.

Cryaster brachyactis (Clark, 1923, p. 293, pl. 11, figs. 1, 2) was dredged in Algoa Bay, South Africa, in 26 and 57 fathoms. It is very different from *Perknaster*. It has shorter and distally broader rays; a definite series of *large inferomarginal plates*, some of which bear a conspicuous spine (shown in Clark's figure); remnants of large abactinal and superomarginal plates which are not tabulate or paxilliform; large actinal plates, and very wide adambulacral plates. The skeleton, other than the ambulacral and adambulacral systems is undergoing degeneration. The body wall is thick and leathery. The species apparently represents a new genus of the Asteropidae (*vide infra*).

In order to differentiate accurately the several nominal forms of *Perknaster* it has been necessary to compare the structure of the spinelets, especially the abactinal, as well as the pedicel of the abactinal plates which carries the spinelets. Whether the small differences are as important as implied in the notes under the different forms only future experience will determine. It has seemed desirable to carry out an analysis of the most tangible or demonstrable details and leave to the future the decision whether we are dealing with a wide-ranging species, having numerous geographical races (each possibly with recognizable formae) or with several species, similarly subdivided.

The difference between *fuscus*, with its low pedicels and broadly clavate spinelets, and *sladeni*, with high pedicels and slender spinelets, seems obvious enough, although superficially the specimens are very similar. The characteristic crowded podia of *aurorae* seems to constitute a fundamental character, especially in conjunction with a spine structure definitely distinguishable from that of *fuscus* and *sladeni*.

It will not be surprising if *P. charcoti* is found to intergrade with *P. fuscus*. It must be recalled that the material of *fuscus* is still meagre and that the species probably reaches a size equivalent to the type of *charcoti*.

Koehler (1917, p. 36) has described *Cribellopsis* based upon *C. rallieri* from Kerguelen (low tide or very shallow water). The figures (pl. 5, figs. 6-10) suggest at once a species allied to *Perknaster charcoti*. The actinal interradial areas are crossed from inferomarginal to adambulacral plates by lines or narrow grooves, and each file of plates, between two lines, corresponds to an adambulacral plate. The creases are doubtless ciliated grooves. These occur in *P. charcoti*. Koehler says: "Les papules que j'ai signalées sur la face dorsale se continuent également sur la face ventrale où elles restent très nombreuses, mais elles n'empiètent pas sur les lignes de séparation des rangées transversales de granules." This is an extraordinary state of affairs: the papulae do not encroach upon the areas of separation between the transverse rows of granules. That is, they are absent from the interval between the lines of plates, where they would be expected to occur. Papulae are difficult to distinguish in some specimens and it is possible that Koehler mistook pustules of skin, which often resemble papulae, for these organs. The matter needs confirmation by examination of the coelomic surface of the actinal interradial areas for *pores*. Of course no *Perknaster* has actinal papulae.

I desire in this connection to render grateful acknowledgments to Mr D. Dilwyn John for having made comparisons of Discovery specimens with the types of *Perknaster fuscus* and *P. densus*, and later for the loan of a cotype of *P. fuscus* for examination.

A study of the actual specimen, it need not be emphasized, provided the only means of attacking a most baffling genus of a family noted for its taxonomic puzzles.

NOTE ON *CRYASTER BRACHYACTIS*¹ CLARK. This species is known from 2 specimens taken in 26 and 57 fathoms, Algoa Bay, South Africa. Dr H. L. Clark has kindly loaned me the paratype.

It is not a *Perknaster* for it has fairly large phanerozonid inferomarginal plates imbedded in the leathery body wall. These may bear, on the lateral face, a considerable group of small spinelets and also sometimes a conspicuous flattened spine, several of which are shown in the figure of the type.

Another peculiarity is the great width of the adambulacral plates as compared to those of *Perknaster*. The proximal plates commonly have 2 furrow spines in longiseries (in one case, 3) and immediately behind these a *larger* subambulacral. The outer two-thirds of plate is covered by skin only. Near the end of ray the spines form a transverse series of 2 or 3 or, rarely, 4; or sometimes only the furrow spine is present. When there is 1 furrow spine its base is broad and occupies all the furrow margin of plate.

Clark states that the "actinal intermediate areas are large, without calcareous plates, spinules, or papulae". In the paratype there are well-marked large actinal plates in irregular chevrons. A series adjacent to adambulacrals extends a little over half length of inferomarginal series, the last plate being subequal to and opposite the sixth inferomarginal. The remaining actinal interradiial triangle is crossed by 3 to 5 irregular arcs of plates, decreasing in size toward the margin and more and more separated as the margin is approached. There are a few scattered small skin-covered spinelets which disintegrate when treated with weak sodium hypochlorite.

The abactinal plates have disappeared except for about a dozen at the tip of ray. These are similar to the actinals, roundish or ovoid, some in contact, some isolated. Also at the tip are a few remnants of the series of large superomarginals. They are covered with very small, mostly degenerated, spinelets and their sacculi, which, after the distal superomarginals are recognized, can be traced to the base of ray. Over most of the ray the superomarginals have disappeared completely.

The numerous, small, slender, tapered or clavate-acute, abactinal spinelets disintegrate when treated with sodium hypochlorite although they show up plainly in a dried specimen.

The madreporite is conspicuous, 3 mm. in diameter, and contiguous to its adcentral border is an equally large primary interradiial plate.

This species, if its skeleton was complete, would have large roundish or slightly lobed abactinal plates, perhaps connected by a few secondaries; large phanerozonid superomarginals and inferomarginals; large actinal plates in chevrons or arcs, and broad but short adambulacrals.

This is not *Perknaster* and probably Mortensen (1933, p. 249) is correct in assigning *Cryaster brachyactis* and the nearly related "*Culcita*" *veneris* to the Asteroipidae. I might add: in the vicinity of *Tylaster*. Since *Cryaster* is strictly synonymous with *Perknaster* it is not available for *brachyactis* which may therefore serve as the type of:

¹ *Cryaster brachyactis* H. L. Clark, 1923, p. 293, pl. 11, figs. 1, 2.—Mortensen, 1933, p. 249, pl. 12, fig. 14.

*Spoladaster*¹ gen.nov. (Asteropidae)

CHARACTERS. Those of the type species.

If I understand correctly Mortensen's remarks concerning *Calcita veneris* Perrier, of St Paul, this would probably belong also in *Spoladaster*. Its actinal interradial areas are covered with fine spines which may occur, also, sporadically on *brachyactis*.

Perknaster fuscus Sladen

(Fig. A, 1-1d, 2-2g, 4; Plate V, fig. 1; Plate VI, fig. 1)

Perknaster fuscus Sladen, 1889, p. 551, pl. 62, fig. 1, pl. 97, figs. 3, 4.

A specimen collected by the Challenger at St. 149D, off Royal Sound, Kerguelen, was forwarded by the authorities of the British Museum, Natural History. It carries the Register Number 90.5.7.870 and measures R 34-35 mm., r 13 mm. It is therefore slightly smaller than the type specimen which was taken at the same station and which measures R 45 mm., r 14 mm. The example under observation may reasonably be considered typical of the species, a fact verified by Mr D. Dilwyn John.

Considering the small size of Sladen's figures of the whole animal and the nature of the subject, the artist was surprisingly successful. The small sacculate spinelets form a coarse nap the exact texture of which is impossible to depict by a small scale line drawing.

In Sladen's fig. 3, pl. 97, the spinelets appear to be rather more closely crowded than in the smaller paratype; but the detailed figure of the abactinal spinelets (pl. 62, fig. 1) gives an excellent idea of these structures when covered by their heavy sheath of skin. The actual spinelets are of course completely obscured by membrane.

The abactinal spinelets are in groups of 3 or 4 on the larger plates, with only 1 or 2 on smaller secondary plates. The fully developed spinelets (fig. A, 1, 1a) are 0.54 or 0.55 mm. long, and the distal half is built up of thin, serrate laminae radiating from the central axial portion in a rather characteristic manner. This gives the spinelets a clavate contour, and when skin-covered they have as a consequence a coarser appearance than in typical *antarcticus* of higher latitudes. The pedicel is distinctly low, as in *antarcticus*, measuring 0.18-0.22 mm. (including thickness of plate), in sharp contrast to *sladeni* in which a comparable pedicel is 0.54 mm. high. In *antarcticus*, also, the spinelet has a different form, lacking the prominent radiating laminae.

After one has compared a series of different forms of *Perknaster*, the inferomarginal plates of *fuscus* seem fairly conspicuous. They are on the actinal face and form a definite border to the actinal intermediate area and may be readily traced along the ray, where, on the outer two-thirds they are adjacent to the adambulacral plates. They carry 5-8 spinelets which do not have so numerous nor such well-developed radiating flanges as the normal abactinals (fig. A, 1c). The form is rather like that of abactinal spinelets from near tip of ray (fig. 1d).

An actinal spinelet from near mouth-plates (fig. 1b) measures 0.65 mm. in length and lacks the radiating flanges of the abactinal spinelets. The plates adjacent to adambula-

¹ Σπολάς, -άδος, a leathern garment.

cials usually have 2 spinelets; the others 3, 2, or 1, with a scattering having 4 or 5, rarely 6 or 7. In this specimen the membrane of the abactinal plates and spinelets is decidedly inflated, perhaps unnaturally so. Fine, rather deep meandering grooves traverse the actinal area from between the inferomarginal plates to the ambulacral furrow, passing between the adambulacrals.

Sladen's small figure gives a misleading idea of the uniformity of the adambulacral armature. The pair of much smaller spinelets which he mentions as occurring on the outer part of the plate really belongs to the first series of actinal plates. They disappear as soon as the inferomarginals come directly in contact with the adambulacral plates. The simplest armature is a transverse series of 3, the furrow spinelet robust, 1.7 mm. long, strongly compressed distally, often truncate, more heavily sheathed at base than at tip. The second and third are decreasingly smaller (e.g. 1.4 and 0.85 mm.) and are rather similar to actinal spines (see figs. 2*d*–2*f* enlarged only $\times 40$). When there are 4 adambulacral spines the fourth usually stands with the third in a longiseries along outer margin of plate or on the aboral margin opposite the interval between the second and third spines. Rather rarely there are 5 spines: an oblique transverse series of 3 and aboral to the outer 2 (the subambulacrals) 2 other similar subambulacrals. It may be stated here that the adambulacral armature of this species conforms absolutely to that of Koehler's *Cryaster*, even to the spatulate furrow spine.

Each mouth-plate has 3 or 4 marginal spines, the innermost the largest, and 3 or 4 smaller suborals closely crowded on the small plates. The marginal spines are generally compressed, but are sometimes subclavate.

The ambulacral furrows are narrow and the tube-feet are not in the least crowded as they are in *Perknaster aurorae*.

The gonads are subspherical, about 3 mm. in diameter. The gonoduct passes upward for a short distance and opens on the dorsal surface near ambitus. It should be recalled that the inferomarginals are actinal in position so that the gonopore is at least a third the distance from inferomarginals to centre of disk.

The inner surface of the abactinal body wall is a muscular sheet as in typical *Cryaster*, but the abactinal plates are rather larger than in comparable specimens of *antarcticus*.

I strongly suspect that *Cribrellopsis rallieri* Koehler, which was collected at Kerguelen, at low tide or in very shallow water, is a close relative of *Perknaster fuscus* despite the reported presence of actinal papulae. Only a comparison of specimens can settle the question.

TYPE LOCALITY. Kerguelen Island (off Royal Sound), 25 fathoms, volcanic mud.

DISTRIBUTION. Typical race known only from region of Kerguelen and Heard Islands, 25–75 fathoms.

Perknaster fuscus antarcticus (Koehler)

(Fig. B, 1–1*a*; Plate VI, fig. 2)

Cryaster antarcticus Koehler, 1906, p. 24, pl. 1, fig. 1; pl. 2, fig. 10.—1911, p. 28, pl. 4, figs. 1, 2.—1912, p. 30, pl. 3, figs. 6, 7.—1920, p. 126, pl. 27, figs. 4, 7, 8–10; pl. 29, fig. 1; pl. 30, figs. 1, 6; pl. 75, fig. 2.

St. 181. Schollaert Channel, Palmer Archipelago, 160–335 m., mud; 2 specimens.

Since the type of *antarcticus* was taken in the same region, these specimens may reasonably be regarded as typical for the size, which is close to that of the specimen of *fuscus*. They measure as follows: R 37 mm., r 12 mm.; R 35 mm., r 10 mm. In general appearance they are very similar to *fuscus* but the groups of spinelets are smaller and more closely placed (hence more numerous), while the spinelets themselves are decidedly more delicate. They measure about 0.5 mm. in length while the pedicel of the abactinal plates is 0.22–0.25 mm. high—about the same as in *fuscus*. The spinelets are slightly clavate, the terminal half being thorny but, as the figure shows, there are no radiating laminae (Fig. B, 1).

These two specimens lack differentiated inferomarginal plates. It is questionable whether much reliance can be placed on this character. The actinal spinelets are less robust than in *fuscus* and the membrane is thinner but the number of spinelets is the same.

The adambulacral spines have very nearly the same arrangement as in *fuscus* but are slenderer. The furrow spine, especially, is less robust; and instead of being chisel-shaped, it gradually tapers to a rather slender extremity. However, Koehler's figure of a large specimen of *antarcticus* from the Palmer Archipelago (1912, pl. 3, fig. 6) indicates very prominent, heavy, furrow spines, as also does his figure (1920, pl. 27, fig. 8) of a medium-sized example from Adélie Land (R 46 mm.). In this, the furrow spine is strongly spatulate. The smaller furrow spines of the Discovery specimens are probably individual variations, unless there exist definite formae with heavier and slenderer spinelets. The gonads are well developed.

Four of the specimens described and figured by Koehler (1920) were taken along the Antarctic coast between 92° E and 166° E, while a fifth (1911) came from Ross Island in the south-western corner of Ross Sea, a region far removed from the type locality, the Antarctic Archipelago. These specimens may ultimately prove to be closer to typical *fuscus* than those from the type locality.

As Koehler has shown, fully grown examples of *antarcticus* undergo a considerable loss of the dorsal skeleton, while the muscular layer of the body wall thickens. Comparison of such specimens with the small type of *fuscus* would be misleading. It is probable that large examples of typical *fuscus* exist in Kerguelen waters, since this region is well within the Antarctic zone. When these are dredged we shall know whether a corresponding reduction of skeleton takes place with advancing age.

TYPE LOCALITY. Probably Palmer Archipelago, near Port Lockroy.

DISTRIBUTION. Probably circumpolar. Records between 92° E and 166° E, 65° S to 77° 32' S (Ross Island). In the American Quadrant, along the Antarctic Archipelago. Bathymetric range, 11–335 m.

Perknaster densus Sladen

(Fig. A, 3–3f; Plate VIII, figs. 1–2)

Perknaster densus Sladen, 1889, p. 552, pl. 97, figs. 1, 2; pl. 98, figs. 11, 12. Off Cumberland Bay, Kerguelen, 127 fathoms.

St. 1563. Off Marion Island, 46° 48.4' S, 37° 49.2' E, 101–106 m., 1 specimen.

DESCRIPTION. The specimen measures R 55 mm., r 15 mm., br 17–18 mm. The disk is slightly smaller, the interbrachial arcs less angular and the rays narrower than in the drawing of the type. The compactness of the abactinal spinulation and spacing of paxillae can best be appreciated from the enlarged photograph. Small abactinal plates are scattered liberally among the larger; the former carry 1–5 spinelets, the latter 8–12, with intergrades in the size and number of spinelets. This abactinal plating passes without obvious change into that of the rounded sides of ray, and thence to actinal surface where the spinelets are slightly longer and, interradially, the plates are arranged in series from the furrow nearly to ambitus. These actinal plates or paxillae also form 4 longitudinal series adjacent to adambulacrals at base of ray, becoming less distinct and reduced to about 2 series distally. The proximal plates of innermost actinal series carry 9 or 10 spinelets about as long as the outermost subambulacrals, and they gradually decrease in length *pari passu* with the latter all along the ray. On the outer third of ray the plates of the adjacent longiseries (the inferomarginals) are larger, bearing 15–20 spinelets, and at very tip of ray touch the adambulacrals. Adorad to middle of R the inconspicuous inferomarginals, following the contour of the widening ray as in other *Perknasters*, reach the interradius on the actinal face a short distance from the actual margin. The plates become separated by the interpolation of secondary plates. One can recognize the limits of the technical abactinal surface by the change from a wrinkled, pustulated skin between the bases of paxillae to the relatively smoother (but still wrinkled) skin of the actinal area; and also by the limitation of the small papulae to the area circumscribed by the abactinal plates. Along the interradiial line between mouth-plates and inferomarginals there are 10–12 actinal plates decreasing in size toward the margin.

The madreporite is 3 by 4 mm. and situated in middle of r; surrounding it are 5 or 6 large paxillae, the largest with 19 spinelets.

The tabulum of the major abactinal plates is distinctly higher (0.45–0.5 mm.) than in *fuscus* (0.18–0.22 mm.) and is about the same as in a comparable specimen of *charcoti*. The spinelets greatly resemble those of small specimens of *charcoti* but appear to be slightly shorter (0.45–0.48 mm.). The longer actinal spinelets measure 0.58–0.7 mm., and the sharp thornlets extend further toward base (Fig. A, 3–3c). The spine sheaths are about as pronounced as in *fuscus*. The abactinal spinelets especially have a paxilli-form appearance. Certain isolated spinelets or small groups, lower than the major paxillae, may easily be mistaken for papulae.

The adambulacral armature consists of 2 prominent spatulate furrow spines about 2 mm. long, the aboral the longer, placed slightly obliquely, edge to furrow. When spines are upright the oblique furrow margin appears sometimes to carry 3 spines. Subambulacrals usually 6, varying to 5 or 7, typically in 3 pairs parallel to furrow spines, each pair successively shorter, the outermost being subequal to the adjacent actinals. Near end of ray there are 7–9 spines to a plate (sporadically 10–12). The distal of the 2 furrow spines usually stands more prominently into the furrow and is more spatulate than its adoral companion.

Mr D. Dilwyn John very kindly examined the type specimen and made *camera lucida* drawings of the armature of 4 adambulacral plates distributed along the ray from the fourth to thirty-eighth. These drawings as well as his accompanying notes indicate that the figures of the type are not quite correct. In the type, the furrow spines are compressed, perhaps less so than in the Marion Island specimen; the distal spine is more prominent into the furrow and is also slightly stronger and longer than the other, and grows progressively more so from the base of ray toward tip. The furrow spines are followed by 3 pairs of spines (varying 5-7), essentially as in the Discovery specimen. This total of 8 spines, varying 7 or 9, holds all along the ray of the type, at least as far as the thirty-eighth plate. At this point in the Discovery specimen, there are 8-10 spinelets, apparently longer than in the type. But the increasing prominence of one of the furrow spines is characteristic. In this specimen there are 75 adambulacral plates and the thirty-eighth is at about middle of ray measured on side. It is beyond the sixtieth plate that the spinelets increase, sporadically, to 10 or 12; the distal 4 or 5 plates have 5 or 6 spinelets, there being obviously one furrow spinelet; the other is squeezed behind it, as in the type.

The mouth-plates each have 4 heavy spatulate marginal spines, increasing in length toward the oral angle, and 7 or 8 suborals graduated in size as are the subambulacrals.

Ambulacral furrows narrow; tube-feet strictly biserial with large sucking disks.

REMARKS. In general appearance this species resembles *fuscus* and *charcoti*, but differs from both in the greater number of adambulacral spines. The Discovery specimen differs from the type in minor details which may represent normal variation of the species, of which only two examples are known.

Perknaster sladeni (Perrier)

(Fig. B, 3-3c, 4-4c; Plate VII, fig. 1)

Cribraster sladeni Perrier, 1891, p. 104, pl. 11, figs. 2a, 2b.—Koehler, 1912, p. 39, pl. 2, fig. 12; pl. 6, fig. 6.

St. 182. Schollaert Channel, Palmer Archipelago, 278-500 m., 1 specimen.

St. 474. One mile west of Shag Rocks, South Georgia, 199 m., 1 specimen.

In general appearance this form is closely similar to the *fuscus-antarcticus-georgianus* series but has the highest paxillae, smallest disk, and smallest actinal interradiial areas. The elongation of the pedicels of the abactinal plates which differentiates *georgianus* from *fuscus* and *antarcticus* is carried still further. The abactinal and actinal spinelets are longer than in any *Perknaster* of comparable size, are slender, terete, only slightly clavate and have the fewest thornlets at the distal end.

The more typical specimen (Fig. B, 3-3c) from St. 474 measures R 50 mm., r 14 mm., R=3.5 r; br 16 mm. The compact ovary has short lobes full of eggs measuring 1 mm. in diameter (11 November 1930).

The disk is high, the rays well arched, almost circular in section, and there is no obvious lateral margin, although with care the marginal plates can be recognized by

their slightly larger groups of spinelets, low on the side of the ray. The abactinal aspect resembles Koehler's figure of *Cribraster sladeni* (1912, pl. 6, fig. 6) except that the madreporite is smaller, a difference of no great importance since there is variation in the size of the madreporite in *georgianus* and *aurorae*. The furrow is narrow and the podia strictly biserial.

The body wall is reinforced by a tough muscular lining. Imbedded in the wall are small, spaced independent ossicles, irregularly oblong, triangular or lozenge-shape—the bases of the papillae. They are narrower than the interspaces, and the papulae are fairly large, not numerous, irregularly distributed and confined to the abactinal surface. Each plate develops a subcylindrical pedicel or tabulum 0.48–0.55 mm. high, the convex top of which carries 2–6 slender spinelets 0.6–0.7 mm. long. The tabulum is higher than in *georgianus*. The spinelets are slender-clavate rather than capitate, and the terminal third is armed with short thorns, shorter, less spiculate, and much less numerous than in *aurorae* of comparable size. What I interpret as the proximal inferomarginal plates carry about 9 spinelets.

The small actinal areas have longer spinelets (0.8–0.9 mm.) essentially like the abactinal in form. These plates usually carry 3 or 4 spinelets in a close group and the groups are rather crowded together.

All the spines are heavily sheathed and look like tapered pointed papillae, between which the rugose skin can be seen, especially on actinal surface. Only when dry do the spines themselves become visible and take their proper shape. The sheathed spinelet is two or three times the diameter at base of the spinelet proper, whence the appearance of conical papillae.

The adambulacral armature is typically "cryasteroid"—either an oblique series of 3, decreasing in size outward from the heavy spatulate furrow spinelet (on aboral side of plate), or else a triangular group of 3 spines, the outer having moved aborally. Sometimes the outer spine is duplicated by a fourth, the two forming a longiseries. The furrow spine is frequently scoop-shaped, and the second spine may also be compressed, or spatulate. There are 4 heavy marginal mouth spines, also compressed, and about 2 suborals.

There is a prominent interbrachial septum, broader above than below, which does not extend across the actinal interradiial area but leaves a wide passage (filled with gonads). It is heavily fortified with ossicles hidden by very tough tissue. The coarse-lobed ovaries open interradially on side of ray above marginal plates. The ampullae are bilobed as in typical "*Cryaster*".

Koehler's photographs are much better than Perrier's. I have already alluded to Koehler's figure of the abactinal aspect. The ventral surface (Koehler, 1912, pl. 2, fig. 12) is in poor condition but the figure shows the coarse flattened, furrow spines. It is to be regretted that Koehler, a master of detailed description, did not give at least some figures of spinelets.

The Shag Rocks specimen is probably not typical since the type came from a faunally different area, the Falkland Plateau.

St. 182 (Fig. B, 4-4c). This specimen is heavily parasitized by an organism forming a large cyst at base of ray opening by a small actinal aperture. The largest cyst measures 15 by 10 by 10 mm. There are at least 6 of these parasites, yet the gonads are well developed. Experience has shown that sea stars parasitized by *Dengrogaster* may suffer an abnormal reduction of skeleton, yet this individual appears to be normal except for distortion caused by the cysts.

R 53 mm., r 16 mm., br about 18 mm. Since this specimen was dredged in the same general locality as the two small examples of *antarcticus* it would be rather natural to refer it to that form. But the paxillae are entirely different, having the elongate pedicels and slender longer spinelets of *sladeni*. The pedicels are commonly 0.45-0.5 mm. high, while the spinelets are 0.6-0.7 long. They are even less robust than those of the Shag Rocks specimen. This is true also of the unmodified actinal spinelets, the differences being best appreciated by a comparison of figures. A considerable number of actinal plates (as in the Shag Rocks specimen) have actinal pedicellariae composed of 2 or 3 modified spinelets bent toward one another (fig. 4c).

The inferomarginal plates are not clearly differentiated; nevertheless, the limits of the actinal intermediate areas can be traced from the fact that the abactinal paxillae are in contact whereas the actinal are slightly spaced. The former carry 2-6 spinelets which appear paxilliform on account of the sacculus. Very little skin is visible between the paxillae. The madreporite is small—2 mm. in diameter.

The adambulacral spinelets are tapered, pointed and provided each with a pulpy investment. The furrow spinelets are therefore not flattened and spatulate as is rather characteristic of the Shag Rocks specimen.

The ambulacral furrow is narrow and the podia strictly biserial.

Koehler¹ has described *Perknaster aurantiacus* from the vicinity of Adelaide Island and Alexander I Island, 92-254 m. Subsequently (1923) he recorded the same species from Shag Rocks and South Georgia (Cumberland Bay), 75-160 m. The type measured R 25 mm., r 6 mm. It is barely possible that the northern examples belong to *P. sladeni*. But the type does not have longish spinelets. Koehler states: "On n'aperçoit qu'un recouvrement de petits piquants serrés, très courts, cylindriques, très légèrement renflés à l'extrémité, qui prend la forme d'une petite tête arrondie, et pas beaucoup plus longs que hauts; ce sont plutôt des granules allongées que des piquants. On ne reconnaît aucun groupement parmi ces piquants, que restent parfaitement isolés les uns des autres, très rapprochés mais non contigus." He says further that the actinal spinelets are also short. These observations having been made from a dried specimen are doubly significant since desiccation emphasizes the pedicels and slender spinelets of *sladeni* and *georgiannus*. By no stretch of the imagination can the spinelets of these forms be considered "elongated granules".

The relationship of *sladeni* and *georgiannus* is a puzzle. The pedicel of the abactinal paxillae of *georgiannus* is about midway between that of *sladeni* and *antarcticus*, yet *sladeni* probably occurs at South Georgia in nearly the same depth as *georgiannus*. The

¹ Koehler, 1912, p. 36, pl. 3, fig. 9; pl. 4, fig. 1; 1923, p. 73.

spinelets of *georgianus* are neither those of *antarcticus* nor *sladeni* but nearer to the latter as are the small actinal interradial areas.

TYPE LOCALITY. Falkland Islands.

DISTRIBUTION. Falkland Islands, Shag Rocks, Palmer Archipelago; 199–500 m.

Perknaster sladeni georgianus subsp. nov.

(Fig. B, 2–2*b*; Plate V, fig. 2; Plate VI, fig. 3)

DIAGNOSIS. Differing from typical *antarcticus* in having an obviously higher tabulum to abactinal plates, slenderer abactinal spinelets which are less swollen at tip and have less prominent thornlets; actinal paxillae higher and usually more closely placed. Type, R 31–35 mm., r 10.5 mm., br 12 mm. R=3r.

DESCRIPTION. Although the 3 specimens are small (R 33 mm. to R 35 mm.) they are sexually mature. The race is in some respects intermediate between *sladeni* and *antarcticus*. It is not close to *fuscus* since the pedicels of the paxillae are decidedly higher (0.4 mm.), while the abactinal and actinal spinelets are slenderer and differently armed.

The abactinal paxillae are also higher than in *antarcticus* owing to the higher tabulum which with plate measures 0.4 mm., while the spinelets measure 0.48–0.54 mm. In *antarcticus* the tabulum measures 0.23–0.27 mm. high and the spinelets 0.45–0.5 mm. When the spinelets are upright on the tabulum, the paxillae of *georgianus* are 0.88–0.94 mm. high (including the somewhat thinner abactinal integument) while those of *antarcticus* are 0.68–0.77 (including a somewhat thicker skin which further shortens the apparent height of the paxillae). These differences seem small but are very apparent when specimens are compared under low magnification. As will be noted from the figures, the abactinal spinelets of *georgianus* are slenderer and not at all capitate as are those of *antarcticus*. In this respect they stand nearer to the spinelets of *sladeni*.

The inferomarginal plates do not form a conspicuous actinal interradial arc as in *aurorae*. The plates can be distinguished from the actinals only by their slightly more numerous spinelets—5–7 in the interradial region, while the actinal plates adjacent carry 2 or 3. The actinal interradial areas are about as small as those of *sladeni*, and smaller than is apparent from the size of disk, since the interradial width of area is only about three-fourths minor radius. The inferomarginals are actinal in position, one-fourth r from ambitus. A few of the plates near furrow have their 2–4 slender spinelets slightly bent and co-ordinated into a pedicellaria, especially in specimens from St. 42.

In *sladeni*, from St. 474, the adambulacral furrow spinelet and often the second spinelet are compressed, while in *georgianus* they are subterete, rather slender, tapered, with occasionally a slight compression of the tip of the furrow spinelet (St. 42). Otherwise the adambulacral armature is fundamentally as in *sladeni* and *fuscus*. There are 3 spines in an oblique transverse series, the furrow spine being on the aboral side of plate. But the outer, smallest spinelet sometimes has an aboral companion, making 4 in all. This fourth spine sometimes stands aborad to the second spine of series. The first adambulacral

may have 2 spines on furrow margin and 2 on the actinal surface of plate, or only 1 furrow spine and 1 subambulacral.

The mouth-plates have 4 or 5 marginal spines and 2 or 3 shorter suborals in a parallel series. They are subterete, slightly tapered, bluntly pointed.

In one specimen from St. 42 the madreporite measures 1.5 by 2 mm.; in the other it is 2.5 by 2.4 mm.; in that from St. 140 it measures 1.5 by 2 mm. This character is therefore unstable, and the disparity between the madreporites of the type of *sladeni* and of the Shag Rocks specimen is probably without taxonomic significance.

Although a specimen measures only R 33 mm., the ovaries are well developed and contain eggs 0.75 mm. in diameter.

Just how to treat this recognizable form is something of a problem. It is as distinct from *antarcticus* as is *fuscus*. Its high paxillae, slender spinelets, and small actinal inter-radial areas appear to relate it to *sladeni*. But the specimen of *sladeni* from the Palmer Archipelago complicates the matter since it indicates a range which would reasonably include that of *georgianus*. No specimen typical of *sladeni* has been taken at South Georgia, proper, and it is possible that *georgianus* does have some geographical or ecological significance. Only more material can answer the question.

TYPE LOCALITY. St. 42. Off mouth of Cumberland Bay, South Georgia, 120–204 m., 2 specimens.

SPECIMENS EXAMINED. In addition to two from St. 42, a paratype from St. 140, Stromness Harbour to Larsen Point, South Georgia, 122–136 m.

Perknaster charcoti (Koehler)

(Fig. B, 5–5e; Plate VII, fig. 3)

Cryaster charcoti Koehler, 1912, p. 33, pl. 2, figs. 8, 9; pl. 3, fig. 8.—1920, p. 132.

St. 39. East Cumberland Bay, South Georgia, 179–235 m., grey mud, 1 specimen (A).

St. 148. Off Cape Saunders, South Georgia, 132–148 m., grey mud, stones, 1 specimen (B).

St. 149. Mouth of East Cumberland Bay, South Georgia, 200–234 m., 1 specimen (C).

The three specimens measure as follows:

Specimen A, St. 39, R 90 mm., r 34 mm., br 34–39 mm. (specimen pressed flat); specimen B, St. 148, R 51 mm., r 16 mm., br 19 mm.; specimen C, St. 149, R 102 mm., r 40 mm., br 43–47 mm.

Specimen B is the only one which is at all comparable to the example of *fuscus*, from Kerguelen, in which R = 34 mm. Although B is larger and a light yellowish brown in colour, while *fuscus* is dark brown, the two are very similar, especially in the features of the actinal surface. The adambulacral spinelets as a rule form a transverse series of 3, precisely as indicated by Sladen in his figure of the type of *fuscus* (1889, pl. 97, fig. 4). The furrow spine is strongly compressed, heavily sheathed, and its base occupies almost the entire length of the plate. The second spine is also compressed, but is about three-fourths as long as the furrow spine, while the third is tapered and about two-thirds the length of the second. Just external to the third is a pair of actinal spines which Sladen

mistook for adambulacrals. As a variation, there may be a fourth small spinelet in line with the series or else placed aborad to the third spinelet. The whole armature forms a cheval-de-frise along the furrow margin very conspicuously higher and heavier than the small actinal spinelets which are in well-spaced groups of 2, less often 3. The interradial area is crossed by the characteristic deep wrinkles or dermal grooves.

The inferomarginal groups of 5 or 6 spinelets clearly mark the border of the actinal area and are actinal in position, at the interradius about $\frac{1}{5}r$ from the ambitus. Above or beyond them the abactinal spinelets are sharply differentiated from the actinals by their heavier investment of skin and the much closer juxtaposition of the paxillae, which carry 1, 2, or 3-5 spinelets. These are normally hidden by a sheath common to the whole paxilla. That is, the group of spinelets is enclosed in a wrinkled bag of pulpy tissue (while in *fuscus* each spinelet is separately visible). The skin between the crowded sacculate groups is raised into lower deeply wrinkled welts among which it is difficult to differentiate the papulae. These are, however, rather evenly scattered all over the abactinal area, being readily seen from the inner surface of the abactinal wall. The latter is much thicker than in *fuscus*, but some of the difference must be discounted owing to the greater size of specimen B. This body wall further thickens in the larger specimens. In C it reminds one of the body wall of a leathery holothurian.

Coming to the details of the spinelets of specimen B (Fig. B, 5*a*), the resemblance is rather close to *aurorae*, but the spicules or thornlets build a smaller head to the spinelet, as a rule. Fig. 5*a* (left) is a young spine, indicating the terminal origin of thornlets. The spinelets are the same length as in equal-sized specimens of *aurorae* (0.53-0.63 mm.). The pedicel, however, is a little higher (0.36-0.45 mm.), and distinctly higher than in *fuscus*. The actinal spinelets are 0.7-0.75 mm. long and the armature of slender thornlets is no more extensive than in the shorter abactinal spinelets. It is therefore much less than in the actinal spinelets of *aurorae*.

In large examples (figs. 5, 5*e*) the thornlets either are absorbed or are broken in the case of the abactinal spinelets since none could be found having the characteristic structure of fig. 5*a*. In specimen C the spinelets (fig. 5, enlarged $\frac{1}{2}$ scale of fig. 5*a*) are around 0.7-0.75 mm. long and appear to represent only about $\frac{2}{3}$ of fig. 3. The actinal spines of large specimens (fig. 5*e*) are also very different. There is no longer any trace of the delicate spicules of specimen C. The terminal third is covered with short asperities, somewhat like rose thorns in shape. Such a transformation is not found in comparable large specimens of *aurorae*.

Koehler has fully described the adult with excellent photographic figures. Certain emendations are necessary since he had only the type from Petermann Island. He emphasizes the peculiarity of the large, spatulate, innermost adambulacralspines with its heavy sheath of tissue which forms a membranous expansion along either edge of the spatula, thereby increasing its apparent width. This spatula is not so wide in the Discovery specimens as in the type, and is often not wide at all, but is narrow and gouge-shaped, with a thickened, slightly bifid truncate end, the extremity being one-third to one-half the width of the end of Koehler's figure (pl. 3, fig. 8). This extremely broad

spine is therefore not characteristic; nor is the number of adambulacral spines 2, as might be inferred from Koehler's description. The prevalent number is 3, in a slightly oblique transverse series, as in specimen B; or a small fourth spine may stand aborad to the median or to the outermost spine.

Koehler states (1920, p. 132) that on the actinal interradiial areas of *charcoti* the spinelets are more developed (developpé) than in *antarcticus* and are sometimes coordinated into small groups; that they have therefore undergone less degeneration than in *antarcticus*. The individual spines are probably larger in *charcoti* but Koehler's comparative figure of *antarcticus* (1912, pl. 3, fig. 1) shows more numerous actinal spinelets than in *charcoti*, and even a slight grouping is indicated. In small specimens of *antarcticus* the spinelets are regularly disposed in small, slightly spaced groups of 2 or 3. In each of the 3 specimens of *charcoti* the small groups of 2 or 3 spinelets are very definite, well spaced. In specimens A and C those groups near the furrow function as primitive spiniform pedicellariae. In such groups the spinelets are usually slightly curved toward each other.

In large specimens the abactinal paxillae are well spaced and in specimen A are submerged in the myriad folds of the highly rugose glandular skin; in specimen C the spinelets extend slightly above this skin as in Koehler's figure (pl. 2, fig. 9). On the lateral part of the *abactinal* area, deeper transverse channels resolve themselves from the maze of intricate folds to continue actinally between the marginal plates and across the actinal area, disappearing between the combs of adambulacral spines.

Although the tube-feet are large, they are not crowded as in *aurorae* and preserve an approximate biserial arrangement.

Specimen B, having R 51 mm., has well-developed subspherical ovaries.

Colour note, specimen C. Pale yellow with red interradiial streaks on interradii and a few vertical red streaks on sides of arms.

TYPE LOCALITY. Petermann Island, Graham Land coast.

DISTRIBUTION. South Georgia and Petermann Island, low tide to 235 m.

Perknaster aurorae (Koehler)

(Fig. C, 1-1c, 2-2a, 3-3d; Plate 7, fig. 2)

Cryaster aurorae Koehler, 1920, p. 120, pl. 27, figs. 1-3, 5, 6; pl. 28, figs. 1-11; pl. 29, figs. 2-6; pl. 30, figs. 2-5; pl. 75, fig. 1.—1923, p. 73.

St. 366. Four cables south of Cook Island, South Sandwich Islands, 77-152 m., 1 specimen.

St. 370. Two miles north-east of Bristol Island, South Sandwich Islands, 18-80 m., 2 specimens.

St. 371. One mile east of Montagu Island, South Sandwich Islands, 99-161 m., 9 specimens.

St. MS 71. East Cumberland Bay, South Georgia, 110-60 m., 1 specimen (see note below).

Perknaster aurorae differs from all other forms in having broader ambulacral furrows, in which the more numerous, larger podia are crowded out of the strictly biserial arrangement. Even in specimens as small as the example of *P. fuscus* this crowding is conspicuous and contrasts very sharply with the condition in *fuscus* where the furrow is so narrow that the furrow spinelets of opposite margins interlock. In every specimen of

aurorae the podia force apart the margins of the furrow. In large examples at the middle of furrow 3, or rarely 4, podia can be counted in a transverse series. In the example of *fuscus* there are 84 podia to a ray while in a slightly smaller example of *aurorae* there are 108.

The dorsal aspect of the 2 species is practically the same. Both are covered with close-set blunt papillae. But the structure of the spinelets is different, those of *aurorae* being almost brush-like from a multitude of sharp thornlets which do not so obviously form the margins of radiating lateral flanges. In contrast to *sladeni* and *georgianus* the pedicel of the paxillae is low, as in *fuscus* and *antarcticus*.

In *aurorae* both series of marginal plates are clearly discernible. In large specimens they become separated in the interbrachial arc by several series of smaller intermarginals similar to the lateral abactinals. The marginals carry 8 or 9 spinules about as large as adjacent actinal spinules.

The largest of the Discovery specimens, from St. 370, measures R 112 mm., r 44 mm., br 48 mm. The smallest specimen, from St. 371, measures R 34 mm., r 12 mm., br 14 mm. The others are scattered between these limits.

The structure of the abactinal spinelets described and figured by Koehler (1920, pl. 75, fig. 1) is highly characteristic. Each spinelet is clavate. The enlarged tip bristles with numerous slender thorns buttressed to their neighbours by trabeculae which increase in number as the thorns or spicules lengthen. Separating the trabeculae are holes of varying size (Figs. C, 2, 2*a*). When the spinelets begin to degenerate as the animal reaches fully adult size, the trabeculae are absorbed first, leaving a row of serrations along the adjacent borders of neighbouring spicules (fig. 2*a*). In some large specimens the spinelets are not so well developed as shown by fig. 2 (St. 366) but may have the shorter spicules of fig. 1 (St. 371) which represents a smaller specimen (R 40-50 mm.). Koehler (1920, pl. 75, fig. 1) gives photomicrographs of spinelets but the figures have suffered by the routing of the background. Koehler's fig. 1*c* is nearest to the spinelets of the Discovery specimens. The pedicels of the abactinal paxillae are usually a trifle higher than those of typical *antarcticus* (figs. 1*b*, 3*d*).

The adambulacral furrow spine, and even the second spine, is usually strongly compressed or spatulate as is clearly shown by Koehler's figures.

A specimen with R 43 mm. already has the gonads well developed.

NOTE ON SPECIMEN FROM ST. MS 71 (Fig. C, 3-3*d*). This specimen from South Georgia is not at all typical but it is nearer to *aurorae* than any other species. It measures R 48 mm., r 16 mm., R=3r, br 18 mm. The gonads are well developed. The spinelets have rather fewer and coarser thornlets than has typical *aurorae* while the pedicel of the paxillae is higher than in typical southern specimens (compare figs. 1*b* and 3*d*). The spinulation of the abactinal surface passes into that of the actinal without a conspicuous break, although small inferomarginals with 5-8 spinelets can be recognized in contrast to the actinals which usually carry 3, but adjacent to furrow, 4 or 5. Most of these groups of actinal spinelets are modified into pedicellariae, the 2-5 spinelets being bent toward a common centre (fig. 3*b*). Although such spiniform pedicellariae are

rather characteristic of *charcoti* and *sladeni* they are not of typical *aurorae* and *antarcticus*. But the tube-feet of this specimen are crowded in the manner of *aurorae*, in sharp contrast to the condition in *sladeni*, which the specimen superficially resembles. Finally, the furrow spinelets are terete and not spatulate.

One might naturally regard this specimen as representing a race of *aurorae* at the northern limit of its distribution. Koehler (1923, p. 73), however, states that his example of *aurorae* (R 40 mm., r 19 mm.) from Shag Rocks is absolutely typical and conforms to a specimen of equal size taken at the type locality. He notes no difference between two small specimens, one from Graham Land and one from Cumberland Bay, South Georgia.

At this same station, MS 71, were taken one small adult (R 25 mm.) and 5 young of a *Cycethra* with slender rays and R ranging from 6.5 mm. to 12 mm. In the absence of adult *Cycethra* from South Georgia, I believe these young would be mistaken for young *Perknaster*. The resemblance is close.

TYPE LOCALITY. Davis Sea, 65° 42' S, 92° 10' E, 60 fathoms.

DISTRIBUTION. Antarctic, probably circumpolar. Recorded by Koehler from the region between 92° and 141° E (64° 32'–66° 32' S), 25–151 fathoms; Graham Land, 150 m.; South Georgia 252–310 m.; Shag Rocks, 160 m. Extreme bathymetric range, 18–310 m.

Family ASTERINIDAE Gray

Genus *Patiriella* Verrill

Patiriella fimbriata (Perrier)

Asterina fimbriata Perrier, 1875, p. 307.—1891, p. 111, pl. 12, figs. 5, 5*b*.—Koehler, 1923, p. 55, pl. 9, figs. 2, 5–8. Literature.

Patiriella fimbriata Verrill, *Amer. J. Sci.* xxxv, 1913, p. 484.—Fisher, 1931, p. 5, pl. 5, figs. 1, 2.

St. WS 81. 8 miles north-west of North Island, West Falkland Island, 81–82 m., sand, 1 specimen.

St. WS 84. 7½ miles south-west of Sea Lion Island, East Falkland Island, 75–74 m., coarse sand, shells, stones, 1 specimen.

St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shell, 11 specimens.

St. WS 221. 48° 23' S, 65° 10' W, 76–91 m., 1 specimen.

St. WS 750. 52° 12' S, 67° 19' W, 95 m., 2 specimens.

St. WS 755. 51° 39' S, 57° 39' W, 77 m., 4 specimens. Ringdove Inlet, 1 specimen.

The specimens vary in size between R 6 mm. (St. WS 84) and 16 mm. (St. WS 750); two from St. WS 85 have R 15 mm.

Although this species is rather characteristic of the Falkland Plateau and the Straits of Magellan, it occurs as far north as Calbuco, Chile, and is reported by Koehler from Graham Land (64° S).

Genus *Anseropoda* Nardo

Anseropoda Nardo, Oken's *Isis*, 1837, p. 716. Type *Anseropoda membranacea* = *A. placenta* (Pennant).

Anseropoda antarctica sp.nov.

(Fig. E, 1-1c; Plate X, fig. 3; Plate XII, fig. 1)

DIAGNOSIS. Rays 5. R 17 mm., r 10-11 mm., br 12-13 mm. (body distorted). Broadly stellate, the general habit that of a thin-edged *Asterina*; disk rather arched and oral region sunken; interradial areas thin but restricted in extent. Abactinal surface covered with small, uniform truncate granules, grouped so as to indicate underlying plates; actinal plates with combs of usually 3 spinelets; adambulacral furrow combs with 6-3 webbed, slender, blunt spinelets; subambulacral combs with 5-3 spinelets; marginal oral spinelets 8, basally webbed.

DESCRIPTION. The general form is more that of an *Asterina* than of a typical *Anseropoda* owing to the arched disk and concave actinal surface. The small size obviates an extensive development of broad thin actinal interradial areas.

The abactinal surface is covered with fairly uniform truncate granuliform spinelets, 0.18-0.22 mm. long, the top of which is subcircular and armed with numerous thornlets. A profile view is shown in fig. 1. The granules, by reason of slightly differentiated spacing, form groups corresponding roughly to underlying plates, most conspicuous in the interradial areas. Larger radial plates carry 12-18 granules; the smaller interradial plates 5 or 6.

The abactinal plates are thin, scale-like and strongly imbricated, with a curved external free edge. In the median radial series this edge is directed toward centre of disk. The other plates are arranged in series parallel with the radial, and also in transverse series; and the curved free edge is toward centre of disk and radial line. On the coelomic side the dorsolateral plates each have a conspicuous process which is directed toward the margin of ray and increases in length in successive plates. This process is characteristic of *Anseropoda* (fig. E, 1a, 1b).

Papulae small, "here and there" on centre of disk, and in two radial series, one on either side of carinal plates—about 12 to a series.

Madreporite 1 mm. in diameter, situated 4 mm. from centre of disk.

Supermarginal plates small, abactinal in position, the margin ray being defined by the outer end of inferomarginals, which form a border outside of the supermarginals nearly as wide as the latter. Supermarginals carry 10-12 granules and the abactinal surface of the inferomarginals about the same number, a trifle smaller in size. There is a distinct groove between the inferomarginals (or the lateral outgrowths of the imbricated plates proper).

The actinal plates are in regular oblique transverse series corresponding each to an inferomarginal (and usually to an adambulacral). The grooves, mentioned above, continue to the ambulacral furrow between the regular lines of actinal plates. A few plates near the oral angle carry a central comb of 4 or 5 short sharp thorny spinelets, but usually there are 3 in a slightly curved comb (1-3 in very small specimens, R 5 mm.). Occasionally the spinelets stand in a group, spinelets 0.3-0.37 mm. long.

Adambulacral armature: a curved furrow comb of 6 webbed slender spinelets, the laterals much shorter than the 4 central. This number diminishes to 5, 4 and 3 as end of ray is approached. The subambulacrals are on an oblique ridge of the surface at a higher level than the marginals. They are a little shorter, more pointed, and very similar to adjacent actinals. The webbed combs usually start with 5 spines and end with 3. Furrow spines: longest 0.75 mm., shortest laterals, 0.22 mm.

Mouth-plates with 8 marginal spinelets, the 16 of an angle basally webbed and decreasing in length laterally from the central pair which are the largest spines on the body. Three or four suborals border the outer half of suture; and usually two somewhat longer ones stand between these and margin.

TYPE LOCALITY. St. 170. Off Cape Bowles, Clarence Island, 342 m., 7 specimens.

REMARKS. The specimens range in size from R 4.5 mm. to R 17 mm. (type). This is probably a small species since the type does not appear to be immature.

The species does not particularly suggest, by its general appearance, an *Anseropoda*. The abactinal granules constitute an aberrant feature since *Anseropoda* typically has delicate spinelets. Although the body is thin, its proportions have not reached the bizarre stage of *A. placenta* and other typical species. The internal processes of the abactinal and actinal plates are proportionately much shorter than in *A. placenta* and the plates of the midradial region are not obviously stellate. In large species the long internal processes are an essential anatomical contrivance in connection with numerous oblique septa all along the ray. They make possible the survival of a creature which is very thin, broad and delicate. If *A. antarctica* grows to a large size these processes undoubtedly greatly lengthen.

A curious feature of *A. antarctica* is the presence of hyaline spicules or thornlets on the dorsal, coelomic, surface of the ambulacral plates. They are best developed on the first 2 ambulacrals where they are prominent and occupy nearly the whole length of the plate, especially on the narrow part between ampullae. Further on, they are confined to the lower half of plate. I find a somewhat similar development in the relatively huge six-rayed *Anseropoda insignis* Fisher of the Hawaiian Islands.

There appears to be no described species closely related to this diminutive *Anseropoda*. The abactinal granulation, alone, is distinctive.

Genus *Kampylaster* Koehler

Kampylaster Koehler, 1920, p. 136. Type *K. incurvatus* Koehler.

Kampylaster incurvatus Koehler

(Fig. D, 3-3d)

Kampylaster gamulatus Koehler, 1920, p. 8 (*nomen nudum*).

Kampylaster incurvatus Koehler, 1920, p. 138, pl. 36, figs. 4, 6, 7, 11; pl. 37, figs. 1, 2, 3; pl. 66, fig. 10.

St. 190. Bismarck Strait, Palmer Archipelago, 93-130 m., 3 specimens.

St. 1660. Ross Sea, 74° 46.4' S, 178° 23.4' E, 351 m., 6 specimens.

Three of the specimens from St. 1660 are perhaps full grown, being the same size as Koehler's type—namely, R 15 mm., r 9–10 mm. The rays are bent strongly ventralward. Two specimens are carrying numerous young in the concavity adjacent to mouth (27 January 1936). Two other examples from this station having R about 10 mm. are strongly folded, while another is simply convex. The three small examples from St. 190 (R 7 mm.) are not folded ventralwards; the disk is simply convex, and in one case the ray tips are curved upward. Except when brooding young the animal probably is spread out in normal sea star fashion as Mortensen found to be the case with living examples of *Stegnaster inflatus* (Hutton). When preserved this species usually is strongly convex (Mortensen, 1925, p. 304, pl. 13, fig. 11).

A few notes need to be added to Koehler's account. He does not mention the papulae. These are difficult to see from the outside, being small and largely obscured by the granules. From the coelomic side of the dorsal surface they may be observed to occupy a radial petaloid area extending from centre of disk two-thirds the distance to end of ray. In this area there are about 16 papulae widely and unequally spaced. Koehler has described the thin overlapping plates, which lack the internal marginally directed process or lobe characteristic of the thin abactinal plates of *Anseropoda*. The abactinal granules, of which figures are given, are characteristically expanded at the base, the whole structure resembling an elaborate holothurian "table". The slightly convex summit is uniformly beset with very numerous sharp thorns. The subcircular base of each spinelet is in contact with its neighbours and is, of course, immersed in the "dermal" layer of the skin. The effect of these "tables" is to form a calcareous layer over the plates proper. The spinelets in alcoholic specimens, on account of their membranous covering, appear to be simply convex granules.

The gonads have short thick lobes, and are attached to the *dorsal* wall a short distance from the margin of interbrachium. In the case of one of the specimens carrying young the oviduct could be traced to the margin but the pore could not be located.

There is a very short stout calcareous interbrachial pillar proceeding upward from each mouth angle to the abactinal wall, the point of contact being less than $\frac{1}{4}$ r from centre. The space between pillar and margin is devoid of a membranous septum.

There are two brooding females. One of these has 26 young in a cavity involving the proximal 5 or 6 adambulacral plates of each ray. These young are 4 mm. in diameter and have about the same proportions as the adult, but the inferomarginal plates, relatively more prominent than in the adult, carry 2 or 3 outstanding spinelets the series of which forms a conspicuous fringe on the ambitus. As the animal grows and new spinelets are added to the plate these original spinelets increase in thickness faster than in length. In a specimen having R 6 mm. this marginal fringe of spinelets longer than the others has disappeared. But in *Mirastrella biradialis* just the opposite has taken place. The marginal fringe is accentuated as the animal grows. In these young there are no actinal plates. There are 7 pairs of tube-feet. The first 4 or 5 adambulacral plates carry a prominent inner spinelet and a small companion external and adoral to it; the next 1 or 2 plates have only the inner spinelet. Each mouth-plate has 2 or 3 marginal

spines. The abactinal granules are uniformly distributed and no bare furrows proceeding inwards from the interval between marginal plates are present, as in *M. biradialis*.

Figures of the spinelets of these young (figs. 3*b*, 3*c*) are of significance for comparison with those of the adult.

Koehler, by comparing *Kampylaster* with *Tremaster* Verrill (Fisher, 1911, p. 254), implies a certain similarity between the two genera which is rather far-fetched. *Tremaster* is peculiar in having 5 interradial perforations similar to those of "key-hole" sand dollars (e.g. *Mellita*). *Stegnaster* Sladen seems to be a much nearer relative and one which also has a habit of folding up when killed in alcohol (Mortensen, 1925, p. 303, pl. 13, fig. 11).

TYPE LOCALITY. Off Adélie Land, 66° 32' S, 141° 39' E, 151 fathoms.

DISTRIBUTION. Probably circumpolar: 97° 20' E-141° 39' E; Ross Sea; Palmer Archipelago; bathymetric range 93-351 m.

Mirastrella gen.nov.

DIAGNOSIS. Similar to *Kampylaster* but differing in having a double series of equivalent abactinal radial plates, tabulate inferomarginal plates, and specialized abactinal interradial grooves. Type *M. biradialis*.

Although there is much similarity in general appearance between *Mirastrella* and *Kampylaster*, the latter does not have the very unusual double row of carinal or radial plates. The plates of its normal single series are separated by encroachment of the adradials of either side which imbricate and force the radial plates apart. As the animal grows, irregularity of plates often obscures the radial series.

The young of *K. incurvatus*, recovered from the brood chamber, much more nearly resemble *Mirastrella* than do the adults. In these young the inferomarginals (4 to a ray) constitute a "phanerozoniate" border but there is no specialized tabulum. On the ventrolateral margin of plates are 2 or 3 prominent spinelets which stand out laterally and form an ambital fringe. Above these on the dorsal surface of plate are 3-5 smaller spinelets a trifle larger than the superomarginals and abactinals. As mentioned under *incurvatus* the young "grow up to" the ventrolateral spinelets which are not enlarged in the adult.

Mirastrella is readily distinguishable from *K. incurvatus* by the presence of this marginal fringe of spinelets, the tabulate character of the inferomarginal plates, and by the abactinal grooves. The spinelets of *Mirastrella* lack the subcircular, perforated, basal expansion found in *Kampylaster* while the membranous investment of the body is much thinner in *Mirastrella*.

Mirastrella superficially resembles *Leilaster* A. H. Clark (1938, p. 1, pl. 1), the type of which is *Korethraster radians* Perrier from off Barbados, 56 fathoms. I have examined a specimen of *Leilaster* which appears to belong to the Ganeriidae. Its produced inferomarginals are similar to those of *Mirastrella* but the abactinal skeleton is very different. There is a normal carinal series of plates and on either side a series of subequal adradials. The adradials of the second series, however, are conspicuously enlarged and form a

border to the abactinal area. Between these 2 rows of enlarged plates are 3 series of smaller ones—that is, the carinal and 2 adradials.

The position of *Mirastrella* is not clear. The thin imbricating abactinal plates and a certain similarity to *Kampylaster* (which in turn is perhaps related to *Stegnaster*) favour the Asterinidae. The produced inferomarginals and general appearance of the actinal surface suggests the Ganeriidae.

The species is sexually mature when R measures only 5.5–6 mm.

Mirastrella biradialis sp.nov.

(Fig. D, 4–4*e*; Plate IX, fig. 1)

DIAGNOSIS. Rays 5, R 5.5–6 mm., r 3 mm., br 3.5 mm. Form broadly stellate with thick disk, convex abactinal surface, concave actinal surface, and marginal rays sharply defined by the prominent tabula of inferomarginal plates, which are bent obliquely downward and carry 2 or 3 spinelets abruptly larger than abactinal granules; a conspicuous abactinal interradiial furrow and series of oblique superomarginal grooves; granules slightly spaced, uniform; outlines of plates indicated by differentiated furrows; adambulacral spines 3 or 4 proximally, usually in oblique transverse series.

DESCRIPTION. The arched abactinal surface is covered with subequal, slightly spaced, relatively coarse granules or granuliform spinelets invested by a very thin membrane and so disposed that individual plates are indicated by channels between the groups of spinelets. Spinelets spaced about half their own diameter, the contour of the enlarged head of spinelet being round. The spinelets lack an expanded base and measure 0.1–0.15 mm. high by 0.09–0.12 mm. broad. Their precise form, for comparison with that of *K. incurvatus*, is best indicated by fig. 4*a*. The structure of these spinelets is that of a mature animal rather than of a young one. The most characteristic features of the abactinal surface are the furrows (undoubtedly richly ciliated in life) which originate in the bare interval between the prominent inferomarginals, pass obliquely upward between the broad superomarginals, and merge with the channels separating the groups of granules. The interradiial sulcus is obviously the largest and is evident after the spinelets have been removed; its inner end meets the outer border of the primary interradiial plate (Fig. D, 4*e*, *x*).

The abactinal plates consist of a small central plate surrounded by 5 primary interradials which overlap. Outside of these is an imbricating ring of plates consisting of 5 primary radials and 5 *pairs* of plates *external* to the interradials. Between the plates of each pair passes the interradiial sulcus. These are the innermost plates of the series marked *AD'* in figs. 4, 4*e*. Between the primary radial and the terminal plate are 2 longitudinal series of imbricating plates occupying the position of the usually single series of radial, or carinal, plates. On either side of this double series (which occupies the crest of ray) are 5 or 6 larger plates composing the first adradial series (*AD*1). Between these and the superomarginals are 3 plates of a second series (*AD*2). Abactinal plates relatively thick. There are no internal processes as in *Anseropoda*.

No madreporic body and no papulae could be found.

The superomarginals carry about 10 granules in 2 series aligned on long axis of plate. On the lateral surface of the inferomarginals is a group of 5 or 6 similar granules while the end carries a series of 3 much stouter spinelets, the median the longer. This spiniferous part of the plate is really the pedicel of a sort of coarse paxilla. Between successive tabula are the characteristic lateral furrows.

A cleaned and dried specimen shows only 3 slender actinal plates to each ray, carrying 1 or 2 small slender spinelets each. On account of the obliquely downward growth of the inferomarginal pedicels and the convexity of disk, the concavity of actinal surface is accentuated.

Adambulacral spinelets slender, subterete, around 0.35 mm. long; proximally 3 or 4, distally 2, rather heavily sheathed and connected by this sheath at base. They are usually arranged in an oblique, transverse arc, the innermost spinelet farthest from mouth. Or 2 may occupy the furrow margin, and 2 or 1 the surface of plate. At end of ray only 2 spinelets stand in a transverse series.

Mouth spinelets, 4 on furrow margin, subequal and similar to adambulacrals.

In the paratype (R 6 mm.) the subspherical ovaries are attached to a superomarginal plate and contain a few relatively large eggs. The entire ovary is only about 0.6 mm. in diameter so that the duct could not be traced in the tiny space available. It probably opens ventrally. The large eggs suggest a "paedophoric" species.

TYPE LOCALITY. St. 160. Near Shag Rocks, 177 m., grey mud, stones.

SPECIMENS EXAMINED. St. 160, 4 specimens, R 3-6 mm.

St. 170. Off Cape Bowles, Clarence Island, 342 m., 1 specimen, R 5 mm.

Family PORANIIDAE Perrier

Genus *Porania* Gray

Porania Gray, *Ann. Mag. Nat. Hist.*, vi, 1840, p. 288. Type *Porania gibbosa* = *Asterias pulvillus* O. F. Müller.

Glabraster A. H. Clark, *J. Wash. Acad. Sci.*, vi, no. 5, 1916, p. 122. Type *G. magellanica* (Studer).

Porania antarctica Smith

Porania antarctica Smith, *Ann. Mag. Nat. Hist.*, ser. 4, xvii, 1876, p. 108.—*Phil. Trans.*, Zool. Kerguelen Island, etc., CLXVIII, 1879, p. 275, pl. 17, fig. 1.—Sladen, 1889, p. 360, pl. 59, fig. 3.—Perrier, 1891, p. 107.—Ludwig, 1905, p. 51, pl. 6, fig. 1.—Koehler, pars, 1923, p. 70 (Burdwood Bank).

Porania magellanica Studer, *Monatsber. preuss. Akad. Wiss. Berlin*, July 1876, p. 459.—Sladen, 1889, p. 363, pl. 59, fig. 5.

Glabraster magellanica A. H. Clark, *J. Wash. Acad. Sci.*, vi, no. 5, 1916, p. 122.

St. WS 80. Falkland Islands, 50° 57' S, 63° 37' W, 152-156 m., fine dark sand, 1 specimen.

St. WS 84. 7½ miles south-west of Sea Lion Island, East Falkland Island, 75-74 m., coarse sand, shells, stone, 2 specimens.

St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shells, 4 specimens.

St. WS 93. West Falkland Islands, 51° 51' S, 61° 30' W, 133-130 m., grey sand, 1 specimen.

St. WS 245. Falkland Islands, 52° 36' S, 63° 40' W, 304-290 m., 1 specimen.

St. WS 824. Falkland Islands $52^{\circ} 29\frac{1}{4}'$ S, $58^{\circ} 27\frac{1}{4}'$ W, 146–137 m., 4 specimens.

St. WS 825. Falkland Islands, $50^{\circ} 50'$ S, $57^{\circ} 15\frac{1}{2}'$ W, 135–144 m., 1 specimen.

St. 1563. Marion Island, $48^{\circ} 48\cdot4'$ S, $37^{\circ} 49\cdot2'$ E, 101–106 m., 2 specimens (intermediate).

St. 1564. Marion Island, $46^{\circ} 36\cdot5'$ S, $38^{\circ} 02\cdot3'$ E, 108–113 m., 4 specimens.

Although it has long been customary to regard *Porania* of the Magellanic region as identical with that of Kerguelen, Crozet, and Prince Edward Islands, the case is far from being established. The only continuity of distribution may well be through the really Antarctic *glabra* which is probably the parent form of both stocks—that of the American Quadrant and that of the African Quadrant. Be that as it may, *P. antarctica* does not range as far south as the Antarctic Convergence except at Kerguelen.

The specimens from St. 1564, Marion Island, slightly north of the Antarctic Convergence, are typical *antarctica* and have longer subambulacral spines and less robust abactinal spines than specimens from the Falkland region. The two examples from St. 1563 have only a few abactinal spines in the radial areas and are intermediate with *glabra*. Three specimens from St. 1562, Marion Island, are also intermediate but nearer to *glabra* (*q.v.*).

I believe a good series of specimens from the African Quadrant north of the Antarctic Convergence would be demonstrably different from the South American form. The few specimens obtained by the 'Discovery' from Marion Island substantiate this conclusion.

The Falkland specimens vary considerably in the number of abactinal spines, some having more numerous and larger spines than Sladen's fig. 5 which represents about the minimum number for adults. Small examples have the fewest spines—sometimes only 3 or 4 along the radial line.

In *glabra* the young may have small tubercular spines but these disappear in the adult, whereas in *antarctica* the number and size increase with age.

A specimen from St. WS 80, with R 60 mm., r 32 mm., has 30–35 *stout* tubercular spines to each ray, not counting a pentagon of 11 in centre of disk. It resembles, dorsally, an arcuate pentagonal Echinasterid such as *Poraniopsis*.

Apparently the dermal spinelets of *glabra* do not occur in this race except as rudiments in young specimens.

Colour note, St. WS 245: abactinal surface brilliant deep scarlet.

TYPE LOCALITY. Kerguelen.

DISTRIBUTION. Prince Edward, Marion, Crozet Islands; Kerguelen; Falkland-Magellan Plateau, north along the Chilean coast to Calbuco ($41^{\circ} 45'$ S).

Porania antarctica glabra Sladen

Porania glaber Sladen, 1889, p. 360, pl. 59, figs. 1, 2.

Porania spiculata Sladen, 1889, p. 362, pl. 59, fig. 4.

Porania antarctica Studer, Die Seesterne Süd-Georgiens, *Jahrb. weiss. Anstalten zu Hamburg*, 1885, p. 160.—Ludwig, 1903, p. 22, pl. 2, figs. 18–20.—Koehler, 1906, p. 10.—1911, p. 27.—1912, p. 66.—1917, p. 42.—1920, p. 178, pl. 33, figs. 6, 7.—1923, pars, p. 74 (Graham Land, South Georgia).

Porania armata Koehler, 1917, p. 43, pl. 7, figs. 3, 4, 7, 12.—Döderlein, 1928, p. 297.

- St. 39. East Cumberland Bay, South Georgia, 179-235 m., grey mud, 2 specimens.
 St. 42. Off mouth of Cumberland Bay, South Georgia, 120-204 m., 4 specimens.
 St. 45. 2.7 miles south-east of Jason Light, South Georgia, 283-270 m., grey mud, 1 specimen.
 St. 123. Off mouth of Cumberland Bay, South Georgia, 230-250 m., grey mud, 4 specimens.
 St. 141. East Cumberland Bay, South Georgia, 17-27 m., 1 specimen.
 St. 148. Off Cape Saunders, South Georgia, 132-148 m., grey mud and stones, 4 specimens.
 St. 149. Mouth of East Cumberland Bay, South Georgia, 200-234 m., mud, 1 specimen.
 St. 156. South Georgia, 53° 51' S, 36° 21' 30" W, 200-236 m., rock, 7 specimens.
 St. 159. South Georgia, 53° 52' 30" S, 36° 08' W, 160 m., rock, 39 specimens.
 St. 160. Near Shag Rocks, 53° 43' 40" S, 40° 57' W, 177 m., grey mud, stones and rock, 9 specimens.
 St. 170. Off Cape Bowles, Clarence Island, 61° 25' 30" S, 53° 46' W, 342 m., rock, 10 specimens.
 St. 175. Bransfield Strait, South Shetlands, 63° 17' 20" S, 59° 48' 15" W, 200 m., mud, stones, gravel, 1 specimen.
 St. 181. Schollaert Channel, Palmer Archipelago, 64° 20' S, 63° 01' W, 160-335 m., mud, 1 specimen.
 St. 187. Neumayr Channel, Palmer Archipelago, 64° 48' 30" S, 63° 31' 30" W, 259 m., mud, 4 specimens.
 St. 190. Bismarck Strait, Palmer Archipelago, 64° 56' S, 63° 35' W, 93-130 m., rock or stones and mud, 3 specimens.
 St. 366. 4 cables south of Cook Island, South Sandwich Islands, 77-152 m., 2 specimens.
 St. 371. 1 mile east of Montagu Island, South Sandwich Islands, 99-161 m., 1 specimen.
 St. 456. 1 mile east of Bouvet Island, 40-45 m., 9 specimens.
 St. 1562. Marion Island, 46° 52' S, 37° 55' E, 97-104 m., 3 intermediate specimens.
 St. 1652. Ross Sea, 75° 56.2' S, 178° 35.5' W, 567 m., 2 specimens.
 St. 1660. Ross Sea, 74° 46.4' S, 178° 23.4' E, 351 m., 2 specimens.
 St. 1952. Between Penguin Island and Lion's Rump, King George Island, South Shetlands, 367-383 m., 1 specimen.
 St. WS 25. Undine Harbour (North), South Georgia, 18-27 m., mud, sand, 5 specimens.
 St. WS 62. Wilson Harbour, South Georgia, 15-45 m., 2 specimens.
 St. WS 65. Undine Harbour (North), South Georgia, shore collection, 1 specimen.
 St. MS 74. East Cumberland Bay, South Georgia, 22-40 m., 1 specimen.

Of the 118 specimens, 36 have R between 30 and 65 mm. and may reasonably be regarded as adult. Nine specimens from St. 456, Bouvet Island, have a few short tubercles scattered along the radial series of plates, or restricted to the outer half of ray where they may occur also on either side of the radial series. All the others, from South Georgia, the Antarctic Archipelago, and Ross Sea, have a perfectly smooth abactinal surface, although imbedded in the skin are a variable number of delicate spinelets which are clearly visible only when the specimen is dried. These spinelets are extremely numerous in the Bouvet Island specimens, occurring on the papular areas as well as plates. They never occur on the actinal surface. They appear to be a normal character of *glabra*, although they are sometimes very small and restricted to the lateral parts of the abactinal area. In small and medium-sized alcoholic specimens in which the membrane is usually thinner than in the adult the spicules, if very numerous, are often visible under a strong hand-lens, but become conspicuous only when dry, giving the abactinal surface a finely spiculate texture.

Sladen's *Porania spiculata* therefore appears to be a normal specimen of *glabra*.

Young specimens may have a variable number of short abactinal tubercles, or rarely of veritable spines, in addition to the integumentary spinelets. Such specimens are likely also to have more prominent and numerous marginal spines and more strongly spatulate subambulacral spines. This form is represented especially well by young specimens from Sts. 159, 170, 175. Apparently these tubercles are later absorbed or remain as scattered survivals (e.g. St. 456). But the spatulate character of the subambulacral spines (with or without more numerous marginals) is found in the adult stage and is characteristic of the Bouvet Island specimens as well as of others (e.g. St. 190).

In contrast to these there are young specimens (e.g. Sts. 45, WS 25, WS 62, WS 65) in which there are no abactinal tubercles while the short marginal spines are restricted to the interradial arc, the plates of the distal half of ray being smooth. The subambulacral spines are not broadly spatulate. Between these two extremes there are intergrades, as for instance at St. 159, where the spinous variation is common.

The matter resolves itself into the fact that (as in many species) there are two extremes in spine development—"multispinous" and "paucispinous", with intergrading stages. Sladen's type of *glabra* represents the paucispinous form while Koehler's *armata* is the multispinous. To the latter the Bouvet Island specimens are referable.

The absence of marginal spines from the distal plates is not a specific character. Neither does the presence of 2 (or even 3) subambulacral spines on distal adambulacral plates constitute a differential character. Even the paucispinous typical adult of *glabra* regularly carries on the distal plates 2 subambulacral spines, the form of which varies from narrowly to broadly spatulate, round-tipped to truncate.

The Shag Rocks specimens are definitely like those of South Georgia, the adults of which are devoid of abactinal tubercles and have the very delicate integumentary spinelets chiefly on the margin of the abactinal area. As might be expected the Ross Sea specimens are typical *glabra*.

One naturally wonders why Koehler, who merged *antarctica*, *magellanica* and *glabra* under one specific designation, was not more suspicious of the qualifications of his *armata*, the general locality of which (Kerguelen) had already yielded *antarctica*, *glabra* and *spiculata*.

Apropos the uniting of *antarctica* and *glabra*, Sladen distinctly states that in a good series of *antarctica* from the Prince Edward and Crozet Islands "The spiny character is present in all stages of growth". Adults of *glabra* with abactinal tubercles occur only as sporadic variations and are in no wise characteristic. It is not obvious that Koehler ever saw a typical specimen of *antarctica*. The Magellanic form which he lists from Burdwood Bank (1923, p. 74) certainly is not. All other specimens listed in his various papers are variants of *glabra*.

Porania glabra appears to be the pan-Antarctic form restricted to the region south of the Antarctic Convergence and ordinarily to moderate depths. *P. antarctica* in reality is sub-Antarctic, and reaches its best development well north of the Convergence.

Colour note, St. 42, South Georgia: two adults; one is orange while the other has the

abactinal surface reticulated whitish with duller papular areas; centre of disk dull orange; 5 abactinal interradial blotches of brilliant orange.

TYPE LOCALITY. Kerguelen Island, 30 and 127 fathoms.

DISTRIBUTION. Circumpolar, Antarctic; 15–567 m.

Family ECHINASTERIDAE Verrill

Genus *Poraniopsis* Perrier

Poraniopsis Perrier, *Comptes rendus*, CVI, 1888, p. 763 (*nomen nudum*).—1891, p. 105. Type *P. echinaster* Perrier.—Leipoldt, 1895, p. 589.—Fisher, *Zool. Anz.*, xxxv, 1910, p. 568.—*Bull. U.S. Nat. Mus.*, no. 76, 1911, p. 260.

Lahillea de Loriol, *Notes pour servir à l'étude des Échinodermes*, ser. 2, fasc. 2, 1904, p. 32. Type *L. mira* de Loriol.

Alexandraster Ludwig, *Mem. Mus. Comp. Zool.*, xxxii, 1905, p. 210. Type *A. mirus* Ludwig.

Ortmannia de Loriol, *Revue critique de paléozoologie*, Paris, x, 1906, p. 78 (proposed to replace *Lahillea*, preoccupied).—Bather, *Revue critique de paléozoologie*, Paris, x, 1906, p. 131.

Labillia de Loriol, *Revue critique de paléozoologie*, x, 1906, p. 77.

Poraniopsis echinaster Perrier

Poraniopsis echinaster Perrier, 1891, p. 106, pl. 10, figs. 2*a*, 2*b*.—Fisher, 1911, pp. 261, 265.—Koehler, 1912, p. 211.—Clark, *H. L.*, 1923, p. 290.

Poraniopsis echinasteroides Perrier, 1891, p. 197, pl. 10, figs. 2*a*, 2*b*.—Leipoldt, 1895, p. 589, pl. 31, fig. 6.

St. 399. 1 mile south-east of south-west point of Gough Island, 141–102 m.

The single specimen measures R 46 mm., r 23 mm., R = 2r; br 23–26 mm.; longest spines as follows: abactinal, 3.5 mm.; superomarginal, 4 mm.; inferomarginal, 4 mm.; subambulacral, 4.25 mm.; furrow, 3.5 mm.; greatest diameter of madreporite, 5 mm.

The abactinal spines are in 3 longiseries; including the superomarginals which border the abactinal area there are 5 series about equidistantly spaced; spines stout, tapered, bluntly pointed and seated on an elevated boss of the usually 4-lobed primary plates. The first 2 or 3 of the 19 inferomarginals carry 1 spine; the next 8–10 plates carry 2 spines, varying to 3 on 1 or 2 plates at midray; then the last 6 or 8 have 1 or 2 spines each. On the diplacanthid and triplacanthid plates the spines form a transverse series and the lower is usually somewhat flattened.

The actinal interradial angle is not heavily armed, there being 3–6 spines (3–3.5 mm. long) to each area. The 2 adambulacral spines (occasionally 3) are strongly flattened, spatulate, subtruncate. Although some of the furrow spines are slightly concave at the tip, the upper side is not strongly grooved as in *inflata*.

There are 4 marginal oral spines, the inner or apical spatulate, shallowly concave on upper side, the others much smaller, and narrower, decreasing rapidly in size toward the first adambulacral; 1 or 2 suboral spines, heavy, concave, like the apical spine.

The madreporite is prominent, convex, and constitutes a plate independent of the adjacent adcentral primary interradial.

Preparation of integument of papular areas reveals numerous embryonic perforated

plates of irregular outline, measuring 0.06–0.18 mm. in diameter, with as many as three layers of trabeculae in the centre. There are no integumentary spinelets or prickles such as characterize *P. mira* (de Loriol).

In comparison with *P. inflata* Fisher this particular specimen has a more flaccid body wall with obviously weaker skeleton, much fewer actinal intermediate spines, 2 inferomarginal spines (instead of 1) over most of ray; while the strong grooving of the actinal, adambulacral and oral spines of *inflata* is only faintly suggested in the furrow spines of *echinaster*. Our specimen of *echinaster* has 1 intermarginal spine at base of 6 out of 10 intermarginal areas. There are only a few inconspicuous intermarginal spinelets on the type of *inflata* but another specimen from the same region (Monterey Bay, California) has 8–13 in 1 or 2 intermarginal series.

P. inflata has been dredged from off Oregon to San Diego, California, 26–159 fathoms (Fisher, 1911, p. 264). *P. inflata flexilis* is apparently a deeper water race (334–600 fathoms) from California and probably extends to the Gulf of Panama, 458 fathoms (Ludwig, 1905, p. 210, as *Alexandraster mirus*). *P. flexilis* has a very delicate skeleton (Fisher, 1911, p. 265, pl. 64; pl. 112, fig. 2), slender acicular spines and no deposits in the abactinal integument.

H. L. Clark has described *P. capensis* from 160 and 230 fathoms, Cape Colony. It closely resembles our specimen of *P. echinaster* which is derived from a station (Gough Island) that is nearer to South Africa than to Tierra del Fuego.

Clark (1923, p. 291) has raised the question whether his species is specifically distinct from *echinaster*. The presence of 2 inferomarginal spines on many of the plates of his second specimen (1926, p. 20) is a character of *echinaster* shared by the Gough Island specimen. His larger specimen (R 68 mm.), with 2 inferomarginal spines, has the spines in general markedly sacculate which is not the case in *echinaster*, nor in *inflata*. Obviously a definitive decision must be postponed until an adequate series of specimens is available.

It is curious that a locality so near to Cape Horn as the Gulf of San Mathias, Argentina, would yield such a distinctly different species as *P. mira* (de Loriol), 1904. In this form the abactinal spines have a flattened, often capitate, tip, and are quite short and tubercular. In addition to the spines, the surface of the body is covered by a multitude of almost microscopic thorny spinelets (de Loriol, 1904, p. 33, pl. 3, fig. 1–1 h).

The only other species which has dermal spinelets is *P. japonica* Fisher from 182 fathoms off Honshu, Japan. This differs from *P. inflata*, the geographically nearest form, in having a decidedly broader abactinal area with more numerous abactinal spines, numerous delicate thorny spinelets immersed in the thick membrane of the papular areas, more widely spaced inferomarginal spines (often 2 to a plate as in *echinaster*) and adambulacral spines without a well-marked groove. The dermal spinelets are smaller, slenderer, and less numerous than those of *P. mira*.

TYPE LOCALITY. Nassau Bay, Tierra del Fuego, 95 m.

Genus *Rhopiella*¹ nov.

DIAGNOSIS. Small Antarctic Echinasteridae superficially resembling *Poraniopsis*, but differing in having a small spine on the furrow face of the adambulacral plates, in lacking intermarginal papulae, and in having gonopores in the actinal interradial area. Differing from *Echinaster*, *sensu stricto*, in the extensive actinal intermediate areas and in the adambulacral armature, which consists of a transverse comb of spines united by delicate membrane essentially as in *Pteraster*. Paedophoric. Type, *Rhopiella koehleri*.

REMARKS. This group includes also *Echinaster hirsutus* Koehler,² *E. pterasteroides* Koehler,³ and possibly *E. smilax* Koehler.⁴ These species have a general facies unlike that of the tropical and warm water species constituting the genera *Echinaster* and *Othilia*, a fact which evidently troubled Koehler (1920, p. 118).

In keeping with the larger disk, the interbrachial septum is rather strongly fortified with calcareous plates. The septal fold extends from the body wall inward to a concave free edge impinging on the stomach, the dorsal "attachment" reaching three-fourths the distance from margin to centre of disk (*R. koehleri*).

The skeleton of Koehler's *Echinaster smilax* is close-knit in contrast to the other species in which it is very open, while the spinelets are more simple. The terminal portion is not expanded, denticulate, and hyaline as in *R. koehleri*, *hirsuta* and *pterasteroides*. Yet in the large disk, proximally swollen rays, and structure of the adambulacral armature *smilax* seems to be nearer to *Rhopiella* than to *Echinaster*.

Rhopiella koehleri sp. nov.

(Fig. E, 2-2*d*; Plate X, figs. 1, 2)

DIAGNOSIS. Resembling *Rhopiella hirsuta* (Koehler),⁵ but with only a few large papulae scattered over the abactinal area; not more than a single papula to a skeletal mesh and numerous meshes without a papula. Whole body covered by a soft opaque skin, forming a thick sheath on spinelets, and a delicate web uniting the transverse comb of usually 5 adambulacral spinelets, R 33 mm., r 10 mm., R = 3.3r; br 10-11 mm.

DESCRIPTION. The general habit and the structure of the skeleton is like that of *hirsuta*. Koehler states that the number of papulae varies, in *hirsuta* from 1 to 5 or 6, according to the dimensions of the skeletal interval. In *koehleri* there is never more than one large papula to an interval and there are numerous meshes without a papula. There are no intermarginal and no actinal papillae.

The primary plates, which are irregularly lobed, carry 1 or 2 spinelets, 1-1.2 mm. long;

¹ Derived from *Rhopia*, Gray, a synonym of *Echinaster*, *sensu stricto*.

² Koehler, 1920, p. 113, pl. 12, fig. 9; pl. 24, figs. 6-9; pl. 66, fig. 2. Type locality, 66° 32' S, 141° 39' E, 151 fathoms.

³ Koehler, 1920, p. 115, pl. 16, figs. 4, 5, 8; pl. 25, figs. 3, 4, 5; pl. 66, fig. 3. Type locality, 64° 44' S, 97° 28' E, 358 fathoms.

⁴ Koehler, 1920, p. 111, pl. 12, fig. 10; pl. 25, figs. 1, 2, 6, 7; pl. 66, fig. 1. Type locality, 66° 8' S, 94° 17' E, 120 fathoms.

⁵ Koehler, 1920, p. 113, pl. 12, fig. 9; pl. 24, figs. 6-9; pl. 66, fig. 2 (as *Echinaster hirsutus*).

while the connecting, secondary plates have 1 or 2 smaller spinelets 0.8–0.9 mm. long. These are all encased in a soft but pulpy sheath which gives them the appearance of conical papillae. Koehler described the abactinal spinelets of *hirsuta* as being cylindrical in the proximal part but flattened in the distal half (also pl. 66, fig. 2). In *koehleri* the spinelets are not at all flattened distally. They are roughly clavate in form. Each spinelet is built of rather numerous radiating irregular longitudinal laminae, coarsely denticulate as shown in Fig. E, 2*b*.

The inferomarginal plates define the ambitus and carry 2–4 spinelets (similar to abactinal) in a transverse basally webbed comb. The plates are fundamentally 4-lobed but are often irregular. The superomarginals are discernible only in a cleared preparation and then cannot be followed satisfactorily proximal to middle of ray. On the outer half of ray the superomarginals, inferomarginals and adambulacrals form 3 adjacent series. Superomarginal spines similar to abactinals.

The extensive actinal intermediate areas are characteristic of the genus. The plates are generally monacanthid, the spaced spinelets forming transverse series between adambulacral and inferomarginal combs but with some irregularities. The innermost spine of the actinal series may be joined to the outer adambulacral spine by a shallow web (Fig. E, 2*c*, AC).

The adambulacral armature is a transverse series of 3 or 4 subambulacrals and 1 furrow spinelet. Fig. 2*c* shows the armature of the sixth plate of type (adoral face) while Fig. 2*d* is drawn from an excised plate (aboral face). The innermost subambulacral spine of consecutive series is involved in an inconspicuous contracted web which runs the length of furrow margin, above the furrow spine, and is homologous with the often conspicuous membrane between the innermost subambulacral spines of *Othilia* and *Echinaster*. It is indicated in Fig. 2*c*, but disappears in dried specimens.

Mouth-plates: deep in furrow a spinelet similar to adambulacral furrow spinelet; on furrow margin 3 or 4 webbed spinelets, the web continued to first subambulacral (and less conspicuously along furrow margin). Subambulacrals, 4–8 in each angle, either webbed in 2 series or variously joined to marginals.

Madreporite very inconspicuous, situated $\frac{1}{3}$ r from centre of disk, and surrounded by a variable number of spinelets.

Gonads, with short lobes, attached interradially on a level with the inferomarginal plates, the duct opening below the inferomarginals in actinal interradiial area.

TYPE LOCALITY. St. 190, Bismarck Strait, Palmer Archipelago, 93–130 m., 1 specimen.

SPECIMENS EXAMINED. St. 181. Schollaert Channel, Palmer Archipelago, 160–335 m., mud, 1 specimen. St. 363. Off Zavodovski Island, South Sandwich Islands, 329–278 m., 8 specimens.

DISTRIBUTION. Known only from Palmer Archipelago and South Sandwich Islands, 93–335 m.

REMARKS. The specimen from St. 181 has the disk strongly arched and the bases of the rays drawn together to form a brood chamber in which, close to mouth, were a few eggs measuring 3–4 mm. in diameter.

It is probable that *Echinaster smithi* Ludwig (1903, p. 34) belongs in *Rhopiella*. It was dredged in 450 m., 71° 18' S, 88° 02' W. The papulae are numerous, 3-6 to the skeletal meshes. In the absence of figures it is not possible to determine whether the species is the same as any one of the three described by Koehler.

Genus *Henricia* Gray

Henricia Gray, *Ann. Mag. Nat. Hist.*, vi, 1840, p. 184. Type *H. oculata* Gray, i.e. *Asterias sanguinolenta* O. F. Müller.

Cribrella Forbes (not *Cribrella* Agassiz, 1835), *British Starfishes*, 1841, p. 100.

Cribrella Lütken, *Vid. Medd. for 1856*, 851, p. 93.

The name *Henricia* is applied to a rather considerable number of extremely unstable entities, for convenience called species, which are similar in a general way to members of the adjacent genera *Echinaster* and *Othilia*. It differs chiefly in lacking the membrane which unites the spines of the furrow edge, in the last 2 genera, into a continuous web along the margin of furrow. Of only a few forms is there enough material for a critical study of the species problem. This task is rendered all the more difficult because, added to the paucity of suitable characters, there is an extraordinary variability, and a marked tendency to what may be termed a structural equivalence in widely separated localities. An instance of this is *Henricia sufflata*, Kermadec Islands, *Henricia aspera*, west coast of North America, and *Henricia obesa*, Falkland region. So far as there are "species" in sea stars, these three are probably perfectly distinct. Yet the extremes of variation of each form very nearly bridge the gaps of structural difference between the three. *Henricia* has large eggs, and, so far as I am aware, pelagic larvae are not known in the genus. It seems probable therefore that any environmental peculiarities would have a maximum effect on individuals, and that here, if ever, we might expect to find small species developing in the inevitably many suitable but different faunal situations available.

This similarity of species from widely separated parts of the globe probably reveals a real relationship. Such equivalent species are subdivisions therefore of a sort of superspecies of wide range. The same idea is carried out in the concept of a wide-ranging species with numerous subspecies.

In the case of *Henricia*, representatives of more than one superspecies may occur in a locality or region. If 2 or 3 such distinct strains (each with its variations) are regarded as varieties of one species, confusion is piled on confusion. An instance of such a confusion is to be found in the classification of the Magellanic-Falkland *Henricias*. Here representatives of two distinct superspecies, *H. obesa* and *H. studeri*, have been united with the representative of yet a third, *H. paginstecheri*. Leiboldt (1895, pp. 578, 579) tossed into this *pot pourri*, also, *H. sufflata*, *H. simplex*, and by implication the then composite *H. sanguinolenta*! If these are one species, then any attempt to classify *Henricia* of the shallow waters of the world becomes absolutely futile.

As representatives of one of these "superspecies" I would adduce *Henricia scabrior* (Michailovskij),¹ *H. aspera* Fisher, *H. obesa* Sladen, *H. sufflata* Sladen. Another is

¹ S. G. Hedging, 1935, p. 31.

represented by *H. abyssalis* (Perrier),¹ *H. compacta* Sladen, *H. studeri* Perrier. *Henricia scabrior* had been submerged as a form of *sanguinolenta* until 1935, but an equivalent species (*aspera*) in the north Pacific was described by me in 1906. There it is sometimes found in the same locality with *H. sanguinolenta*.

The point of the above remarks is the belief that *Henricia pagenstecheri*, *H. obesa*, and *H. studeri* are each a segment of 3 distinct strains of very wide distribution.

I believe the only solution possible for the *Henricia* puzzle is to reduce it to a problem of a natural faunal region; to analyse these faunas one by one; and finally to trace through a mosaic of all *Henricia* faunas available the pattern of the superspecies. This was the idea I had in mind in analysing the north Pacific fauna (Fisher, 1911, pp. 266-305; 1930, pp. 194-6). Hedding (1935, pp. 16-34) has made a similar attempt for the north Atlantic region.

Henricia studeri (Perrier)

(Plate XI, fig. 1)

Cribrella studeri Perrier, 1891, p. 102, pl. 9, figs. 2a-2d.

Cribrella pagenstecheri pars, Leipoldt, 1895; Meissner, 1904; Ludwig, 1905.

St. WS 81. 8 miles north-west of North Island, West Falkland Island, 81-82 m., sand, 3 specimens.

St. WS 82. Falkland Islands, 51° 30' S, 61° 15' W, 140-144 m., 1 specimen.

St. WS 84. 7½ miles south-west of Sea Lion Island, East Falkland Island, 75-74 m., coarse sand, shell, stones, 1 specimen.

St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shell, 6 specimens.

St. WS 86. Falkland Islands, 53° 53' 30" S, 60° 34' 30" W, 151-147 m., sand, shell, stones, 31 specimens.

St. WS 87. Falkland Islands, 54° 07' 30" S, 58° 16' W, 96-127 m., sand, shell, stones, 1 specimen.

St. WS 97. Falkland Plateau, 49° 30' S, 61° 58' W, 146-145 m., 1 specimen.

St. WS 246. Falkland Islands, 52° 25' S, 61° W, 267-208 m., coarse green sand and pebbles, 1 specimen.

St. WS 824. South-east of East Island, 52° 29½' S, 58° 27½' W, 146-137 m., 1 specimen.

St. WS 871. Falkland Islands, 53° 16' S, 64° 12' W, 336-341 m., 1 specimen.

St. WS 872. Falkland Islands, 53° 48' S, 64° 18½' W, 139-141 m., 1 specimen.

This species, submerged heretofore as a synonym of *pagenstecheri*, is readily separable from that form since its relationships lie in another direction. *H. studeri* is a link in a chain of species, encircling the southern hemisphere, which are the antithesis of *pagenstecheri* in being characterized by having numerous spinelets compactly placed on the plates, especially the marginal, actinal, and adambulacral. The actinal series of plates extends well beyond the middle of ray, sometimes nearly to the tip. This chain of species includes *H. abyssalis* (Perrier) Mortensen, Cape of Good Hope; *H. praestans* (Sladen) Crozet Islands; *H. compacta* (Sladen) New Zealand; *H. studeri*. Probably the multispinous deep-water species, which regularly have 2 or 3 adambulacral spinelets deep in the furrow, are also related to this *compacta-studeri* group. Such, *inter alia*, are *H. pauperrima* Fisher, Hawaiian Islands, *H. densispina* (Sladen), Philippines to Korea;

¹ Mortensen, 1933, p. 265.

H. microplax Fisher, Mindanao Sea; *H. arcystata* Fisher, Philippines; *H. polyacantha* and *H. clarki* Fisher, Pacific coast of North America.

In the absence of a series of *H. compacta* it is not possible to determine what may constitute the real differences which separate it from *studerii*, for there is no reason to expect that *compacta* is less variable than other species.

I believe we can safely conclude at this time, that *studerii* and *compacta* are "divisions" of a wide-ranging subantarctic multispinous stock (as distinguished from the *simplex-pagenstecheri* stock). So far as there are species in *Henricia* these widely separated "colonies" can conveniently be called species. But the task of putting into words exactly what characters distinguish each is vastly complicated by the wide range of parallel variations which each species reveals as soon as sufficient specimens are assembled. Perhaps we shall never agree on specific limits in *Henricia* for the simple reason that Linnaean species probably do not exist.

Where *studerii* and *obesa* range together, as at St. WS 86, a few specimens may reasonably be regarded as intergrades. They are intermediate in what are assumed to be specific characters and are intergrades in the sense that they are probably hybrids. An exactly similar situation exists in the north Pacific whenever independent stocks of *Henricia* overlap in their ranges.

Studerii may be distinguished from *obesa* by the smaller skeletal intervals between the abactinal primary plates and the typically more numerous and slightly larger delicate spinelets of these plates. The adambulacral plates frequently have 2 spinelets deep in furrow and 12–16 subambulacral spines, of which three commonly stand on the furrow margin. There is less interval between successive plates in *studerii*. The plates of actinal surface are more densely spined and have smaller skeletal intervals. The series of actinal plates in specimens of approximately equal size extends farther along the ray in *studerii*, sometimes to the tip, whereas in *obesa* this series adjacent to the adambulacrals usually dies out at the middle of ray. This is a useful guide character for doubtful specimens but must be used in connection with the *sum* of other diagnostic features.

The general appearance of most of the specimens from St. WS 86 is closely similar to that of *H. microplax*, 200 fathoms, Mindanao Sea (Fisher, 1919, pl. 120, figs. 3, 5; pl. 121, fig. 2).

A colour note attached to a specimen from St. WS 81 reads "Orange yellow to light red dorsally, dull yellow ventrally".

TYPE LOCALITY. South of Cape Horn, 99 m.

DISTRIBUTION. Cape Horn—Falkland plateau, 74–341 m.

Henricia obesa (Sladen)

(Plate XI, fig. 2)

Cribrella obesa Sladen, 1889, p. 544, pl. 96, figs. 3, 4; pl. 98, figs. 5, 6.

Cribrella hyadesi Perrier, 1891, p. 100, pl. 9, figs. 1a–1d.—Leipoldt, 1895, p. 578, pars.—Meissner, 1896, p. 99.

Cribrella pagenstecheri Meissner, 1904, p. 13.—Ludwig, 1905, p. 68.

Henricia obesa Fisher, 1906, p. 1091.

Henricia hyadesi Clark, H. L., 1910, p. 336, pl. 2, fig. 5.

Henricia pagenstecheri Koehler, pars, 1923, p. 60.

St. WS 81. 8 miles north-west of North Island, West Falkland Island, 81–82 m., sand, 6 specimens.

St. WS 84. $7\frac{1}{2}$ miles south-west of Sea Lion Island, East Falkland Island, 75–74 m., coarse sand, shell, stones, 8 specimens.

St. WS 85. Falkland Islands, $52^{\circ} 09' S$, $58^{\circ} 14' W$, 79 m., sand and shell, 11 specimens.

St. WS 86. Falkland Islands, $53^{\circ} 53' 30'' S$, $60^{\circ} 34' 30'' W$, 151–147 m., sand, shell, stones, 19 specimens.

St. WS 93. West Falkland Island, $51^{\circ} 51' S$, $61^{\circ} 30' W$, 133–130 m., grey sand, 3 specimens.

St. WS 108. Falkland Island, $48^{\circ} 30' 45'' S$, $63^{\circ} 33' 45'' W$, 118–120 m., fine dark sand, 1 specimen.

St. WS 109. Falkland Islands, $50^{\circ} 18' 48'' S$, $58^{\circ} 28' 30'' W$, 145 m., fine dark sand, 1 specimen.

St. WS 220. South-east of Cape Tres Puntas, $47^{\circ} 56' S$, $62^{\circ} 38' W$, 108–104 m., 1 specimen.

St. WS 243. North-east of Falkland Island, $51^{\circ} 06' S$, $64^{\circ} 30' W$, 144–141 m., coarse dark sand, 13 specimens.

St. WS 248. Falkland Island, $52^{\circ} 40' S$, $58^{\circ} 30' W$, 210–242 m., fine green sand, pebbles, shells, 4 specimens.

St. WS 576. Berkeley Sound, $51^{\circ} 35' S$, $57^{\circ} 49\frac{3}{4}' W$, 34–24 m., 1 specimen.

St. WS 776. Off Cape Tres Puntas, Argentina, 107–99 m., 2 specimens.

St. WS 782A. North Falkland Island, $50^{\circ} 29\frac{1}{4}' S$, $58^{\circ} 23\frac{3}{4}' W$, 141–146 m., 1 specimen.

St. WS 791. North-east of Cape Tres Puntas, $45^{\circ} 38' S$, $62^{\circ} 57' W$, 97–96 m., 1 specimen.

St. WS 796B. South-east of Cape Tres Puntas, $47^{\circ} 53\frac{1}{2}' S$, $63^{\circ} 32\frac{1}{2}' W$, 108–112 m., 1 specimen.

St. WS 804. North-west of West Island, Falkland Islands, 150–143 m., 1 specimen.

St. WS 807. East of Porto Santa Cruz, $49^{\circ} 50\frac{1}{2}' S$, $65^{\circ} 03' W$, 125–126 m., 1 specimen.

This species differs from *H. studeri* (Perrier) in having a rather large-meshed abactinal skeleton—a characteristic which is illustrated by Sladen's and Perrier's figures. The actinal skeleton is also more open, with larger meshes and smaller plates. In both species 3 longitudinal, regular series of plates are usually present, representing 1 actinal (contiguous with adambulacrals) and 2 marginal series. The actinal series extends to about the middle of ray, and in robust specimens of *obesa*, a second, shorter actinal series is present exterior to the first. As a matter of fact this second series is present also in slenderer rayed specimens (similar to the type of *hyadesi*) but the skeletal spaces are smaller. Similarly, 1–3 short longiseries of intermarginal plates are present at base of ray, the length of series and spacing varying with robustness of ray.

There are about 6–9 subambulacral spines, usually arranged with 1, sometimes 2, on the furrow margin (above the curved, generic, furrow spinelet), followed by 2 not very regular trans-series of 3 or 4 spines each; or the innermost spine is followed by 1 or 2 similar but slightly shorter ones, and then a group of 3–6 spinelets. There is considerable variation in arrangement but the spinelets are fewer in number than in *H. studeri*. In very small specimens occasionally plates carry a single transverse series of 5 or 6 spinelets after the manner of *pagenstecheri* (q.v.).

It hardly seems useful to divide this species into named formae such as forma *obesa* and forma *hyadesi*, on account of the large number of intermediate variations not quite typical of either. One variant (e.g. from Sts. WS 248 and 782A) does not show a clear

serial arrangement of the actinal and marginal plates, which gives the specimens a very abnormal appearance. An analogous, sporadic, variation occurs in *Henricia leviuscula* of the Pacific coast of the United States.

The largest specimen (St. WS 791) measures R 72 mm., r 16 mm., br 18–21 mm.

A specimen from St. WS 81 carries a colour note: orange red dorsally and dull yellow ventrally.

Clark (1916, p. 60) has recorded as *hyadesi* 11 specimens from Tasmania, Bass Strait, south of Gabo Island (Victoria), and Great Australian Bight, 50–200 fathoms. Dr Clark has sent me a specimen from each locality except Bass Strait. While they undoubtedly closely resemble the Magellanic species, an extensive series of *obesa* and *studer* throws a different light on the matter. The specimen from south of Gabo Island seems to me to be a slender-rayed form of *H. sufflata*, Kermadec Islands. That from 78 fathoms, east of Maria Island, Tasmania, is possibly also a form of *sufflata* (but definitely not *hyadesi*); while that from the Great Australian Bight is of the *compacta* group, with numerous adambulacral spines.

Whether or not this interpretation is correct, it is, nevertheless, evident that in the waters south of Australia there are forms closely similar to both *studer* and *obesa*, just as in the Auckland-Campbell Islands there is a form equivalent to *pagenstecheri* of South Georgia.

TYPE LOCALITY. Challenger St. 315, Port William, Falkland Islands, 12 fathoms, sand, gravel.

DISTRIBUTION. Typically a species of the Falkland Plateau and Magellan region; north on the Pacific side of Iquique, Chile (Meissner) and on the Atlantic side to north-east of Cape Tres Puntas, Argentina; 24–242 m. in the Falkland region; as deep as 245 fathoms off entrance to Smyth Channel (Challenger). It is possible that the record from Iquique, Chile, may refer to another, nearly related form. *H. australis* Barattini (1938) off Uruguay, closely resembles *obesa* and may be one of its numerous variants.

Henricia pagenstecheri (Studer)

(Plate XI, fig. 4)

Cribrella pagenstecheri Studer, 1885, p. 158, pl. 2, figs. 6a, 6b.

Henricia pagenstecheri Koehler, pars, 1923, p. 60 (Shag Rocks).

- St. 6. Tristan da Cunha, 80–140 m., rock, 1 specimen.
- St. 25. 19 miles north-east of Jason Light, South Georgia, 18–27 m., 2 specimens.
- St. 39. East Cumberland Bay, South Georgia, 179–235 m., grey mud, 1 specimen.
- St. 123. Off mouth of Cumberland Bay, South Georgia, 230–250 m., grey mud, 1 specimen.
- St. 140. Stromness Harbour to Larsen Point, South Georgia, 122–136 m., green mud and stones, 4 specimens.
- St. 141. East Cumberland Bay, South Georgia, 17–27 m., 1 specimen.
- St. 148. Off Cape Saunders, South Georgia, 132–148 m., grey mud and stones, 1 specimen.
- St. 149. Mouth of East Cumberland Bay, South Georgia, 200–234 m., mud, 1 specimen.
- St. 156. South Georgia, 53° 51' S, 36° 21' 30" W, 200–236 m., rock, 1 specimen.
- St. 160. Near Shag Rocks, 53° 43' 30" S, 40° 57' W, 177 m., grey mud, stones, rock, 5 specimens.
- St. 474. 1 mile west of Shag Rocks, 199 m., 1 specimen.
- St. WS 27. South Georgia, 53° 55' S, 38° 01' W, 106–109 m., gravel, 1 specimen.

The largest specimen, St. 39, measures R 17 mm., r 5 mm., br 5 mm. Kochler (1923) records 2 specimens from Shag Rocks, 160 m., having R 30 and 36 mm. It is probable that the species never attains a size comparable to that of *obesa*. Rays slender to medium robust.

The adambulacral armature consists of a transverse series of 4 or 5 prominent subambulacral spinelets, decreasing in length from furrow outward, and in addition 1, or occasionally 2, shorter, but still prominent spinelets deep in furrow. The subambulacral spinelets are the longest on the body. The consecutive series are well spaced from one another and constitute a conspicuous cheval-de-frise all along the furrow margin. The single series of actinal plates extends to middle of ray and each carries 1 to sometimes 2 or 3 delicate spinelets, shorter than the outer subambulacrals (and much shorter than the longer furrow members of series). The marginal plates do not form very regular series. The inferomarginals carry 3-5 short spinelets in a transverse series or a group, while the superomarginals (not always recognizable) are like the abactinals and carry usually 1-3 short spinelets in irregularly spaced groups.

The papulae are dorsally 1 or sometimes 2 to each mesh of the skeleton; laterally and ventrally they are single, and extend to the adambulacral plates, adjacent to which there is a regular series for the entire length of the ray. (This series is entirely lacking in the fine specimen of *simplex* from Marion Island. In this the papulae do not cross the inferomarginal plates, *there being no true actinal papulae.*)

The tiny specimen from Tristan da Cunha has R 6 mm. and r 2 mm. It has actinal papulae and is not distinguishable from an equal sized specimen from St. 140.

Mortensen (1925, p. 304, pl. 13, figs. 1, 2) has given notes on *H. lukinsii* of the Auckland-Campbell Islands and has differentiated it from *pagenstecheri*. It is probably a valid "small species", but it is only fair to record that some of the peculiarities of *lukinsii* are not so apparent when a good series of *pagenstecheri* is examined. For instance, in the latter the spinelets of the proximal marginal plates often form transverse series with those of the adambulacral and actinal intermediate plates. The true furrow spine of *pagenstecheri* is not always directed horizontally but may be bent upward (as viewed from actinal aspect). There is sometimes (e.g. St. 25) a conspicuous actinal interradiar naked area, or slight depression, in the angle outside the oral plates, as stated by Mortensen, but this area may also be nearly or quite obliterated by small spinelets, singly or in twos (Sts. 39, 123). The rays of *lukinsii* are stouter and the disk larger than in any of my specimens of *pagenstecheri*.

In spite of these apparent discrepancies I agree with Mortensen that there is an average difference between the two forms both of which are small in size and hence most difficult to evaluate accurately.

TYPE LOCALITY. South Georgia.

DISTRIBUTION. South Georgia, Shag Rocks, Tristan da Cunha, 18-250 m.

Henricia pagenstecheri parva (Koehler)

Cribrella parva Koehler, 1912, p. 40, pl. 4, figs. 3, 8.—1920, p. 118, pl. 25, fig. 10; pl. 26, figs. 1–11; pl. 66, fig. 4.

St. 170. Off Cape Bowles, Clarence Island, South Shetland Islands, 61° 25' 30" S, 53° 46' W, 342 m., rock, 1 specimen.

St. 1948. North-east of Clarence Island, 60° 49' 4' S, 52° 40' W, 490–610 m., 1 specimen.

This race is close to *pagenstecheri* from which it differs chiefly in having slightly larger abactinal plates carrying upward of 10 small spinelets which, like those of the South Georgia species, are minutely thorny. The adambulacral spinelets are not particularly different from those of *pagenstecheri* other than being slightly more numerous. Ordinarily there are 5 or 6 subambulacral spines in a single transverse series, the 2 ranks of combs on either side of furrow forming a prominent cheval-de-frise. But on the first 2 or 3 plates there are 7 or 8 spinelets in 2 complete or incomplete series. Here and there the adambulacral armature is aligned with the actinal and inferomarginal spinelets which are in close-set groups of 3–8 and do not form regular longiseries. The small single papulae extend to the adambulacral plates.

The specimen from St. 1948 measures R 22 mm., r 6 mm., br 6.5 mm.

The example from St. 170, measuring R 18 mm., r 4.5 mm., br 5 mm., is not at all typical in respect to adambulacral armature. The plates of the proximal half of ray in addition to a prominent furrow spinelet (or occasionally 2) have 7–9 subambulacral spinelets, arranged in the equivalent of 2 transverse series as a rule, but very irregularly so. Far along ray there is often a transverse series of 3 spines and a group of 3 or 4 smaller spinelets on the outer part of plate.

Koehler (1920) reported *parva* from off Adélie Land and Queen Mary Land, 110–151 fathoms. Abactinally, these resemble *pagenstecheri* quite as much as they do *parva*.

TYPE LOCALITY. Admiralty Bay, King George Island, South Shetlands, 420 m.

DISTRIBUTION. Antarctic, circumpolar; 191–610 m.

Henricia simplex (Sladen)

(Plate XI, fig. 3)

Cribrella simplex Sladen, 1889, p. 547, pl. 97, figs. 5, 6; pl. 98, figs. 9, 10.

St. 1564. Off Marion Island, 46° 36' 5' S, 38° 02' 3' E, 108–113 m., 1 specimen.

The specimen measures R 36 mm., r 8 mm., br, beyond constriction, 10 mm. The photographic figure is introduced to indicate wherein this relatively large specimen varies from that illustrated by Sladen. There are usually 4 subambulacral spines in a single transverse series and these combs are aligned with the 1 or 2 actinal and 2–4 inferomarginal spinelets. The actinal plates extend about one-third length of ray measured on side. The supermarginals are not well marked except on outer third of ray; at the base of ray they are separated from the inferomarginals by a lateral wedge-shaped area of intermarginals—3 or 4 plates wide at interradius. The lowermost regular series of papulae lies just under the supermarginals on the lateral face of ray. *There are*

no papulae between the inferomarginals and actinals, nor between the latter and the adambulacrals. If the absence of actinal papulae is constant in specimens from Marion, Prince Edward, and the Crozets, then *simplex* may be readily distinguished from *pagenstecheri* in which there are actinal papulae even in specimens having R only 6 mm.

Sladen has recorded *simplex* from Tristan da Cunha where the 'Discovery' secured a tiny specimen of *pagenstecheri*. It would be an easy matter to confuse the two forms for they are not distinguishable on spine characters alone. Since Sladen describes abactinal and intermarginal papulae, but no actinal papulae, it seems almost certain that he had in hand *simplex* and not *pagenstecheri*.

DISTRIBUTION. Prince Edward Island, Marion Island, Crozet Islands, Tristan da Cunha, 50-150 fathoms.

Henricia diffidens (Koehler)

Echinaster diffidens Koehler, 1923, p. 58, pl. 8, figs. 1, 2; pl. 9, figs. 9, 10.

St. WS 840. 53° 52' S, 61° 49' W, 368-463 m., 1 specimen.

St. WS 871. 53° 16' S, 64° 12' W, 336-341 m., 3 specimens.

The largest specimen, from WS 840, measures R 17 mm., r 5.5 mm., br 6.5 mm.

The spines are somewhat longer than those of Koehler's specimens, particularly the types from Graham Land, indicating the possible existence of a different race on the Falkland Plateau.

It is not evident why Koehler placed this species in *Echinaster*, as it is of the general habit of *Henricia*, and very small specimens greatly resemble equal sized *H. pagenstecheri* but have more numerous, longer abactinal spines, fewer and less obvious actinal papulae. In the largest specimen the true actinal papulae appear at about the end of the proximal third of furrow (measured from mouth) at about the point where the actinal plates end. From this point to end of ray the spaced papulae lie between the inferomarginal and adambulacrals plates. Proximal to that point actinal papulae do not regularly occur.

H. diffidens greatly resembles two north Pacific species: *H. asthenactis* Fisher¹ and *H. longispina* Fisher.²

At St. WS 871 was taken also one specimen of *H. studeri*.

TYPE LOCALITY. Graham Land (Swedish Antarctic Expedition, St. 5) 64° 20' S, 56° 38' W, 150 m., sand and gravel.

DISTRIBUTION. Graham Land, South Georgia, Falkland Plateau, 75-463 m.

¹ Fisher, 1911, p. 297, pl. 77, fig. 1; pl. 111, figs. 4, 4a. Vicinity of Santa Barbara Island, California, to Bering Sea, 178-682 fathoms.

² Fisher, 1911, p. 299, pl. 76, figs. 1, 2; pl. 111, figs. 3, 3a. Vancouver Island to southern Alaska, 41-134 fathoms. A race of *longispina* occurs near Attu, Aleutian Islands, 135 fathoms (*H. longispina aleutica*, p. 300, pl. 77, fig. 2).

Family SOLASTERIDAE Perrier, emended

Genus *Lophaster* Verrill

Lophaster Verrill, *Amer. J. Sci. Arts*, ser. 3, xvi, 1878, p. 214. Type *Solaster fureifer* Düben & Koren.
Sarkaster Ludwig, *Mem. Mus. Comp. Zool.*, xxxii, July, 1905, p. 185. Type *Sarkaster validus* Ludwig.

DIAGNOSIS. Five-rayed¹ Solasteridae with cruciform or lobed abactinal paxilliform plates (without intermediate connecting ossicles) forming a skeleton of quadrate or polygonal meshes; with 2 well-developed series of marginal paxillae, and with usually a single series of spaced actinal intermediate plates, with or without a paxilliform tuft of spinelets, extending far along the ray; adambulacral armature not essentially different from that of *Solaster*; an interbrachial calcareous pillar from actinal to abactinal surface, but no membranous interbrachial septum between it and interbrachial angle as in *Crossaster*.

Lophaster stellans Sladen

(Fig. E, 3, 3a)

Lophaster stellans Sladen, 1889, p. 460, pl. 71, figs. 4, 5; pl. 72, figs. 11, 12.—Ludwig, 1903, p. 27, pl. 3, figs. 23, 24 (western Antarctica, not typical).—Koehler, 1920, p. 151.

Lophaster pentactis Perrier, 1891, p. 112, pl. 9, fig. 3, 3a-3e.—See Koehler, 1920, p. 151, pl. 31, figs. 6, 7; pl. 68, fig. 3 (type).

Lophaster levinseni Perrier, 1891, p. 7 (*lapsus*).

St. WS 81. 8 miles N, 11° W of North Island, West Falkland Island, 81-82 m., sand, 3 specimens.

St. WS 83. 14 miles S, 64° W of George Island, East Falkland Island, 137-129 m., fine green sand and shell, 2 specimens.

St. WS 243. North-east of Falkland Islands, 51° 06' S, 64° 30' W, 144-141 m., coarse dark sand, 7 specimens.

St. WS 244. Falkland Islands, 52° S, 62° 40' W, 253-247 m., fine dark sand and mud, 1 specimen.

St. WS 246. Falkland Islands, 52° 25' S, 61° W, 267-208 m., coarse green sand, 2 specimens.

St. WS 799. South-east of Cape Tres Puntas, 48° 04' S, 62° 48' 07" W, 141-137 m., 1 specimen.

St. WS 825. North-east of East Island, Falkland Islands, 50° 50' S, 57° 15' W, 135 m., 1 specimen.

St. WS 840. 53° 52' S, 61° 49' W, 368-463 m., 1 specimen.

St. WS 848. North-east of Atlantic Entrance to Strait of Magellan, 115-117 m., 2 specimens.

If there were any utility in recognizing 2 formae in this species, names are available. Forma *stellans*, illustrated by Sladen, has a large disk and broad rays tapering evenly to a pointed extremity. Two specimens from St. WS 83, with R 36 mm. and 30 mm., are typical. Forma *pentactis*, illustrated photographically by Koehler, has slender rays and the sides of the ray are at first subparallel and then taper gradually on the outer part. The marginal paxillae have longer pedicels. This form was taken at all the other stations except WS 799. One specimen from this station and one of those from WS 81 have the longer marginal paxillae, but the rays are intermediate between the two extremes.

¹ Exceptionally six-rayed, as a meristic variation.

Sladen's specimen from 1325 fathoms off the Chonos Archipelago merits further examination on account of the great depth. One suspects the existence of a deep water form analogous to *L. furcilliger*, Alaska to Galapagos Islands, 192-1100 fathoms.

Ludwig's figures (1903, pl. 3, fig. 23) do not represent typical abactinal spinelets of *stellans*, judging by specimens from the Falkland Plateau illustrated herewith, although they are similar to Kochler's photographs of the type of *L. pentactis* (1920, pl. 68, fig. 3).

TYPE LOCALITY. Not given. Taken by the 'Challenger' at three localities, off the coast of Chile, between $45^{\circ} 31' S$ and $50^{\circ} 56' S$, 40-1325 fathoms.

DISTRIBUTION. Falkland Plateau to $48^{\circ} S$; Strait of Magellan; coast of Chile to $45^{\circ} 31' S$, 80-267 m. (except Sladen's record of 1325 fathoms which is open to question). (Western Antarctica, e.g. $71^{\circ} 14' - 71^{\circ} 19' S$, $87^{\circ} - 89^{\circ} W$, 450 m., Ludwig; possibly a different race.)

Lophaster marionis sp.nov.

(Fig. F, 1-1d; Plate XIII, fig. 1)

DIAGNOSIS. Similar in general form to *L. furcilliger* Fisher, having narrow rays, small disk, and long pedicelled, penicillate paxillae, the inferomarginal being especially prominent; differs in lacking a definite series of actinal plates on ray and in details of spinulation especially in the more numerous unequal spinelets of marginal paxillae. R 30 mm., r 9 mm., br 10 mm. including marginal paxillae.

DESCRIPTION. Paxillae not crowded but distinctly spaced, penicillate, with 15-20 delicate, divaricate, usually 3-pronged, glassy spinelets about 0.8 mm. long on disk; pedicel slender, about as long as spinelets. Paxillae rapidly diminishing in size on outer half of ray where the pedicels are shorter than the 3-6 or 7 spinelets. The cruciform delicate abactinal plates (base of paxillae) are arranged in chevrons pointed toward centre of disk; the first chevron has 11 plates from side to side of ray, not counting the much larger superomarginals. The number then drops to 9, 7, and on outer third of ray to 5, although some irregularity exists. The plates are also aligned parallel to the superomarginals, but lateral-most row contains more plates than superomarginal series. Papulae few, 3-5 or 6 per area on disk; 2 or 3 on proximal part of ray; 1 or 0 on outer third. Madreporite small, 0.9 mm. in diameter, situated at mid-r.

Marginal plates one above the other, 20 to a ray in each series. Superomarginal paxillae abruptly larger than dorsolaterals; spinelets on proximal paxillae 12-15, similar to abactinal but a little stouter and varying in length from 0.75 to 0.85 mm.; proximal pedicels longer than spinelets.

Inferomarginal paxillae with terminally compressed pedicels slightly longer and decidedly stouter than superomarginal; spinelets proximally about 20, those on dorsal side of tip 0.6 mm. long, increasing to 1.1 mm. on ventral. The shorter have 3 or 4 prominent prongs but are broader distally than the abactinal spinelets. The longer spinelets have 4-7 prongs (Fig. F, 1b). The first 1 or 2 inferomarginals are smaller than the succeeding. On distal third of ray the pedicels rather rapidly shorten and are about half as long as the proximal.

Actinal intermediate plates about 8, carrying 1-4 delicate thorny spinelets, and not extending beyond third or fourth adambulacral plate, except for 1 or 2 rudimentary plates near middle of some of the rays.

Adambulacral plates very short but broad with prominent muscular intervals. Furrow comb consisting of proximally 4 or 3 (exceptionally 5) delicate, slender, long, basally webbed spines; and a transverse actinal comb of usually 4 or 3 subambulacrals of which characteristically the outer 2 (or 1) are much thornier and a little shorter than the inner 2 (the former 1.6 mm., the latter 1.8 mm., Fig. F, 1c, 1d). The spine numbers run as follows along one side of ray, the Roman numerals of each couplet being subambulacral, 4-IV; 4-IV; 3-V; 3-IV; 3-III; 3-III; 3-III. On another ray it runs 5-IV; 3-V; 4-IV; 4-IV; 4-II; 3-III; 3-IV; 3-IV; 3-III; 3-III; 3-IV; 3-IV; 3-III. On outer part of ray the 2 furrow spinelets gradually align themselves with the subambulacrals so that there is a single transverse fan of 5 or 6 spinelets to a plate.

Marginal mouth spines 7 or 8, similar to adambulacrals, basally webbed; on the convex outer part of mouth-plates, 3-5 slender subambulacrals, the inner slightly the longer.

Tube-feet with sucking disk about as broad as column.

TYPE LOCALITY. St. 1563, Marion Island, 46° 48' 4" S, 37° 49' 2" E, 101-106 m., 1 specimen.

REMARKS. The similarity of this species to *L. furcilliger*¹ Fisher, Alaska to Galapagos Islands, 192-1100 fathoms, has been mentioned in the diagnosis. In that form the abactinal 2- and 3-pronged glassy spinelets, 1-1.2 mm. long, radiate in all directions forming a subspherical group. The spinelets of the marginal paxillae are not markedly unequal in length nor is the pedicel of the inferomarginals compressed at the end. A series of spaced actinal platelets extends along the ray. In *L. suluensis*² Fisher the pedicels of abactinal and marginal paxillae are conspicuously shorter than the spinelets, which are not trifurcate; the subambulacral spines are much longer than the furrow spines, and are longer than marginal paxillae with their spines. *L. marionis* is probably most nearly related to *L. quadrispinus* Clark from the Cape region, South Africa. Clark compares *quadrispinus* to *L. furcilliger* but it is more like *L. stellans* Sladen. There is a well-developed series of actinal paxillae extending nearly to tip of ray and 8-12 similar but smaller paxillae in the remainder of the interradial area. Clark states that *quadrispinus* has much more numerous actinal paxillae than has *stellans*. But *stellans* also has a series of well-developed actinal paxillae extending to end of ray, while *marionis* has none. I think *quadrispinus* and *stellans* are closely related. In the matter of proportions and general habit my specimens of *stellans* agree with Clark's rather poor figures; and in addition to the series of actinal paxillae adjacent to the adambulacral plates there are 4-10 small paxillae in each interradial angle—a number which overlaps the 8-12 of *quadrispinus*. In *stellans* the furrow spines are generally 4, 3, 2; but also, as in *quadrispinus*, there may be 5 or 6³ at base of ray. In *quadrispinus* the reported number of

¹ Fisher, 1911, p. 334, pl. 79, figs. 1, 2; pl. 114, figs. 1-1g; pl. 116, fig. 5.—1930, p. 198.

² Fisher, 1919, p. 449, pl. 123, fig. 2; pl. 124, fig. 3; pl. 132, figs. 8, 8a.

³ Mortensen, 1933, p. 272.

subambulacra is 4, 3, 2; in *stellans* it is 6 or 5, and 4 only sporadically, or at tip of ray. The abactinal paxillar spinelets of *stellans* (0.7–0.9 mm. long) have 5 or 6 sharp prongs (Fig. E, 3*a*) rather than the 3 or 4 of *marionis*. Ludwig's figures (1903, pl. 3, fig. 23) do not represent typical abactinal spinelets of the *stellans* of Falkland region but are similar to Kochler's figures of the spinelets of *L. pentactis* Perrier (Kochler, 1920, pl. 68, fig. 3). Spines of *L. quadrispinus* have not been figured.

Out of this emerges the probability that *stellans* and *quadrispinus* are representative small species of the eastern and western hemispheres, connected by a pan-Antarctic species (or series of small species) of which *marionis* is a northern representative.

Lophaster gaini Kochler

Lophaster gaini Kochler, 1912, p. 42, pl. 4, figs. 4, 5, 12, 13.—1920, p. 143, pl. 31, figs. 8, 9; pl. 66, fig. 8.

St. 187. Neumayr Channel, Palmer Archipelago, 64° 48' 30" S, 63° 31' 30" W, 259 m., mud, 1 specimen.

St. 599. West coast of Adelaide Island, 67° 08' S, 69° 06½' W, 203 m., 1 specimen.

Kochler has fully described and figured this species, which appears to have no very close relatives. One might quite naturally assume it to be an Antarctic equivalent of *L. stellans* of the Cape Horn-Falkland region but this seems to be definitely not the case. *L. gaini* has highly characteristic abactinal spinelets which are needle-like and end in a single hyaline point, while in *stellans* these spinelets are characteristically 3- or 4-pronged as illustrated by Ludwig (1903) and Kochler (1920, pl. 68, fig. 3). I have verified the spine characters of both species. In *L. gaini* the marginal, especially the inferomarginal, spines are unusually coarse, rather few in number, and acicular in form (see Kochler, 1920, pl. 31, fig. 8). About 5 of the spines are conspicuously larger than the others and on the outer part of the ray they form a transverse comb, flanked on the adoral side by a group or series of 5 or 6 shorter spines. On the outer third of the ray the marginal plates and spines resemble those of *Gaueria*.

TYPE LOCALITY. South Shetland Islands (King George Island) 420 m., mud and stones.

DISTRIBUTION. South Shetland Islands, Palmer Archipelago, and Adelaide Island, 203–420 m. Adélie Land, 318–400 fathoms; Queen Mary Land, 110 fathoms. Probably a continuous circumpolar distribution.

Lophaster densus sp.nov.

(Fig. E, 4–4*c*; Plate XIII, figs. 2, 3)

DIAGNOSIS. Rays 5; R 19 mm., r 7.5 mm., br 8 mm. Disk rather high and rays strongly convex, the marginals being on the actinolateral border; paxillae close-set, low, compact, the abactinal view suggesting a short-rayed *Leptychaster*; marginal paxillae close-set, low, not projecting as in typical *Lophaster*, the very even surface of the abactinal spinulation passing without a break into that of inferomarginal paxillae; actinal surface with well-developed actinal interradial areas and suggesting a five-rayed *Solaster*.

DESCRIPTION. The paxillae are low, flat-topped, spaced less than the diameter of the crown of compactly placed short spinelets which form a co-ordinated group. Spinelets 15–30, usually 20–30, to a paxilla, slightly longer than the low tabulum which springs from a 4-lobed base. Spinelets with 3 deeply excavated sides, broadening conspicuously to a convex truncated summit beset with numerous points. Spinelets 0.3–0.4 mm. long and not obviously bound together by membrane, although there is a very delicate membrane at the base, continuous with the thin dermal investment of spinule.

The abactinal plates are squarish with rounded corners and shallowly excavated sides. They strongly overlap by these incipient lobes and the very small interstices accommodate a single papula. Plates form fairly regular transverse series, the regularity of which is interrupted at midradial line.

Madreporite 1.5 mm. in diameter, situated in middle of r and hidden by paxillae.

Superomarginals alternate with inferomarginals. They are conspicuously larger than adjacent small abactinals but on outer part of ray the difference is not so marked. The crown does not extend above the level of the abactinal paxillae, although the spinelets are slightly coarser and number about the same as on large abactinal paxillae (i.e. 20–30).

Inferomarginal paxillae 20, conspicuously larger than the superomarginals, with about the same number of still heavier spines which increase conspicuously in size from the dorsal to ventral margin of tabulum. The inferomarginals have a shorter pedicel and more compact appearance than in *L. stellans*. The largest spines are about 0.6 mm. long, while a few small ones from dorsal margin are as small as 0.3–0.4 mm. (Fig. E, 4*b*).

The actinal interradiar area is well developed for so small a specimen, containing 3 chevrons of plates. The first series extends to end of ray. The plates on the disk have 6–9 divaricate spines on a slight convexity. Beyond the second or third inferomarginal the plates become spaced and carry 3 or 4 spinelets, then 2, and finally only 1. At middle of ray there are 6 actinals to 3 inferomarginals. The second chevron does not extend beyond the second inferomarginal; while the third consists of 3–5 plates adjacent to the first inferomarginal of neighbouring series.

Adambulacral furrow spines 5, 4, 3, 2 from base to end of ray. They are rather coarse, subterete, round-tipped when covered with membrane. The 2 or 3 median are much longer than the laterals of the comb and all are united by web to mid-height. Subambulacrals in a curved transverse series of 4 or 5 spines increasing in size from outer to inner. The inner 2 or 3 are much coarser but not much longer than the median furrow spines and are from 1 to 1.2 mm. long (Fig. E, 4*c*).

The oral plates are characteristic of *Lophaster* in form and armature; marginal spines 6–8, webbed increasing in length to innermost, which, being slightly longer than subambulacrals, are the largest spines on body. Suborals 9 or 10 in two poorly defined series adjacent to median suture and widely spaced from the marginal spines.

Gonads interradiar, opening on upper border of first superomarginal plate. There is a slender calcified interbrachial pillar extending from odontophore to abactinal wall, but no membranous septum joins this pillar to the wall of body at interbrachium, as in *Crossaster*. There is no trace of the characteristic muscles of *Myoraster*.

TYPE LOCALITY. St. 175, Bransfield Strait, South Shetlands, 63° 17' 20" S, 59° 48' 15" W, 200 m., mud, stones, gravel. The type and a specimen with R 7.5 mm. Taken also at St. 1948, north-east of Clarence Island, 60° 49.4' S, 52° 40' W, 490–610 m., 1 specimen.

DISTRIBUTION. Known only from South Shetland Islands.

REMARKS. The specimen having R 7.5 mm. has the arched abactinal surface and neat appearance of the type, but the actinal interradial areas are very small. Only the first adambulacral plate has 5 furrow spinelets; subambulacrals proximally 4. The number of abactinal spinelets is of course variable but is of the order of 15 on the larger plates.

The specimen from St. 1948, received long after the original collection, has R 19 mm., r 8 mm., br 9 mm., and shows no important variations.

L. densus is very different from any described species. As stated in the diagnosis its dorsal aspect is that of a *Leptychaster*, while the close-set marginals on the actinolateral border are so different from those of *L. stellans* that one may say the divergence in general habit is as great as that between *Solaster endeca* and *Crossaster papposus*.

The type was dredged at the same station with *Myoraster antarcticus*. Of course this species is distinguished at once by its generic peculiarity, the actinolateral muscle. But superficially the paxillae are rather similar, though the spinelets differ in form. The inferomarginals of *Myoraster* are much more prominent than those of *densus* and the actinal interradial areas are distinctly smaller.

Genus *Paralophaster* nov.

DIAGNOSIS. Five-rayed Solasteridae closely similar to *Lophaster*, but without differentiated superomarginal paxillae. Type *Solaster godefroyi* Koehler.

REMARKS. Koehler described 4 species of Antarctic Solasteridae having five rays but differing from *Lophaster* in lacking differentiated superomarginal paxillae. These species are: *Solaster lorioli*¹ from 2500 fathoms, 67° 33' S, 36° 35' W; *S. godefroyi*² from 250 to 400 m., southern Bellingshausen Sea and off Queen Mary Land; *S. incertus*,³ Kerguelen, shallow water; *S. asperatus*,⁴ 110 fathoms, off Queen Mary Land.

Since Koehler's *Solaster* included also *Crossaster*, it is probable that he had the latter type in mind. In *Crossaster* the paxillae are penicillate and spaced; the superomarginal are subequal to the abactinal, while the inferomarginal are abruptly much larger. In *Solaster* (e.g. *S. endeca*) there are definite, differentiated superomarginal paxillae, although they are much smaller than the inferomarginals.

Paralophaster has the appearance of a 5-rayed *Crossaster*, but it lacks the membranous interbrachial septum of *Crossaster* (absent also in *Lophaster* and *Solaster*). The abactinal paxillae are arranged in oblique transverse rows as in *Solaster*, *Lophaster*, *Myoraster*, but not as in *Crossaster*.

¹ Koehler, 1908, p. 558, pl. 4, figs. 40, 41.

² Koehler, 1912, p. 50, pl. 4, figs. 2, 6, 9, 10, 11; 1920, p. 153, pl. 31, fig. 1; pl. 35, figs. 1–4; pl. 66, fig. 9.

³ Koehler, 1917, p. 40, pl. 5, figs. 2, 3; pl. 9, figs. 21, 22.

⁴ Koehler, 1920, p. 157, pl. 33, figs. 8, 9; pl. 65, fig. 3.

Paralophaster godefroyi, *asperatus* and *lorioli* form a homogeneous group. The only known specimen of *lorioli* is immature (R 22 mm., r 5 mm.).

Solaster incertus is probably not a *Paralophaster*. The type is small, dried, and imperfect (R 15 mm., r 5.5 mm.). There are no differentiated superomarginals.

Paralophaster godefroyi meseres n.subsp.

(Fig. F, 2-2*b*; Plate XII, figs. 2, 3)

DIAGNOSIS. Differing from *P. godefroyi* (Koehler) in the following particulars: adambulacral furrow spines 2 (3 on first few plates and 1 on distal); inferomarginal spines at middle of ray 20-25; abactinal paxillae with short pedicel carrying, on disk and base of rays, from 5 to 8 subequal, delicate, spinelets irregularly denticulate on the distal half; paxillae of outer half of ray with 2-5 spinelets; marginal mouth spines 6 or 7, suborals 3 or 4; actinal intermediate spines 2-5. R 28 mm., r 8 mm., R=3.5r; br at interradius, 9 mm.

DESCRIPTION. In the specimens of *godefroyi* from the type locality, the abactinal paxillae carry 2-4 central, and 6-10 peripheral spinelets, smaller than the central. In *meseres* the spinelets are fewer and very nearly equal; there is no differentiated central group. The superomarginal paxillae in both species are not distinguishable from the other abactinal paxillae. In the large example of *godefroyi* from off Queen Mary Land the abactinal paxillae have 15-20 spinelets while the large inferomarginals carry 15 spinelets—the same number as in the much smaller type. The obviously larger number of inferomarginal spinelets of *meseres* is the more surprising since the abactinal paxillae have fewer spines than in *godefroyi*.

In *godefroyi* the abactinal spinelets (0.9-1 mm. long) are three-edged (prismatic with deeply excavated sides) and taper to a sharp point or occasionally two (Koehler, 1920, p. 154, pl. 66, fig. 9*a*). The dorsal spinelets of *meseres* are structurally the same but the edge of the 3 flanges is sparsely and irregularly denticulated, as indicated by figures of 4 abactinal spinelets. Koehler's figures of *godefroyi* indicate that the 3 flanges are well developed but without lateral teeth. In *meseres* the inferomarginal spines are smooth edged with 1 or 2 slight denticulations at tip, usually on only one of the flanges. These flanges are better developed in *godefroyi*.

Actinal interradiial areas do not reach the distal margin of second inferomarginal. They contain about 12 roundish plates which carry a divaricate group of 3-6 very slender spinelets. A single series of very small actinal plates extends two-thirds length of ray. Beyond fourth or fifth inferomarginal there is only one plate to each inferomarginal, at its adoral end.

Adambulacral furrow spines basally webbed, long and slender, 2 to a plate except for the first to third plates, which carry 3, and those near tip of ray, which carry 1. Subambulacrals proximally 4, varying to 3 on middle range of ray; then on distal third of ray, 5. The spines are basally webbed and this web is continued from the innermost suboral to the base of the distal furrow spine. On the most distal plates, with 1 furrow spine, the

armature consists of a transverse webbed comb of 6 spines, the innermost being the furrow spine. The adambulacral plates are much broader than long, and the muscular interval between the plates is twice as wide as the spine-bearing crest of the plate. The suboral combs occupy only the inner of furrow half of this crest, so that there is a definite spineless zone along ray between the outer subambulacral and the base of the inferomarginal paxillae. The longest subambulacral spines are 1.8 mm. and 3 are figured for comparison with *S. godefroyi*. Furrow spines proximally are subequal to the subambulacrals; distally they are definitely shorter.

Marginal mouth spines 6 or 7, similar to adambulacrals; suborals smaller, 3 or 4, in a single series along median suture.

TYPE LOCALITY. St. 1652, Ross Sea, $76^{\circ} 56.2' S$, $178^{\circ} 35.5' W$, 567 m.

SPECIMENS EXAMINED. The type.

REMARKS. *Paralophaster godefroyi* was described from 3 small specimens (R 37, 14, and 4 mm.) taken by the second Charcot Expedition near Alexander I Island and west of Charcot Island, 250–400 m., sandy mud, pebbles and rocks (Koehler, 1912, p. 50, pl. 4, figs. 2, 6, 7, 9, 10, 11). A larger specimen, having R 70–80 mm. was described and figured by Koehler from off Queen Mary Land, $64^{\circ} 32' S$, $97^{\circ} 20' E$, 110 fathoms (1920, p. 153, pl. 31, fig. 1; pl. 35, figs. 1–4; pl. 66, fig. 9).

In the same dredge haul with this large specimen was taken a very immature *Paralophaster* which Koehler has described as *Solaster asperatus* (1920, p. 157, pl. 33, figs. 8, 9; pl. 65, fig. 3; R 8.5 and 9 mm., r 4 mm.). The denticulated spinelets of the abactinal paxillae are somewhat similar to those of *meseres*, but the inferomarginal are not. Even in such a tiny specimen Koehler found 12 spinelets on the largest paxillae and 10 on the others. Koehler states that the inferomarginal paxillae “se distinguent de celles du reste de la face dorsale, non pas par le développement particulier de leurs pignants qui ne sont pas plus grands que les autres, mais par l'épaississement et l'allongement de leur tige”. In *meseres* the inferomarginal spinelets are not only larger and more numerous than those of the abactinal paxillae but they are of a different form. They lack the conspicuous denticulations characteristic of the abactinal spinelets.

This small type of *Paralophaster asperatus* has 4 furrow spines, and 3 subambulacrals “très forts et allongés”. Koehler states that the spines have “une structure analogue à ceux des paxilles dorsales, mais ils sont plus forts et leurs denticulations terminales sont un peu plus nombreuses”. That is, the denticulations are in excess of 2–4 on each of the 3 flanges. In *meseres* the subambulacrals have only a few terminal denticles as shown in 2*b*, left, but exceptionally as many as shown in 2*b*, right. They seem nearer to the typical subambulacral of *godefroyi* figured by Koehler (1920, pl. 65, fig. 9, *d*).

Finally, in spite of having more numerous adambulacral furrow spines than *meseres*, *asperatus* has only 5 marginal mouth spines. In respect to general appearance it is evident that *meseres*, with its prominent inferomarginal paxillae and their numerous spinelets conspicuously longer than the abactinals, more nearly resembles *P. godefroyi*. But it must be remembered that the specimen of *asperatus* is too young to afford a definitive picture of the species. It appears, however, to be distinct from *godefroyi*.

Genus *Solaster* Forbes

Solaster Forbes, *Mem. Wernerian Nat. Hist. Soc.*, VIII, 1839, p. 120. Type *Asterias endeca* Linnaeus.

Solaster regularis Sladen

Solaster regularis Sladen, 1889, pl. 60, fig. 1; pl. 62, figs. 5, 6.—Fisher, 1911, p. 323.

Crossaster australis Perrier, 1891, p. 113, pl. 10, figs. 1a-1d.

Solaster australis Ludwig, 1905, p. 63.—Fisher, 1911, p. 323.

St. WS 80. Falkland Islands, 50° 57' S, 63° 37' 30" W, 152-156 m., fine dark sand, 2 specimens.

St. WS 97. Falkland Islands, 49° S, 61° 58' W, 146-145 m., 1 specimen.

St. WS 108. Falkland Islands, 48° 30' 45" S, 63° 33' 45" W, 118-120 m., fine dark sand, 1 specimen.

St. WS 243. North-east of Falkland Islands, 51° 06' S, 64° 30' W, 144-141 m., coarse dark sand, 2 specimens.

St. WS 773. East of Cape Tres Puntas, 47° 28' S, 60° 51' W, 291 m., 1 specimen.

St. WS 804. Falkland Plateau, 50° 22 $\frac{3}{4}$ ' S, 62° 49' W, 150-143 m., 1 specimen.

St. 824. South-east of East Island, Falkland Islands, 52° 29 $\frac{1}{4}$ ' S, 58° 27 $\frac{1}{4}$ ' W, 146-137 m., 1 specimen.

Eight specimens have 9 rays and one has 10 rays (St. WS 243). The type has 8 rays, Ludwig's specimen 10, Perrier's, 9 or 10.

This species is as variable as the north Pacific *Solaster paxillatus* Sladen and *S. borealis* Fisher. As in these species, there is a form with small paxillae, one with large, and intermediates. Sladen's figure represents an aberrant extreme, just as his figure does in the case of *paxillatus*, in which, also, the rays vary from 8 to 10.

There are scarcely 2 specimens of *regularis* from different localities which are alike. The example from St. WS 824 (R 84 mm., r 25 mm., br 17 mm.) has relatively large, close-set paxillae with numerous (e.g. 18) slender, sometimes terminally expanded, thorny spinelets which appear stout, blunt and papilliform on account of the soft pulpy investment. The proximal furrow combs have usually 5, long, slender, basally webbed spines, also appearing blunt and stout on account of the sheath. These diminish to 3 on outer part of ray. Proximally the transverse, curved, subambulacral comb usually has 6 slightly longer, heavily sheathed spines; distally there are 5. In a specimen from St. WS 80 there are 7 with a smaller eighth at outer end of series. These spines are stout, subterete, tapered, but usually appear coarser and blunter than they really are on account of the sheath. Each mouth-plate carries about 9 marginal spines, the inner enlarged and terminally bifid, while parallel to median suture there are 7 or 8 suboral spines, the inner of which is subequal to the 2 "teeth". Inferomarginals of conspicuous size, broader than long, much like those of *S. paxillatus* (Fisher, 1911, pl. 88). The first 10 correspond to the first 17 or 18 adambulacrals.

There is a specimen from St. WS 243 (R 100 mm., r 36 mm., br 26 mm.) referable to the same forma but, owing to inflation of disk and rays, the paxillae are not so closely placed. The sheath of all the spines is unusually thick and pulpy.

Forms with small paxillae are represented by figures of Sladen's type and those of *Crossaster australis* Perrier. In the latter the dorsal integument is unduly shrunken by

preservation or drying. Specimens from Sts. WS 80 and WS 97 are examples. Paxillae carry usually 6–10 delicate but “pulpy” sheathed spinelets; R 73 mm., r 22 mm., br 12–13 mm. Slenderer, less inflated rays among other things allow the inferomarginals to stand out more prominently and alter the general appearance. When the ray is strongly inflated the marginals of the proximal half or two-thirds of ray are hidden when viewed directly from above, whereas in a slender-rayed form, such as that having R 110 mm., br 17–19 mm. (St. WS 108), all or nearly all can be seen from above, and stand out prominently on the sides of the ray. Such a specimen seems to belong to an entirely different species from the large puffy example from St. WS 243.

The stomach of a large specimen from St. WS 243 contained the remains of a *Pteraster*.

TYPE LOCALITY. Challenger Station 308, south of Wellington Island, Chile, $50^{\circ} 8' 30''$ S, $74^{\circ} 41'$ W, 175 fathoms, blue mud.

DISTRIBUTION. Cape Horn region and Falkland Plateau, north on the Pacific side to 50° and on the Atlantic to $47^{\circ} 28'$; 65–350 m., mud, sand.

Solaster regularis subarcuatus Sladen

Solaster subarcuatus Sladen, 1889, p. 455, pl. 60, fig. 2; pl. 62, figs. 7, 8.—Döderlein, 1928, p. 296, pl. 12, fig. 4.

Solaster octoradiatus Ludwig, 1903, p. 25, pl. 3, figs. 21, 22.—Bell, 1908, p. 11.

St. 170. Off Cape Bowles, Clarence Island, $61^{\circ} 25' 30''$ S, $53^{\circ} 46'$ W, 242 m., rock, 2 specimens.

Both specimens have 8 rays. The type has 9 rays; 5 specimens reported by Ludwig had 8 rays and one had 7 rays. Bell's specimen, which I have in hand, is 8-rayed, as was Döderlein's specimen.

The larger of the 2 specimens has R 40 mm., r 14 mm. The abactinal paxillae are a little larger than those of the type. The largest have 9 or 10 peripheral and 4–7 central, blunt, denticulate spinelets. The papulae are not numerous in the close meshes of the skeleton—usually 3 or 4 to a group. The mouth-plates each have about 9 marginal spines of which the 3 inner are decidedly elongated. Bell's specimen from Coulman Island has 7 (R 31 mm.) while the small example from St. 170 also has 7 (R 10 mm.). The ambulacral plates of this specimen have, proximally, 2 furrow spinelets, distally only 1, while the larger specimen has 5, 4, 3, 2, 1, from base to extremity of ray. The transverse subambulacral combs contain 5 or 4 stout spines, conspicuously longer than the marginal. In the young specimen there are usually 4.

Subarcuatus is obviously close to *regularis*. Indeed the resemblance is apparent from Sladen's figures which stand side by side on Pl. 60, and these represent but random samples. When one observes the latitude of variation in *regularis* he is somewhat put to it to discover wherein *subarcuatus* differs. Both “species” have forms with larger and smaller paxillae; both have the same general appearance and the same number of rays. So far as is known *subarcuatus* does not grow so large as *regularis*; there are 4 or 5, rather than 6 or 7, subambulacral spines; and in comparison to the latter the furrow spinelets are much shorter, especially in the Coulman Island specimen. In *subarcuatus* the

abactinal paxillar spinelets are shorter and stouter, somewhat clavate in general contour, with the rather numerous thornlets at the tip, and usually only a slight distance below the tip. In *regularis* the spinelets are usually slender, somewhat tapered in general contour with far fewer terminal spinelets and other prominent thorns occurring irregularly on the side of shaft half-way to the base (but not in all spinelets). These are not invariable characters but rather the habit of the two forms.

I think it will be convenient to maintain *subarcuatus* as the antarctic representative of *regularis*; but as I have indicated in the synonymy there seems to be no place for *O. octoradiatus*.

TYPE LOCALITY. Challenger St. 150. Between Kerguelen and Heard Islands, $52^{\circ} 4' S$, $71^{\circ} 22' E$, 150 fathoms, coarse gravel, bottom temperature $35.2^{\circ} F$.

DISTRIBUTION. Probably circumpolar. Between 80° and $88^{\circ} W$, 70° – $71^{\circ} 18' S$, 450–500 m. ('Belgica'); Coulman Island, $73^{\circ} 30' S$, $170^{\circ} E$, 100 fathoms; South Shetland Islands, 242 m. ('Discovery').

Genus *Crossaster* Müller & Troschel

Crossaster Müller and Troschel, *Monatsber. preuss. Akad. Wiss.*, 1840, p. 103. Type *Asterias papposa* Linnaeus.

Crossaster penicillatus Sladen

Crossaster penicillatus Sladen, 1889, p. 446, pl. 60, fig. 5; pl. 62, figs. 9, 10.—Koehler, 1908, p. 560 (Gough I.).—Bell, 1905, p. 249.—Clark, 1923, p. 295.—Mortensen, 1933, p. 272.

St. H. Cape Trawler, $34^{\circ} 4' S$, $17^{\circ} 36' E$, 272–402 m., 1 specimen.

The specimen has 10 rays; R 65 mm., r 20 mm., br 11–14 mm. Clark's specimens had from 8 to 10 rays—the young 8 or 9, and the adults (R 55–60 mm.) 9 or 10 rays. The furrow spines are long and slender, basally webbed, 5 at the base of ray, then 4, 3, 2, and finally 1 near the end. This single spine is co-ordinated with the curved transverse comb so that the adambulacral armature consists of essentially a single transverse series, which, so far as the 3 innermost spines are concerned, descends somewhat upon the furrow face of the plate. The subambulacral spines are long, slender, tapered and pointed. The combs are transverse or obliquely transverse, curved, with the convexity adoral. The first few combs consist of about 5 basally webbed spines, rapidly increasing to 7 and 8; then to 7, 6, 5 on outer fourth of ray. The spines stand on a curved convexity or crest of the plate, which becomes more prominent on the outer part of ray. Each mouth-plate has 10 furrow spines, the inner 3 or 4 conspicuously longer than the others, and about 10 long subambulacral spines. Abactinal spinelets are numerous, long, very delicate. It will be seen from the above that the spines are not much more numerous than in Sladen's type, in which R is 34–36 mm.

TYPE LOCALITY. Challenger St. 135c, off Nightingale Island, Tristan da Cunha, 110 fathoms.

DISTRIBUTION. Tristan da Cunha and Gough Islands, South Africa; Marion Island; 80–800 m., sand, mud. The range is therefore in the sector between $40^{\circ} E$ – $15^{\circ} W$ and 33° – $47^{\circ} S$.

Genus *Myoraster* nov.

DIAGNOSIS. Rays 5. Differing from *Solaster*, *Crossaster*, and *Lophaster* in having a specialized internal longitudinal muscle lying between adambulacral and superomarginal plates and extending from end of ray to interbrachial angle, whence it continues to the tip of adjacent ray. Abactinal paxillae resembling those of *Lophaster*; marginal plates of *Solaster endeca* type; actinal and adambulacral armature not essentially different from that of *Lophaster*. Type, *Lophaster antarcticus* Koehler.

REMARKS. The specialized actinolateral muscle is the most characteristic feature of this genus, which otherwise resembles a combination of *Solaster* and *Lophaster*. The marginal plates, for example, are like those of typical *Solaster*, since the inferomarginal paxillae are compressed, somewhat fan-shaped, while the superomarginal paxillae are only a trifle larger than the abactinal paxillae and usually stand above the interspaces between the inferomarginals, as in *Solaster endeca*. In typical *Lophaster* the conspicuously enlarged superomarginal paxilla stands above the inferomarginal and the combined plates form a single strong dorsoventral calcareous ridge, very apparent when viewed from the coelom.

It is of course not possible to make a definitive evaluation of such a character as the actinolateral, or marginal, muscle which appears thus in an isolated species. The slight rudiment of it, as a faint narrow band, can be detected in some specimens of *Solaster endeca*, where it can hardly be of functional importance. I can find no trace of it in *Lophaster*. An actinal muscle layer, of which at least a part is homologous with this marginal muscle, occurs in *Cuenotaster*, a genus very distinct from all other Solasterids.

An interesting feature of the type species is a specialized spinelet terminating in 3 lobes, rather than 3 sharp prongs. The variations have been fully figured by Koehler (1920, pl. 67, fig. 3). This special spinelet occurs in addition to the normal spinelets with 3 sharp terminal prongs, and has not been described in any other Solasterid.

It is possible that *Solaster incertus* Koehler (1917, p. 40, pl. 5, figs. 2, 3; pl. 9, figs. 21, 22) belongs to this genus. The type and only known specimen from Kerguelen is too small (R 15 mm.) to indicate adult characters.

Lophaster tenuis Koehler, based upon a single small specimen (R 21–22 mm.) from 64° 32' S, 97° 20' E, 110 fathoms, has very special spine characters which separate it from *antarcticus*. It may belong to *Myoraster* (Koehler, 1920, p. 151, pl. 32, figs. 1–7; pl. 68, fig. 5).

Myoraster antarcticus (Koehler)

Lophaster antarcticus Koehler, 1912, p. 46, pl. 3, figs. 4, 5.—1920, p. 144, pl. 32, figs. 8–11; pl. 33, figs. 3, 4; pl. 67, figs. 1–5; pl. 68, figs. 1, 2.—1923, p. 75.

St. 148. Off Cape Saunders, South Georgia, 132–148 m., grey mud, stones, 4 specimens.

St. 175. Bransfield Strait, South Shetlands, 63° 17' 20" S, 59° 48' 15" W, 200 m., mud, stones, gravel, 1 very small specimen.

St. 181. Schollaert Channel, Palmer Archipelago, 64° 20' S, 63° 01' W, 160–335 m., mud, 5 specimens.

St. 182. Schollaert Channel, Palmer Archipelago, 278–500 m., 1 specimen.

St. 371. One mile east of Montagu Island, South Sandwich Islands, 99–161 m., 1 specimen.

St. 599. West coast of Adelaide Island, 67° 08' S, 69° 06½' W, 203 m., 3 specimens.

The largest specimens measure as follows: St. 181, R 142 mm., r 42 mm., br 45 mm.; St. 148 (South Georgia), R 160 mm., r 46 mm., br 50 mm.

Koehler has fully described and figured the external features of this species, including the characteristic spinelets. His type specimen from Adelaide Island and Alexander I Land were all small, none exceeding R 28 mm. However, the Australasian Antarctic Expedition secured material from off Adélie Land, the largest specimen of which has R 120 mm.

St. 599 is very near the type locality and the largest specimen has R 74 mm., r 21 mm., br 22 mm., and conforms well to Koehler's description. A curious feature of this specimen, as well as others from different localities, is the position of the subambulacral comb which consists of 3-5 basally webbed spines. The normal position of the comb is probably a slightly curved, obliquely transverse, line from the outer adoral to the inner aboral corner of the plate. However, this line shifts so that the slightly curved comb (convex side adoral) is almost at a right angle to furrow; or the axis of the comb may shift so that the comb becomes more nearly parallel with the furrow series and closer to it. This last posture is rather characteristic of the specimens from Schollaert Channel, Palmer Archipelago, although oblique transverse combs are found—especially on the outer part of ray. In contrast the specimens from other localities such as Adelaide Island, South Sandwich Islands, South Georgia, while showing the extremes of variation have the majority of the subambulacral combs obliquely cross-wise on the plate.

A variable feature of the species is the size of the actinal interradial area which is associated with size of the disk. The type form has the smallest disk (Koehler, 1912, pl. 3, fig. 5, young; 1920, pl. 32, fig. 9, adult). The disk may become much broader, and the interbrachia more rounded than in Koehler's pl. 33, fig. 4 (1920), with correspondingly enlarged actinal interradial areas. This holds true for all the South Georgia specimens, the large specimen from St. 181, that from St. 182, but not for the example from St. 371 (R 122 mm.). It is difficult to express the difference in terms of actinal plates, as they are of about the same number in large specimens but differ in spacing. Eight to ten paxillae may be counted along the interradial line from mouth-plates to margin. The series parallel to furrow is not always very regular, outside the first, which reaches to within a short distance of tip of ray. In the triangular actinal interradial area there are usually about 6 chevrons of paxillae, with a few irregular additional paxillae next to the first inferomarginals.

The abactinal skeleton is a close mesh, fairly regularly 4-sided on the lateral parts of the area but irregular along a broad radial band. The lateral abactinal plates (the bases of the paxillae) have 4 rather long lobes which touch or overlap 4 neighbouring plates. In the radial area the plates are irregular and are frequently 3- to 5-lobed, with short connecting ossicles in old specimens. The papulae are found all over the ray and disk and there are commonly 2-5 to an area in large specimens, but only 1 to an area in small examples (and on outer third of ray of large specimens).

The interbrachial calcified pillar is slender and flexible, and expands slightly where it joins the abactinal skeleton. The membranous septum in which the pillar lies expands

fan-wise at the dorsal end, but below is scarcely more extensive than the pillar. It does not extend interradially to the margin as there is a wide free passage between the adjacent rays.

Gonads are interradial in position and empty dorsally about one-fourth r from inter-brachial angle.

In one of the large specimens from South Georgia the abactinal plates of the disk and radial region of proximal half of ray have disappeared along with the basal portion and in some cases all of the shaft of the paxilla. The condition is possibly pathological, as in the other large example from the same station the skeleton is intact.

The remarkable muscular system which differentiates this species from *Lophaster*, *Solaster* and *Crossaster* is essentially a compound bundle of conspicuous size which lies at the lower end of the ambulacral ossicles, against the adambulacral plates to each of which a strand is attached. It therefore is very slender at the end of ray but rapidly increases in size toward the base. At the distal limit of the actinal interradial area it leaves the adambulacral plates and follows the ambitus as a continuous structure into the adjacent ray where it follows an identical course to the tip. Over the coelomic surface of the actinal interradial area a thinner sheet of muscle, composed in part of strands originating in the marginal bundle, passes to the adambulacral plates. In addition, narrow muscles which branch off abundantly from the conspicuous dorsal radial muscle, on reaching this longitudinal muscle, become transformed into thin raised ridges which cross the marginal muscle. Some of these attach themselves to the adambulacral plates, while others unite and continue (as a fairly symmetrical series of ridges) between the lower ends of the ambulacrals. These ridges are conspicuous across the actinal interradial area. The fascicles of the marginal muscle (which is the pertinent innovation) are therefore roughly at right angles (and somewhat covered by) these extensions of the normal dorsal muscular system.

In a specimen from St. 371 having R 120 mm. the marginal muscle measures at the interradius 3.5 mm. dorso-ventrally, by 2.5 mm. horizontally—after evident shrinkage from alcohol.

I have found what is probably the equivalent of the marginal muscle, in a very rudimentary form, in *Solaster endeca*. It is a very thin band, less than 1 mm. in width, lying under the actinal extension of the dorsal muscular system, described above as traversing at right angles the thick marginal muscle of *Myoraster*. There is no trace of the muscle in *Lophaster*, nor of the actinal interradial muscle sheet.

TYPE LOCALITY. Between Jenny Island and Adelaide Island, 67° 43' S, 70° 45' 42" W, 254 m., rocks and gravel.

DISTRIBUTION. South Georgia to Adelaide Island (67° 43' S) and off Adélie Land; probably circumpolar; 99–750 m.; rocks and mud.

Genus *Cuenotaster* M. P. Thiery

Leucaster Koehler (not Gauthier, 1887), 1912, p. 54. Type *L. involutus* Koehler.
Cuenotaster Thiery, ex Koehler, 1920, p. 159.

Koehler by inadvertence compared *Leucaster* to *Crenaster* Perrier, a name without status but regarded as synonymous with *Dytaster*. He intended to write *Ctenaster* Perrier, 1884, which is also without status since it is preoccupied by *Ctenaster* Agassiz, 1835. *Ctenaster* Perrier, renamed *Laetmaster* by Fisher (*Smithsonian Miscell. Coll.*, LII, 1908, p. 88), contains only one species, *L. spectabilis*, dredged in the West Indies in 1920 fathoms.

Although in *Laetmaster* the abactinal plates are very numerous and independent as in adult *Cuenotaster*, the adambulacral armature consists of a furrow comb of about 5 spinelets, and a subambulacral comb at a right angle to furrow, after the common Solasterid pattern. The inferomarginal plates, less prominent and less widely spaced than in *Cuenotaster*, show no trace of the latter's characteristic actinal double transverse ridges, or keels, associated with the marginals. As in *Cuenotaster* the superomarginal paxillae are not differentiated. So far as I am aware the only known specimen of *Laetmaster* is the type which I have examined at the Museum of Comparative Zoology, Cambridge, Massachusetts.

Cuenotaster involutus (Koehler)

Leucaster involutus Koehler, 1912, p. 55, pl. 5, figs. 1, 2, 3, 6, 7, 10, 11.

Cuenotaster involutus Koehler, 1920, p. 159, pl. 33, fig. 5; pl. 65, fig. 4.—1923, p. 75.—Döderlein, 1928, p. 295.

St. 42. Off mouth of Cumberland Bay, South Georgia, 120–204 m., 4 specimens.

St. 45. Off Jason Light, South Georgia, 238–270 m., grey mud, 1 specimen.

St. 140. Stromness Harbour to Larsen Point, South Georgia, 122–136 m., green mud, stones, 2 specimens.

St. 148. Off Cape Saunders, South Georgia, 132–148 m., grey mud, stones, 2 specimens.

St. 167. Off Signy Island, South Orkneys, 244–344 m., green mud, 2 specimens.

St. 195. Admiralty Bay, King George Island, South Shetlands, 391 m., 7 specimens. This is the type locality.

St. 1952. Between Penguin Island and Lion's Rump, King George Island, South Shetlands, 367–383 m., 1 specimen.

St. MS 71. East Cumberland Bay, South Georgia, 120–60 m., 1 specimen.

Koehler has described and figured the external features of this species which is readily recognized by the single series of prominent, bristling, spaced, marginal paxillae from the base of which a double ridge passes to the adambulacral plates. The adambulacral armature consists of a transverse series of 4 or 5 bristling tapered spines—the furrow spine and the subambulacrals co-ordinated in a single series. In young examples the abactinal skeleton is a very irregular, open mesh, enclosing small isolated irregular plates. With advancing age (R 70 mm.) the plates of the mesh become entirely dissociated and immersed in the thick integument, which also increases in thickness with age. These plates are very unequal in size, irregular, longer than wide, with tapered ends.

Those which formed nodal points of the reticulum are lobed. The originally isolated platelets of the younger stage are the smallest among the dissociated elements and bear paxillae of secondary size. It is probable that the plates also alter in shape with age, as the lobes are less well marked in large specimens.

In young specimens, as Koehler points out, the low paxillar groups of spinelets are easily recognizable, but with age become involved in the thickening (glandular) epidermis and lose their identity, precisely as in *Perknaster*. In a specimen with R 35 mm., primary paxillae with upward of 12 short spinelets (see Koehler, 1920, pl. 65, fig. 4) can be differentiated from smaller and lower groups of 2-4 spinelets. The primary groups are elements of the continuous reticulum, while the others stand on the independent, secondary, platelets. In very small specimens the secondaries are few in number, and the meshes of the reticulum are naturally smaller in proportion to the size of the enclosing plates.

The papulae are fairly large, not closely placed, and occur all over the abactinal surface.

The dorsoventral interradiial, calcareous pillar is slender, flexible, and the upper end joins the abactinal surface about one-third r from interbrachial angle. A narrow membranous septum (of which it is a part) impinges on the stomach, but between pillar and interbrachium there is no septum.

Gonads open dorsally about half way between upper end of calcareous pillar and margin. In a specimen with R 78 mm. the large eggs are fully formed (1 April 1926, St. 42).

The actinal floor of both disk and rays is covered with a conspicuous sheet of muscle, which is continuous with a thinner dorsal layer. In the rays the actinal portion appears to be homologous with the marginal muscle bundle of *Myoraster*. Its coelomic face is crossed by oblique ridges of tissue, in part muscular as in *Myoraster*, which pass between the lower ends of the ambulacral plates. As dissepiments these die out on the side of ray but their muscular elements appear to be continuous with the branched dorsal system which overlies (as seen from coelom) the continuous thin sheet. The marginal muscle is not obviously differentiated from the ventral (longitudinal) sheet as in *Myoraster*.

The rays of *Cuenotaster* are very flexible and are sometimes coiled ventrally. It seems obvious that this special ventral sheet of muscle (as well as the dorsal sheet and the disconnected dorsal plates) co-operate in some special locomotor behaviour. The animal may perform undulating movements of the rays and walk on the tips of its extended podia, as do some species of *Luidia*.

A specimen from St. 42 was dull greenish grey in life.

TYPE LOCALITY. Admiralty Bay, King George Island, South Shetlands, 75 m.

DISTRIBUTION. Probably circumpolar. From south of Adelaide Island (68° S) to Shag Rocks, 60-391 m., mostly hard bottom (rocks, gravel, with mud); Emperor William II Land to Adélie Land (89° E to 142° E, 64° 32' S to 66° 50' S), 120-700 m.

Family KORETHRUSTERIDAE Danielssen & Koren

KORETHRUSTERIDAE Danielssen & Koren, 1884; Bell, 1892; Gregory, 1900; Fisher, 1905, 1911, p. 340 (*q.v.*).

KORETHRUSTERINAE Sladen, 1889; Perrier, 1904.

Spinulosa superficially resembling the Solasteridae but differing in lacking a calcified interbrachial septum, actinal intermediate plates, paxilliform inferomarginals; armature of adambulacral plates forms with that of inferomarginal a single transverse series of spines, never webbed; abactinal skeleton composed of roundish plates or lobed plates, in *Peribolaster* connected by slender ossicles forming an open mesh; abactinal plates bearing a tuft of acicular or flattened spatulate spinelets, either independent or united by a sacculus; mouth-plates resembling those of Pterasteridae, but spines never webbed.

Genus *Remaster* Perrier

Remaster (subgenus) Perrier, 1894, p. 161. Type *Korethruster palmatus* Perrier.

Remaster gourdoni Koehler

Remaster gourdoni Koehler, 1912, p. 60, pl. 5, figs. 4, 5, 9, 12; pl. 8, fig. 7.—1923, p. 76, pl. 9, fig. 1.

St. 140. Stromness Harbour to Larsen Point, South Georgia, 122–136 m., green mud and stones, 1 specimen.

St. 141. East Cumberland Bay, South Georgia, 17–27 m., 6 specimens.

St. 145. Stromness Harbour, South Georgia, 26–35 m., 1 specimen.

St. 159. South Georgia, 53° 52' 30" S, 36° 08' W, 160 m., rock, 19 specimens.

St. 170. Off Cape Bowles, Clarence Island, 61° 25' 30" S, 53° 46' W, 342 m., rock, 5 specimens.

St. WS 177. South Georgia, 54° 58' S, 35° W, 97 m., 1 specimen.

St. MS 71. East Cumberland Bay, South Georgia, 120–60 m., 1 specimen.

Large specimens, sexually mature, measure: R 10–12 mm., r 6–7 mm., measured to apparent interbrachial angle and not bottom of sulcus. Koehler's largest example measured R 11.5 mm., r 6 mm.

The external characters of this species have been described and figured by Koehler who was the first to accord the group generic rank. There is one unfortunate error in Koehler's description. He states (1912, p. 62): "Entre la rangée marginale ventrale et les plaques adambulacraires, s'étendent, sur toute la longueur des bras, deux rangées régulières de plaques latéro-ventrales, dont chacune porte un piquant composé, élargi à l'extrémité et comparable à ceux de la rangée marginale ventrale, mais moins épais et comprenant un nombre moins élevé de piquants élémentaires" (that is, each spine has fewer dorsoventral calcareous rods).

As a matter of fact there are no actinal intermediate (lateroventral) plates whatsoever. The very broad, but short adambulacral plates overlap the inferomarginal series, but do not correspond plate for plate with the latter. The proximal inferomarginal plates are also wide, but rapidly shorten beyond the basal third of the ray.

The two series of lateroventral spines of Koehler's description are in reality the outer 2 of the transverse series of 3 prominent subambulacral spines. On the proximal half of

the ray the plates usually carry a much smaller, fourth, furrow spinelet. The first adambulacral plate is much shorter than the second, and is wedged between the second plate and the mouth-plate. However, it carries 4 spines, but the inner subambulacral is forced to the furrow margin, so that there are apparently 2 furrow spines (the distal much the smaller). This accounts for the 2 furrow spines of the first plate, as described by Koehler.

If the actinal integument is gradually removed by means of sodium hypochlorite (strong alcohol being used to arrest the disintegration) it is possible to define clearly the boundaries of the adambulacral plates and their relation to the inferomarginals. The outer end of the adambulacrals overlaps, as a rule, the inner half of the ventral surface of a pair of inferomarginals. This alternation of the plates of the 2 series is not absolutely regular.

The narrow, obviously specialized, interradial sulcus which this genus has in common with *Koelhraster* is bordered and sometimes concealed by 2 regular rows of paxillae. The groove is paved by 2 series of modified flattish abactinal plates closely in contact and of course devoid of tabulum and spines. These form a sort of fold, the edge of which is turned toward the coelom. They actually constitute a strong interradial arch, superficial in position, the lower end of which is joined to the odontophore by a pair of rather elongate flattish plates with rounded ends. These may represent the first inferomarginals. A true interbrachial septum of plates is lacking. The actinostome is wide and flexible, the frame plates being elongate. The gonads are interradial.

The abactinal plates have four well-developed lobes by which the plates imbricate regularly. In the smaller interspaces there is a single papula; in the larger, 1 or 2.

A highly characteristic feature of this genus is to be found in the curious scoop-shaped abactinal spines which form hollow funnel-shaped fascicles on each plate. Each fascicle is enclosed in a common sacculus, concave at the summit of the group. These have been well described by Koehler, who speaks of the longitudinal elements of the spines as "petits piquants élémentaires". This is satisfactory as a figure of speech; but there is no evidence whatever that broadened spines are compound in the sense of being composed of several ankylosed spinelets. Each very small spine is so modified that the elements are spread out in two dimensions, rather than crowded into the three dimensions of the ordinary cylindrical spine.

This type of spine occurs on the marginal and adambulacral plates of *Koelhraster* but not on the abactinal plates.

Koehler intimates that the abactinal plates are not regularly arranged, but this idea is due in part to the slightly dishevelled condition of his material. The key to the arrangement is the specialized interradial sulcus. The plates are in fairly regular series parallel to this. For each ray therefore the plates are in chevrons, the odd, apical, plate of which is a carinal plate. The first chevron is formed by the plates bordering the sulcus of two neighbouring interradia and the apical plate is the primary radial or first carinal. The 5 primary radials are close to the anus (which is covered by 6 or 7 converging blunt calcareous valves or modified spines). Those spines of the paxilla on the side of the plate

toward the anus are conspicuously longer than those of the opposite half of the circle and thus suggest the arrangement in the "oscular" paxillae of *Pteraster*. When the paxillar spines of *Remaster* are spread to their fullest extent they nearly or quite touch those of neighbouring paxillae. The membrane forming the end of each fascicle is stretched taut and the abactinal surface has a tessellated appearance. The supradorsal branchial space is nearly as effectively protected from outside contamination as in *Pteraster*.

The actinal surface of *Remaster* is not strikingly different from that of *Korethraster*. The divergence is seen in the abactinal surface. Perrier's diagnosis of *Remaster* may be superseded by the following:

Korethrasteridae having 4-lobed abactinal plates united in a small-meshed skeleton with 1 or 2 papulae to each interspace; abactinal and superomarginal plates with a fasciculate, obconic group of specialized, broadened, often scoop-shaped, denticulate spines enclosed in a sacculus enveloping the whole group; no actinal intermediate plates; no true calcified interradiial septum; gonads interradiial; adambulacral plates short and broad with a simple transverse series of prominent subambulacral spines, and usually a small furrow spine.

TYPE LOCALITY OF *REMASTER GOURDONI*. $64^{\circ} 49' 35''$ S, $65^{\circ} 49' 18''$ W, off Port Lockroy, Palmer Archipelago, 70 m., mud and pebbles.

DISTRIBUTION. Graham Land (south-east of Seymour Island); Palmer Archipelago; South Shetland Islands; South Georgia; Shag Rocks; Falkland Islands; 10–342 m.

Genus *Peribolaster* Sladen

Peribolaster Sladen, 1889, p. 464. Type *P. folliculatus* Sladen.—Fisher, 1911, p. 341 (diagnosis; *vide infra*).

Peribolaster folliculatus Sladen

(Fig. C, 5)

Peribolaster folliculatus Sladen, 1889, p. 465, pl. 73, figs. 4–7.—Fisher, 1911, pp. 341, 343.—Kochler, 1920, p. 164.

St. 1562. Off Marion Island, $46^{\circ} 52' S$, $37^{\circ} 55' E$, 97–104 m., 1 specimen.

St. WS 81. North-west of North Island, West Falkland Island, 81–82 m., sand, 1 very large specimen.

St. WS 93. West Falkland Island, 133–130 m., grey sand, 1 small specimen.

The specimen from St. WS 81 is much larger than Sladen's type and of an entirely different form. It measures: R 90 mm., r 52 mm., br 60 mm. The rays at base are thus two-thirds R in breadth. The gonads are greatly developed, causing the very flaccid, collapsed, abactinal wall to bulge at either side of the base of ray, so that from the actinal aspect a considerable portion of it is visible beyond the superomarginal plates. This is not true of the smallest example (St. WS 93) which measures R 31 mm., r 12 mm. (to actual interradiial angle, not end of spines); br 16 mm. (measured to end of spines). Even this specimen has broader rays than Sladen's type but the difference is due largely to the somewhat longer abactinal spines. The extreme breadth of ray of the large specimen would be greatly lessened if the body were turgid and the abactinal wall

elevated. As the internal organs are badly macerated, it may well be that the body form is not at all what it would be in life.

I have figured (Fisher, 1911, pl. 115, fig. 5) the abactinal skeleton of *P. biserialis*. It seems obvious from an examination of a prepared sample of the large specimen that there is no fundamental difference between the two species. In *folliculatus* an increase in the number of cruciform primary plates does not keep pace with increase in size of the animal. As a consequence the tufts of spines become widely spaced and the skeletal intervals greatly enlarged. The slender, secondary, spineless ossicles lengthen and, instead of 1, 2 or 3 connect the nodal points of the skeletal net. The character of the spinelets is similar in the two species, 4 or 5 being a common number for each abactinal fascicle. In the large specimen the papulae are much more numerous, and more conspicuous on account of the spacing of the fascicles of spines. In the small specimen (in which the skeletal net has smaller meshes than in *P. biserialis*) the papulae per area range from 1 to 5, but in the large specimen there are commonly 8-12.

The madreporite is very large, with an irregularly lobed contour; extreme diameters 17 and 19 mm.

Sladen gives good figures of the actinal surface and description of the actinal armature. He could not determine, without mutilating the type and only specimen, how many spines belong to the adambulacral plates. I have made preparations of portions of the actinal surface of both Falkland specimens. The "behaviour" of the plates is highly peculiar.

SMALL SPECIMEN. The lateral-most series of fascicles (each with 3 spines) represents the superomarginals. Between each superomarginal fascicle and the furrow is a transverse series of 5 slender acicular spines encased in a thick sheath as shown in Sladen's fig. 7, pl. 73. The sixth or outer "spine" in his figure is really the *superomarginal fascicle*. The next spine toward furrow is the single inferomarginal, and the other 4 are adambulacral. A sodium hypochlorite preparation cleared in glycerin shows that the superomarginal plate, which is roughly oval in shape, is ankylosed to the dorsal and distal face of the outer third of the adambulacral plate. Owing to difference of refraction the two plates are easily identified. The inferomarginal can even be separated from the adambulacral but at this stage ankylosis has actually taken place. The lobed superomarginals overlap the inferomarginal ossicle.

LARGE SPECIMEN. Ankylosis of inferomarginal and adambulacral is complete. At the outer end of the adambulacral, the inferomarginal portion bends slightly distad. The angle is more marked on the dorsal aspect. On this side, the faint outline of the inner portion of the inferomarginal can sometimes be discerned overlying the outer half of the adambulacral, on its distal side, as in the small specimen. On the proximal two-thirds of ray the superomarginals (with 3-5 spines), are widely separated from the inferomarginals, the integument being devoid of any connecting skeletal elements. In middle of ray this zone is 5 mm. wide.

The adambulacral plates carry 1 or 2 short acicular furrow spines, and then a transverse series of 5 slender acicular subambulacrals graduated in length from the inner

(5.5 mm.) to the outer (6.5 mm.). The stouter inferomarginal (7 mm.) is spaced from the outermost subambulacral about twice the distance between the 2 outer subambulacrals. All these spines are encased in a rather voluminous sheath which extends as a sacculus beyond the tip, making of the actinal armature a crowded confusion of long pulpy papillae.

The mouth-plates have a broad actinostomial border, and are deeply excavated on the furrow margin to accommodate the first tube foot. On the actinostomial border are three prominent spines; the inner is long, flattened, heavy; the next two are smaller, and the outer of these stands on a prominent angle of the margin. Near it, on furrow margin, is a fourth subequal spine, and then a fifth nearly as large as the apical spine. A suboral stands just back of the apical spine but is not so robust. There is considerable variation in the size of all these spines.

Tube-feet are large, and crowded roughly (as to tips) in 4 series. They remind one of *Diplopteraster*.

There is an extensive, complete, membranous interbrachial septum attached on all sides except that adjacent to eversible stomach. This free inner edge is about even with border of actinostome. The interradian extent of the septum is about 40 mm.; the dorsoventral, doubtless quite variable, is 15 mm.

The voluminous gonads are attached at the junction of the interradian septum with the abactinal wall, from the interradian angle, at ambitus, nearly to the inner free edge of septum, or along about 30 mm. They open by several pores into an unspecialized interradian sulcus. The outermost gonopore is fair sized and is at the ambitus. Two or three others can be detected when the integument is stretched under clear alcohol.

These two Falkland specimens differ from Sladen's type in having stouter rays and longer abactinal spines, and may represent a definite forma. But there are such marked differences between the two specimens that it is unwise to draw any conclusions until more material is available, the more so since the range of variation of the type form may be extensive. Sladen described and figured a unique specimen.

The specimen from off Marion Island measures R 64 mm., r 22 mm. (actual, not to end of spines), br 30 mm. (to end of spines). There are 1 or 2 furrow spines and usually 4 subambulacrals. It appears to be typical *folliculatus*.

I add here a diagnosis of *Peribolaster* emended slightly from that which I published in 1911 (p. 341).

Korethrasteridae having the abactinal surface paved with cruciform plates whose delicate lobes are connected by supplementary ossicles, forming a fairly regular network of large quadrangular meshes over the entire surface. On the centre of each primary abactinal plate is borne, on a small boss, a fascicle of delicate subequal spinelets enveloped in membranous sheaths united in the interior of the fascicle. One to numerous papulae in each mesh; no actinal papulae. No actinal intermediate plates, the adambulacral plates imbricating with and sometimes fusing with the inferomarginals. Superomarginal plates cruciform and bearing a fascicle of spinelets; inferomarginals with a single prominent acicular spine, which forms with the similar adambulacral spines a

transverse series of 4-6, spaced and sheathed separately in membrane. Mouth-plates fairly large, of the type of the Pterasteridae, and with a prominent median keel; a few marginal spines and a single or no suboral spine. Membranous interradial septum; gonads opening dorsally; tube-feet in 2 or 4 rows with fleshy, button-like terminal disk, devoid of deposits. No pedicellariae.

TYPE LOCALITY OF *P. FOLLICULATUS*. Challenger St. 304, off the Peninsula of Tres Montes, Chile, $46^{\circ} 53' 15''$ S, $75^{\circ} 12'$ W, 45 fathoms, green mud.

DISTRIBUTION. Southern Chile, the Falkland Plateau, and off Marion Island, 81-133 m.

Peribolaster macleani Koehler

Peribolaster MacLeani Koehler, 1920, p. 161, pl. 31, figs. 2, 5; pl. 33, figs. 1 and 2; pl. 68, fig. 4. St. 1660. Ross Sea, $74^{\circ} 46.4'$ S, $178^{\circ} 23.4'$ E, 351 m., 1 specimen.

The type specimen measured R 24 mm., r 9.5 mm., whereas the Discovery specimen has R 9 mm., r 3 mm. As Koehler has indicated the species is nearer to *P. biserialis* Fisher of the north Pacific than to *P. folliculatus*. But the subambulacral and marginal spines are entirely different to those of *biserialis*, being more or less flattened, broader at tip than near base, and terminated by several unequal, sharp awns (Koehler, pl. 68, fig. 4, *b, c*).

TYPE LOCALITY. $66^{\circ} 32'$ S, $141^{\circ} 39'$ E, 151 fathoms.

DISTRIBUTION. Antarctica (Australian Quadrant) from Queen Mary Land east to Ross Sea (longitude 94° - 178° E) never far north of summer ice (latitude $64^{\circ} 32'$ - $74^{\circ} 46.4'$); 191-581 m.

Family PTERASTERIDAE Perrier, 1875

Genus *Pteraster* Müller & Troschel

Pteraster Müller & Troschel, 1842, p. 128.—Type *Asterias militaris* O. F. Müller (monotypic).
Retaster Perrier, *Nouv. Arch. Mus. Hist. Nat.*, 2^e ser., 1, 1878, p. 56.—Type *Pteraster capensis* Gray, by designation, Fisher, 1919, p. 460.
Hexaster Perrier, *Comptes rendus*, CXII, no. 21, 1 May 1891, p. 1227; *Mém. soc. zool. France*, IV, 1891, p. 267. Type *Hexaster obscurus* (monotypic).
Temmaster Verrill (subgenus), *Proc. U.S. Nat. Mus.*, XVII, 1894, p. 275; *Amer. J. Sci.*, XLIX, 1905, p. 202 (as genus). Type *Pteraster (Temmaster) hexactis* = *Pteraster obscurus* (Perrier).
Lophopteraster Verrill, *Amer. J. Sci.*, XLIX, 1895, p. 202. Type *Pteraster abyssorum* Verrill.
Pterasterides Verrill, *Amer. Naturalist*, XLIII, 1909, p. 547, footnote. Type *Pteraster aporus* Ludwig = *Pteraster militaris* (O. F. M.).

The genus *Pteraster* has now accumulated a considerable number of nominal species. Within this assemblage there appears to be at least three natural groups, or sections. These are hardly of generic importance, but as subgenera will be of distinct service. By allocating a new species to its particular group, the task of identification is simplified at the outset. Subgenera can also lessen the danger of contrasting a new form with irrelevant species, on the ground of geographical proximity. The literature of every large

genus has numerous instances of misleading comparisons. Such are, of course, unavoidable, but none the less harmful.

The key to the subdivision of *Pteraster* seems to lie in the marginal spines of the mouth-plates. In the subgenus *Pteraster* the spines of each plate form an independent web and are hence most nearly like the webs of the adambulacral plates of which the mouth-plates are a modification. A majority of species have the actinolateral membrane narrow, a condition which may be regarded as less specialized than that in which the actinolateral spines reach or even pass the margin.

In *Retaster* the union of the oral spines goes a step further. A web is present between the apical spines, so that all the spines of a mouth angle are co-ordinated into a single webbed series—not two series as in *Pteraster*. In this group, species with a narrow actinolateral membrane are slightly more numerous than those with a medium or broad membrane.

In *Apterodon* the marginal mouth spines are not webbed at all. Sometimes a short abortive web unites the bases of two spines but this is in the nature of an individual variation. In this group the actinolateral membrane averages wider than in the two preceding subgenera.

The keys to the species of *Pteraster* which Clark (1908) and I (1911) published served their purpose but are now no longer reliable. Both Clark and I allowed too little latitude of variation in the number of adambulacral spines. In the following partitioning of species among three subgenera no attempt has been made to construct a key. What is needed now is a critical comparison of specimens, which are not available.

Subgenus *Pteraster* s.s. (including *Pterasterides*)

Pteraster, in which the series of marginal spines of each oral plate is independently webbed.

A. With abundant or sparse calcareous deposits in supradorsal membrane:

Pteraster militaris, type species. Bering Sea, Arctic Ocean, North Atlantic.

Pteraster lebruni Perrier. Falkland and Magellanic region, and neighbouring Antarctic.

Pteraster lebruni brachiatus Koehler. Kerguelen region; Marion Island.

Pteraster rugatus Sladen. Between Kerguelen and Heard Islands.

Pteraster trigonodon Fisher. Southern California.

Pteraster marsippus Fisher. Bering Sea.

B. Deposits of supradorsal membrane absent, or not reported:

Pteraster jordani Fisher. Pacific Coast of North America (Washington to Lower California).

Pteraster affinis Smith. Kerguelen; South Africa.

Pteraster aculeatus Koehler. Davis Sea (65° S, 96° E). Possibly the same as, or a race of, *affinis*.

Pteraster flabellifer Mortensen. South Africa.

Pteraster personatus Sladen. South-east of Ireland.

Pteraster reductus Koehler, off Azores.

Pteraster sordidus Perrier. Off Morocco.

Pteraster alveolatus Perrier. Near Azores.

Subgenus *Retaster* Perrier (including *Hexaster*, *Temnaster*)

Pteraster, in which the oral web is continuous across the point of the jaw so that all the marginal spines of an oral angle are united by one continuous membrane. Occasionally the small, outermost, spine may be free, or partly so.

Pteraster capensis Gray, type species by designation (Fisher, 1919, p. 460). South Africa.

Pteraster gibber (Sladen). Magellanic region.

Pteraster tessellatus Ives. West coast of North America from Strait of Fuca to Bering Sea.

Pteraster tessellatus arcuatus Fisher. Monterey Bay, California.

Pteraster putvillus Sars. North Atlantic, Arctic Ocean, Bering Sea.

Pteraster multiporus Clark. Japan.

Pteraster corynetes Fisher. Molucca Passage.

Pteraster temnochiton Fisher. Aleutian Islands.

Pteraster obscurus (Perrier). Arctic Ocean, North Atlantic, Bering Sea.

Subgenus *Apterodon* nov.

Pteraster, in which the marginal mouth spines are not united by a web.

Pteraster stellifer Sladen, type species. Antarctic, circumpolar, north to Falkland Plateau.

Pteraster danae Verrill. Atlantic Ocean off coast of South America. Perhaps this and *stellifer* are races of the same species.

Pteraster coscinopeplus Fisher. California.

Pteraster reticulatus Fisher. Hawaiian Islands.

Pteraster fornicatus Mortensen. South Africa.

Pteraster obesus Clark. Japan.

Pteraster obesus myonotus Fisher. Philippine Islands.

Pteraster tetracanthus Clark. Victoria, Australia.

Pteraster carribaeus Perrier. Lesser Antilles.

The use of *Retaster* for a subgenus of *Pteraster* is necessitated by the fact that I made *capensis* the type species because Perrier placed it first, and since his description of Gray's *capensis* indicates a typical *Retaster* in the old sense. Several years later Clark (1923) and Mortensen (1933) found that *capensis* is not congeneric with *cribrosus* nor *insignis*. See below, under *Pteraster gibber*.

Pteraster florifer Koehler, 64° 34' S, 127° 18' E, 1700 fathoms, is not included in any of the above lists since the damaged type specimen lacks mouth-plates. I surmise that the species will ultimately fall in *Pteraster* s.s.

Pteraster ingouffi Perrier, in my opinion, is a synonym of *Diplopteraster verrucosus*; *Pteraster hunteri* Koehler, a synonym of *stellifer* Sladen, which may possibly later be merged with *danae* Verrill. *Pt. multispinus* Clark and *Pt. gracilis* Clark are probably synonyms of *Pt. tessellatus* along with *Pt. hebes* Verrill. *Pt. aporus* Ludwig is a synonym of *Pt. militaris*. *Pt. obscurus* includes *Pt. hexactis* and *Pt. octaster* Verrill.

Subgenus *Pteraster**Pteraster lebruni* Perrier

Pteraster lebruni Perrier, 1891, p. 144, pl. 13, figs. 4a-4b.—Ludwig, 1903, p. 29, pl. 3, figs. 25-28.—

Clark, 1908, p. 286 (key).—Fisher, 1911, p. 369 (key).—Koehler, 1917, pp. 49-52.—1920, p. 170.

St. 148. Off Cape Saunders, South Georgia, 132-148 m., grey mud, stones, 1 specimen.

St. 1958. 61° 17' 9" S, 52° 50' 8" W, 740 m., 1 specimen.

St. WS 81. 8 miles north-west of North Island, West Falkland Islands, 81-82 m., sand, 5 specimens.

St. WS 84. 7½ miles south-west of Sea Lion Island, East Falkland Island, 75-74 m., coarse sand, shells, stones, 1 specimen.

St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shells, 2 specimens.

St. WS 93. West Falkland Island, 51° 51' S, 61° 30' W, 133-130 m., grey sand, 3 specimens.

St. WS 97. North of Falkland Islands, 49° 00' 30" S, 61° 58' W, 146-145 m., 1 specimen.

St. WS 210. Falkland Islands, 50° 17' S, 60° 06' W, 161 m., green sand, 1 specimen.

St. WS 243. North-east of Falkland Islands, 51° 06' S, 64° 30' W, 144-141 m., coarse dark sand, 2 specimens.

St. WS 782A. North of Falkland Islands, 50° 29¼' S, 58° 23¾' W, 141-146 m., 1 specimen.

St. WS 831. 50° 50' 30" S, 66° 10' 30" W, 98-102 m., 3 specimens.

St. WS 871. 53° 16' S, 64° 12' W, 336-341 m., 7 specimens.

The largest specimen has R 72 mm., r 30-32 mm., R=2.25 r, br 35-36 mm. (St. WS 782).

This species so closely resembles *Pt. militaris* in general habit that the figures of the latter species published by me in 1911 would serve almost equally well for *lebruni*. The observation applies especially to the actinal surface. The width of the actinolateral membrane and the manner in which the adambulacral web extends beyond the outer spine of its comb across the actinolateral membrane is characteristic of both species.

The appearance of the supradorsal membrane is variable, as in all species of *Pteraster*, due, in part, to accidents of preservation, crowding in containers, etc. In some specimens it appears thick and folded, with no spinelets visible, as in my figure of *Pt. militaris* (Fisher, 1911, pl. 98, fig. 1). In the largest specimen, and a number of others (e.g. St. WS 81), the supradorsal membrane is not well hardened so that the ends of numerous spines protrude, very much as in my figure of *Pt. marsippus* and *Pt. jordani* (Fisher, 1911, pl. 100). The supradorsal membrane is crowded with deposits which have been figured by Ludwig. The abactinal paxillae have a low pedicel and usually three much longer spinelets, of which one is commonly stouter than the other two.

The adambulacral combs of large specimens have as many as 7 or 8 spines, and the mouth-plates 6-8 marginal spines, of which the two or three innermost are much longer than the others. The series of each plate is independently webbed. The first adambulacral webs of a mouth angle are not continuous across the interradius.

The suboral spines are variable in size and shape, but are always much thicker than the innermost marginal spine. Although usually subcircular in section almost to the tip, the terminal fourth or fifth may be triangular in section. In some specimens (e.g. Sts. WS 81, WS 871), however, this triangular condition extends throughout the distal

hyaline portion of the spine (about half total length). Less often (Sts. 148, WS 81) the three sides are concave in the middle region of the spine, greatly accentuating the three-edged condition (Fisher, 1911, pl. 116, fig. 3*b*, *Pt. temnochiton*). The edges are rounded, rather than sharp. Rarely a fusiform suboral spine has a flattened tip terminating in 3 or 4 small, sharp, points.

The tube-feet of the proximal half of ray are more crowded than in the strictly biserial arrangement, but it is probably an exaggeration to call them quadriserial. In the largest specimen the crowding continues to end of ray. The same condition exists in *militaris*, and is still more accentuated in *marsippus* and *jordani* (Fisher, 1911, pls. 98, 101).

The specimen from St. 148, South Georgia, measures R 37 mm., r 14 mm., $R=2.57r$. The adambulacral combs contain usually 5 or 6 spines. Marginal mouth spines 4-6; suboral spine, rather more slender than usual, 3-edged throughout the distal hyaline half, and the facets of the spine concave. Normally, of course, the spine is heavily sheathed, except the triangular point. It is questionable whether even this protrudes in life. The general habit is in no wise fundamentally different from the Falkland Plateau specimens.

The range of variation in the number of adambulacral and oral spines is in line with that of other species where the series of specimens is large enough to yield pertinent information. The variation in the shape of the suboral spine is somewhat disconcerting since the extremes have been used in differentiating species. In this series of *Pt. lebruni* we probably have indicated two formae, but there is far too little material to reach any conclusion.

This series indicates that *Pt. lebruni* is much more closely related to *Pt. militaris* than either Clark (1908) or I (1911) supposed when we compiled our "keys" to the species of *Pteraster*. For instance, we distinguished *militaris* from *lebruni* on the difference in the number of adambulacral spines which proves to be insignificant. Also I state that the suboral spine is not three-edged, whereas it sometimes is. No harm is done by this since the contrasted species, *trigonodon*, has long paxilla stalks carrying 6 spines.

Species of the southern hemisphere which are related to *lebruni* are:

- brachiatus* Koehler, 1917, p. 49, pl. 7, figs. 1, 2, 6; pl. 10, fig. 6. Kerguelen, 2 specimens. This seems to be a race of *lebruni*.
- aculeatus* Koehler, 1920, p. 168, pl. 38, figs. 3, 4, 5; pl. 65, fig. 6. 65° 06' S, 96° 13' E, 325 fathoms, 1 young specimen probably close to, or the same as, *Pt. affinis* Smith.
- rugatus* Sladen, 1889, p. 473, pl. 74, figs. 3, 4; pl. 77, figs. 3, 4. Between Kerguelen and Heard Islands, 150 fathoms.
- marplatensis* Bernasconi, 1937, p. 169, figs. 1, 2; pl. 1, figs. 1-4; pl. 2, figs. 3, 4. Argentina, 39° S, 57° 10' W, 45-97 fathoms. Also four other localities between 37° 40' and 38° 25' S, at 56° 30' W, 48-55 fathoms.
- argentinus* Bernasconi 1937, p. 173, fig. 3; pl. 2, figs. 1, 2. Argentina, 39° 26' S, 56° 25' W, 55 fathoms.

Pt. marplatensis Bernasconi is very closely related to *lebruni* and seems to me to be at best a race of that species. Bernasconi states that it differs from *lebruni* in the greater number of oral and adambulacral spines. But this number (7 or 8) is not greater than I find in large specimens of *lebruni*.

Pt. argentinus Bernasconi is also closely related to *lebruni*. It has the characteristic short paxillar pedicels and 3 (or 4) spinelets, one of which is longer than the others. Adambulacral and oral spines 6, the suboral long, tapered, slightly curved. The three known specimens have 6 rays.

The type and only specimen of *rugatus* is obviously young, measuring R 9.5 mm., r 6.5 mm. The form is pentagonal, paxillar spinelets 5-6; adambulacral spinelets 3 or 4; oral spines 3, webbed, the two webs of a mouth angle separated; suboral, longer than the other oral spines, "exceedingly thick, translucent triangular". Supradorsal membrane "indurated with minute spicules averaging 0.03-0.04 mm. in length, small, irregular, and angularly branching bodies, subdendriform in appearance and fairly well spaced".

A specimen of *lebruni* measuring R 9 mm. and r 5 mm. is distinctly stellate with angular interbrachia; paxillae with usually 3 spinelets; adambulacral spines 5 proximally; oral spines usually 5; suboral spine terminally triangular; actinolateral membrane proximally much narrower than in *rugatus* and, unlike that of *rugatus*, it narrows very gradually toward tip of ray.

Pt. affinis Smith, Kerguelen (possibly including *aculeatus* Koehler), has 5-10 paxillar spinelets, 4 adambulacral spines, 4 oral and a tricarinate (triangular) suboral. Both *affinis* and *aculeatus* appear to have a thin supradorsal membrane, without spicules.

TYPE LOCALITY OF *PTERASTER LEBRUNI*. Magellan region: "Washington Canal", 80 m.

DISTRIBUTION. Magellan and Falkland Plateau, to South Georgia on the east and Bellingshausen Sea on the south-west ($71^{\circ} 24' S$, $89^{\circ} 12' W$); 74-450 m.

Pteraster lebruni brachiatus Koehler

Pteraster brachiatus Koehler, 1917, p. 49, pl. 7, figs. 1, 2, 6; pl. 10, figs. 6-10.

St. 1562. Off Marion Island, $46^{\circ} 52' S$, $37^{\circ} 55' E$. 97-104 m., 7 specimens.

St. 1563. Off Marion Island, $46^{\circ} 48.4' S$, $37^{\circ} 49.2' E$, 101-106 m., 3 specimens.

The largest specimen (St. 1562) measures R 48 mm., r 15 mm., br 18 mm., height of ray at base, 15 mm. The rays are narrower than in typical *lebruni*. The supradorsal membrane is thick, rugose, and crowded with deposits. In this specimen the osculum is as small as the diameter of a fine sewing needle, but in other specimens is well defined though small. It is probable that the osculum nearly or quite disappears in some specimens, as evidently happened in the case of a specimen of *Pt. militaris* from Bering Sea which Ludwig named *Pt. aporus* and which later Verrill designated as the type of *Pterasterides*.

The pedicel of paxillae is appreciably slenderer than in typical *lebruni* and there are ordinarily 3 or 4 slender paxillar spines of which one is slightly the heavier. Near the osculum there are sometimes 5.

What the photographs do not show clearly is that adambulacral combs have proximally 7 spines and distally 6. As in *lebruni* the web is continued across the actinolateral membrane as a series of parallel folds. In each of the 2 marginal fans of each oral angle are 8 spines while the suboral is heavy, clavate, with a sharp, prismatic hyaline tip. Small

examples (e.g. R 13 mm.) have usually 5 ambulacral and 5 oral spines and the same number of paxillar spines as the adult.

It is probable that these specimens are not typical *brachiatus*, but are near to that race and emphasize its close similarity to *lebruni*. Koehler states that the paxillae of his type "ne comprennent guère qu'une demi-douzaine de piquants divergents, dont l'un, plus développé, soulève la tente dorsale et la perce pour faire saillie au dehors". "Scarcely half a dozen" is not greatly different from 3 to 5, while the puncturing of the supradorsal membrane is not a normal condition, but an accident either of handling or preservation.

One stomach contained some remains of branching bryozoans and miscellaneous organic debris.

TYPE LOCALITY. Kerguelen.

Subgenus *Retaster*

Pteraster gibber (Sladen)

Retaster gibber Sladen, 1889, p. 481, pl. 74, figs. 5 and 6; pl. 77, figs. 7 and 8.—Ludwig, 1905, p. 65, pl. 6, figs. 6 and 7.—Bernasconi, 1937, p. 185.

St. WS 248. Falkland Islands, 52° 40' S, 58° 30' W, 210–242 m., fine green sand, pebbles, shells, 1 specimen.

The specimen is smaller than Sladen's type, with broader rays, so that the contour is subpentagonal. R 20 mm., r 12 mm. \pm , R=1.6 r. The abactinal surface is arched, the body being thick and cushion-like. The supradorsal membrane shows the characteristic quadrate and pentagonal reticulum figured by Sladen. The actinolateral membrane is very narrow. The adambulacral combs contain 6 spines instead of the 5 figured by Sladen. The innermost or furrow spinelet is small and the fan here curves distad. Each oral plate carries a marginal series of 8 spines (the outermost 4 being small). The 16 are united in a single web. Sladen states that the type carries 3 oral spines per plate. This is a big discrepancy even for variable *Pteraster*. It seems likely that the outer spinelets were overlooked, as Ludwig (1905, p. 66) has indicated. Ludwig's larger specimen carried 6 oral spines (R 18 mm.).

The largest paxillae, supporting the interradiolateral portion of the supradorsal membrane, consist of an elongate pedicel and 7–9 peripheral spinelets meeting the supradorsal membrane on the periphery of the areoles. There is a central group of 3 or 4 spinelets, slenderer and more acute than the peripheral, the tips of which are usually slightly clavate and thorny.

Pt. gibber is closely related to *Pt. tessellatus* Ives¹ and *Pt. capensis* (Perrier).² The first ranges from Bering Sea to Washington; the second is from the Cape region of Africa.

Clark remarks on the close resemblance of *Pt. capensis* and *Pt. tessellatus*, stating that the only constant difference between the two species "seems to be in the structure of the paxilla: in *capensis* each paxilla has a single central spinelet of a size about equal to the surrounding series of 6 or 7 similar spinelets, while in *tessellatus* instead of this central

¹ Fisher, 1911, p. 359, pl. 104, figs. 1–5.

² Clark, 1923, p. 299, pl. 9, figs. 3 and 4. Mortensen, 1933, p. 267, pl. 14, figs. 1–3; text-fig. 9.

spinelet is a cluster of smaller and more slender spinelets". If this character is constant in *capensis*, then *gibber*, with a small tuft of slender central spinelets, is more like *tesselatus*. In full-grown specimens of *tesselatus* there are 7 or 8 stout peripheral spines and upward of 18 much more delicate ones in a central group.

The colour of the 3 is much the same—dark or pale violet: *capensis* sometimes has a dark angular ring on the upper surface on a paler ground colour. *Tesselatus* is usually mottled with fawn colour, but may also have darker markings. *Gibber* seems to have been dark violet grey in life.

The figure of the oral plates of *capensis* (Mortensen, *loc. cit.*, text-fig. 8) would serve almost as well for *gibber*. In our specimen the suboral spines are slightly longer and heavier, but circular in section (as in *capensis*). Ludwig's specimen of *gibber* had 6 marginal spines. In *capensis* the number (*vide* Clark) varies from 5 to 7.

GENERIC POSITION OF *PTERASTER GIBBER*. The close similarity of *gibber* to *tesselatus* and *capensis*, which are regarded as *Pteraster*, naturally excludes it from *Retaster*. Clark (1923, p. 298) has restricted *Retaster* to *cribrosus* von Martens and *insignis* Sladen. He designated *cribrosus* as the type species, under the impression that this formality had never been complied with. When Perrier instituted the genus¹ he listed *Pteraster capensis* and *Pt. cribrosus* without fixing either as type. Sladen² was the first to give the group a standing but neglected also to designate a type. In 1919³ the present writer chose Perrier's first species, *Pteraster capensis*, for the type of *Retaster*. At that time, this seemed to be a perfectly safe procedure since Perrier (1875, p. 382) had seen the type of Gray's *capensis* and stated: "Par la structure de leur tégument dorsal, soutenu par un réseau à large mailles formées de ligaments unissant les épines qui le soutiennent, et par leur grande taille, ces deux espèces (*capensis* and *cribrosus*) s'éloignent des autres *Pteraster*, et peut-être faudra-t-il créer pour elles un genre spécial.

"Un échantillon unique desséché au British Museum.—Du cap de Bonne-Espérance."

Unfortunately, since *Retaster* has been formally attached to *Pteraster capensis* Gray it becomes, for the time being at least, a synonym of *Pteraster* in its widest sense.

The genus heretofore known as *Retaster* may appropriately be called *Euretaster*, type *Retaster insignis* Sladen. Included species: the type and *Pteraster cribrosus* von Martens. The reasons for choosing *insignis* for the type are: there is a definite, well-preserved type specimen from Challenger St. 189,⁴ Arafura Sea, 25 fathoms; Sladen's illustrations are excellent and detailed. Since *Pt. cribrosus* has been designated (though erroneously) the genotype of *Retaster*, it seems inadvisable to employ it again as the genotype of *Euretaster*.

TYPE LOCALITY OF *PTERASTER GIBBER*. Challenger St. 311, off entrance to Smyth Channel, 52° 45' 30" S, 73° 46' W, 245 fathoms, blue mud, bottom temperature 46° F.

DISTRIBUTION OF *PTERASTER GIBBER*. Strait of Magellan and appropriate depths on both coasts; 27–500 m., blue mud, fine sand, pebbles, shells.

¹ *Nouv. arch. Mus. Hist. Nat.* 2^e ser., 1878, 1, p. 56.

² Sladen, 1889, p. 477.

⁴ Designated as type locality, Fisher, 1919, p. 461.

³ Fisher, 1919, p. 460.

Subgenus *Apterodon**Pteraster stellifer* Sladen

Pteraster stellifer Sladen, *J. Linn. Soc. Lond. (Zool.)*, xvi, p. 193.—1889, p. 474, pl. 74, figs. 1, 2; pl. 77, figs. 1, 2.—Bernasconi, 1937, p. 176.

Pteraster hunteri Koehler, 1920, p. 165, pl. 37, figs. 4-10; pl. 38, fig. 8; pl. 75, fig. 8.—1923, p. 81.—Bernasconi, 1937, p. 176.

St. 175. Bransfield Strait, South Shetlands, 200 m., 1 specimen.

St. 652. Burdwood Bank, 169-171 m., 2 specimens.

St. WS 81. 8 miles north-west of North Island, West Falkland Islands, 81-82 m., sand, 3 specimens.

St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shells, 5 specimens.

St. WS 88. Falkland Islands, 54° S, 64° 57' 30" W, 96-127 m., shell and stones, 1 specimen.

St. WS 216. Falkland Plateau, 47° 37' S, 60° 50' W, 219-133 m., fine sand, 2 specimens.

St. WS 224. Falkland Plateau, 50° 18' S, 65° 07' W, 124-126 m., 1 specimen.

St. WS 228. Falkland Plateau, 50° 50' S, 56° 58' W, 229-236 m., 23 young.

St. WS 231. Falkland Plateau, 50° 10' S, 58° 42' W, 167-159 m., fine green sand, 2 young.

St. WS 237. Falkland Plateau, 46° S, 60° 05' W, 150-256 m., coarse brown sand and shells, 48 young.

St. WS 243. North-east of Falkland Islands, 51° 06' S, 64° 30' W, 144-141 m., coarse dark sand, 1 young.

St. WS 246. Falkland Islands, 52° 25' S, 61° W, 267-208 m., coarse green sand and pebbles, 1 young.

St. WS 248. Falkland Islands, 52° 40' S, 58° 30' W, 210-242 m., fine green sand, pebbles, shells, 1 specimen.

St. WS 781. Falkland Islands, 50° 30' S, 58° 50' W, 148 m., 1 specimen.

St. WS 795. East of Cape Tres Puntas, 46° 14' S, 60° 24' W, 157-161 m., 1 specimen.

St. WS 800. 48° 15' 45" S, 62° 09' 52" W, 137-139 m., 1 specimen.

St. WS 824. Falkland Islands, 52° 29¼' S, 58° 27¼' W, 146-137 m., 13 specimens.

St. WS 831. 50° 50' 30" S, 66° 10' 30" W, 98-102 m., 2 young.

St. WS 871. 53° 16' S, 64° 12' W, 336-341 m., 2 young.

The largest specimen (St. WS 85) measures R 23 mm., r 13 mm., and is therefore smaller than the type, in which these dimensions are respectively 34 and 23 mm. Sladen's figures show the general habit satisfactorily, although in this series of specimens the stellate protuberances of the supradorsal membrane are seldom so prominent as shown by Sladen, and are masked altogether in a very considerable proportion of the specimens. The condition pictured by Sladen is approached closely by the series from St. WS 824. Here the 6-8 peripheral paxillar spines radiate more or less symmetrically from the pedicel top, and there is usually a single central spine. A feature characteristic of most specimens is the conspicuous lateral fringe of actinolateral spines, and the deeply emarginated web of their membrane. While in some specimens this from above defines the entire ambitus, in others from the same station it is visible only on outer part of ray. It is not indicated in Sladen's pl. 74, fig. 1.

The figures of the actinal surface given by Sladen are good, although the form of the adambulacral comb must not be interpreted too literally as it varies even in the same specimen. If the membrane is greatly contracted the adambulacral spines seem to

protrude above the border of a deeply emarginated web. The slightly emarginated web figured by Sladen (pl. 77, fig. 2) is not characteristic of the species, although I find an exactly similar condition on the proximal part of the rays of a specimen from St. WS 216; but on the distal part the spines protrude much more than in Sladen's figure. The continuous web of the first pair of adambulacrals over the outer end of oral plates is well shown by Sladen in pl. 74, fig. 2. The adambulacral spines, stated by Sladen to be 5, are frequently 6.

Each oral plate has 5 or 6 marginal spines entirely without connecting web. The suboral spine is slender, tapered, sharp, and normally entirely encased in membrane. It is very similar to the innermost marginal spine. This latter in some instances moves outward upon the actinal surface of the plate so that there are then 2 suboral spines (St. WS 85). These two form with the second marginal spine (now somewhat enlarged) a curved interradiial series and give to the mouth angle a very abnormal appearance, since the suboral spines are also more robust than in typical specimens.

A number of specimens are carrying young which can be seen in the nidamental cavity through the supradorsal membrane. In one of these which measures R 12 mm., the young are very small with 2 pairs of podia and a ventral yolk sac. Already a supradorsal membrane, showing a large central osculum, has developed (St. WS 824, 19 January 1932). In another specimen, R 11 mm., the young, about 2.25 mm. in diameter and irregularly circular, have 4 pairs of podia and a large terminal "tentacle". The actinolateral web is very prominent, extending as a pair of webs or fans on either side well beyond the end of the radius. The remains of the yolk sack is a convex mass on the mouth. The adambulacral and oral spines are differentiated but too delicate to count accurately, St. 652.

Pt. hunteri is rather typical *Pt. stellifer*. Koehler adduces as the principal difference (the spine counts being the same) the fact that paxillar spinelets of *hunteri* do not have the symmetrical posture shown by Sladen's figure. This is rather a naïve viewpoint for a veteran worker! Sladen obviously describes and figures a specimen, not a species. Scarcely any structure in the entire gamut of sea star morphology is more liable to modification by preservatives, or subsequent crowding, or maceration, than the supradorsal membrane of *Pteraster*. A specimen from St. WS 85 exhibits the stellate posture of the paxillar spinelets on two rays, but elsewhere on the abactinal surface (to quote Koehler) "la disposition régulière des pignants des paxilles est complètement différente". Koehler (1920, pl. 37, figs. 4-10) gives excellent photographic figures of the variations of the abactinal surface. Fig. 9 shows well the ambital fringe of actinolateral spines and web mentioned above. Furthermore, Koehler (1923) records his *hunteri* from east of the Falklands.

TYPE LOCALITY. Challenger St. 311. Off entrance to Smyth Channel, 52° 45' 30" N, 73° 46' W, 245 fathoms, blue mud, bottom temperature 46° F.

DISTRIBUTION. Magellanic and Falkland region to South Shetland Islands, 79-500 m.; south Indian Ocean, 64° to 66° S, 96° to 140° S, 110-358 fathoms. Circumpolar, and probably divisible into local forms.

Genus *Diplopteraster* Verrill*Diplopteraster verrucosus* (Sladen)

Retaster verrucosus Sladen, *J. Linn. Soc. Lond. (Zool.)*, xvi, 1882, p. 196.—1889, p. 478, pl. 76, figs. 1, 2; pl. 77, figs. 9, 10.—Koehler, 1908, p. 550.

Pteraster Ingouffi Perrier, 1891, p. 144, pl. 12, figs. 4a, 4b.—Bernasconi, 1937, p. 176.

Pteraster ingolji (error typ.) Fisher, 1911, p. 370 (key).—1919, p. 458.

Diplopteraster verrucosus Fisher, 1911, p. 370.—Koehler, 1923, p. 76, pl. 11, fig. 5; pl. 12, fig. 1.—Bernasconi, 1939, p. 183, pl. 7, fig. 2; pl. 8, fig. 2.

Diplopteraster Nordenskjöldi Koehler, 1923, p. 77, pl. 10, figs. 4–8.—Bernasconi, 1937, p. 184, pl. 7, fig. 1; pl. 8, fig. 1.

The Roman numerals V–VIII indicate number of rays; e.g. 29 V, 1 VI = 29 five-rayed and 1 six-rayed.

St. WS 81. 8 miles north-west of North Island, West Falkland Island, 81–82 m., sand, specimens 29 V, 1 VI.

St. WS 84. $7\frac{1}{2}$ miles south-west of Sea Lion Island, East Falkland Island, 75–74 m., coarse sand, shells, stones, specimens 5 V.

St. WS 85. Falkland Islands, $52^{\circ} 09' S$, $58^{\circ} 14' W$, 79 m., sand and shells, specimens 6 V.

St. WS 90. 13 miles north-east of Cape Virgins Light, Argentina, 82–81 m., fine dark sand, specimens 1 VI.

St. WS 91. Tierra del Fuego, $52^{\circ} 53' 45'' S$, $64^{\circ} 37' 30'' W$, 191–205 m., fine dark sand, shell, specimens 2 VI.

St. WS 92. Between Falkland Island and Straits of Magellan entrance, $51^{\circ} 58' 30'' S$, $65^{\circ} 01' W$, 143–145 m., specimens 5 VI.

St. WS 93. South-west of Beaver Island, West Falkland Island, 135–130 m., specimens 1 V, 1 VI.

St. WS 109. Falkland Islands, $50^{\circ} 18' 48'' S$, $58^{\circ} 28' 30'' W$, 145 m., fine dark sand, specimens 1 V.

St. WS 210. Falkland Islands, $50^{\circ} 17' S$, $60^{\circ} 06' W$, 161 m., green sand, specimens 2 V.

St. WS 243. North-east of Falkland Islands, $51^{\circ} 06' S$, $64^{\circ} 30' W$, 144–141 m., coarse dark sand, specimens 6 VI, 1 VII, 1 VIII.

St. 776. Off Cape Tres Puntas, Argentina, 107–99 m., specimen 1 V.

St. 781. Falkland Plateau, $50^{\circ} 31' S$, $58^{\circ} 50' W$, 148 m., specimen 1 V.

St. 782A. Falkland Plateau, $50^{\circ} 29\frac{1}{4}' S$, $58^{\circ} 23\frac{3}{4}' W$, 141–146 m., specimen 2 V.

St. WS 784. $49^{\circ} 47' S$, $61^{\circ} 05' W$, 170 m., dark green sand, specimen 1 V.

St. WS 813. $51^{\circ} 35\frac{1}{4}' S$, $67^{\circ} 16\frac{1}{4}' W$, 106–92 m., specimen 2 VI.

St. WS 816. $52^{\circ} 09\frac{3}{4}' S$, $64^{\circ} 56' W$, 150–160 m., specimen 1 VI.

The largest 5-rayed specimen (St. WS 782) measures: R 76 mm., r 51 mm. The abactinal aspect agrees with Sladen's figure. The actinolateral membrane is somewhat broader. The apparent width of the actinolateral membrane is modified by the posture of the adambulacral combs, and to a slight degree by retraction during preservation. In this large specimen there are usually 5 spines in both sorts of adambulacral combs; but in the less prominent comb 1 or 2 spines next to furrow are small. The number of spines per comb starting with the first plate run as follows, an asterisk marking the alternate, smaller plate: 5, 5*, 5, 5*, 5, 5*, 5, 4*, 5, 4*, 4, 5*, 6, 5*, 5, 5*, 5, etc. There are usually 5 marginal spines to each oral plate or 10 to a mouth angle, completely webbed. This number is not invariable, for one plate may have 4 spines, the other 5; or, as in the largest example, 5 and 6. The suboral spine, relatively slender and completely sheathed in

membrane, equals or slightly exceeds in length the longest marginal spine. Sometimes a short accessory suboral is present on outer half of plate.

The largest specimen having more than 5 rays (6-rayed) measures: R 56 mm., r 38 mm. The 7-rayed example measures: R 35 mm., r 21 mm. The 8-rayed example measures: R 40 mm., r 29 mm. In all respects other than number of rays these specimens are typical *verrucosus*. The differences which Koehler believed sufficient to justify a new species, *nordenskjöldi*, are either not constant or else not characteristic. For instance, the difference in the appearance of the abactinal surface (Koehler, 1923, p. 80) is merely a difference such as may exist between two 5-rayed specimens, as well as between a 5-rayed and 6-rayed. Sladen's figure of the abactinal surface of the type of *verrucosus* indicates the areolated, or honey-combed, condition which is even more accentuated in some of the 5- and 6-rayed examples before me. The supradorsal membrane in such specimens is sunken within the circle of props formed by $10 \pm$ peripheral paxillar spines; while the longer, heavier central spine of the paxilla forms a characteristic eminence in the middle of each areole (Sladen, pl. 77, fig. 9). Sometimes, due to a variety of causes (such as crowding in container), the supradorsal membrane does not exhibit this areolated appearance. There appears to be no essential difference between the 5-rayed and 6- to 8-rayed examples in the adambulacral and oral armature nor in the size of the tube-feet.

Fortunately, a 5-rayed specimen having R 50 mm. (St. WS 85, 25 March 1927) was found to be carrying young in the supradorsal space. These occupied chiefly the lateral portions of the interradii, but smaller young were found in one ray two-thirds the distance to tip. The number of young in each interradius was as follows: A, 1 with 4 rays, 3 with 5 rays; B, 2 with 5 rays, 2 with 6 rays; C, 4 with 5 rays, 2 with 6 rays; D, 2 with 5 rays, 2 with 6 rays, 1 with 5 mouth angles but 6 rays; E, 5 with 5 rays, 1 with 6 rays. Total: 25, of which 16 had 5 rays, 8 had 6 rays and 1 had 4 rays. It is therefore obvious that the 6-rayed condition is much more fundamental than in *multipes* where it is very rare.

The largest of these 25 young has 5 rays and measures R 9 mm., r 6 mm. The first adambulacral comb contains 4 spines; the next, 5, the innermost being very small; then 3 plates with 4 spines; then one with 5, innermost very small; then 3 plates with 4 spines, etc. The oral angle has a fan of 8 completely webbed spines. The crowding of the tube-feet is already very apparent but the adambulacral plates have not yet become differentiated into two sorts. The actinolateral membrane is about as broad as in the adult. There are about 8 peripheral paxillar spinelets and 1 central. The osculum is as well developed as in the adult.

A 6-rayed young, with R 5 mm., found in the same interradius, has essentially the same spine counts.

The smallest of the 25 has 6 rays with R 3.5 mm. It was found together with a 5-rayed young rather far along the ray. Adambulacral combs contain mostly 4 spinelets each.

In a 6-rayed specimen (St. WS 243, 17 July 1928), having R 38 mm., nine 6-rayed young and one 5-rayed were found. Two 6-rayed young, with R 6.5 and 7.5 mm. were about

ready to leave the marsupium, but the other eight were quite small, R ranging from 1.25 to 2.5 mm. The smallest (6-rayed) specimen has 3 adambulacral spinelets and 3 oral spinelets per plate. The actinolateral membrane, with 5 spines on either side of each ray, extends conspicuously beyond the border and tip of the ray proper as in *Hymenaster*. The terminal papilla of radial water tube is large and there are 6 pairs of tube-feet to each ray.

From this glimpse into the genetics of the species it is evident that the 6-rayed specimens are not specifically distinct. It is significant that the majority of the young of a 5-rayed parent are 5-rayed; and of a 6-rayed parent preponderantly 6-rayed. It is probable that the 7- and 8-rayed specimens are from 6-rayed rather than from 5-rayed parents (or from 7- and 8-rayed parents).

Pteraster obscurus of the north Atlantic, Arctic Ocean and Bering Sea has 6-9 rays. In a large 7-rayed specimen I found two 6-rayed young,¹ and in two adults with 8 rays I found one 9-rayed, three 8-rayed and two 7-rayed young—all three sorts occurring in the same parent. *Pteraster obscurus*, although aberrant for the genus, seems to be much nearer to *Pteraster* than to *Diplopteraster*.

Perrier's figures of *Pteraster ingouffi*, although small, indicate clearly the general habit and crowded tube-feet of *Diplopteraster verrucosus*. With a lens one can distinguish the two sorts of adambulacral combs. *Ingouffi* is described as having a slender suboral spine encased in membrane and a fan of 10 oral spines completely webbed. This describes *verrucosus* exactly, as no other *Pteraster* of the region has this oral armature. *Pt. gibber* has the marginal spines united by membrane but the suboral is heavy not slender, and the actinolateral membrane is characteristically narrow—entirely unlike that of *ingouffi*.

TYPE LOCALITY. Challenger St. 313. Near the Atlantic entrance to the Strait of Magellan, 55 fathoms, sand; bottom temperature, 47.8° F.

DISTRIBUTION. Falkland Plateau, north to latitude 40°, coast of Argentina; south to Navarin Island (Perrier) and Burdwood Bank (Koehler); 74-270 m.

Diplopteraster semireticulatus (Sladen)

Pteraster semireticulatus Sladen, *J. Linn. Soc. Lond. (Zool.)*, xvi, 1882, p. 195; 1889, p. 475, pl. 75, figs. 5, 6; pl. 77, figs. 5, 6.

St. 1562. Off Marion Island, 46° 52' S, 37° 55' E, 99-104 m., 3 specimens.

The smallest and only perfect specimen measures R 13 mm., r 8 mm., and is therefore for all purposes the same size as the type, the figures of which it closely resembles. This specimen has 4 or 5 adambulacral spines in irregular alternation, the innermost of the series (and sometimes the second in the case of 5 spines) being conspicuously shorter than the others. The supradorsal membrane is semi-transparent. The paxillae have 6 or 7 rather long delicate spinelets surrounding a central one, essentially as in the type specimen (Sladen, pl. 77, fig. 5). The tube-feet are crowded, incipiently quadriserial, but

¹ Fisher, 1911, p. 365, pl. 105, fig. 1.

the adambulacral combs have not yet become differentiated whereby alternate fans project farther into the furrow. Except for a rather wider actinolateral membrane this specimen resembles an equal-sized young of *D. verrucosus* (St. WS 210) which likewise lacks any marked differentiation of alternate adambulacral combs and has only incipiently quadriserial tube-feet.

Unfortunately the adult specimen, as well as a medium sized one, is incomplete through maceration. The size before softening was probably close to R 45 mm., r 22 mm. The supradorsal membrane is thick and verrucose as in *D. verrucosus*. Near the centre of disk the paxillae have 8-10 long slender peripheral divaricate spinelets and an obviously stouter central one surmounting a slightly longer slender pedicel, which is longer in interradii than on radial area; on outer half of ray the pedicels rapidly shorten and there are commonly 8 peripheral spines.

Along the only complete series of adambulacral plates the spine counts run as follows: mouth-plates 5, first adambulacral 4, then 5, 5, 4*, 5, 4*, 5, 4*, 4, 4*, 4, 4*, 4, 4*, etc. The "recessive" series are marked *. When the prominent series has 4 spines, the furrow member is nearly as long as the second spine, while in the recessive series it is usually less than half as long. The suboral spine is long and slender, close to the innermost marginal oral spine to which it is united by a web (not present in the other 2 specimens). The web of the first adambulacral series is continued across interradius uniting with the other first series, behind mouth-plates. The two second series nearly meet.

It should be noted that Sladen's type of *reticulatus* was immature, that it already showed a reticulate dorsal membrane and crowded tube-feet. The differentiation of the adambulacral combs is not at all obvious in *D. verrucosus* until R is 20 mm. It is not apparent in specimens as small as the type of *D. reticulatus*.

This species is closely related to *verrucosus* and *multipes*. *D. perigrinator* (Sladen) from off Kerguelen has furrow combs of 7 or 8 spines alternating with combs of 5. But it will not be surprising if the three ultimately prove to be forms of one species.

TYPE LOCALITY. Off Marion Island, 69 fathoms, volcanic sand.

Family BRISINGIDAE G. O. Sars

Genus *Odinella* nov.

DIAGNOSIS. Related to *Odinia* but differing in having a more specialized genital region confined to first 4 skeletal arches, the intervals between which are without plates on sides of ray; first intercostal area laterally modified in female to form part of a specialized axillary brood chamber; sacculi of lateral and some of abactinal spines of ray extremely thick, ovoid to subglobular in form. Papulae appearing late, not numerous, confined to disk and genital region; pedicellariae very small, confined to sacculi and absent from abactinal area of disk; gonads 2 to each ray, opening laterally in first intercostal space; interradiial plate (odontophore) hidden by abactinal integument of interbrachial angle; first post-oral adambulacral of each mouth angle closely apposed to its fellow, and above them a pair of small closely joined inferomarginal plates (Fig. H, 1);

ray breaks at muscular joint between first and second adambulacrals (no adambulacrals syzygial joints). Type, *O. nutrix*.

REMARKS. This genus differs from all known Brisingidae in having in each inter-radius a highly specialized, axial, brood chamber, in which young are protected until they attain a diameter of at least 6 mm. The number of rays, 11-14, is determined at the outset of development and is not increased by later additions, as in *Labidiaster*.

Odinella may be regarded as an off-shoot of *Odinia* stock with which it agrees in the possession of papulae on both disk and rays, a single subambulacralspines, and probably in the general structure of the actinostomial ring. In *Odinella* there is no completely syzygial joint among the proximal adambulacrals plates such as is found in *Brisinga*, *Craterobrisinga*, *Brisingella*, and *Astrostephane*, *inter alia*. It is probable that no complete syzygy occurs in *Odinia*, notwithstanding my statement to the contrary.¹ Doubt is cast on the matter by a ray of *Odinia magister* apparently broken from the disk between first and second adambulacrals. There are remnants of muscle on the proximal face of what I take to be the second adambulacrals. The succeeding joints are muscular ones except possibly the upper part of the second-to-third. I do not have adequate material to examine this question in other species of *Odinia*.

No known Brisingid has a genital region as concentrated as that of *Odinella*. On this basal inflation of the ray are numerous dorsolateral spines, some of which grow fast to the opposite body wall, locking together, in gravid males and females, all the genital regions into a sort of circular accessory disk, bristling with spines longer than those of the disk proper. As a special adaptation this contrivance undoubtedly prevents loss of rays which have at best a flimsy attachment to the disk. In the female these spine-bridges, as well as the numerous interdigitating but free spines, form a basket work which effectively confines the eggs and developing young to the brood chambers, into which fresh water is driven by cilia. The functional part of the arm for locomotion and trapping of crustacea (by means of the pedicellariae) is restricted to the flexible region distal to the genital inflation.

In *Odinia*, the sides of the proximal part of ray between the skeletal arches is provided with numerous stout plates in a close irregular mesh. The arches are rather poorly defined near disk. Very numerous papulae occur on the sides as well as dorsal surface of the genital inflation, which extends along ray, for 9 or 10 well-spaced arches and reaches its greatest size at about its middle, not anywhere close to disk. In *O. magister* the male gonad opens near base of ray (as in *Odinella*) either in the first or second intercostal area which are here heavily plated and difficult to distinguish from the primary arches.

Brisingaster de Loriol, which strongly suggests *Odinia* except that the intercostal plates are embryonic and there are no papulae, differs from both *Odinella* and *Odinia* also in having gonads in a series of 8 or 9 proximally just above the adambulacrals plates. There appears to be a syzygy between first and second adambulacrals plates. Throughout the genital area of 9 or 10 well-spaced complete arches, the subambulacrals spine has a modified expanded truncate tip. First pair of adambulacrals plates (and sometimes most

¹ Fisher, 1919, p. 501: 1928, p. 4.

of second pair) united interradially; directly above them is the united pair of first infero-marginals, conspicuously larger than in *Odinella*, their inner ends broadly engaging the lower outer end of interradial plate, which is much more conspicuous superficially than in *Odinella*.

STRUCTURE OF ACTINOSTOMIAL RING (Fig. H). The relative size and position of the plates of the ventral skeleton of the disk, known as the actinostomial ring, is usually super-specific. To a certain extent their form is also characteristic of genera rather than species, especially in the case of the mouth-plates.

The actinostomial ring consists of two concentric circles of plates intimately joined. Each radial sector of the inner circle consists of the first pair of ambulacral plates locked between a single mouth-plate on either side (Fig. H, 6, 7). The odontophore, called the interradial plate, forms a keystone above the mouth-plates, which are further bound together by muscles (Fig. H, 6, *o'*, *o''*). The outer circle consists, radially, of the second pair of ambulacrals, and a pair of first adambulacrals; interradially, of a pair of inferomarginals whose size and position is of considerable importance (Fig. H, 1, 6, 8, *m*). Also of importance is whether the joint between the first and second adambulacrals is a muscular or a non-muscular symphysis (syzygy).

The structure of the actinostomial ring may not be ignored if the affiliations of a species, new or old, are to be determined. The *Brisinga* of Asbjørnsen, G. O. Sars, Sladen, and Ludwig was not homogeneous. The relations of the plates of the ring gave the clue to a subdivision into more natural generic groups. The same is true of *Freyella*.¹

In Fig. H is recorded the structure of the actinostomial plates of *Odinella* and for comparison, those of *Brisingella*. This comparison must be worked out in connection with the explanation of the figures, as a description would be of doubtful value. Attention may be called to certain significant points. In the interbrachial angle, the relation of the first adambulacrals and first inferomarginals, *inter se*, presents almost the extremes of contrast in *Odinella* and *Brisingella*. Of a type similar to that of *Odinella* is the arrangement in *Odinia*, *Brisingenes*, *Brisingaster*, *Brisinga*, *Craterobrisinga*, *Aprostophane*. Irrespective of details of difference in the ring plates these genera can be separated as follows:

- a*¹. Papulae on disk and rays; no true syzygy between first and second adambulacrals; gonads 2 to each ray.
 - b*¹. Genital area elongate with stout intercostal plates on side of rays; no brood pouch. *Odinia*.
 - b*². Genital inflation very short, without intercostal plates on sides of rays; specialized brood pouch. *Odinella*.
- a*². Papulae on disk only; a syzygy between first and second adambulacral plates; gonads in series on each side of ray. *Brisingenes*.
- a*³. No papulae; a syzygy between first and second adambulacral plates.
 - b*¹. Gonads 2 to each ray.
 - c*¹. Integument between costae without plates. *Aprostophane*.
 - c*². Integument between plates crowded with spineless plates. *Stegnobrisinga*.

¹ Fisher, *Ann. Mag. Nat. Hist.*, ser 8, xx, 1917, p. 418; also, 1919, p. 502; 1928, p. 4.

- b*². Gonads numerous, in series on either side of base of ray.
- c*¹. Disk plates small, bearing one to several small spinelets; on the ray only one lateral or marginal spine (never a comb of several); no intercostal embryonic plates; furrow spine or spines present.
- d*¹. Proximal subambulacral spine or spinus acicular; second subambulacral when present at adoral end of plate; adambulacral armature not dense and crowded. *Brisinga*.
- d*². Proximal subambulacral spines with modified, capitate, often truncate tip; a second, prominent subambulacral regularly present near aboral end of plate, armature crowded. *Craterobrisinga*.
- c*². Disk plates large, with 1-3 fairly large acicular spines; a vertical series of 4 conspicuous lateral spines to each successive skeletal arch of ray; integument between costae with spaced embryonic plates; no furrow spinelets; 1 prominent subambulacral with modified capitate tip throughout genital region. *Brisingaster*.

A comparison of Figs. 2 and 3, 5 and 7, indicates a considerable difference in the form of mouth-plate. In descriptions of species only the exposed oral face of the plate is considered, whereas the dorsal and lateral extensions which are intimately concerned in the structure of the ring are really of greater importance. With modifications of the mouth-plates are linked changes in the first ambulacrals.

The odontophore exhibits considerable individuality.

Even in genera, having the general arrangement of first adambulacrals and marginals indicated above, the marginals differ in size and posture and the distal joint of the adambulacral may be muscular or non-muscular.

The development of muscles between adjacent mouth-plates (Fig. H, 6, *o'*, *o''*) varies in different genera.

Odinella nutrix sp.nov.

(Figs. G, 1-6; H, 1-9; Plates XIV, XV, XVI, figs. 1-11; Plate XVII, figs. 1-3)

DIAGNOSIS. Rays 11-14, usually 12 or 13. R 75-80 mm., r 7 mm. (type). Rays abruptly swollen at base into a specialized genital region with numerous irregularly placed abactinal spines, which dorsolaterally and laterally interlock with those of adjacent rays and sometimes form permanent bridges, protecting, in axils of female, a specialized brood chamber; beyond genital area, ray narrow, very flexible, with a series of lateral, slender, spaced costae bearing 3 or 2 acicular spines immersed in ovoid sacculi covered with pedicellariae; 1 subambulacral spine with lateral succulus; 1 suboral and 2-4 marginal oral spines; disk small, sunken below level of the rays, the spinelets devoid of pedicellariae; papulae on disk and genital region only; pedicellariae very small, the oral different in form from those of rays. A 12-rayed specimen (St. 123) measures R 100 mm., r 7 mm.; br, at disk, 2-3.5 mm.; at middle of genital inflation 5-13 mm.; at middle of R 3.5 mm.

DESCRIPTION. The general appearance, well shown by the figures of entire specimens, is highly characteristic and very different from that of any known *Brisingid*. In mature specimens the genital region of the ray is inflated, irregularly spiny and papulose, in close contact with adjacent rays, and slightly longer than width of disk. The distal

portion is abruptly narrower than the genital, and devoid of plating except for the regular lateral, spaced costae, which, except for the first 1 or 2 beyond the genital region, do not reach entirely across the ray but simply support the thin integument as props extending upward from, usually, each fourth adambulacral. These lateral "ribs" carry a vertical series of 3 acicular long spines enveloped in an ovoid fleshy sacculus covered with minute pedicellariae. These thick sacculi are found also on some of the abactinal spines of the genital region, and possibly in living specimens are still more numerous but have been lost by abrasion in the dredge.

The disk is dorsally convex, the convexity accentuated by the dorso-ventrally constricted ray at its opening into disk (Pl. XVI, fig. 4). Its abactinal wall is reinforced by irregularly roundish or short-lobed, slightly imbricating plates 0.5-1 mm. in diameter and carrying 1, 2, or 3 skin-covered spinelets, subacicular or variously pronged. Some examples are given in accompanying figures. Apparently the disk spinelets never carry the clavate sacculus. Scattered large papulae are more numerous in a marginal zone than at centre of disk. Pronged spinelets are more numerous in immature specimens than in fully adult; that is, later additional spinelets are more likely to be of the acicular type.

The abactinal skeleton of the genital region, like that of disk, is normally obscured by the skin and is more open, with very irregular elements. A study of growth stages does not indicate that the abactinal plates of the genital region, in excess of those of the simple arches, represent ancestral arches partly suppressed. On the abactinal surface between arches II-III, and III-IV the extra plates have, in medium-sized specimens, an easily discernible transverse alignment (Pl. XVI, fig. 3). On the proximal part of the genital region the larger plates have 2 or 3 lobes and carry 1-3 sharp acicular spines while the oblong connectives which join them and achieve thus a very irregular reticulum carry usually a shorter one. On the sides of this region the arches of plates are arranged, with slight variations as in Pl. XVI, fig. 3, which represents a medium-sized male with gonopore in the middle of the large intercostal space I. This area of thin skin becomes, in the female, one side of the nidamental cavity (Pl. XVII, fig. 1). This area is always bounded proximally by arch I, the lower end of which is formed by inferomarginal 2 resting on adambulacrals 2 and 3. Inferomarginal 1 and adambulacral 1 remain on the disk when a ray is detached. When the nidamental cavity is functioning, arch II is not so straight as shown in Pl. XVI, fig. 3, but is strongly bowed or bent distally. The oviduct opens at about mid-height on its proximal border. Arches III and IV extend completely across the ray from side to side; but arch V is represented on either side by a "rib" of 3 or 4 plates, each bearing a spine. From arch V or VI onwards, each rib of plates consists of an inferomarginal, a superomarginal, and a dorsolateral plate, each carrying a long spine covered by a fleshy sacculus (Pl. XVI, figs. 1, 2). Toward end of ray there may be only 2 lateral plates and spines. In the type there are 4 complete arches plus 19 pairs of lateral ribs.

Small isolated radial plates occur sporadically along the radial line and carry groups of pedicellariae sometimes without a central spinelet.

The terminal plate, though small, is modified to protect the relatively large terminal

sense organ (Pl. XVI, figs. 6-8). It is deeply hollowed on the actinal face, and the border of the distal half carries, on either side, 6-8 acicular spines which support a fleshy cushion of tissue (coalesced sacculi) thickly beset with pedicellariae. In the young, this compound sacculus appears very early and its pedicellariae are the first to be developed, indicating the importance of the terminal sense organ (Pl. XVI, figs. 9-11). The form and relative size of the sense organ are indicated in the figures.

In fully developed specimens papulae occur on the disk, as indicated above; on the dorsal surface of the genital region, irregularly according to the skeletal meshes, dwindling to 1 or 2 dorsally in intercostal spaces VI or VII; on the *lower* part of intercostal spaces I to VI where, in the type, space I has 2 or 3; II and III have 5 or 6 each; IV has 2 (but numerous ones on dorsolateral region); V has 1; VI has 1 or 0. In the medium-sized specimen figured (Pl. XVI, fig. 3) only the first 3 spaces have papulae in this position. The dorsal and dorsolateral papulae are omitted to avoid confusion of lines. Apparently the papulae never encroach upon the upper part of the intercostal space I. In a specimen (St. 123) having R 18 mm. (Pl. XVII, fig. 2) I can find no papulae. In a specimen with R 37 mm. (St. 172) papulae have appeared sparingly in a marginal zone on disk, dorsally on the short, developing genital region, and ventrolaterally in intercostal spaces I and II (1 papula to each) (see also Growth stages, 4).

Intercostal space I, in the female, becomes the side of the nidamental cavity and, with the growth of the young, is forced inward to the sagittal plane until it presses against the similarly stretched wall of the other side of ray. The hepatic coeca occupy the arched upper portion of the swollen genital region and their connection with the stomach is through the very constricted opening of the base of ray (Pl. XVI, fig. 4). The already small aperture afforded by the first skeletal arch is further decreased by a membranous diaphragm in the dorsal part of the first arch, as indicated in the figure. In fully grown specimens this diaphragm is even more extensive than in the figure and the passage to ray is correspondingly smaller.

The general facies of actinal surface is well shown by the photograph. The adambulacral plates, short at base of ray and gradually becoming longer and lower as is characteristic of Brisingids, bear each a single acicular spine on the actinal surface. This spine is similar and subequal to the lateral spines at base of ray, but soon the latter are decidedly the longer. It carries a lateral flap of tissue covered with pedicellariae and the tip of the proximal spines is not in the least degree modified. No furrow spinelets present. The first adambulacral plate remains on the disk when a ray breaks off. The joint between the first and second plates is a muscular one, not different from the preceding nor the third and following ones, except that the muscular space widens slightly as the flexible portion of ray is reached. At each mouth angle the first pair of adambulacral plates is tightly apposed by the lateral face, and the second pair to a less extent, that part which is involved being indicated by dots in Pl. XVII, fig. 5. Above the first united pair of adambulacrals is a pair of small inferomarginals forming a part of the disk skeleton; while above adambulacrals 2 and 3 is inferomarginal 2 (Pl. XVI, fig. 5), a portion of the lateral face of which (dotted) is joined to its fellow of the adjacent ray.

The superficial portion of the mouth-plates slopes downward from the outer end to the broad actinostomial margin, which is close to peristomial membrane and carries 6-8 skin-covered spines to each pair of plates. The median, longest, of the fan are about as long as the median suture and slightly shorter than the pair of suboral spines, which stand on the distal margin and are in all respects like the first adambulacral spines. The median marginal spines carry a few to a conspicuous tuft of pedicellariae; the laterals have a few or none. These lateral members of each comb overlap those of the adjacent "jaws" and close the narrow entrance to the ambulacral furrow.

The madreporite is on the extreme margin of disk and difficult to find in large alcoholic specimens owing to crowding of the swollen genital region of ray. In young specimens it has a single groove (interradial in direction) and resembles a miniature "bivalve". This groove next becomes sinuous (R 47 mm.).

PEDICELLARIAE. The pedicellariae are all very small. Those which thickly cover the surface of the sacculi measure, in adults, 0.115-0.14 mm., measured on the long axis of the figures (Fig. G, 5-5*b*). The first to be developed are on the terminal sacculus of ray (stage 2 under "Development"); next (stage 4) they appear on the primary radial plate and a very few on the adambulacral spines. The first of the lateral sacculi of the ray probably do not develop until after the young leave the brood chamber. All these pedicellariae are essentially similar in shape and size. When the animal is practically adult the larger and differently formed pedicellariae of the marginal mouth spines appear on slight flanges of tissue. These measure 0.16-0.185 mm. high. The base of each blade or jaw is greatly developed and flares outward as may be appreciated from the figures (Fig G, 6*a*, 6*b*). The middle piece (*mp*) is very large, while the excessively fine teeth of centre of jaw are much more numerous than in the common type of pedicellaria. It is probable that the oral pedicellariae, appearing as they do rather late, will be more valuable as a generic character than the other type, which resemble, in a general way, the small pedicellariae of *Odinia*, *Brisingaster*, and even those of the distantly related *Briusingella* and *Freyellaster*.

GONADS. The gonads when ripe are voluminous and form two clusters to each ray, almost filling the genital chamber at its base. The ovary opens on distal margin of the first intercostal area at about mid-height of the second skeletal arch; while the male gonopore is in the centre of the area.

NIDAMENTAL CAVITY. In each interradius or axilla, so that the interradian angle (with its 2 first skeletal arches) forms part of its walls, is the cavity where eggs are deposited and develop. The very concave intercostal area 1 forms either side wall; while interdigitating spines of arches II and III and of the dorsal plates, above area 1, constitute a sort of basket work, with small passages through which water can circulate. The manner in which these dorsolateral spines interlock is evident from the photographs, but what is not clearly shown is that some of the spines form a continuous organic bridge between adjacent rays. These sharp spines, either by their growth or by the expansion of the body wall deeply pierce the integument of the opposite ray, and the sheath of the spine coalesces with the skin of the opposite ray. When the rays are forced apart the

spine sheath ruptures leaving the spine-tip bare and part of the sheath attached to the opposite body wall.

As the 5-9 eggs of each "basket" develop, the first intercostal membrane becomes more and more concave. The young usually have their ventral surface against the sides of this basin-like hollow, but not invariably. There are usually 2 or 3 which are developed much further than the rest. Those shown in the enlarged photograph are probably nearly ready to escape. Beneath such young, crowded against the pouch wall, there may be several very immature ones, or even eggs.

In a sample brood chamber of the large 13-armed specimen, St. 123, were 8 young in 2 stages: (1) three in the youngest stage as described below, rays 12, 13, 14; (2) five with 13 rays in stage 4. The next pouch, B, has 2 eggs; three young in the first stage (one with 11 rays, two with 13 rays); three (with 13 rays) in stage 4. Pouch C, same specimen, had a cluster of 6 eggs and three 13-rayed young in stage 1.

This is the first instance of brooding reported for the Brisingidae and is noteworthy for the position of the nursery as well as for the details of adaptation. *Especially extraordinary are the permanent spine bridges across the dorsal side of the chamber.*

DEVELOPMENTAL STAGES. The eggs found in brood pouches are subspherical, sometimes slightly flattened on one side, 1.5 mm. in diameter. One ellipsoid 2 mm. by 1.4 mm. was found.

Stage 1. In the earliest stage encountered (Fig. G, 4) the total diameter is 2.5 mm. The disk is low hemispherical and the rays from above are scarcely more than buds 0.3-0.4 mm. long. The disk is beset with widely spaced spine buds. The circle of the actinostome occupies most of the actinal surface. The nerve, terminal organ, and 3 or sometimes 4 pairs of tube-feet have appeared, and swellings of the end of ray on either side of the terminal tentacle indicate the first terminal spinelets. The oral angle is sketched in but there are no calcareous plates. Distance from oral angle to tip of ray, 0.65-0.75 mm. A specimen prepared in sodium hypochlorite has the beginnings of the following plates: abactinal of disk (4*b-d*); 4 pairs of ambulacrals, 2 of adambulacrals (no spinelets); terminal (2 spinelets). All these are in a very embryonic state. There is no trace of pedicellariae.

Stage 2 (Pl. XVI, fig. 9). Diameter about 3.5 mm. The chief advance is the appearance of numerous pedicellariae on the conspicuous sheath in which the 4 or 5 terminal spinelets are immersed. The rays are relatively longer to the still strongly convex disk; disk spinelets longer; tiny mouth pore; 2 adambulacral spines; rudimental mouth-plates; 4 pairs of tube-feet. Distance from actinostome to end of ray, 1 mm. (1 example from type).

Stage 3. Diameter 4.25 mm. Rays slightly longer, but no abactinal spinelets; disk strongly convex with subcircular embryonic plates, their spinelets slightly longer than in 2; terminal ruff of pedicellariae larger; 6 terminal spinelets, 4 pairs of tube-feet with rudiments of fifth pair on some rays, the proximal 3 pairs relatively slightly larger than in 2, and with strong sucking disks; 3 adambulacral spinelets on each side of furrow; the rudiment of a lateral oral spine to each mouth-plate (as in stage 2, Pl. XVI, fig. 9) but

definitely no suboral spine; hepatic diverticula visible through transparent peristome. Distance from mouth-plates to end of ray, 1.25 mm.

Stage 4. Diameter 5 mm.; diameter of peristome 1.7 mm.; distance from mouth-plates to end of ray 1.6–1.7 mm. The disk is now only slightly convex; the disk plates are subcircular (Fig. G, 3) and as well marked as in stage 5; the spinelets (3 *a-b*) end in 3 or 4 short thorns. On the rays the rudiments of the first arch have appeared: 3 dorsal plates, the median or radial with a spinelet and a circle of 6–10 pedicellariae; the laterals (superomarginals) with the bud of a spine; next to the adambulacrals on either side is the rudiment of an inferomarginal plate. The 3 adambulacral spinelets are now much more conspicuous and may carry several pedicellariae. The mouth-plates are larger, with a short suboral spine, and the second shorter marginal spine adjacent to median suture. The terminal ruff of pedicellariae is still larger and there are 8 slender conspicuous terminal spines. The outline of the stomach and hepatic diverticula is clear through the transparent peristome but the mouth and lips seem to be covered by tissue.

Stage 5 (Pl. XVI, figs. 10, 11). Diameter 6–6.2 mm.; diameter of peristome, 2.5 mm.; distance from mouth-plates to tip of ray, 1.85 mm. This differs from the last chiefly in increase in size. The rays are slightly longer and there are 6 pairs of tube-feet and 4 prominent adambulacral spines, but no additional oral spines nor abactinal ray spines, and no spine on the rudimentary inferomarginal plate. This is the stage shown in photographs, and it seems probable that the young soon leave the nursery through the ventral side of the brood "basket".

GROWTH STAGES. (1) The youngest post-nursery stage is a 12-rayed specimen from St. 123 having the following dimensions: diameter 14 mm., R 6–7 mm., r 2.5 mm.

The disk is not convex and is paved with relatively large, roundish, thin, overlapping plates bearing each a 3-pronged spine. This plating ceases abruptly at base of ray, to be followed after a very narrow interval of skin by the first skeletal arch composed of 7 plates, of which the unpaired mid-dorsal is usually 3-lobed, larger than the others, and carries a prominent sacculated acicular spine; the other shorter spines without a sacculus. The second arch, well spaced from the first, has a tiny mid-dorsal spine and 3 conspicuous sacculated laterals. Then there are two widely spaced arches with 2 lateral sacculated spines, and rudimentary dorsal plates; and finally a rudimentary fifth arch near the conspicuous terminal sacculus.

The adambulacral and mouth spines are relative to length of ray much longer than in adult, and the former bear a lateral sacculus of pedicellariae. The second marginal mouth spine to be developed is now longer than the lateral. The first pair of adambulacrals only touch by their inner ends adjacent to oral plates, and the first and following interadambulacral joints show no sign of a syzygy. These proximal adambulacrals are more elongated than in the adult. This condition and the separation of the first pair of adambulacrals at oral angle is similar to the structure of *Brisingella*.

(2) The next larger specimen (St. 39) is somewhat mangled but two of the 13 rays can be measured: diameter 24 mm., R 11–12 mm. r 3.75 mm. There are now 7 skeletal arches. The first 3 are clearly complete. The fourth to sixth are technically completed by

a flat, embryonic midradial plate without a spinelet. These are probably the isolated radial plates of the adult that are usually out of alignment with the paired costae. The seventh arch near the terminal "complex" appears to have this radial plate. Irregularity of plates at base of ray (arches 1 and 2) is foreshadowed by the appearance of secondary plates and spinelets—the beginning of the differentiation of a genital region. The primary radial plate can be recognized. In the third to seventh arches the spines are so spaced as to give the appearance of a complete arch of spines of which there are 8 on the second to fourth arches and 6 on the fifth to seventh. Proximally, 3 spines on either side have a heavy sacculus, distally 2. Many of the mouth-plates have 3, but a few of them 2 marginal spines. In each mouth angle there has been a rapprochement of the first adambulacral plates which are now nearly as in the adult.

Some of the disk plates have an additional spinelet. The prongs of the spines are slightly longer than in the preceding stage.

(3) St. 123 (Pl. XVII, fig. 2); extreme diameter 34 mm.; R 13–17 mm., r 3.75 mm. The disk diameter of this well-preserved 13-rayed specimen is the same as that of the preceding, but the unequal rays are longer, comprising 10 or 11 skeletal arches which do not differ in character from those of the preceding specimen. The trilobate primary radial plate with its prominently sacculate, aciculate spine is conspicuous. A smaller dorso-lateral spine on either side usually has a smaller sacculus. The 3 or 2 lateral sacculi of succeeding arches are large. Two spinelets, 0.57 and 0.6 mm. long, from disk of this specimen, are figured (Fig. G, 1, 1a). Only one of the 26 mouth-plates has 3 spines; the other have 2.

(4) St. WS 42. Extreme diameter 60 mm.; R 23–37 mm., r 5 mm. The short rays may be regenerating the tips. Rays 13. The first appearance of papulae, there being about 10 on the disk, situated interradially near margin. One ray has a papula near the base. The genital region is swollen so that base of ray is convex and higher than plane of disk. The lateral aspect of ray is *similar* to Pl. XVI, fig. 3, but smaller, and no papulae are present adjacent to adambulacral plates. The base of rays are closely appressed and dorsolateral spinelets interdigitate, but no permanent spine bridges have been formed. There are 18 skeletal arches, complete and incomplete, and the dorsal aspect of ray is similar to adult. The sacculi are large and subglobose. Most of the lateral ribs have 3 spines and sacculi; sometimes on outer part of ray, only 2, as in the fully adult. Each mouth-plate has 4 or 3 marginal spines.

FOOD. Samples of stomach contents of specimens from Sts. 42 and 123 were submitted to Dr Isabella Gordon for determination.

St. 39. The exoskeletons of 4 Cumacea, probably *Gaussicuma* were found in the stomach of the type. (W. K. F.)

St. 42. Specimen A: remains of Cumacea and small Mysidae. (W. K. F.) Specimen B. "Cumacea of the family Bodotriidae (as used by Zimmer, 1927). Appear to be males of *Gaussicuma*, a genus hitherto know only from females." (Gordon.)

St. 123. Largest specimen (R 100 mm.), a few Cumacea. (W. K. F.)

Small specimen (Pl. XVII, fig. 2). When first removed from bottle a number of

small Mysidae were held fast by the pedicellariae. (Gordon.) Possibly these were caught while in the trawl. The stomach contained fragments of a cumacean and appendages of a mysid.

COLOUR NOTE. Specimen from St. 42: disk whitish cream, arm bases light pink criss-crossed with white calcareous network; arms (beyond genital area) whitish cream; sacculi orange.

TYPE LOCALITY. St. 39, East Cumberland Bay, South Georgia, 179–235 m., grey mud. 25 March 1926, 1 large, 1 medium sized, 1 small specimen.

SPECIMENS EXAMINED. In addition to three from type locality, the following:

St. 42. Off mouth of Cumberland Bay, South Georgia, 120–204 m., 1 April 1926, 2 specimens.

St. 123. Off mouth of Cumberland Bay, South Georgia, 230–250 m., grey mud, 15 December 1926, 2 adults, 2 immature.

St. 172. Off Deception Island, South Shetland Islands, 525 m., 26 February 1927, 1 immature specimen.

St. WS 42. South Georgia, $54^{\circ} 41' 45''$ S, $36^{\circ} 47'$ W, 198 m., mud, stones, 7 January 1926, 1 immature specimen.

St. WS 766. $44^{\circ} 58'$ S, $60^{\circ} 05'$ W, 545 m., 1 immature specimen in bad condition.

Family ASTERIIDAE Gray, emended

(See Fisher, 1928, p. 56 for synopsis of subfamilies.)

Subfamily PEDICELLASTERINAE Fisher

Pedicellasterinae Fisher, 1918, p. 108.—1923, p. 249.—1928, p. 57.

Genus *Pedicellaster* Sars

Pedicellaster Sars, *Översigt af Norges Echinodermer*, Christiania, 1861, p. 77. Type *P. typicus* Sars.—Fisher, 1923, p. 251; 1928, p. 58 (revision).

Pedicellaster hypernotius Sladen

(Fig. F, 3)

Pedicellaster hypernotius Sladen, 1889, p. 558, pl. 105, figs. 5–7.

Pedicellaster antarcticus Ludwig, 1903, p. 35, pl. 4, figs. 32–38.—Kochler, 1920, pp. 106–109, pl. 16, fig. 11; pl. 17, figs. 8, 9.

St. 156. South Georgia, $53^{\circ} 51'$ S, $36^{\circ} 21' 30''$ W, 200–236 m., rock, 1 specimen.

St. 160. Near Shag Rocks, $53^{\circ} 43' 40''$ S, $43^{\circ} 57'$ W, 177 m., grey mud, stones and rock, 7 specimens.

St. 170. Off Cape Bowles, Clarence Island, $61^{\circ} 25' 30''$ S, $53^{\circ} 46'$ W, 342 m., rock, 2 specimens.

St. 181. Schollaert Channel, Palmer Archipelago, $64^{\circ} 20'$ S, $63^{\circ} 01'$ W, 160–335 m., mud, 2 specimens.

St. 190. Bismarck Strait, Palmer Archipelago, $64^{\circ} 56'$ S, $63^{\circ} 35'$ W, 93–130 m., rock or stones and mud, 2 specimens.

St. 1955. South Shetland Islands, $61^{\circ} 35' 1''$ S, $57^{\circ} 23' 3''$ W, 440–410 m., 1 specimen.

In the largest specimen, St. 156, $R=23.5$ mm., $r=3.5$ mm. It is sexually mature. In the type specimen, collected by the 'Challenger', off Marion Island, 140 fathoms,

R = 25 mm., r = 5 mm. The type of *P. antarcticus*, from Bellingshausen Sea, 450 m., measures R 30 mm., r 5 mm.

The principal difference between *antarcticus* and *hypernotius*, according to Ludwig, is the presence of 3 spinelets on each carinal plate of the former and only one in the latter species. In the Discovery specimens the number varies from 1 to 3, and occasionally to 4.

The larger of the two varieties of crossed pedicellariae is abundant on the sides of ray and distally they encroach upon the abactinal surface. They are very similar to those of *P. magister* Fisher¹ a relatively gigantic species from Bering Sea and the Alaskan coast, but are unlike the major crossed pedicellariae of *P. typicus* (Fisher, 1928, pl. 26, fig. 1). The jaw varies between 0.3 and 0.4 mm. in length. The minor pedicellariae are *circa* 0.22 mm. long. There are also pedicellariae intermediate in size and form between the major and minor varieties. Very small, blunt, triangular straight pedicellariae (0.15 mm. long) occur along the furrow margin, as figured by Sladen (1889, pl. 105, fig. 7). In the specimen from St. 1955, in which R is only 9 mm., the two sorts of crossed pedicellariae are well differentiated.

In these small specimens there is only 1 series of actinal plates. The extraordinary development of the actinal system of *P. magister* is not even suggested.

The only other Antarctic *Pedicellaster* is *formatus* Koehler (1920, p. 106, pl. 16, figs. 1, 9, 10; pl. 17, figs. 6, 7; pl. 58, fig. 4) from 120 fathoms, 66° 08' S, 94° 17' E. It differs chiefly in having stouter plates and may ultimately prove to be a form of *hypernotius*.

The Discovery specimens extend the known range of the species from Bellingshausen Sea along the Antarctic Archipelago to South Georgia and Shag Rocks.

Genus *Anteliaster* Fisher

Anteliaster Fisher, 1923, p. 252; 1928, p. 69. Type *A. coscinactis* Fisher.

Anteliaster australis sp. nov.

(Fig. I, 1-1d; Plate IX, figs. 2, 3)

DIAGNOSIS. Differing from *C. coscinactis* Fisher in lacking unguiculate straight pedicellariae and in having a relatively close-knit skeleton with usually only 1 papula to each area of disk and rays; spinelets short, close-set, interspersed with numerous crossed pedicellariae, attached to the plates, giving the body a uniform finely granulose appearance; to the touch the texture is like that of fine sand-paper. R 35 mm., r 5 mm., br 6 mm., R=7r.

DESCRIPTION. The body is covered with slender, short, thorny tipped spinelets, rather uniformly spaced about their own length; 1-3 spinelets to a plate. Everywhere between the spinelets are crossed pedicellariae, attached to surface of plates and also to membrane of papular areas. The spinelets, only slightly longer than the pedicellariae, combine with them to give the surface a rather uniform granular appearance.

¹ Fisher, 1928, p. 63, pl. 26, fig. 2; pl. 27, fig. 2.

Marginal plates lateral in position. Supermarginals with 3 spinelets, reduced to 2 and 1 at end of ray. Inferomarginals with 2 spinelets, reduced to 1 distally, before the reduction of supermarginal spinelets occurs. Actinals with 1 spinelet.

The skeleton is basically like that of *A. coscinactis* (Fisher, 1928, pl. 29, fig. 1) but the skeletal intervals relative to size of plates are much smaller; that is, the mesh is less open. If the specimen were larger (R 63 mm. in *coscinactis*) it is possible the difference would be less. The secondary ossicles uniting inferomarginals to actinals of *coscinactis* are lacking in *australis*, while the secondary intermarginal ossicles extend only a fourth the length of ray (in larger specimens, undoubtedly farther). The dorsolateral skeleton is irregular as in *coscinactis*, the plates 3- and 4-lobed, and the smaller papular areas are in about 3 irregular longiseries. There is one series of actinals extending far along ray and a short second series about one-third length of ray. The papular areas are distributed as in the figure of *coscinactis* but contain a single papula, except for a few intermarginal areas proximally which have 2.

In a smaller specimen (St. WS 86) most of the proximal dorsolaterals are 3-lobed and imbricate more regularly.

Adambulacral spines conspicuously longer than marginals and actinals, disposed in transverse series, 4 on first 3 or 4 plates, then 3. The outermost spine is clavate, the furrow spine terete and much more slender, while the middle one is intermediate. Each mouth-plate has 2 short spinelets on the inner border, extending over the peristome; and in line with the inner spinelet is a series of 3 successively longer ones on the surface of the narrow plates. On the distal furrow corner of plate is a spinelet conspicuously shorter and slenderer than outermost suboral. The first pair of adambulacrals behind mouth-plates is separated by a slight interval. The disposition of oral spines is closely similar to that of *A. coscinactis* (Fisher, 1928, pl. 29, fig. 1*b*).

Madreporic body small, with few coarse striae, situated near margin at top of inter-brachial sulcus.

There are no straight pedicellariae. The crossed closely resemble those of *A. coscinactis*, differing only in minor details. They vary in length from 0.18 to 0.4 mm., the greater number being 0.27-0.35 mm. in length. The largest are found on the actinal and inferomarginal plates where they are mixed with average sized; while the smallest are on the abactinal surface, there mixed with medium sized which are slightly smaller than the actinal average.

The gonads open in the interval between the inferomarginal and actinal plates, 3 or 4 mm. from the interbrachial angle. Each gonad consists of a cluster of relatively large branched tufts, the lobules being irregular in form and unequal in length. The inter-brachial septum is very rudimentary, practically non-existent, the coelom of disk being therefore undivided. This is an advantage to the animal which ingests its food entire. In the stomach of a specimen with disk diameter of 9 mm. were two gastropod shells, the larger a sharp cone 9 mm. long.

TYPE LOCALITY. St. WS 248, East Falkland Island, 52° 40' S, 58° 30' W, 210-242 m., fine green sand, pebbles, shells, 3 specimens.

SPECIMENS EXAMINED. Including the above, 11 specimens.

St. 156. South Georgia, south-east of Larsen Point, 260 m., mud, 1 specimen.

St. 160. Near Shag Rocks, 177 m., grey mud, stones and rock, 2 specimens.

St. WS 81. North-west of North Island, West Falkland Island, 81-82 m., 1 specimen.

St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shell, 2 specimens.

St. WS 825. North-east of East Island, Falkland Islands, 135-144 m., 1 specimen.

St. WS 871. Falkland Islands, 53° 16' S, 64° 12' W, 336-341 m., 1 specimen.

REMARKS. At Sts. 156 and 160 *Pedicellaster hypernotius* was taken. There is considerable superficial resemblance between the two species.

If the identification of the specimens listed as *Anteliaster scaber* (Smith) is correct, *australis* is a very different species. The spinelets of *scaber* are longer and the crossed pedicellariae have a different form.

Anteliaster scaber (Smith)

(Fig. F, 4, 4a)

Pedicellaster scaber Smith, *Ann. Mag. Nat. Hist.*, ser. 4, xvii, p. 107; *Phil. Trans.*, Zoology, Kerguelen Island, CLXVIII, 1879, p. 274, pl. 16, fig. 3.

St. 1563. Off Marion Island, 46° 48.4' S, 37° 49.2' E, 101-106 m., 2 specimens.

St. 1564. Off Marion Island, 46° 36.5' S, 38° 02.3' E, 108-113 m., 2 specimens.

In the absence of type material for comparison the identification of these small specimens must be regarded as provisional. The largest measures R 10 mm., r 2.5 mm. Since they were taken so near to the type locality of *Pedicellaster hypernotius*, they have been examined with that species in mind. However, there are no straight pedicellariae on the furrow margin and the proximal adambulacrals, as well as numerous others here and there along the ray are triplacanthid. There is only one kind of crossed pedicellaria (0.2 mm. long). The species is therefore not a *Pedicellaster* but an *Anteliaster*.

In the largest specimen there is one series of actinal plates which extends half the length of ray; each plate with 1 small spinelet. The intermarginal papular areas are the largest. One inframarginal series of small areas extends as far as the actinal plates; dorsolateral areas small. Dorsal plates and spinelets not in definite longiseries. The actinal surface has the bristling appearance depicted by Smith's figure.

Subfamily LABIDIASTERINAE Verrill, emended

Labidiasterinae Verrill, 1914, p. 26.—Fisher, 1919, p. 492; 1928, p. 88.

Rays numerous (9-50), long, slender; inferomarginal spines prominent, single, enveloped in a sheath carrying on the usually expanded distal surface a conspicuous wreath of crossed pedicellariae; abactinal skeleton either very open with large squarish meshes or else abortive with scattered independent plates; crossed pedicellariae in abactinal spinal wreaths or thick ruffs; no actinal plates; gonads two to each ray, opening upon the side a short distance from base; tube-feet numerous, biserial to quadriserial, each with a single ampulla.

The subfamily as here understood is rather isolated and contains *Coronaster* Perrier, *Rathbunaster* Fisher (eastern north Pacific) and *Labidiaster* Lütken.

REMARKS. Verrill included only *Labidiaster* and the synonymous *Labidiastrella* in this subfamily, which he placed in the Brisingidae, following the usual treatment of *Labidiaster*.

Labidiaster differs from *Brisinga*, *Odiuia*, *Freyella*, and similar Brisingids in the following important particulars: (1) its abactinal skeleton is not duplicated in the Brisingidae; (2) forciform, or straight, pedicellariae are present; (3) the adambulacral plates are crowded, very short in proportion to width, and entirely unlike in form and armature the same highly peculiar plates of all Brisingidae; (4) the adambulacralia are shorter, especially the dorsal ends, which overlap, or imbricate with, the next adoral ambulacral plate, while in the Brisingidae there is no sign of imbrication, the ambulacralia resembling the centra of chordate vertebrae, with vertical articulating adoral and aboral facets.

In the Brisingidae (less *Labidiaster*) the abactinal skeleton of the rays is variable, being in the form of transverse, independent, parallel ridges or costae, separated by areas of integument without plates; or the intervals may be partially or completely filled in with more or less imperfectly developed plates immersed in the body wall; or the arches may be absent and a tessellation of thin plates may cover the genital region of the ray; or there may be thin plates, more or less spiniferous, together with differentiated transverse costae.

In *Labidiaster* the skeleton of the ray is closely similar to that of *Coronaster*. There is a longitudinal series of trilobate inferomarginal plates, one of quadrilobate or cruciform superomarginal plates, and one of cruciform median radial plates. The marginals and radials form regular transverse series. On the basal portion of the ray there is a more or less irregular zigzag series of trilobate dorsolateral plates. The primary plates either connect directly by their slender lobes, or these are joined by 1 or 2 overlapping, oblong, intermediate ossicles. There results an open, fairly regular, reticulate skeleton having large tetragonal meshes (except where the dorsolateral plates frame pentagonal openings). On the outer part of ray the longitudinally oriented, intermediate, connectives and similarly oriented lobes of marginals and radials gradually disappear on the outer part of ray, so that there remains only a series of independent, transverse, slender, skeletal bands. Even the abactinal elements of these are absorbed in *Labidiaster annulatus*. The skeletal meshes contain numerous papulae. The form and armature of the adambulacral plates are as in *Coronaster*. The arrangement of the pedicellariae either in retractile wreaths surrounding the spines or on retractile transverse cushions is not unlike that found in *Coronaster*. The mouth-plates of the Brisingidae, of *Coronaster*, *Pedicellaster*, and of *Labidiaster* are similar in general form, those of *Labidiaster* being relatively the smallest.

The features which are chiefly relied upon to distinguish the Brisingidae, and to which the family in part owes its characteristic appearance, are conspicuous by their different form in *Labidiaster*. Such, in the Brisingidae, are the elongate and peculiarly

formed adambulacral plates; the long needle-like subambulacral and marginal spines, with their characteristic sacculate sheaths; the variable but always non-reticulate abactinal skeleton of the rays; the presence of only crossed pedicellariae.

The genus *Rathbunaster* is notable for the suppression of the alternate superomarginal plates and the reduction of the abactinal skeleton to spaced circular plates without trace of connectives. The marginal and abactinal plates bear an acicular spine surrounded by a retractile sheath with an expanded distal crown covered with numerous pedicellariae. The ambulacral, adambulacral, and oral plates are similar to those of *Coronaster*.

In *Labidiaster*, *Coronaster*, *Rathbunaster*, and certain genera of the Brisingidae there are 2 gonads to each ray; each gonad opens upon the side of the ray at some distance from the base. All three genera, as well as the Brisingidae, have a single ampulla to each tube-foot.

Genus *Labidiaster* Lütken

Labidiaster Lütken, *Videnskab. Medd. naturh. Foren. i Kjøbenhavn*, 1871, p. 289. Type *L. radius* Lütken.

Labidiastrella Verrill, 1914, p. 352. Type *L. annulatus* Sladen.

Labidiaster annulatus Sladen

(Fig. 1, 3-3e)

Labidiaster annulatus Sladen, 1889, p. 595, pl. 108, fig. 1.—Kochler, 1917, p. 7, pl. 1, figs. 2, 4, 5.

Labidiaster radius Kochler, 1906, p. 24.—1912, p. 7, pl. 1, fig. 1.

Labidiastrella annulata Verrill, 1914, pp. 352, 373.

St. 148. Off Cape Saunders, South Georgia, from $54^{\circ} 03' S$, $36^{\circ} 39' W$ to $54^{\circ} 05' S$, $36^{\circ} 36' 30'' W$, 132-148 m., grey mud and stones, 2 specimens.

St. 156. South Georgia, $53^{\circ} 51' S$, $36^{\circ} 21' 30'' W$, 200-236 m., rock, 2 specimens.

St. 159. South Georgia, $53^{\circ} 32' 30'' S$, $36^{\circ} 08' W$, 160 m., rock, 1 specimen.

St. 160. Near Shag Rocks, $53^{\circ} 43' 40'' S$, $40^{\circ} 57' W$, 177 m., grey mud, stones, 4 specimens.

St. 167. Off Signy Island, South Orkneys, $60^{\circ} 50' 30'' S$, $46^{\circ} 15' W$, 244-344 m., green mud, 1 specimen.

St. 182. Schollaert Channel, Palmer Archipelago, 278-500 m., 1 specimen.

St. 187. Neumayr Channel, Palmer Archipelago, $64^{\circ} 48' 30'' S$, $63^{\circ} 31' 30'' W$, 259 m., mud, 1 specimen.

St. 190. Bismarck Strait, Palmer Archipelago, $64^{\circ} 56' S$, $63^{\circ} 35' W$, 93-130 m., rock or stones and mud, 8 specimens.

St. 371. 1 mile east of Montagu Island, South Sandwich Islands, 99-161 m., 3 specimens.

St. MS 68. East Cumberland Bay, South Georgia, 220-247 m., 2 specimens.

St. 1873. Off Clarence Island, South Shetland Islands, $61^{\circ} 20.8' S$, $54^{\circ} 04.2' W$, 200-137 m., 2 specimens.

St. 1955. South Shetland Islands, $61^{\circ} 35.1' S$, $57^{\circ} 23.3' W$, 440-410 m., 2 specimens.

The smallest specimen (St. 160), with R 15-17 mm. and r 4 mm., has 16 subequal rays and the bud of a new one. The specimen with longest rays (St. MS 68) with R 340-370 mm. and r 45 mm. has 45 rays. Of these, 21 are only 15-50 mm. long and represent regenerating rays from margin of disk. The following are the maximum number of rays observed: 47 rays, R 270 mm. (St. 156); 48 rays, R 260 mm. (St. 167);

49 rays, R 185 mm. (St. 1955); 50 rays, R 180 mm. (St. 167). So far as I am aware this is the greatest number of rays observed in any sea star and is slightly in excess of twice the maximum number (24) ever reported for the large north Pacific *Pycnopodia helianthoides*.

The outstanding characters of this species are the very large crossed pedicellariae carried by the abactinal transverse integumentary welts of ray; and the rapid atrophy of the abactinal skeleton beyond the proximal third of the ray. At first the longitudinally oriented ossicles of the skeleton disappear leaving rather widely spaced transverse arches of slender plates, corresponding to the lateral pairs of marginals. Then the abactinal elements of these arches disappear, leaving the marginal plates, which become smaller and smaller as end of ray is approached. On the outer third of ray they are scarcely more than rudiments. A very small inferomarginal spinelet persists nearly to end of ray but is quite hidden by the thick integument and pedicellariae.

The transverse welts, or thickening, of the integument, which proximally overlies the skeletal arches, are continued to the end of the ray and are more prominent after the disappearance of the abactinal plates. These heavier cushions distal to the region of more or less complete abactinal skeleton carry the largest pedicellariae in considerable numbers, as shown by Koehler's figures (1917, pl. 1, figs. 2, 4). Over the proximal, so-called genital area, the crossed pedicellariae are fewer and smaller, their place to some extent being taken by numerous large and small laceolate straight pedicellariae.

On fully grown specimens (e.g. with R 180 mm.) the characteristic large crossed pedicellariae are 1-1.5 mm. long and on the largest examples upward of 1.75 mm. long (Fig. 1, 3). On the marginal spines and proximal abactinal plates are numerous smaller pedicellariae approximately 0.4 mm. (Fig. 3c); and on the outer adambulacral spines a cushion of still smaller ones, 0.25-0.3 mm. (Fig. 3b).

Crossed pedicellariae are practically absent from the disk, but in place of them are very numerous small and large lanceolate straight pedicellariae, the largest as long as the acicular spinelets but much thicker.

Sladen does not mention the mouth-plates. They are more easily observed in small than in large specimens, for in the latter the entire circumference of actinostome is a *cheval-de-frise* of crowded spines and very numerous large straight pedicellariae which hide the plates. In a small specimen, with disk-diameter 25 mm. and 36 rays, the inner end of all but 5 of the ambulacral furrows is bridged by a fusion of the inner lateral angles of the mouth-plates of either side of furrow. In a large specimen with 49 rays only 4 furrows are open at the inner end. This is obviously caused by a crowding of the mouth angles. The organic bridge consists at first of tissue only, but as growth proceeds the opposing plates are wedged tightly together so that at best only a narrow suture separates them. In old examples actual ankylosis takes place. In early stages a sort of epineural tube represents the inner end of the ambulacral furrow, but in later stages of fusion this tube is often very small—so small in fact that one wonders how the radial nerve avoids compression during active movements of the animal. The armature of the plates is variable, partly due to suppression of the lateral marginal spines by this fusion. Each plate has on the actinostomial margin adjacent to median suture a prominent

slender acicular spine and two shorter ones at mouth of furrow. One or both of these lateral spinelets may be suppressed by fusion of plates. Actually the actinostomial margin of the combined mouth-plates of any oral angle carries 2 or 3 unequal spines, except when one "corner" has failed to fuse. On that particular plate there are 3 spines, the apical and 2 laterals. The companion plate of that angle (if fused with its *εἰς-ἀ-εἰς* of the next angle) has only the apical spine surviving. The very constricted outer part of each oral pair carries 1-3 prominent slender acicular suborals irregularly placed.

The circle of mostly fused mouth-plates overhangs the outer part of the peristome so that the circumoral nerve is at the rear, or bottom, of a rather deep groove above the projecting oral angles. The *cheval-de-frise* of spines and large pedunculate straight pedicellariae evidently provide an efficient protection to the nerve.

Behind the oral pair of plates there is an extensive adoral carina composed of 6-8 pairs of juxtaposed adambulacral plates of adjacent rays. Each of these plates carries 1 spine, the inner of the pair characteristic of adambulacrals of the free part of the ray.

In spite of a certain amount of variation in detail, the two species of *Labidiaster* are easy to distinguish, the general habit of medium-sized specimens being well shown by Sladen's figures which, however, do not do justice to the disparity in size of the crossed pedicellariae. In *radiosus* these pedicellariae are not only smaller, but differ slightly in detail. The skeletal arches, in a rudimentary form, persist to the end of ray. The disk is smaller, while a scattering of primary spines is conspicuously larger than the secondaries; in *annulatus* there is no such disparity, the spines being uniformly small and more numerous. In *radiosus* straight pedicellariae are not numerous, but this feature may prove to be variable.

In young specimens of *annulatus* (e.g. R 50 mm., r 12 mm.) the transverse skeletal arches persist to the end of the ray as in adult *radiosus*. Verrill made a "book-genus", *Labidiastrella* for *L. annulatus*,¹ based upon the absence of the dorsal skeleton distally. The difference between *radiosus* and *annulatus* in this respect is one of degree, not kind. The abactinal skeleton of *radiosus* is incomplete distally, but the degeneration has not been carried so far as in *annulatus*. Compensating for the loss of abactinal plates, *annulatus* has developed a remarkable equipment of crossed pedicellariae of very large size.

As in *Pycnopodia*, the loss of the abactinal skeleton undoubtedly confers a high degree of flexibility to the rays. Active prey can be detained long enough by the large crossed pedicellariae for the tube-feet of adjacent rays to be brought into action. Rapid torsion of rays is of distinct advantage. In the stomach of a rather small example, with disk diameter of 30 mm., are fragments of a *Euphausia* (probably *superba*) about 40 mm. long (St. 190). A specimen from St. 371 and one from St. 1955 have captured isopods; one from St. 148 contains a small ophiuran. In general the mouth is widely open and sometimes the stomach is partly everted.

Koehler's records of *L. radiosus* from the Antarctic Archipelago refer to *L. annulatus*. His figure (1912, pl. 1, fig. 1) of a specimen from 64° 48' S, 65° 51' W is clearly referable to *annulatus*.

¹ Verrill, 1914, p. 352.

TYPE LOCALITY. Not stated. Original specimens from 75 to 150 fathoms off Kerguelen and Heard Islands and between the two.

DISTRIBUTION. South of the Antarctic Convergence: Kerguelen, Heard; Antarctic Archipelago; South Orkneys, South Sandwich Islands, South Georgia, Shag Rocks; 93-440 m.

The record of this species from Challenger St. 191, 800 fathoms, Arafura Sea needs confirmation by new material.

Labidiaster radiosus Lütken

(Fig. I, 2-2b)

Labidiaster radiosus Lütken, *Videnskab. Medd. naturh. Foren. i Kjobenhavn*, 1871, p. 293.—Studer, 1884, pp. 14-25, pls. 2, 3, fig. 4a-y.—Sladen, 1889, p. 595, pl. 108, fig. 2.—Perrier, 1891, p. 72, 149-159, pl. 8, figs. 2-11.—Ludwig, 1903, p. 58, pl. 4, fig. 39; 1905, p. 71.—Koehler, 1917, pl. 1, fig. 3.—1923, p. 6, pl. 1, fig. 3.

Labidiaster crassus Koehler, 1923, p. 7, pl. 1, figs. 1, 2.

St. 48. 8.3 miles north, 53° E of William Point Beacon, Port William, East Falkland Island, 105-115 m., 3 specimens.

St. 51. Off Eddystone Rock, East Falkland Island, 105-115 m., fine sand, 18 specimens.

St. WS 72. Falkland Islands, 51° 07' S, 57° 34' W, 79 m., sand and shell, 5 specimens.

St. WS 79. Falkland Islands, 51° 01' 30" S, 64° 59' 30" W, 131-132 m., fine dark sand, 5 specimens.

St. WS 83. 14 miles south, 64° W of George Island, East Falkland Island, 137-129 m., fine green sand and shell, 1 specimen.

St. WS 84. 7½ miles south, 9° W of Sea Lion Island, East Falkland Island, 75-74 m., coarse sand, shell, stones, 17 specimens.

St. WS 91. Tierra del Fuego, 52° 53' 45" S, 64° 37' 30" W, 191-205 m., fine dark sand and shell, 1 specimen.

St. WS 93. West Falkland Island, 51° 51' S, 61° 30' W, 133-130 m., grey sand, 1 specimen.

St. WS 97. Falkland Plateau, 49° 00' 30" S, 61° 58' W, 146-145 m., 1 specimen.

St. WS 225. Falkland Islands, 50° 20' S, 62° 30' W, 162-161 m., green sand, shells and pebbles, 1 specimen.

St. WS 226. Falkland Islands, 49° 20' S, 62° 30' W, 144-152 m., 1 specimen.

St. WS 249. Falkland Islands, 52° 10' S, 57° 30' W, 166 m., fine brown and green sand, shells, stones, 1 specimen.

St. WS 583. Falkland Islands, 53° 39' S, 70° 54½' W, 14-78 m., 1 specimen.

St. WS 801. South-east of Cape Tres Puntas, 48° 26¼' S, 61° 28' W, 165 m., 1 specimen.

St. WS 824. Falkland Islands, 52° 29¼' S, 58° 27¼' W, 146-137 m., 3 specimens.

St. WS 825. Falkland Islands, 50° 50' S, 57° 15¼' W, 135-144 m., 1 specimen.

This species has been erroneously reported from the Antarctic Archipelago by Koehler, as noted under synonymy of *L. annulatus*. Even specimens from as near the Falkland area as Shag Rocks are referable to *annulatus*.

The two species are readily distinguishable by the persistence, in *radiosus*, of the abactinal arcs of plates to the end of the ray; by the smaller crossed pedicellariae of the transverse integumentary cushions, relatively few abactinal straight pedicellariae, and by large primary abactinal spines of disk in addition to distinctly smaller secondary ones. Although there are no specimens of *radiosus* large enough to compare with the fully

grown examples of *annulatus*, in medium-sized examples of comparable size (e.g. 100 mm.) there is a decided difference in the dimensions of the largest crossed pedicellariae. These are 0.55–0.65 mm. in *radiosus* and in *annulatus*, 0.9–1.3 mm. In fully grown examples of *annulatus* they are still larger (1.75 mm.). In addition to these large pedicellariae there are also perfectly formed small ones on the order of 0.2 mm. long in *radiosus* and 0.27–0.4 in *annulatus*. Slight differences in details are observable in the crossed pedicellariae of the two species (see figures).

Fusion of the mouth-plates occurs in this species as in *annulatus* and has been noted and figured by Perrier (1891, p. 73, pl. 8, fig. 4). In a specimen with 34 rays and disk diameter of 35 mm. (R 95 mm.) there are only 5 scattered furrows which are "open" at the adoral end. There are rather fewer oral straight pedicellariae than in *annulatus*. The adoral carina is composed of 5–7 pairs of adambulacral plates.

Labidiaster crassus Koehler, without locality, seems to be a variety of *radiosus* with stout, abnormally short rays.

In the stomachs of several individuals from St. 51 were found the remains of Serolid isopods. At this station were taken 3 species of *Serolis*—*schythei*, *convexa*, *exigua* (see Sheppard, 1933, *Discovery Report*, VII, p. 259). There were 5 young *Muuuda*, looking like *gregaria* (identifications by Mr Dilwyn John).

DISTRIBUTION. The Falkland plateau and southern end of South America, north to latitude 41° S on the Pacific coast and to 38° S on the Atlantic; 0–183 m.

Subfamily COSCINASTERIINAE Fisher

Coscinasteriinae Fisher, 1923, p. 249.—1928, p. 93 (key to genera).

Genus *Lethasterias* Fisher

Lethasterias Fisher, 1923, p. 258; 1928, p. 131. Type *Asterias nanimensis* Verrill.

Lethasterias australis sp.nov.

(Fig. L, 1–1g, 2; Plate XVII, fig. 5)

DIAGNOSIS. R 32 mm., r 7 mm., br 7 mm. Resembling a small *Sclerasterias* abactinally; ray pentagonal in section, swollen beyond base. Differing from north Pacific forms in lacking unguiculate straight pedicellariae, blackish tips to abactinal spines, and in the different form of the straight pedicellariae which have a more extensive terminal lip.

DESCRIPTION. The type strongly resembles a small *Sclerasterias* but is debarred from this genus by the presence of a cushion of crossed pedicellariae on both inferomarginal spines and by the absence of even any sign of an enlarged lateral tooth on the terminal lip of the crossed pedicellariae. In *Distolasterias* the crossed pedicellariae have an even more conspicuously enlarged terminal tooth on each side of the terminal lip.¹ The abactinal surface slopes downward on either side of the carinal ridge to the superomarginal plates, each carinal and superomarginal plate carrying 1 stout capitate spine, the swollen end being vertically grooved. Smaller, well-spaced dorsolateral spines are

¹ See Fisher, 1928, p. 95, pl. 60, figs. 1–3.

scattered between these two series in the equivalent of two irregular longiseries. All carry heavy basal wreaths of crossed pedicellariae which increase in size from the carinal (0.27–0.36 mm.) to the superomarginal (0.40–0.45 mm.). The lateral, vertical face of ray is about half as wide as the dorsolateral. The first 5–8 inferomarginals carry 1 spatulate, heavy spine, then two until near end of ray where there may be either 1 or 2. Each spine, or pair of spines, carries a pad of crossed pedicellariae on the upper and outer side. (For form and dimensions of spines see Fig. L, 1a–1e). Between the inferomarginals and adambulacrals is a short series of slender, spineless actinal plates hidden by the integument.

The adambulacrals are regularly diplacanthid except the first 1, 2, or 3. The spines are subterete, round-tipped, relative to the inferomarginals, rather slender. Each narrow mouth-plate has 1 long and 1 short actinostomial spine, and 1 still longer suboral like the first few adambulacrals. The first pair of adambulacrals are in close contact behind the mouth-plates, the second and third pairs not so close; the fourth pair definitely separated.

The abactinal skeleton is not very regular. The carinal plates imbricate directly one with the other but form a sinuous series. The spiniferous dorsolaterals do not form well-defined longiseries and it seems probable that in an older specimen the skeleton will lose rather than gain in regularity, as in the case of *L. nanimensis*. The surface of the superomarginal plates lacks any trace of hyaline pebbling such as is found in *Sclerasterias*.

Good sized papulae occur singly or in two's on the dorsolateral area and disk; singly along the intermarginal channel; and a short series proximally in the actinal channel. Integument thick and wrinkled.

In addition to the characteristic crossed pedicellariae, which occur on abactinal and marginal spines, there is a moderate number of lanceolate, pedunculate straight pedicellariae on the mouth and adambulacral plates (furrow face), and 1 or 2 on each actinal interradiial area (0.75 mm. long).

Madreporite small, sunken, situated at mid-r.

Gonads rudimentary.

TYPE LOCALITY. St. WS 235, 47° 56' S, 61° 10' W, 155 m., 1 specimen.

REMARKS. The type is immature and the species possibly attains a large size, as in the case of *L. nanimensis* and *L. nanimensis chelifera*.¹ It is not improbable that such large specimens will be provided with unguiculate straight pedicellariae. The crossed pedicellariae of *australis* have a more extensive terminal lip than is found in the northern forms. This is most easily appreciated by a comparison of drawings of lateral views (Fisher, 1928, pl. 60, figs. 4, 5).

Genus *Notasterias* Koehler .

Notasterias Koehler, 1911, p. 35. Type *N. armata* Koehler.—Fisher, 1930, p. 243.

Autasterias Koehler, 1911, p. 38. Type *Asterias pedicellaris* Koehler.—Fisher, 1930, p. 244.

Notasteriinae Fisher, 1930, p. 243.

DIAGNOSIS. With crossed pedicellariae of a peculiar type, sometimes of very large size, having hooked terminally crossed, somewhat falcate jaws, the bases of which flare

¹ Fisher, 1928, pp. 132, 134.

apart to accommodate an unusual development of muscles (*macrocephalus* Koehler); together with a less modified form (*pirocephalus*), and conventional crossed pedicellariae. Dorsal skeleton and spines essentially as in less modified Coscinasteriinae, consisting of large, cruciform typically monacanthid carinals (alternating sometimes with secondary smaller plates) which connect with similar superomarginals by short transverse arcs of a few plates; marginals large, cruciform, monacanthid; 1 series of monacanthid actinals; papulae in 2 dorsolateral, 1 intermarginal, and, in one species, 1 actinal series; adambulacral plates predominantly diplacanthid, or monacanthid, or a combination of the two, the spines without attached pedicellariae; major pedicellariae attached to spine sheath at base of spine, or aggregated in wreaths on collar-like thickenings of the sheath, or scattered over dorsal surface; gonads in one species (*armata*) open ventrally.

REMARKS. In the light of the Discovery material it is not possible to maintain *Autasterias* on the basis of the number of adambulacral spines. Its type species (*pedicellaris*) is probably immature. *Autasterias bongraini*, as shown below, is not exclusively monacanthid; and it more closely resembles the diplacanthid *Notasterias stolophora* than it does the type of *Autasterias*. Both *Autasterias pedicellaris* and *Notasterias haswelli* have the major pedicellariae attached to plates rather than to the spine sheaths, as have the other species. The one has predominantly monacanthid adambulacrals, the other diplacanthid. It is not at all clear that these two constitute a natural generic group.

There is nothing in the structure of the skeleton and spines which justifies the removal of *Notasterias* from the Coscinasteriinae. The shape of the plates (Fig. K, 1) and distribution of the single spines are as in typical Coscinasteriinae—even to occurrence of spines on alternate superomarginals and carinals. The macrocephalous pedicellariae (which are sometimes absent) have not diverged further from the normal crossed type than have the peculiar falcate straight pedicellariae of *Pisaster* from the conventional straight pedicellaria. I have therefore placed the Notasteriinae in the synonymy of the genus.

Notasterias armata Koehler

(Fig. J, 2*a*, 4-4*b*; Fig. K, 1)

Notasterias armata Koehler, 1911, p. 39, pl. 5, figs. 6-11; pl. 6, figs. 1-8.—1912, p. 25, pl. 1, fig. 8.—1920, p. 58, pl. 7, figs. 7-9; pl. 8, figs. 2-8; pl. 9, figs. 1-6; pl. 10, figs. 1-9; pl. 60, fig. 1; pl. 61, fig. 1.—Fisher, 1930, p. 244.

St. 1658. Ross Sea, 76° 09.6' S, 168° 40' E, 520 m., 1 specimen.

St. 1660. Ross Sea, 74° 46.4' S, 178° 23.4' E, 351 m., 3 specimens.

Koehler has described and figured this species in great detail. It is remarkable for the large size of the macrocephalous pedicellariae, of which 1, and rather seldom 2 or 3, are attached to the base of the carinal and superomarginal spines (R 66 mm., St. 1658). The inferomarginal pedicellariae are much smaller and simpler. Two or three are attached to the spine sheath above the base, while on the actinal spines similar ones are at about mid-height. It is probable that even the giant pedicellariae can be elevated to end of the spine. The largest macrocephalous pedicellariae measure 3 mm. in length and 2 mm. broad at base. I find no minor crossed pedicellariae, nor spatulate straight pedicellariae.

There is much variation in the frequency of diplacanthid adambulacral plates. In the largest specimen (R 66 mm.) only the plates of the proximal third of ray are diplacanthid, the rest having 1 spine, with a few scattered plates bearing 2.

There is no trace of papulae between the inferomarginal and actinal spines, nor any between the latter and adambulacral plates.

In the largest specimen, on the actinal surface on either side of interradial line, and between inferomarginal and actinal plates, is what I interpret as a gonopore. There are thus two in each actinal interradial area. The gonads are attached to body wall at lower end of first superomarginal plate, thus well above the pore.

DISTRIBUTION. Ross Sea and South Victoria Land, 30–351 m.; Antarctic Archipelago (Alexander I Island), 297 m.; latitude $64^{\circ} 32'$ to $66^{\circ} 55'$ S and longitude 92° to $145^{\circ} 51'$ E, 60–354 fathoms; hence probably circumpolar.

Notasterias stolophora sp.nov.

(Fig. J, 1–1e, 2b; Plate XVII, fig. 4)

DIAGNOSIS. Differing from *N. armata* in having smaller macrocephalous pedicellariae distributed in true circumspinal wreaths on the carinal plates and half wreaths on the marginal, and in having actinal papulae. R 27 mm., r 6.5 mm., br 7 mm. Colour in life pale yellow-green.

DESCRIPTION. Spines subequal, prominent, spaced, with compressed, truncate or subclavate tips, in 5 longiseries. The carinal spines are on every plate on the proximal third of ray, then on alternate plates. The superomarginals are generally in alternate plates, while each inferomarginal plate carries 1 spine. The carinal plates carry prominent wreaths of pedicellariae while the marginals have half-wreaths on the upper or adcarinal side. The skeleton is similar to that of *N. armata*. There are two dorsolateral series of single papulae (1 series close to carinals and 1 close to superomarginals), 1 intermarginal series, and a short actinal series, comprising 3–5 single papulae. The intermarginal papulae, mostly single, are large and the intermarginal area is as broad as the dorsolateral.

Integument thick and wrinkled, as are the spine sheaths except at spine tips where skin is strongly contracted. Well-defined transverse channels extend from dorsal surface between marginal plates to ambulacrum and include between them usually three adambulacral plates.

Adambulacral plates diplacanthid except for first 1–3, which are monacanthid. Spines slender, terete, blunt, subequal to inferomarginals but much less robust. At each mouth angle are 4 spines, the middle pair longer than the lateral spine and shorter than the adambulacrals. Behind these are two prominent suborals slightly larger than adambulacrals. The adoral carina is composed of the first 2 pairs of adambulacral plates.

Crossed pedicellariae are solely of the large macrocephalous variety in different stages of development. When fully developed they are 0.75–0.8 mm. long and 0.3–0.4 mm. broad at the basal piece. They are thus very much smaller than in *armata*, as

well as different in form. They are characteristically more numerous, since the heavy spine-sheaths carry at about mid-height of the disk and carinal spines 5-8 in a complete wreath. On the side of the superomarginal spines toward carinals there are 1-5, and on the inferomarginals 1-3 on the upper side. Along the furrow face of adambulacral plates is a moderate number (which will undoubtedly increase with age) of lanceolate pedicellariae. Typical pedicellariae from different locations are figured.

The presence of 1 or 2 rudimentary actinal spines probably indicates that the series is well developed in large specimens, as are probably also dorsolateral spines. Madreporic plate small, situated at mid-r on outer side of a small primary interradial spine.

TYPE LOCALITY. St. 1872, east of Joinville Island, Antarctic Archipelago, 63° 29.6' S, 54° 03.1' W, 247 m., 2 specimens, 1 very small (R 6.5 mm.).

REMARKS. There is no chance of confusing this species with *N. armata*, which carries 1 or 2 enormous major pedicellariae at the base of abactinal and superomarginal spines. *N. haswelli* has uniformly small major pedicellariae (usually 0.45 mm. in length) which are distributed in great abundance all over the dorsal surface. These pedicellariae resemble those of *stolophora* in having short "handles" to the blades, or jaws. These handles are more developed however than in *stolophora*, much less so than in *armata* and *bongraini*. The pedicellariae alone will distinguish the form I have called *bongraini* in which the large (1.8-2 mm. long) major pedicellariae are attached to the thickened sheath of the carinal spines, forming what is essentially a circumspinal wreath.

The young specimen has R 6.5 mm., r 2.5 mm., 6 carinal, 6 superomarginal, 6 or 7 inferomarginal spines. The major crossed pedicellariae, few in number, are at the stage of development shown in Fig. J, 1d.

Notasterias bongraini (Koehler)

(Fig. J, 3-3a, 2c, d, e)

Autasterias bongraini Koehler, 1912, p. 26, pl. 2, figs. 10, 11; 1920, p. 74, pl. 6, figs. 5-10; pl. 59, fig. 1.—Fisher, 1920, p. 244.

St. 1957. Off south side Clarence Island, South Shetlands, 830 m., 3 specimens.

The largest specimen measures R 53 mm., r 10 mm., br 11-12 mm. The other two are small having R 17 and 20 mm.

Although Koehler's original specimens were taken at King George Island, South Shetlands, 420 m., the Discovery specimens are different in having more numerous macrocephalous pedicellariae and by no means uniformly monacanthid adambulacral plates. In the large specimen, for instance, in one adambulacral series chosen at random the following plates, counting from base of ray, have 2 spines: 15, 28, 38, 48, 52, 54, 56, 72, 79, 81, 88, 89 (series ends at 106). The incidence on another ray is 2, 10, 11, 15, 16, 17, 40, 51, 52, 67, 69, 75. Although Koehler states that the adambulacral spines are in a single series, the photograph of a type (1912, pl. 2, fig. 11) shows a very few diplacanthid plates. Of the two small specimens one has very few diplacanthid plates while in the

other they are as numerous as in a young example of *armata* (R 17 mm.) where some of the proximal plates and all of the distal half of ray are monacanthid.

The macrocephalous pedicellariae are closely similar to those figured by Kochler (1920) but are more numerous in the large specimen where the carinal plates carry a battery of from 2 to 5 and disk spines, 5-8, attached to the swollen base of the spine sheath. A short series of dorsolateral spines carries 1 or 2 of these major pedicellariae. The superomarginal spines have a complete wreath of ordinary pedicellariae extending half the height of spine, and in addition the proximal spines carry 1 or 2 major pedicellariae. The inferomarginals each have a thick pad of numerous minor pedicellariae on the outer side, while actinals are similarly armed with about 10 minor pedicellariae. The inferomarginal spines are all united at the base by a web of skin which would obviously be broader if the pads of pedicellariae were advanced to the end of spines. The prominence of this ventrolateral web (which is present in *N. armata*) depends upon the contraction of sheath muscles. A similar web occurs in typical *Coscinasteriinae*.

There is no trace of actinal papulae.

The young specimens (R 17 and 20 mm.) already have the minor crossed pedicellariae developed on supero- and inferomarginal spines, whereas in the much larger *armata* and *stolophora* they are absent. These small specimens also carry 1 or 2 macrocephalous pedicellariae at base of the central, primary radial, and about half of the carinal spines. Some of them belong to the pirocephalous variety of Kochler and appear to be incompletely developed macrocephalous, lacking the long hyaline spine at end of jaw.

I do not believe a generic distinction, based upon number of adambulacral spines, can be drawn between *N. armata* and *N. bongraini*.

DISTRIBUTION. South Shetland Islands, 420-830 m., latitude 65° 42' to 66° 55' S, longitude 92° 10' to 145° 21' E, 60-318 fathoms.

Notasterias species

St. 195. Admiralty Bay, King George Island, South Shetlands, 391 m., 3 specimens.

St. 599. West coast of Adelaide Island, 67° 08' S, 69° 06½' W, 203 m., 1 specimen.

The specimen from St. 599 has R 18 mm. and definitely *diplocanthid* adambulacrals. There are no specialized major pedicellariae. The carinal, some of the few dorsolateral, the superomarginal, and inferomarginal spines carry 1 or sometimes 2 normal crossed pedicellariae, *circa* 0.4 mm. long, resembling those of *N. bongraini* (Fig. 3a) but with a straighter terminal lip as seen in profile. Along the furrow margin at base of about every third or fourth spine is a broadly lanceolate straight pedicellaria.

The largest specimen from St. 195, representing probably a second species, has R 15 mm. and monacanthid adambulacrals. It has a few normal straight pedicellariae but no major pedicellariae. The other specimens (R 8 and 5 mm.) have still fewer crossed pedicellariae. The largest specimen has only a few furrow straight pedicellariae, the others none.

The important feature of these specimens is the absence of the specialized major

crossed pedicellariae. These are present in an example of *N. bongraini* having R 17 mm., and in one of *stolophora* as small as 6.5 mm., so that age alone cannot account for their absence. It may well be that they do not occur in some of the less specialized species of the genus.

Genus *Psalidaster* nov.

DIAGNOSIS. Superficially resembling *Saliasterias* Koehler, but differing in having large, crossed pedicellariae of *Notasterias* type, abactinal and marginal spines single, the latter (surrounded by rosettes of crossed pedicellariae) forming two prominent lateral series. Abactinal and intermarginal papulae; no actinal plates or papulae; adambulacral plates diplacanthid, sporadically monacanthid and triplacanthid; actinostome small, mouth-plates small, adoral carina, long, narrow (5 or 6 plates); ambulacral furrow not abnormally wide; tube-feet slender, four ranked; abactinal skeleton proximally very irregularly reticulate, weak, disintegrated distally into separated small primary plates; gonopores conspicuous, two to each constricted actinal interradial area.

Type *Ps. mordax* sp. nov.

REMARKS. This new polybrachiate type cannot be confused with either *Saliasterias* Koehler or *Cryptasterias* Verrill, since its crossed pedicellariae, nearly 1 mm. long, have a highly characteristic form totally unlike the very small conventional pedicellariae of the above named genera. This is rather a fortunate circumstance for the abactinal skeleton, like that of so many Antarctic Asteroiidae, is weak, reticulated, and without any special clues to relationship; while the mostly monacanthid marginals are also without outstanding characteristics. The ovaries are small with large eggs, as in *Cryptasterias*, and open ventrally. The skin, though soft and finely wrinkled, is not of the thick pustulate type characteristic of *Cryptasterias*.

The crossed pedicellariae resemble those of *Notasterias* in having a broad base for the accommodation of heavier muscles, the jaws being swollen, with a large cavity. The constricted distal end of the jaw is produced into two principal teeth which interlock with those of the other jaw, instead of crossing. The suppression of one tooth would produce a pedicellaria closely similar to those which predominate on the inferomarginal and actinal spines of *Notasterias armata* (compare Fig. J, 4*b* with Fig. K, 2*f*, 2*g*).

As to the place of this genus in the system, I believe that it may be regarded as allied to *Coscinasteriinae* rather than to typical *Asteriinae* such as *Diplasterias*.

Psalidaster mordax sp. nov.

(Fig. K, 2-2*g*, 3-3*b*; Plate XVIII, figs. 1, 2)

DIAGNOSIS. Rays 11; R 135 mm., r 27 mm., br 15-16 mm. Paratype R 110 mm., r 23 mm., br 12 mm. Rays flexible, slender, with evenly convex pliant abactinal surface uniformly beset with short soft papillae representing small spinelets, their associated crossed pedicellariae and smaller interspersed papulae; abactinal skin soft, not thick, not thrown into heavy welts, although finely wrinkled; marginal spines larger than abactinal, in two regular longiseries, carrying rosettes of pedicellariae; no actinal plates;

adambulacral spines 2 (varying to 1 or 3), long, slender, terete, in a transverse series; actinostome small, mostly occluded by the long teeth (a pair to each mouth angle); furrows not wide; tube-feet slender, 4 ranked.

DESCRIPTION. The convex abactinal wall is beset with widely spaced slender acicular thorny spinelets (0.9–2 mm. long), the retracted sheath of which forms a soft collar at the base and carries 1 or 2 to 5 or 6 characteristic crossed pedicellariae. The integument is soft and until dried hides the skeleton. Between the spines are abundant papulae, singly or in two's and three's, and here and there a lanceolate straight pedicellaria. In alcoholic specimens the abactinal surface, under low magnification, has the appearance of being covered with low papillae—a confused mixture of papulae, skin-covered pedicellariae and spinelets. There is considerable difference between the two specimens in the number of pedicellariae. In the smaller, most of the abactinal spinelets of ray carry 1 or 2, and of the disk 2 or 3; whereas in the type the number is 5 or 6 for ray and 5–10 for disk. Madreporic body small (3 mm. diameter), situated at mid-r.

On the side of the ray are two longiseries of acicular spines conspicuously larger than the abactinal and surrounded by thick basal collars of crossed pedicellariae like the abactinal. The upper or superomarginal are 2–2.25 mm. long by 0.35 mm. just above base and carry 6–8 crossed pedicellariae, while the inferomarginal spines (sometimes 2 spines to a plate) are 2.9 mm. long by 0.5 mm. thick at base, and the fleshy sheath carries upward of 25 crossed pedicellariae. The spines correspond to about every fourth adambulacral plate and as the superomarginal plates are oriented obliquely to the inferomarginals the superomarginal spine is usually above the interval between 2 inferomarginal spines. There is a series of single inconspicuous intermarginal papulae which may represent encroachments of the abactinal system.

Between the inferomarginal and outer adambulacral spine is a narrow zone of bare skin devoid of papulae. The adambulacral spines are usually two in a transverse series on the inner half of plate; often there are 3, or only 1. They are long, slender (proximally 3.5 by 0.4 mm.), blunt, of nearly uniform diameter, and the proximal are a little longer than the inferomarginals. The furrow face of the adambulacral plates carries numerous small pedunculate straight pedicellariae of the common lanceolate form, 0.6–0.7 mm. in length, and 0.35 mm. broad at base.

The mouth-plates are small with a narrow actinostomial border, there being at each mouth angle two long "teeth" extending over the peristome; at outer end of each mouth pair are two spines intermediate in size between the teeth and the first adambulacrals. The narrow adoral carina, just back of mouth-plates, is composed of 5 or 6 pairs of juxtaposed adambulacrals which generally carry only one spine each; but sometimes a second smaller one is present on the fourth to sixth. The mouth-plates carry an abundance of small straight pedicellariae, exactly like the adambulacral.

Phylogenetically the abactinal skeleton is degenerating. It is composed of very numerous small plates forming a fantastically irregular reticulate structure, the irregularly spaced nodes of which are formed by 3- or 4-lobed primary plates, bearing single spinelets. The secondary plates are slender, overlapping, and the meshes are small, very

unequal in size and irregular in shape. A meandering series of slightly larger carinal plates can be readily distinguished in a prepared specimen. Their spinelets are closer together than elsewhere because the carinal plates imbricate directly, or through one spineless plate between; whereas on the dorsolateral region 3 or 4 elongate ossicles may separate two primary plates. The form and imbrication of the marginals can best be appreciated from the figure (Fig. K, 3*b*). There is no trace of actinal plates. The above obtains on the proximal half of ray. Distally the mesh-work gradually becomes disconnected through the absence of intermediate ossicles until on the outer fourth of ray there are only spaced primary spiniferous plates. What really happens, of course, is that on the distal younger part of the ray the primary plates appear first, and only later, during further growth, the connecting ossicles develop. On the distal part of the ray the inferomarginals imbricate in a complete series. To the upper lobes of each is imbricated an oblique superomarginal. These are separated one from another by a conspicuous interval of membrane, encroached upon sometimes by a small disconnected abactinal plate. Even on the proximal half of ray the superomarginal plates are sometimes disconnected; or they are joined directly by overlapping lobes or by intermediate plates belonging to the abactinal system.

The crossed pedicellariae are diagnostic and recall those characteristic of *Notasterias*. The most frequent size varies between 0.7 and 0.93 mm. in length, but almost as numerous are various smaller sizes down to 0.6 mm., and a few as small as 0.5 mm. Each jaw is wide at the base and tapers to a narrow tip having 2 prominent teeth between which are usually several smaller ones. On the vertical inner edge of each jaw the denticles are numerous but very variable in details. At the attached end, the pedicellariae are wide and each jaw has a relatively large cavity for the accommodation of powerful "biting" muscles, as in the case of *Notasterias*.

The gonoducts open ventrally by prominent pores in the very constricted actinal interradiial area. The pores are not symmetrically placed side by side but one is nearer margin than the other. Those of the female (smaller specimen) are larger than in the male (type). The small ovaries are attached lower on the side of the interbrachial septum (coalesced sides of rays) than the voluminous testes. The interbrachial septum contains calcareous plates. The tube-feet are crowded into 4 ranks and their anpullae are single, pyriform, voluminous.

TYPE LOCALITY. St. WS 821. Falkland Islands, 52° 55 $\frac{3}{4}$ ' S, 60° 55' W, 351-367 m., 2 specimens.

Subfamily ASTERIINAE Verrill (emended)

Asteriinae Verrill, 1914, p. 42.—Fisher, 1923, p. 250; 1928, p. 57; 1930, pp. 2, 217 (key to genera).

Genus *Anasterias* Perrier

Anasterias Perrier, 1875, p. 81; 1891, p. 91. Type *Anasterias minuta* Perrier.—Fisher, *Smithsonian Misc. Coll.*, LII, 1908, p. 52; *Zool. Aus.*, XXXIII, 1908, p. 356; *Ann. Mag. Nat. Hist.*, ser. 9, x, 1922, p. 592; XVIII, 1926, p. 197; 1930, p. 221; 1931, p. 6.

Asteroderma Perrier, *Comptes Rendus*, CVI, no. 11, 1888, p. 763; 1891, p. 96. Type *Asteroderma papillosum* Perrier.

Sporasterias Perrier, *Expéd. Sci. Travailleur et Talisman*, 1894, p. 107, Type *Asterias rugispina* Stimpson.—Ludwig, 1903, p. 39.—Koehler, 1917, 1920, 1923.—Verrill, 1914.—Fisher, 1922, p. 596; 1923, p. 605; 1930, p. 239; 1931, p. 9.
Calvasterias Sladen (not Perrier), 1889, p. 590.
Parastichaster Koehler, 1920, p. 89. Type *P. mazoni* Koehler.
Kalyptasterias Koehler, 1923, p. 43. Type *K. conferta* Koehler.

Anasterias is the oldest name for the group commonly called *Sporasterias*, which includes, in the Cape Horn region, a number of variable and puzzling forms having a weak, often degenerated, dorsal skeleton and a thick skin. The type species, *Anasterias minuta*, is one of these forms. The type specimen is unfortunately immature, and although probably not referable to *A. antarctica*, is obviously closely related. This relationship was clearly recognized by Perrier in 1891, in a series of 37 specimens from the Cape Horn region. He indicated that the reduced dorsal skeleton was too variable to warrant a new genus. Nevertheless, in 1894 he created *Sporasterias* for *Asterias rugispina* (*antarctica*), using its more fully developed abactinal skeleton as the criterion of difference.

In 1903 Ludwig adopted the name *Anasterias* for a group of Antarctic, mostly small, sea stars, the first species of which was the *A. perrieri* of Studer (1885). Although this *Anasterias* of Ludwig did not include *A. minuta*, the type, it was rather generally accepted, even by Verrill, a great stickler for nomenclatorial proprieties. It was renamed *Lysasterias* by me in 1908. The matter is of minor importance since *Lysasterias* is poorly differentiated from the real *Anasterias*.

The type specimen of *A. minuta* is in the Museum d'Histoire Naturelle and is labelled E 792 M. M. Hombron et Jacquinot, 1847. It obviously takes precedence over the series of specimens brought back by the Mission Scientifique du Cap Horn (1882–1883), some of which Koehler examined and erroneously treated as types.

Perrier (1891, p. 95) arranged this series of 37 specimens into 18 groups according to the development of the abactinal skeleton in such a manner that the first members of the list have the best developed skeleton and approach nearest the characters of *Asterias spirabilis*. The last are those which have the least development of skeleton "et qui, par conséquent, présentent davantage les caractères du genre *Anasterias*". In groups 1–10 the skeleton has the best development and there are numerous abactinal spinelets; in 11–14 the dorsal spinelets of the rays become less and less numerous but those of disk are still apparent and on the disk is a pentagonal figure formed by the skeletal plates bearing each a group of spinelets. From 15 to 18 the spines and plates are indistinct, which also means that the integument is thicker.

The specimens examined by Koehler may have been derived largely from the first 10 groups of Perrier and hence have been immature *antarctica*, since 11 specimens came from "Baie Orange", from whence Perrier lists a large number of *antarctica* (as *spirabilis*).

Koehler states: "Je dois dire que j'ai eu en communication plusieurs *Anasterias minuta* du Jardin des Plantes et j'ai pu constater que toutes étaient parfaitement identique

à de jeunes *Sporasteria antarctica*." He adds the somewhat singular observation: "J'estime donc l'*A. minuta* forme jeune d'une *Sporasterias* ou peut-être d'une autre *Anasterias*, ne doit pas figurer parmi les espèces du genre *Anasterias*."

The type of *Anasterias minuta*, which is the only specimen which can fix the identity of the species, is in alcohol. The rays are short, R 12 mm., r 6 mm. The integument entirely conceals the abactinal skeleton. I treated one ray with caustic potash which revealed a fairly regular series of small carinal plates, between which and the regular series of superomarginals (each with 1 short spine) is an irregular very open incomplete net of plates, strongest next to the superomarginals. The net is in part composed of about 14 irregular transverse tongues of plates on either side, extending inward toward the carinals and each corresponds roughly to a superomarginal plate. The inferomarginals have 2 spines, which are the largest on the body and are separated from the smaller single superomarginal by a fairly broad channel provided with a row of papulae. Actinal spines not developed; adambulacral plates strictly monacanthid. The abactinal surface is soft and somewhat pulpy, but not conspicuously papillose or pustulate; abactinal spinelets few and scattered.

This specimen obviously falls within Perrier's third group, and my sketch of the abactinal skeleton of the type agrees with the skeleton of the *A. minuta* of the present report. This sketch is not essentially different from Koehler's figures of young *A. pedicellaris* (which are possibly referable to *minuta*). *A. conferta*, in the young stages, has a variably weak abactinal skeleton of the same sort, and is difficult to separate from *minuta*. *Minuta* is closely related to *pedicellaris* (some varieties of which have an abactinal skeleton as well developed as that of *antarctica* and *studerii*).

The practical difficulty of assigning names to the multitude of variants which one encounters in this complex of "small species" is very trying to the patience. One is bound to sympathize with Leipoldt who lumps them all together as one species!

Anasterias antarctica (Lütken)

(Plate XIX, fig. 1)

Asteracanthion antarcticum Lütken, *Vidensk. Meddel.*, 1856, p. 105.

Asterias rugispina Stimpson, *Proc. Boston Soc. Nat. Hist.*, VIII, 1860, p. 267.—Leipoldt, *Zeit. Wiss. Zool.*, 1895, p. 563; literature.

Asterias cunninghami Perrier, *Rév. Stell.*, 1875, p. 75.

Asterias spirabilis Bell., *Proc. Zool. Soc. Lond.*, 1881, p. 513, pl. 48, fig. 4.

Asterias verrilli Bell, *Proc. Zool. Soc. Lond.*, 1881, p. 513, pl. 47, figs. 3, 3a.

Asterias hyadesi Perrier, *Comptes-rend.*, 1886, p. 1146.

Sporasterias spirabilis Perrier, *Expéd. sci. Travailleux et Talisman*, 1894, p. 107.

Asterias (Sporasterias) antarctica Meissner, *Arch. Naturges.*, 1896, p. 105, pl. 6, figs. 7, 7a-7b; literature.

Sporasterias antarctica Ludwig, *Expéd. antarct. Belge*, 1903, p. 39; 1905, p. 70.—Koehler, 1917, p. 10; 1920, p. 78, pl. 18, figs. 1-4; pl. 28, figs. 1-4; 1923, p. 14, pl. 7, fig. 4.—Fisher, 1930, p. 240; 1931, p. 9.

Anasterias antarctica Fisher, *Ann. Mag. Nat. Hist.*, ser. 9, XVIII, 1926, p. 197.

To this synonymy Leipoldt, 1895, p. 563, adds: *Asteracanthion varium* Philippi, *A. fulgens* Philippi, as well as several species, such as *Anasterias minuta*, *Asterias perrieri* Smith, *Asterias rupicola* Verrill, and *Calvasterias stolidota* Sladen, which I consider to be distinct.

St. 52. Port William, East Falkland Island, 17 m., 1 specimen.

St. 724. Fortescue Bay, Magellan Strait, 0-5 m., 11 specimens.

St. 1902. $49^{\circ} 48' 0''$ S, $67^{\circ} 39' 5''$ W, Cape San Francisco de Paula Lighthouse bearing 328° , distance 4 miles, 47 m., 1 specimen.

St. WS 90. 13 miles north 83° E of Cape Virgins Light, Argentina, 81-82 m., fine dark sand, 2 specimens.

St. WS 755. $51^{\circ} 39'$ S, $57^{\circ} 39'$ W, 77 m., 10 specimens.

St. WS 798. $47^{\circ} 32'$ S, $65^{\circ} 02'$ W, 49-66 m., 3 specimens.

St. WS 834. $52^{\circ} 57\frac{3}{4}'$ S, $68^{\circ} 08\frac{1}{4}'$ W, 27-38 m., 2 specimens.

St. WS 836. South-east of Atlantic entrance to Magellan Strait, 64 m., 3 specimens.

St. WS 841. Falkland Islands, $54^{\circ} 11\frac{3}{4}'$ S, $60^{\circ} 21\frac{1}{2}'$ W, 110-120 m., 2 specimens.

St. WS 848. North-east of Atlantic entrance to Magellan Strait, $50^{\circ} 37\frac{1}{2}'$ S, $66^{\circ} 24'$ W, 115-117 m., 2 specimens.

The largest specimen measures R 90 mm., r 20 mm., br 22 mm. (dry); the smallest measures R 6.5 mm., r 2.5 mm. Typical specimens have a great abundance of crossed pedicellariae all over the abactinal surface (on the plates and around the borders of the papular areas), around the superomarginal spines, and on the upper side of outermost inferomarginal spine. In the interradiial channels there is a variable number of conspicuous straight pedicellariae considerably longer than broad, either tapered or blunt ended while a variable number of similar ones are found in the actinal and intermarginal channels. In little specimens they are entirely lacking. Along the ventrolateral border of ray is a series of oblique combs of 3 or 4 spines the innermost of which is an actinal, the others inferomarginal. There is a series of actinal papulae. Very small specimens lack actinal plates, spines, and papulae, or have only a short series.

In this species the abactinal skeleton is normally stout, but specimens are occasionally met with in which the skeleton is weak and the crossed pedicellariae few in number (Teal Inlet, Falkland Islands, Fisher, 1931, p. 8, pl. 8). In young examples the abactinal skeleton is nearly always weak and only a little better developed than in small examples of *minuta*. The latter differs in having a thicker pustulate skin, few abactinal spinelets and few pedicellariae.

Anasterias studeri Perrier

(Plate XIX, fig. 2)

Anasterias studeri Perrier, 1891, p. 99.—Koehler, 1920, p. 13, pl. 2, fig. 6; pl. 12, fig. 11; pl. 57, fig. 2.
Lysasterias studeri Fisher, 1930, p. 236.

St. WS 91. Tierra del Fuego, $52^{\circ} 53' 45''$ S, $64^{\circ} 37' 30''$ W, 191-205 m., fine dark sand, 11 specimens.

St. WS 92. $51^{\circ} 58' 30''$ S, $65^{\circ} 01'$ W, 145-143 m., 11 specimens.

St. WS 93. West Falkland Island, 133-130 m., 1 juv.

St. WS 814. $51^{\circ} 45\frac{1}{4}'$ S, $66^{\circ} 40'$ W, 111-118 m., 1 specimen.

St. WS 816. $52^{\circ} 09\frac{3}{4}'$ S, $64^{\circ} 56'$ W, 150-160 m., 2 specimens.

St. WS 818. $52^{\circ} 31\frac{1}{4}'$ S, $63^{\circ} 25'$ W, 272-278 m., 1 specimen.

St. WS 847A. Off Porto Santa Cruz, Argentina, $50^{\circ} 15\frac{3}{4}'$ S, $67^{\circ} 57'$ W, 51–56 m., 3 specimens, intermediate.

St. WS 847B. Off Porto Santa Cruz, Argentina, $50^{\circ} 18\frac{3}{4}'$ S, $67^{\circ} 44'$ W, 56–84 m., 6 specimens, intermediate.

St. WS 867. $51^{\circ} 10'$ S, $64^{\circ} 15' 30''$ W, 150–147 m., 2 specimens.

Typical large examples are very distinct from *antarctica* by reason of the abundance of large triangular straight pedicellariae, the jaws of which are as broad at base as the height. There is a good representation of apparently fully grown specimens. The largest measures R 110 mm., r 30 mm., br 25 mm. In addition to the numerous characteristic abactinal straight pedicellariae there is usually an abundance of crossed, distributed as in *antarctica*; but in a large specimen from St. 92 these are relatively few. The crossed pedicellariae are broader than in *antarctica*. In the latter species, the rounded end of jaw is 0.26–0.30 mm. broad while in *studerii* it measures 0.35–0.38 mm. In typical *studerii* the abactinal spinelets are decidedly slenderer and generally obviously more numerous than in *antarctica*. The actinal papular areas contain 2–4 papulae while in large *antarctica* there is only 1. As in *antarctica*, in the ventrolateral combs there are 3 or 4 (rarely 5) prominent spines, of which the inner belongs to an actinal plate.

In medium-sized specimens (R 50 mm.) the straight pedicellariae are confined to side of rays, only a very few occurring on the adambulacral furrow face. From Sts. WS 91 and WS 92 are 2 series illustrating growth stages from R 11 mm. to R 100 mm. One can be reasonably sure that these are all of one species. Up to R 30 mm. there are no straight pedicellariae; or at base of ray only 1 or 2 of a broadly lanceolate form such as is found in *antarctica* and *pedicellaris*.

Without the accompanying adults these small examples would undoubtedly be classified as *antarctica*, although their abactinal spinelets are more numerous and the crossed pedicellariae very much less numerous than in typical small *antarctica*.

The abactinal skeleton is well developed with numerous small irregular meshes. In young specimens the skeleton is rather stronger and the meshes smaller than in corresponding sizes of *antarctica*. The species therefore is in nowise closely related to *Lysasterias perrieri* or to other species having a degenerated dorsal skeleton. Koehler who examined and photographed the type rather unaccountably placed it in his "*Anasterias*", which led me to list it as *Lysasterias* (1930, p. 236). It is, as a matter of fact, very close to *A. antarctica* and possibly may regularly intergrade with that species at intermediate depths. There certainly is no occasion to make the species the type of a new genus on account of its pedicellariae, as Koehler thought might be necessary.

Typical specimens of *studerii* are found in deeper water than *antarctica*. The specimens from St. WS 847, 51 to 84 fathoms, are not typical in having fewer and coarser abactinal spines and fewer straight pedicellariae which, in one specimen, are narrower than in the typical form. The very numerous crossed pedicellariae are of the broader type, and actinal papulae 2 or 3 to an area. One of the 3 specimens is the largest, having R 110 mm.

A large specimen (St. 92, 8 April 1927) is carrying a coalesced mass of eggs 20 mm. in diameter. Each egg is 2.5 mm. in diameter.

TYPE LOCALITY. Falkland Islands, 320 m.

Anasterias pedicellaris (Koehler)

(Plate XIX, fig. 3)

Sporasterias pedicellaris Koehler, 1923, p. 18, pl. 5, figs. 1-6; pl. 6, figs. 1-5, 7-10.*Sporasterias antarctica* Koehler, 1920, p. 78, pl. 18, fig. 4.*Anasterias pedicellaris* Fisher, 1930; p. 225; 1931, p. 8.

St. 55. Port Stanley, East Falkland Island, 10-16 m., 2 specimens.

St. WS 81. 8 miles north, 11° W of North Island, West Falkland Island, 81-82 m., sand, 10 specimens.

St. WS 84. 7½ miles south, 9° W of Sea Lion Island, East Falkland Island, 75-74 m., shells and stones, 13 specimens.

St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shell, 14 specimens.

St. WS 221. Off Argentina, 48° 23' S, 65° 10' W, 76-91 m., 1 specimen.

St. WS 576. 51° 35' S, 57° 50' W, 34-24 m., 1 specimen.

St. WS 823. 52° 14½' S, 60° 01' W, 80-95 m., 1 specimen.

Koehler has described in detail this form which is very variable in respect to the robustness of skeleton and the number of both sorts of pedicellariae. The rays are longer and narrower than in *antarctica*, the abactinal skeleton usually weaker, the abactinal spinelets more delicate (and sometimes much more numerous) and the crossed pedicellariae (of about the same size) less numerous. In typical *antarctica* the superomarginal spines are surrounded by numerous crossed pedicellariae, but in *pedicellaris* as in *studerii* these are scarce or absent on the proximal half of ray. The characteristic lanceolate straight pedicellariae are found abundantly only in large specimens; in small ones they are scarce or absent. In general, such small specimens differ from small *antarctica* in having more numerous abactinal spinelets, with not many more crossed pedicellariae than spinelets scattered over the abactinal surface. Without accompanying adults it is questionable if one can be certain of the identification of these young.

A characteristic feature of the species is the variability of the abactinal skeleton, already described and figured by Koehler. When at its weakest it is no better developed than in the type specimen of Perrier's *Anasterias minuta* (see Koehler, 1923, pl. 5, fig. 5). But I am not sure that Koehler's pl. 6, figs. 3 and 10 are not *minuta* rather than *pedicellaris*. They are quite unlike young *pedicellaris* from St. WS 85, at which typical adults were taken. These young have narrow convex rays with a reticulate skeleton and numerous delicate spinelets. But adults may have a skeleton obviously weaker than in typical "*Sporasterias*" (Koehler, pl. 5, fig. 1). I have such specimens from St. WS 85. It is futile therefore to base genera upon the "more or less" development of the abactinal skeleton, where one species exhibits such instability.

The integument is soft and rather thick but not pustulated in the ordinary sense. The abactinal, intermarginal, and actinal pedicellariae are large, the last usually 2 or 3 to an area.

This seems to be a shallow water form, whereas *studerii* is found in much deeper water and differs *inter alia* in having shorter and broader, more triangular, straight pedicellariae.

DISTRIBUTION. Tierra de Fuego, Falkland Islands, north to 48° 23' S, 7-95 m.

Anasterias minuta Perrier

(Plate XIX, fig. 4)

Anasterias minuta Perrier, 1875, p. 81; 1891, p. 93 (in part).—Fisher, 1930, p. 223; 1931, p. 6, pl. 6, pl. 7, figs. 1, 2.

?*Asteroderma papillosum* Perrier, *Comptes Rendus*, cv1, 1888, p. 765; 1891, p. 96.

?*Asterias minuta* var. *Asteroderma papillosum* Perrier, 1891, pl. 10, figs. 3*a*–3*c*.

Sporasterias pedicellaris, part, Koehler, 1923, p. 18.

St. 53. Port Stanley, East Falkland Island, 0–3 m., 4 specimens.

St. 55. Entrance to Port Stanley, East Falkland Island, 10–16 m., 7 specimens.

St. 58. Port Stanley, East Falkland Island, 1–2 m., 1 specimen.

The specimens range in size from R 8 mm., r 4 mm. to R 37 mm., r 10 mm. All have a thick pulpy skin which is subdivided into small unequal areas by deep creases. These soft cushions of skin are not essentially different from the more inflated “pustules” of the skin of *Lysasterias perrieri* which the specimens somewhat resemble.

The abactinal surface has a very few scattered small spinelets and crossed pedicellariae placed here and there, but these, as well as the underlying skeleton, are completely hidden unless dried. Only a few superomarginal spinelets are present as rudiments here and there, but a double series of well-developed inferomarginal spines occurs on the ventrolateral border of ray. Between these and the single series of adambulacrals is a longiseries of large single papulae. Intermarginally there are very large papulae, 2 or 3 to an area, and a series of large ones above the superomarginal plates, but on the rest of the abactinal area they are difficult to differentiate from the pustules. On the abactinal plates interradially, on the superomarginals, inferomarginals, along actinal groove, and on furrow face of the adambulacrals is a quite variable number of conspicuous, elongate, stout, lanceolate straight pedicellariae. Only a very few crossed pedicellariae are scattered on the marginals. In the smallest specimen there is a superomarginal spinelet to each plate, and to each ray about 12 abactinal spinelets, which are definitely longer than the crossed pedicellariae, papulae, and intervening folds of skin. There are no actinal papulae as yet, but large intermarginal ones are present. This specimen has about the same spine development as the type specimen.

The abactinal skeleton is weak and incomplete, but there is variation in the incompleteness. In a specimen having R 24 mm. it consists of a short tongue of 1–3 small ossicles extending mesially from the dorsal lobe of each superomarginal. Between these 2 lateral series are unevenly scattered independent plates, or 2 or 3 in series disconnected from the rest. The vestiges of the carinal series are present on outer half of ray. Such a skeleton is obviously identical with what is found in some specimens of *Lysasterias*. Another specimen of *minuta* has a wide meshed skeleton of slender ossicles consisting chiefly of carinal plates and complete or interrupted sinuous transverse series which extend mesially from the superomarginals. On the distal half of ray, the skeleton is less connected than proximally. This specimen represents the condition of skeleton of the type specimen, of which mention has been made under the genus.

So far as the essential structure of skeleton is concerned this species completely bridges the gap between *Anasterias* and *Lysasterias*.

The type of *A. minuta* is in the Museum d'Histoire Naturelle (E 792 Hombron et Jacquinet, 1847, alcohol). Perrier considered the type locality to be Port Famine, Magellan Strait, and hence probably from very shallow water.

I have also studied 2 dried specimens from Darwin Harbour, Choiseul Sound, Falkland Islands (No. 2623 Museum of Comparative Zoology). The smaller measures R 18 mm., r 6 mm.; the larger R 48 mm., r 13 mm. In the smaller example the abactinal skeleton is clearly visible and consists of a weak, irregular reticulum resembling the condition of *A. pedicellaris* as figured by Koehler (1923, pl. 5, figs. 1, 4) and closely similar to that of the type specimen of *minuta*. Most of the superomarginals carry one spinelet and the inferomarginals two, while scattered along the intermarginal channel and inside the furrow margin are rather numerous, lanceolate, straight pedicellariae two-thirds the length of the superomarginal spinelets. In the larger specimen, however, the abactinal integument is thickened and conceals the skeleton, which is quite weak and irregular as in Koehler's pl. 5, fig. 1, alluded to above. The proportions are about as in fig. 4. There are a few actinal plates and spines at the base of the ray and the adoral carina is composed of 3 pairs of contiguous adambulacrals, the first pair larger than second, and the second larger than third. The superomarginal spines have been mostly absorbed; pedicellariae as in the small example. A third specimen (no. 2624) carries a cluster of young.

In the United States National Museum are 25 specimens from Port Stanley collected by Dr W. L. Schmitt (Fisher, 1931, p. 7).

None of the young of *pedicellaris* (accompanied by adults) which I have examined exhibit such a degeneration of skeleton as is shown in Koehler's figures (1923, pl. 5, fig. 5; pl. 6, figs. 3, 10). The specimens which I feel fairly certain are young stages of the adults called *pedicellaris* have narrow rays, numerous abactinal spinelets, a small meshed, complete abactinal skeleton, and a thinner skin lacking pustules. Lanceolate pedicellariae small, few or lacking.

But one specimen of *minuta* (R 31 mm.) from St. 55 has more numerous abactinal spinelets and thinner skin than the others, and at the same time differs from an example of *pedicellaris* (R 36 mm.) from the same station in having a weaker skeleton, much fewer straight and crossed pedicellariae.

The explanation of the confusion may be that *minuta* is the not fully grown stage of a weak-skeleton forma of *pedicellaris* such as Koehler's pl. 5, fig. 1, from West Point Island, West Falkland. This form would usually have few abactinal spinelets and few crossed pedicellariae, but numerous straight pedicellariae. The other extreme would be represented by the multispinous young and adults with a close-knit complete abactinal skeleton and usually abundant crossed pedicellariae, but with very few straight ones when R is less than 25 mm.

So far as *skeleton* is concerned the varieties of such a polymorphic species would fall in *Sporasterias*, *Anasterias* and *Lysasterias*!

Anasterias conferta (Koehler)

(Plate XIX, fig. 5)

Kalyptasterias conferta Koehler, 1923, p. 43, pl. 4, figs. 1-7.—Fisher, 1930, p. 234.*Anasterias conferta* Fisher, 1931, p. 9.

St. 53. Port Stanley, East Falkland Island, 0-2 m., 19 specimens.

Koehler gives good figures of alcoholic and dried specimens which are probably adult, as R varies from 60 to 70 mm. They were taken in 4-7 m. at Port Louis, Falkland Islands.

The Discovery specimens range in size from R 4.5 mm. to R 34 mm. The larger agree with Koehler's figures. The small ones closely resemble specimens of *A. minuta* but, generally speaking, have a more arched disk and more convex rays which taper from a broader base. The straight pedicellariae are few and smaller.

The abactinal skeleton consists of a weak, very irregular and open reticulum in which the small carinals form a sinuous interrupted series much weaker than in the type of *A. stolidota*. The superomarginals are well developed, imbricate strongly and usually carry a small spinelet. There is, however, great variability in these features. In a specimen which I reported (1931, p. 9) from Teal Inlet, Falkland Islands, the abactinal plates have degenerated so that they are entirely disconnected. The skeleton is represented by scattered small circular and slender elongate ossicles. Similarly, the marginal plates are reduced in size, the spineless superomarginals forming a slender sinuous longiseries as in the type of *Kalyptasterias conferta*.

Koehler (1923, p. 46) was handicapped by lack of knowledge of the skeleton of *Calvasterias stolidota* Sladen, which greatly resembles *conferta*. It may be stated that *stolidota* is not a *Calvasterias* but is an *Anasterias* closely related to *conferta*. The two may be forms of the same species. The small specimen of *stolidota* recorded by Sladen (1889, p. 591) from Port William is probably referable to *conferta*.

The type of *stolidota* measures R 44 mm. and is from the Messier Channel between Wellington Island and the west coast of Chili. In 1928 the late Mr G. A. Smith of the British Museum (Natural History) made for me photographs of the skeleton of a ray, which I think will serve a very useful purpose in the present connection (Pl. XIX, fig. 6).

As will be seen the skeleton is of the reticulate type with strong imbricating carinals and stout spiniferous superomarginals. The dorsolateral mesh consists of normally developed plates. The whole might illustrate *A. antarctica* or *A. studeri*.

Genus *Lysasterias* Fisher

Lysasterias Fisher, *Smithsonian Miscell. Coll.*, LII, May 1908, p. 88; *Zool. Anz.*, xxxiii, August 1908, p. 356. Type *Anasterias perrieri* Studer, 1885, but not Perrier, 1891.—Fisher, 1922, p. 594; 1923, p. 606; 1926, p. 197; 1930, p. 235.

Anasterias Ludwig, 1903, p. 42.—Koehler, 1906, p. 12; 1908, p. 566; 1912, p. 10; 1920, p. 11; 1923, p. 11.—Verrill, 1914, p. 354.—Not *Anasterias* Perrier, 1875; not *Asteroderma* Perrier, 1875.

Paedasterias Verrill, 1914, p. 355. Type *Anasterias chiophora* Ludwig.—Koehler, 1920, pp. 16, 30.

DIAGNOSIS. Differing from *Anasterias* in a further reduction of the abactinal and marginal skeleton, which in its poorest development consists of lateral transverse tongues of plates (composed of two reduced marginals plus one to several abactinal elements) abutting on the adambulacral plates; dorsal surface with much reduced, disconnected, scattered platelets, or a sketchy rudimentary reticulum (principally on disk); or, especially in mature specimens, no plates; integument thick, raised in mammillated pustules which represent elaborated spine sheaths; adambulacral plates monacanthid; no actinal spines, the actinal plates rudimentary, confined to disk, or present as an inconspicuous series crowded between the inferomarginals and adambulacrals; gonads open ventrally—paedophoric.

REMARKS. This is the *Anasterias* of most authors. It is closely related to true *Anasterias* and differs chiefly in the development of the spine sheaths into glandular pustules (probably *pari passu* with the disappearance of spines and dorsal plates) and in the disappearance of functional actinal plates. Various degrees of degeneration of the dorsal and marginal skeleton are met with in the type species, *perrieri*. In some varieties the abactinal skeleton is as well developed as in *Anasterias*; in others it is practically absent. There is direct evidence in specimens of *perrieri* from South Georgia that there is a gradual degeneration of abactinal and marginal skeleton as the animal grows, as if the calcium were required for the growth of the more important axial skeleton and essential spines (i.e. the actinostomial ring, the ambulacral and adambulacral systems). In this graded series the abactinal skeleton disappears with increasing age while the marginal plates shrink in size, change their shape, and certain superomarginal connectives disappear entirely.

Verrill's genus *Paedasterias* was founded pretty largely upon an erroneous translation. Ludwig (1903, p. 42), in a synopsis of "*Anasterias*", says: "Die Spagen haben (mit Ausnahme der Armspitze) *keinen oberen Randstachel*; grosse Tatzepedicellarien vorhanden. . . . *An. chiophora* n.sp." Verrill diagnoses the genus: ". . . the upper marginal plates being absent except as rudiments distally". But Ludwig in a major division of his synopsis states that the upper marginal plates are present in *chiophora*. Koehler (1920, p. 30) adopted *Paedasterias*, and added a new species, *joffrei*. As a matter of observation it may be stated that there are reduced superomarginal plates in the species supposed to lack them and that there is no valid generic hiatus between the forms with reduced marginals and those having well-developed marginal plates and spines, such as *adeliae* and *perrieri*. In fact the new species described below, *L. hemiora*, with greatly reduced marginals, may turn out to be a variant of *perrieri*, incredible as it now appears.

Lysasterias is pretty much a genus of convenience. It appears to be an Antarctic offshoot of *Anasterias* which has suffered, along with *Perkuaster* and some other genera, a grave disturbance of calcium metabolism.

Lysasterias perrieri (Studer)

- Anasterias perrieri* Studer, Die Seesterne Süd Georgiens, *Jahrb. wiss. Anst. Hamburg*, 11, 1885, p. 153.—Koehler, 1920, p. 17.
Anasterias tenera Koehler, 1906, p. 12, pl. 2, figs. 11–16; pl. 3, figs. 27, 28; pl. 4, fig. 41; 1908, p. 569; 1912, p. 10; 1920, pp. 11, 17, pl. 2, figs. 1–4, 10; 1923, p. 11.
Anasterias cupulifera Koehler, 1908, p. 566, pl. 5, fig. 52; pl. 6, figs. 58, 59; 1920, p. 16.
Anasterias lysasteria Verrill, 1914, p. 354 (unnecessary substitute name; see Fisher, 1922, p. 593).
 ?*Anasterias Studeri* Koehler, *Sci. Bull. Brooklyn Inst. Arts and Sci.*, 11, no. 4, 5 November 1914, p. 61, very young.
Anasteria Victoriae Koehler, 1920, p. 17, pl. 2, fig. 5; pl. 3, figs. 1–6; pl. 4, figs. 1–4; pl. 5, figs. 1–10; pl. 6, figs. 1–4; pl. 57, fig. 1; 1923, p. 12.
Lysasterias perrieri Fisher, 1930, p. 236.
Lysasteris cupulifera Fisher, 1930, p. 236.
Lysasterias tenera Fisher, 1930, p. 236.
Lysasterias victoriae Fisher, 1930, p. 237.

St. 140. Stromness Harbour to Larsen Point, South Georgia, 122–136 m., green mud and stones, 1 specimen.

St. 141. East Cumberland Bay, South Georgia, 17–27 m., 1 specimen.

St. 145. Stromness Harbour, South Georgia, 26–35 m., 23 specimens.

St. 156. South Georgia, 53° 51' S, 36° 21' 30" W, 200–236 m., rock, 1 specimen.

St. 159. South Georgia, 53° 52' 30" S, 36° 08' W, 160 m., rock, 11 specimens.

St. 164. East end of Normannia Strait, South Orkneys, near Cape Hansen, Coronation Island, 24–36 m., 1 specimen.

St. 170. Off Cape Bowles, Clarence Island, 61° 25' 30" S, 53° 46' W, 342 m., rock, 4 specimens.

St. 175. Bransfield Strait, South Shetlands, 63° 17' 20" S, 59° 48' 15" W, 200 m., mud, stones, gravel, 1 specimen.

St. 456. 1 mile east of Bouvet Island, 40–45 m., 3 specimens.

St. 1873. Off Clarence Island, 61° 20' 8" S, 54° 04' 2" W, 200–137 m., 18 specimens.

St. 1941. Leith Harbour, South Georgia, 55–22 m., 8 specimens.

St. 1959. Scotia Bay Anchorage, South Orkneys, 5 m. (fish trap), 1 specimen.

St. WS 25. Undine Harbour (North) South Georgia, 18–27 m., mud, sand, 1 specimen.

St. WS 62. Wilson Harbour, South Georgia, 15–45 m., 1 specimen.

St. MS 6. East Cumberland Bay, South Georgia, 27 m., 4 specimens.

St. MS 10. Same, 26 m., 1 specimen.

St. MS 62. Same, 31–40 m., 1 specimen.

St. MS 63. Same, 23 m., 1 specimen.

St. MS 67. Same, 38 m., 3 specimens.

St. MS 68. Same, 220–247 m., 1 specimen.

Cumberland Bay, South Georgia, 2 specimens.

Numerous figures and detailed descriptions of this polymorphic species are given by Koehler (1906, 1920, 1923). It is fairly common at South Georgia in shallow and moderate depths, and it is therefore not strange that it was encountered by early collectors and was the first species of the genus to be described. I have no doubt whatever that Studer's species is the same as that recorded by Koehler in 1923 as *tenera* and *victoriae*. The dispersed abactinal straight pedicellariae characteristic of some specimens are mentioned by Studer.

In the same haul I find representatives of Koehler's two species, which are based largely upon the presence or absence of straight pedicellariae on the dorsal surface. This is a character subject to great individual variation. If there are actinal or intermarginal straight pedicellariae but no abactinal in some specimens, certain others are sure to have few or many in addition on the abactinal surface. An "infection" of straight pedicellariae is sure to spread. The alleged difference in the width of the intermarginal channel proximally simply does not hold up. Specimens with abactinal pedicellariae and a good development of abactinal skeleton will also have as broad a channel as those with no abactinal skeleton on rays, and no abactinal straight pedicellariae. The size of the marginal plates varies with age and also with locality.

In fact, local varieties are the rule rather than otherwise with this species. There is a tendency in some localities for the spines to be resorbed with increasing age, and this is accompanied by a resorption of plates—first the abactinal, then the superomarginal. Koehler notes as a "curious circumstance" that in South Orkney specimens the lateral spinelets are better marked and more constant in small than in large individuals. The same effect can be seen in the growth series from St. 145. It is apparently normal in some localities but much less marked in others where the superomarginal plates are less reduced in size and the series of spines more perfect.

The degree of development of abactinal skeleton varies with locality and age. It ranges from a skeleton similar to that of *Anasterias minuta* through a condition of scattered plates to no plates on rays and only a feeble ring of them on the disk. The size and shape of the abactinal pustules is also very variable. *L. cupulifera* (Koehler), South Orkneys, seems to me nothing more than an individual variation of *perrieri*, some of its peculiarities due to accidents of preservation.

The range of variation in the specimens included in the above list of localities is no whit greater than is generally accepted for *Diplasterias brandti*. In fact, one variation is analogous, namely a dispersal of pedicellariae between spinelets (or their residuary pustules) in contrast to a localization around spinelets.

Koehler (1923, p. 12) records *L. victoriae* from Port Louis, Falkland Islands. I believe this to be an error of label or of identification; if the latter, the specimen might conceivably be an *Anasterias pedicellaris* with an unusually weak dorsal skeleton. If a well-developed series of actinal plates and a certain number of actinal spines are present, it is *pedicellaris*. The specimen was dry.

The largest specimen in the Discovery collection is from St. 164 and measure R 117 mm., r 23 mm., br 25 mm. One series of superomarginals and 2 series of inferomarginal spines are well developed. A few small carinal spinelets immersed in their compound pustules survive at base of ray. The pustules are unequal, small, very numerous. The specimen is labelled "cream buff with orange ova". The specimen from St. 1959, Scotia Bay, South Orkneys, R 85 mm. is almost identical in appearance and is labelled: "Dorsal surface very rich, deep, creamy yellow, pale yellow below."

Something in the environment of East Cumberland Bay, South Georgia, seems to be detrimental to skeletons, as the large specimens (R 90–95 mm.) from here are very

flaccid, the marginals small, and the marginal spines are soft as if undergoing resorption. Many have already disappeared.

The 23 specimens from St. 145, Stromness Harbour, South Georgia, form a well-graded series from R 10 mm. to R 80 mm. and are typical in having very little in the way of an abactinal skeleton. The body wall of a specimen with R 32 mm. and one with R 80 mm. was cleared. In the former there are indications of a meandering, interrupted carinal series, with parts of an interrupted net on either side; and from the dorsal lobe of the superomarginal plates, 0-3 small ossicles form (when present) a transversely oriented bar. The superomarginals are articulated *in series* by 1 or 2 oblong intermediate ossicles while the inferomarginals imbricate by their lobes. At base of ray are a few very small actinal ossicles wedged between the inferomarginals and adambulacrals. Abactinal spinelets are few, the numerous pustules containing a single crossed or a larger lanceolate straight pedicellaria. In the larger specimen, the abactinal system is reduced to widely separated grains, bearing small spinelets, in the radial area; the *supramarginal* tongues of plates have mostly disappeared, *as have the superomarginal connectives*. The spineless actinals have advanced beyond middle of ray, but only the proximal are of significant size. The very numerous abactinal pustules contain mostly single straight pedicellariae with a scattering of crossed; the voluminous superomarginal and inferomarginal compound cup-shaped pustules contain mostly crossed, with a few slightly larger straight, but with conspicuously larger straight ones in the narrow actinal channel. The greatest variation exists in the number of straight pedicellariae and it is futile to base even a forma on their presence, much less to invoke them as a specific character (for *victoriae*). Both "species" can be formed in this growth series.

The series from St. 1873 (Clarence Island), however, is notable for having, in the random samples which were dried or cleaned, only crossed pedicellariae, except for a series of straight ones on furrow margin. Moreover, the abactinal plates form a loose, weak, wide-meshed incomplete reticulum on the median or radial region of ray. In some specimens there are numerous slender abactinal spinelets surrounded by a stole of pedicellariae, while in others the spinelets are very few and the circular or polygonal stole becomes a compound pustule or cupule filled with pedicellariae. In general the smaller specimens have the best spine development. Size limits R 15 mm. to R 60 mm. Although this form lacks abactinal and marginal straight pedicellariae it differs from the typical forma *tenera* of Koehler (1906) from Booth Wandel Island in having a better developed abactinal skeleton and spinelets. However, Koehler's specimens ranged from R 65 mm. to R 120 mm. and the spines and skeleton may have been resorbed.

A modification of the above form is found in specimens from Sts. 170 and 175 in which there is about the same development of abactinal skeleton and spinelets but the crossed pedicellariae are mostly scattered thickly over the abactinal surface, only 1 or 2 being attached to the spinelets. The pustules are weakly developed. The single superomarginal and double inferomarginal spines have numerous associated crossed pedicellariae. The specimens from St. 456, Bouvet Island, are a variety of this form, poorer in pedicellariae. The largest example (R 50 mm.) resembles Koehler's figure of *tenera* (1906).

TYPE LOCALITY. South Georgia.

DISTRIBUTION. Probably circumpolar: South Orkneys, South Shetlands, Graham Coast; latitude 64° to 67° S and longitude 92° to 145° E; north to Bouvet Island and South Georgia. Shallow water to 647 m.

Lysasterias adeliae (Koehler)

Anasterias adeliae Koehler, 1920, p. 26, pl. 1, figs. 1, 2, 5-10; pl. 56, fig. 1.

Lysasterias adeliae Fisher, 1930, p. 236.

St. 181. Schollaert Channel, Palmer Archipelago, $64^{\circ} 20' S$, $63^{\circ} 01' W$, 160-335 m., mud, 1 specimen.

Koehler's 2 specimens were taken in 12 fathoms, Adélie Land. The largest measured R 38 to 44 mm., r 10 mm. The present specimen measures R 65 mm., r 12 mm., br 13 mm. The rays are decidedly longer and more attenuate distally, and ray tip more pointed than in Koehler's illustrations. It differs also in having rather numerous, conspicuous abactinal straight pedicellariae which are narrowly lanceolate, acute.

The marginal plates are as well developed as in *perrieri* and the intermarginal channel is broad proximally. The superomarginal plates soon become disconnected and spaced from one another. There is a definite series of superomarginal and one of inferomarginal spines. Attached to the cupule-like sheaths are from 1 to 5 large crossed pedicellariae (0.9-1 mm. long), and on the inferomarginals also several small ones, hardly half as long together with one to several lanceolate straight pedicellariae. The abactinal crossed pedicellariae seem to be only of the small size—not large and small mixed as I infer to be the case in *L. belgicae* (Ludwig). The roundish or lobed abactinal plates of the rays are mostly isolated, widely spaced, and carry usually an acicular spinelet. On the disk is an irregular ring of connected plates, which includes (at mid-r) a large madreporite, and carries about 30 spaced spinelets. Within the circle are about 10 spinelets springing from mostly isolated plates.

Although this specimen is not typical I have little hesitation in referring it to *adeliae*. The extension to abactinal area of the straight pedicellariae is an item of scarcely varietal importance as this is a matter in which the Asteriidae exhibit very wide individual variation.

L. adeliae differs from *perrieri* chiefly in the disparity in size of the abactinal and marginal pedicellariae. *L. belgicae* has both large and small crossed pedicellariae, but Ludwig does not state that the large size is marginal only. *Belgicae* has very small marginal plates and therefore would seem to be more nearly related to *joffrei* than to *adeliae*. In *joffrei* the inferomarginal crossed pedicellariae are also abruptly larger than the abactinal.

Adélie Land and Palmer Archipelago are the only known records for this species. Bathymetric range 22-335 m.

Lysasterias joffrei (Koehler)

Paedasterias joffrei Koehler, 1920, p. 30, pl. 1, figs. 3, 4, 9; pl. 2, figs. 7, 8, 9; pl. 56, fig. 2.

Lysasterias joffrei Fisher, 1930, p. 236.

St. 1660. Ross Sea, $74^{\circ} 46.4' S$, $178^{\circ} 23.4' E$, 351 m., 1 specimen.

St. 1957. Off south side Clarence Island, South Shetlands, 785–810 m., 1 specimen.

Koehler's only specimen, having R 80–85 mm., r 13 mm., was taken in 354 fathoms in D'Urville Sea, off Adélie Land ($66^{\circ} 50' S$, $142^{\circ} 06' E$). The specimen from St. 1660 measures R 53 mm., r 8–9 mm., br 10 mm. The rays are narrow, evenly tapered and high arched, being as high at base as width.

This species and *chirophora* are notable for the great reduction of the marginal plates. I examined a portion of the body wall at base of the ray. The inferomarginals are very small, much longer than high as seen from the coelomic side and touch end to end. A small ovate or elliptical superomarginal is imbricated to the upper lobe of each inferomarginal, and therefore widely separated one from another. There are no superomarginal spinelets except 2 or 3 very small ones at tip of ray. The series of superomarginal sheaths or pustules can, however, be traced to base of ray as they are a little larger than the superjacent abactinal pustules. The inferomarginal spines are single and the thick compound sheaths with numerous large crossed pedicellariae press against the upright adambulacral spines.

The conspicuous pedunculate straight pedicellariae (1.4 mm. long) which Koehler names "en palette" are only slightly different from ordinary lanceolate ones, the jaws being more oblong than tapered, with rounded ends without conspicuous teeth. Occasionally they resemble a very narrow turtle's head in miniature. They are somewhat more widely distributed than in the type for, in addition to being fairly numerous on the abactinal area and sides of rays, they occur also in the actinal interradial areas, on the mouth-plates, and furrow face of the first few adambulacrals, being succeeded on the remainder by conspicuously smaller ones not greatly different in shape.

In this specimen the inferomarginal crossed pedicellariae are larger than the abactinal and are the same size as in type (1 mm. long).

The small specimen, St. 1957, R about 24 mm., r 6 mm., is placed here with some misgivings. The marginal plates, still fairly robust, seem to be undergoing degeneration. In the arm axils are 1 or 2 conspicuous spatulate pedicellariae without teeth.

Lysasterias hemiora sp.nov.

(Fig. L, 3; Plate XX, fig. 2)

DIAGNOSIS. In general appearance resembling a narrow-rayed *L. perrieri* but lacking a series of superomarginal spinelets or of substitute differentiated pustules, the small roundish abactinal pustules appearing to extend right up to the abruptly larger inferomarginal spines and their enclosing sheaths. R 66 mm., r 13 mm., br 13 mm., height of ray at base 12 mm.; ray narrow, very gradually tapered to bluntly pointed extremity,

high arched, the inferomarginals, close to the single adambulacrals, defining border of the subplane actinal surface.

DESCRIPTION. The abactinal and lateral pustules are very small and numerous, closer together than the space between. Nearly all of them enclose a small crossed pedicellaria of one size, 35–38 μ m. in length. The lowermost series of these small pustules represents the superomarginals. At end of ray the last 1 or 2 pustules have a tiny central spinelet. These are probably resorbed and the material used in the next distal plate to be formed. The proximal 6–12 slender inferomarginal plates carry 1 spinelet, the remainder 2. They measure 2.25–2.75 mm. in length and their sheaths contain a few crossed pedicellariae 0.33–0.45 mm. long, and a lanceolate straight pedicellaria 0.5 mm. long.

The abactinal skeleton of rays is reduced to tiny scattered plates sometimes carrying a tiny spinelet. The antiambulacral bars have 3 or 2 plates proximally and are opposite every fourth or fifth adambulacral. The small inferomarginal elements are slightly separated in the sample examined.

The papulae of disk and proximal half of ray are in numerous groups of 2 or 3; distally they are mostly single. The actinal channel is smooth, soft, and crossed by transverse furrows between inferomarginal plates.

Along furrow margin, from mouth-plates, is a series of pedunculate straight pedicellariae with narrow round-tipped valves; length *circa* 0.6–0.7 mm.

In the actinal interradial channel can be seen 2 gonopores. In the interbrachial channel are a few small pedunculate straight pedicellariae.

TYPE LOCALITY. St. 189. Port Lockroy, Weincke Island, Palmer Archipelago, 70 m., 1 specimen.

REMARKS. This species, if species it is, belongs to the section of the genus with much reduced marginal plates, wherein the marginal or antiambulacral skeleton consists of a series of spaced transverse bars along the side of ray. In this species there are two or three pieces to each bar, the third, when present, representing an abactinal element. In young examples one would expect to find 5, 6 or even more plates, perhaps connecting up with an incomplete or sketchily outlined abactinal reticulum.

L. hemiora differs from other species belonging in this group, namely *chirophora*, *lactea*, *belgicae*, *joffrei* in lacking differentiated superomarginal pustules, or spines, and in having crossed pedicellariae of one general size. If *chirophora* has varieties lacking the broad unguiculate straight pedicellariae, the crossed should nevertheless appear in two sizes, namely, 0.6–0.9 mm. for the larger and 0.3–0.37 mm. for the smaller. In *L. belgicae* the two sizes are 0.9–1.17 and 0.4 mm. In *lactea* the inferomarginal and lateral crossed pedicellariae measure 0.65–0.73 mm., the dorsal slightly less; while the representatives of the small sort, described as numerous, are only 0.2–0.22 mm. long. The only known specimen of *lactea* has well-differentiated superomarginal spines.

When all this is said, the remote possibility remains that *hemiora* may represent a freakish sort of mutation of the variable *perrieri*.

Lysasterias heteractis sp.nov.(Fig. L, 4-4*b*; Plate XX, fig. 1)

DIAGNOSIS. Resembling a specimen of *L. perrieri* having 8 slender rays. R 87 mm., r 20 mm., br 16 mm., R = 4r plus.

DESCRIPTION. Abactinal surface with very numerous small pustules of unequal size, enclosing a delicate terete spinelet and 2 or 3 small crossed pedicellariae, or the latter only. These pustules are irregular in outline and separated by narrow grooves except on central area of disk where they are spaced, and the puffy skin can be seen between them. Numerous small papulae, most conspicuous in the interbrachial channels. Spinelets range from 1 to 1.7 mm. long by 0.25 mm. thick at base, and the tip is minutely thorny. The pedicellariae are 0.45-0.55 mm. long, the tip broad and bluntly rounded. In profile the outside of terminal lip is long.

The abactinal skeleton is represented by irregularly and widely scattered separate small plates, or sinuous lines of them suggesting a degenerate reticulation. On side of ray the marginal plates (plus 1 or 2 small abactinals proximally) form weak oblique costae opposite, on an average, every fourth ambulacral. The inferomarginals touch one another proximally but are separated distally. The superomarginals are transversely elongate and do not touch one another.

On sides of ray are 2 series of much larger marginal pustules. Superomarginal spinelets (2.5-3.5 mm.) abruptly longer than abactinal, generally 1 to a pustule but occasionally 2 at base of ray, and surrounded by about 5 crossed pedicellariae larger than the abactinal (0.75-0.85 mm.). Inferomarginal spinelets slightly thicker than superomarginal, 2 at base of ray and 1 on outer half or two-thirds, accompanied by 5-8 crossed pedicellariae similar to the superomarginal. Sometimes each proximal inferomarginal spine is surrounded by its own pustule so that there are three in a vertical series. There are a very few inconspicuous small lanceolate marginal pedicellariae.

The adambulacral spines are slender, rather long (3-3.5 mm.), close-set, and one to a plate. The narrow space between them and the inferomarginal spines is devoid of papulae although intermarginal papulae are present. The swollen inferomarginal pustules usually abut on the upright adambulacral spines.

The mouth angle is constricted, about 4 pairs of adambulacrals behind the oral plates being in contact. The small oral plates have 4 spines on the actinostomial border of each angle, and close behind these a pair of longer suborals exactly like the following adambulacrals. On the mouth-plate and along the furrow face of the adambulacrals are simple lanceolate straight pedicellariae (sometimes with one valve tip hooked over the other) averaging 0.7 mm. long by 0.38 mm. broad at base.

The madreporite is circular, 3.5 mm. in diameter, and situated at mid-r.

The ambulacral furrow is wide, the tube-feet numerous and crowded. One can sometimes count 5 in a transverse series.

The gonads (testes) are attached to the interbrachial septum 5 mm. from the interbrachial sulcus on a level with the intermarginal line. The duct opens at the tip of

a papilla (there being a pair close together) in each constricted actinal interradial area.

TYPE LOCALITY. St. 170. Off Cape Bowles, Clarence Island, 342 m., rock, 1 specimen.

Genus *Diplasterias* Perrier

Diplasterias Perrier, *Comptes-rendus*, CVI, no. 11, 1888, p. 765; 1891, p. 77. Type *Diplasterias lütkeni* Perrier.—Fisher, *Smithsonian Miscell. Coll.*, LI, 1908, p. 89 (error in assignment of *sulcifera* as type); 1930, p. 229.

Podasterias Perrier, 1894, pp. 107, 108; 1896, p. 35. Type *Diplasterias lütkeni* Perrier (not *Podasterias* Perrier, 1891, p. 160).—Fisher, 1923, p. 603; *Zool. Anz.*, XXXIII, 1908, p. 358.

Koehleraster Fisher, 1922, p. 596; 1930, p. 234. Type *Anasterias octoradiata* Koehler.

Bathyasterias Fisher, 1930, p. 231. Type *Asterias vesiculosa* Sladen.

DIAGNOSIS. Adambulacral plates diplacanthid, the spines without attached pedicellariae; abactinal skeleton irregularly reticulate; the plates with one to several slender spines surrounded by a collar of pedicellariae and more or less heavily sheathed with membrane which usually obscures skeleton, or without spines; marginal plates well developed; superomarginal spines 1 or 2, conspicuous, clearly differentiated from abactinal and surrounded by pedicellariae; inferomarginal spines usually 2, sporadically 3, bearing pedicellariae and forming definite longitudinal series separated from superomarginals by a well-defined intermarginal channel; actinal spines with attached pedicellariae, in 1 longiseries (actinals exceptionally spineless); 2–4 pairs of contiguous postoral adambulacral plates; not fissiparous; gonads opening ventrally; young brooded by adult; straight pedicellariae lanceolate, typically not enlarged nor unguiculate. Differing from *Anasterias* in having a stronger abactinal skeleton and diplacanthid adambulacral plates.

REMARKS. In the first reference to *Diplasterias* (1888) Perrier cites *D. lütkeni* Perrier and *D. steineni* Studer as species which brood their young. He adds: "Je classe dans le genre *Diplasterias* les *Asterias* qui ont deux rangées au moins de piquants adambulacraires."

In the Cape Horn report, published three years later, *Diplasterias* is entered as a new genus, with the same diagnosis. Five species are enumerated and described: *D. sulcifera* (Perrier, 1869), *D. loveni* Perrier, *D. lütkeni* Perrier, *D. spinosa* Perrier, *D. steineni* (Studer).

Diplasterias was thus formally published in connection with definite species from which a type may be selected. If the first reference is to be regarded as a *nomen nudum*, as I suggested in 1908 (Fisher, 1908, p. 89), the enumeration of *D. lütkeni* and *D. steineni* is useful as an indication of the species which Perrier had in mind for his new, if somewhat indefinite, genus. While Perrier's Cape Horn report was in the press, Sladen used Perrier's first species, *D. sulcifera*, for the type of *Cosmasterias*. My choice, in 1908, of *D. sulcifera* as the type of *Diplasterias* was ill advised, due to a strict adherence to the "first species rule" for the determination of a type when none is indicated by the author. It seems to me that the oldest known species, *Asterias brandti* Bell, which includes both *Diplasterias lütkeni* and *loveni* (cited by Perrier in 1891) should be chosen, especially as *D. lütkeni* appears in the first, or *Comptes Rendus*, citation.

Diplasterias obviously antedates *Podasterias* Perrier, 1894, even if the generic diagnosis is vague in the light of modern information. *Diplasterias* made no deep impression on Perrier's mind, because he readily abandons it on p. 160 of the Cape Horn paper, in a comment on Sladen's recently published subdivisions of *Asterias*. Here he merges his *Diplasterias* with Sladen's *Asterias*.

On the same page (1891, p. 160) he unfortunately introduces *Podasterias* for the *Asterias sulcifera* group, stating that *Cosmasterias* has priority for this generic division. This is the first occurrence of *Podasterias* in literature. But in 1894,¹ disregarding his *Podasterias* of 1891, he introduced a quite different *Podasterias* for species near *A. lütkeni*. This is precisely synonymous with his *Diplasterias* of 1891, and is the *Podasterias* used by Verrill, Koehler after 1917, and Fisher, 1923. *Podasterias* of 1891 must obviously be discarded for *Cosmasterias*, while that of 1894 had no status when proposed, being a homonym of the first, as well as a synonym of *Diplasterias*.

Disregarding his *Diplasterias* of 1891, Perrier in 1894¹ employs *Diplasterias* in a different sense, namely, for *Asterias* Linnaeus. In this paper the Asteroiidae lack a genus *Asterias*.

In 1896² *Podasterias* is preserved for *Diplasterias lütkeni*, *Asterias* is reinstated, and *Diplasterias* discarded entirely.

Ludwig in 1903³ used *Diplasterias* in the sense in which I advocate employing it. Meissner in 1904⁴ employed the name for *Cosmasterias* plus *Diplasterias*. Koehler in 1906, 1908, and 1912, used *Diplasterias* to include also *Cryptasterias* Verrill, 1914. In 1917, and subsequent papers, Koehler adopted *Podasterias* with very nearly the limits I have assigned to *Diplasterias*. In 1914 Verrill⁵ used *Podasterias* for *Diplasterias* but assigned *Asterias brandti* Bell, *A. alba* Bell, *A. neglecta* Bell, and *A. obtusispinosa* Bell to *Cosmasterias*, the last three as possible synonyms of *C. lurida* (Philippi).

In 1930 I placed Studer's *Asterias steineni* along with his *A. georgiana* in a new genus *Neosmilaster*, leaving in *Diplasterias*, *brandti* (Bell), *brucei* (Koehler), *fochi* (Koehler), *kerguelensis* (Koehler), *meridionalis* (Perrier), and *vesiculosa* (Sladen).

Diplasterias brandti (Bell)

Asterias brandti Bell, 1881, p. 91, pl. 9.

Asterias neglecta Bell, 1881, p. 94, pl. 9.

[*Asterias alba* Bell, 1881, pp. 92, 506.]

[*Asterias obtusispinosa* Bell, 1881, pp. 92, 93.]

Asterias belli Studer, *Abh. Akad. Berlin*, 1884, pp. 12, 13, pl. 1.

Asterias glomerata Sladen, 1889, p. 571, pl. 105, figs. 1-4.

Diplasterias loveni Perrier, 1891, p. 80.

Diplasterias lütkeni Perrier, 1891, p. 81.—Ludwig, 1903, p. 41.

¹ *Expéd. Travailleur et Tatisman*, pp. 107, 108 (key).

² *Résultats camp. sci. Prince de Monaco*, fasc. 11, 1896, pp. 34, 35.

³ *Expédition Antarctique Belge, Scesterne*, p. 41.

⁴ *Hamburger Magalhaensische Sammelreise, Asteroideen*, pp. 5-9.

⁵ *Shallow-water Starfishes*, p. 361.

- Diplasterias brandti* Meissner, 1904, p. 7.—Koehler, 1908, p. 572, pl. 5, figs. 50, 51; 1912, p. 19, pl. 1, figs. 3, 5, 6.—Fisher, 1930, p. 230.
- Podasterias brandti* Koehler, 1917, p. 26, pl. 4, figs. 16, 17; pl. 5, figs. 11, 13, 14; 1920, pp. 41, 51, pl. 13, fig. 11; pl. 16, figs. 5, 6; 1923, p. 27, pl. 2, figs. 2, 3.—Grieg, 1929, p. 7.
- Podasterias brandti* var. *glomerata* Koehler, 1923, p. 29, pl. 2, fig. 4.
- St. 51. Off Eddystone Rock, East Falkland Island, 105–115 m., fine sand, 1 young.
- St. 55. Entrance to Port Stanley, East Falkland Island, 10–16 m., 2 specimens.
- St. 1873. Off Clarence Island, 61° 20' 8" S, 54° 04' 2" W, 200–137 m., 2 specimens.
- St. WS 73. Falkland Islands, 51° 01' S, 58° 54' W, 121 m., fine dark sand, 1 young.
- St. WS 80. Falkland Islands, 50° 57' S, 63° 37' 30" W, 152–156 m., fine dark sand, 1 specimen.
- St. WS 81. 8 miles north 11° W of North Island, West Falkland Island, 81–82 m., sand, 15 specimens.
- St. WS 84. 7½ miles south, 9° W of Sea Lion Island, East Falkland Island, 75–74 m., coarse sand, shells, stones, 5 specimens, 1 carrying young (24 March 1927).
- St. WS 85. Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shells, 2 specimens.
- St. WS 91. Tierra del Fuego, 52° 53' 45" S, 64° 37' 30" W, 191–205 m., fine dark sand and shell, 14 specimens.
- St. WS 92. 51° 58' 30" S, 65° 01' W, 145–143 m., 2 specimens.
- St. WS 98. Falkland Islands, 49° 54' 15" S, 60° 35' 30" W, 171–173 m., 9 specimens.
- St. WS 99. Falkland Islands, 49° 42' S, 59° 14' 30" W, 251–225 m., fine dark sand, 6 specimens.
- St. WS 109. Falkland Islands, 50° 18' 48" S, 58° 28' 30" W, 145 m., fine dark sand, 1 specimen.
- St. WS 210. Falkland Islands, 50° 17' S, 60° 06' W, 161 m., green sand, 2 specimens.
- St. WS 211. Same as 210, 174 m., 4 specimens.
- St. WS 230. Falkland Islands, 50° 10' S, 58° 42' W, 210–271 m., 1 specimen.
- St. WS 233. Falkland Islands, 49° 25' S, 59° 45' W, 185–175 m., fine green sand, 5 specimens.
- St. WS 243. North-east of Falkland Islands, 51° 06' S, 64° 30' W, 144–141 m., coarse dark sand, 1 specimen.
- St. WS 755. Falkland Islands, 51° 39' S, 57° 39' W, 75 m., 2 specimens.
- St. WS 782A. North Falkland Island, 50° 29¼' S, 58° 23¾' W, 141 m., 1 specimen.
- St. WS 815. Between Falkland Islands and Strait of Magellan entrance, 51° 51¼' S, 65° 44' W, 132–162 m., 1 specimen.
- St. WS 816. Same, 52° 09¾' S, 64° 56' W, 150–160 m., 2 specimens.
- St. WS 817. Same, 52° 23' S, 64° 19' W, 191–202 m., 3 specimens.
- St. WS 823. Falkland Islands, 52° 14½' S, 60° 01' W, 80–95 m., 1 specimen.
- St. WS 825. Falkland Islands, 50° 50' S, 57° 15¼' W, 135–144 m., 2 specimens.
- St. WS 836. South-east of eastern entrance to Strait of Magellan, 53° 05½' S, 67° 38' W, 64 m. 1 specimen.
- St. WS 867. 51° 10' S, 64° 15' 30" W, 150–147 m., 1 specimen.
- St. WS 869. 52° 15' 30" S, 64° 13' 45" W, 187 m., 1 specimen.

It has been customary to include in the synonymy of this species *Asterias alba* Bell and *A. obtusispinosa* Bell (1891, pp. 92, 93). Many years ago I examined at the British Museum (Natural History) the type specimens. My notes state that the superomarginals are high on the side of the ray; that there are two series of actinal spines; that the gonads appear to open dorsally in *obtusispinosa*. I have not observed more than one series of actinal spines in *brandti*. Possibly *alba* and *obtusispinosa* belong in *Cosmasterias*.

This species is very variable and in the southern part of the range there is a chance of confusing young specimens with those of *D. brucei*. The most obvious variation in Falkland specimens is in the number of crossed pedicellariae and the thickness of the

sheath of tissue surrounding the spines. *Asterias neglecta* Bell and *A. glomerata* Sladen are representatives of a form with heavy circumspinal sheaths and well-developed crossed pedicellariae. Koehler has already recognized this as variety *glomerata* (1923, p. 29) but *neglecta* Bell has priority.

In another form the tissue of the sheath is well developed but there are few pedicellariae, as in *brucei*. However, the latter has distinctly smaller crossed pedicellariae and fewer dorsolateral spines. In both formae there are "broader and slenderer" rayed specimens.

Two inferomarginal spines with chisel-shaped end and terete base occur with greatest frequency but this number varies sporadically to 1, less often to 3. Certain examples, especially in the southern part of the species-range have a single spine more often than 2. A specimen with R 76 mm. from St. 84 has the disk arched and the bases of rays approximated to form a nidamental cavity in which are 161 young, 5-7 mm. in diameter. All have 5 rays.

DISTRIBUTION. Falkland Islands; Magellan region, north to latitude $44^{\circ} 14' S$ and longitude $53^{\circ} 43' W$; South Georgia; South Shetland Islands; Antarctic Archipelago south to Alexander I Island, $68^{\circ} 35' S$, $72^{\circ} 40' W$; Bellingshausen Sea, $70^{\circ} 23' S$.

Diplasterias meridionalis (Perrier)

(Fig. M, 2-2b; Plate XXI, fig. 4; Plate XXII, fig. 1)

Asterias meridionalis Perrier, 1875, p. 76.—Smith, 1879, p. 272, pl. 16, fig. 1.

Asterias mollis Studer, *Abh. Akad. Wiss. Berlin*, 1884, p. 8.

Asterias studeri Bell, 1881, p. 91.—Studer, *Abh. Akad. Wiss. Berlin*, 1884, p. 8, pl. 1, fig. 1.

Podasterias meridionalis Koehler, 1917, p. 20, pl. 2, figs. 11, 12; pl. 3, figs. 1, 2, 4, 5, 6, 7; pl. 6, fig. 8; pl. 7, fig. 9; 1923, p. 31, pl. 2, fig. 1 (not pl. 13, fig. 1).—Döderlein, 1928, p. 294.

Diplasterias meridionalis Perrier, 1891, p. 7.—Meissner, 1904, p. 8.—Koehler, 1912, pp. 211, 213, 220, 223, 252.—Fisher, 1930, p. 231.

St. 42. Off mouth of Cumberland Bay, South Georgia, 120-204 m., 2 young specimens.

St. 140. Stronness Harbour to Larsen Point, South Georgia, 122-136 m., green mud and stones, 4 specimens (2 with 7 rays).

St. 141. East Cumberland Bay, South Georgia, 17-27 m., 1 specimen.

St. 149. Mouth of East Cumberland Bay, South Georgia, 200-234 m., mud, 2 young specimens.

St. 160. Near Shag Rocks, $53^{\circ} 43' 40'' S$, $43^{\circ} 57' W$, 177 m., grey mud, stones, 2 young specimens.

St. 1562. Off Marion Island, $46^{\circ} 52' S$, $37^{\circ} 55' E$, 97-104 m., 3 young specimens.

St. 1563. Off Marion Island, $46^{\circ} 48' 4 S'$, $37^{\circ} 49' 2 E$, 101-106 m., 6 specimens.

St. WS 25. Undine Harbour (North), South Georgia, 18-27 m., mud and sand, 2 young specimens.

St. WS 27. West Cumberland Bay, South Georgia, 106-109 m., gravel, 1 young specimen.

St. MS 6. East Cumberland Bay, South Georgia, 27 m., 2 specimens.

St. MS 10. Same, 26 m., 3 specimens.

St. MS 67. Same, 38 m., 2 young specimens.

St. MS 71. Same, 110-60 m., 2 specimens.

St. MS 74. Same, 22-40 m., 1 young specimen.

Cumberland Bay, South Georgia, 1 young specimen.

Government Jetty, Grytviken, South Georgia, 1 specimen.

Koehler has materially added to the knowledge of this species, and a rather full account is given in his Kerguelen paper. In his report on the results of the Swedish Antarctic Expedition he includes a 6-rayed form from Antarctic Bay, South Georgia (1923, p. 33, pl. 13, fig. 1) which, apart from the number of rays, more closely resembles *D. brucei* than *meridionalis*. Similar specimens have been listed in this report under *brucei*. In typical *meridionalis* there are numerous stubby irregularly scattered dorso-lateral spines subequal to the carinals which are not aligned in a sharply differentiated fairly regular longiseries. In the problematical specimens the carinal spines are heavily stoled, are in as regular a series as in *brucei* and are occasionally even more sharply differentiated from the smaller dorsolateral spines. In my specimens the differentiation is more marked than in Koehler's figure; and the cushion of tissue around the spines is in one case (St. MS 71) distinctly larger than in *brucei*, where it is variable in size—not rather constant as Koehler thought. In *brucei* there is a series of actinal spines. In *meridionalis* there are no actinal spines, and the plates are small, wedged between the well-developed inferomarginals and adambulacrals, and invisible in alcoholic specimens. But young specimens of *brucei* do not have any actinal spines, and if small enough, no actinal plates either. As the pedicellariae are very similar in the two species there will always be great uncertainty in determining young 6-rayed specimens. Since *meridionalis* also has a few 5-rayed young it is obvious that these will be confused with young *brucei* until adult characters are developed.

A typical specimen from St. MS 10 (14 February 1925) with R 110 mm. has 50 young in the nidamental cavity; 46 have 6 rays and 4 have 5 rays. From St. 140 are 2 small 7-rayed specimens, placed in this species rather than *octoradiata* on account of preponderance of diplacanthid adambulacrals.

A specimen from St. MS 6, having R 105 mm., is occupied by 3 large parasitic ascothoracid cirripedes, *Dendrogaster*, lying in the coelom. The central portion of each of the 4-branched bodies lies between the dorsal and ventral stomachs, while the space between the hepatic diverticula and the ventral wall is completely filled (for half or three-quarters length of ray) by the many lobed branches. Branches of the upper parasite extend into rays 1, 2, 4, 5; while the middle occupies rays 1, 4, 5, 6; and the lowermost, rays 3 (2 branches) 5, 6. Ray 6 therefore is crowded with a branch of each parasite. In spite of all this competition for space the hepatic diverticula appear to be normal and all 10 gonads functional. It is difficult to understand how the stomach could have functioned adequately. The body wall is flaccid and the elements of the skeleton are weak—precisely the condition which I found in an almost equal-sized *Leplasterias polaris accervata*, from Bering Sea, parasitized by several large *Dendrogasters*; and in a specimen of *Hippasteria californica* (Fisher, 1911, p. 237, pl. 111, fig. 1) containing one large *D. arbuscula*.

DISTRIBUTION. South Georgia; Marion Island; Kerguelen (type locality); low tide to 234 m.

Diplasterias brucei (Koehler)

Stolasterias brucei Koehler, 1908, p. 569, pl. 5, figs. 46, 47.

Coscinasterias brucei Koehler, 1911, p. 30, pl. 5, fig. 5.

Coscinasterias victoriae Koehler, 1911, p. 32, pl. 5, figs. 3, 4; 1912, p. 24.

Podasterias brucei, 1920, p. 42, pl. 11, figs. 5-7; pl. 13, figs. 1-9; pl. 14, figs. 4, 7-11; pl. 15, figs. 4, 5; 1923, p. 35, pl. 13, figs. 1, 2.—Döderlein, 1928, p. 295.—Grieg, 1929, p. 5.

Diplasterias brucei Fisher, 1930, p. 231.

McMurdo Strait, Victoria Land (W.Q. hole 12), 2 young specimens.

St. 181. Schollaert Channel, Palmer Archipelago, 64° 20' S, 63° 01' W, 160-335 m., mud, 2 specimens.

St. 123. Off mouth of Cumberland Bay, South Georgia, 230-250 m., grey mud, 2 specimens (6 rays).

St. 148. Off Cape Saunders, South Georgia, 132-148 m., grey mud, stones, 3 specimens (6 rays).

St. 170. Off Cape Bowles, Clarence Island, 342 m., rock, 1 young specimen (5 rays).

St. 181. Schollaert Channel, Palmer Archipelago, 64° 20' S, 63° 01' W, 160-335 m., mud, 2 specimens.

St. 366. South of Cook Island, South Sandwich Islands, 77-152 m., 3 specimens (5 rays).

St. 371. 1 mile east of Montagu Island, South Sandwich Islands, 99-161 m., 1 specimen 5-rayed carrying young.

St. 1941. Leith Harbour, South Georgia, 53-22 m., 3 young (6 rays).

St. MS 71. East Cumberland Bay, South Georgia, 110-60 m., 1 specimen (6 rays).

All the specimens from South Georgia have 6 rays and are therefore not typical *brucei*. Koehler regards this 6-rayed form as a variant of *meridionalis* and has published a figure and notes on a specimen from 250 m., Antarctic Bay, South Georgia (1923, p. 33, pl. 13, fig. 1). It is only necessary to compare this figure with one of *brucei* on the same plate (fig. 2) to see that it resembles *brucei* much more closely than it does typical *meridionalis* (Koehler, 1917, 1923). In fact two medium-sized specimens (R 78 and 93 mm.) outdo typical *brucei*, of about the same size, in the reduction or suppression of the dorsolateral spinelets, and the accentuation of the carinal and superomarginal spines along with the circumspinal cushions of tissue. These cushions are not necessarily larger in (5-rayed) *brucei*, as Koehler believed, but may be actually smaller than in the 6-rayed form (e.g. 1 from St. M 71 as compared to typical *brucei*, Sts. 366, 371). The only difference mentioned by Koehler which seems to hold is the more constant development of actinal spines in *brucei*, these extending farther along ray than in the 6-armed form. There are two very large specimens from St. 148 having 6 rays and the general habit of *brucei*. One measures R 160 mm., r 28 mm.; the other, R 245 mm., r 38 mm. In these, well-developed actinal spines extend $\frac{1}{2}$ R along ray while in a specimen of *brucei* from St. 366 (R about 90 mm.) they extend rather more than $\frac{2}{3}$ R. (In an equal-sized 6-rayed specimen they extend about $\frac{1}{2}$ R but the spines are smaller.) But *D. meridionalis* differs from these in lacking actinal spines altogether and in having reduced hidden, actinal plates.

No typical 5-rayed *brucei* has yet been taken near South Georgia. As the matter now stands these 6-rayed specimens look exactly like typical *brucei* except for the number of rays and a poorer development of actinal spines. To add somewhat to the confusion a

typical specimen of *meridionalis* (St. MS 10) has 4 out of 50 young with only 5 rays. Possibly in deeper water near South Georgia there may be typical *brucei*, of which these 6-rayed specimens constitute a shallower water form.

A specimen of typical *brucei* (St. 371) is carrying 65 young about 6 mm. in diameter and all are 5-rayed.

DISTRIBUTION. South Georgia (6-rayed form); South Sandwich group, South Orkneys, South Shetlands; Graham Coast; Antarctic Coast from 92° E to 166° 12' E and 77° 32' S (McMurdo Sound, South Victoria Land); probably circumpolar; 0-581 m.

Diplasterias octoradiata (Studer)

(Fig. M, 1-1c; Plate XXI, figs. 1-3; Plate XXII, fig. 2)

Pedicellaster octoradiatus Studer, 1885, p. 147, pl. 1, figs. 1a-d.

Anasterias octoradiata Koehler, *Brooklyn Institute Museum, Sci. Bull.*, 11, no. 4, 1914, p. 64, pl. 14, figs. 1-7; 1923, p. 14, pl. 6, fig. 6.—Fisher, 1922, p. 595.—Grieg, 1929a, p. 7.

Koehleraster octoradiatus Fisher, 1930, p. 234.

St. 145. Stromness Harbour, South Georgia, 26-35 m., 1 specimen, typical, 8 rays.

St. 1941. Leith Harbour, South Georgia, 55-22 m., 1 specimen, f. *eunota*, 8 rays.

St. WS 25. Undine Harbour (North), South Georgia, 18-27 m., mud, sand, 1 specimen, f. *eunota*, 9 rays.

St. WS 62. Wilson Harbour, South Georgia, 15-45 m., 1 specimen, typical, 8 rays.

St. MS 6. East Cumberland Bay, South Georgia, 27 m., typical, 3 specimens, 8 rays; one, 9 rays.

St. MS 10. Same, 26 m., 10 specimens, typical, 3 (7r), 5 (8r), 1 (9r).

St. MS 67. Same, 38 m., 1 specimen, juv., 8 rays.

St. MS 74. Same, 22-40 m., 1 specimen, subtypical, 7 rays.

Undine Harbour, South Georgia, 20 m., 2 specimens, f. *eunota*, 9 rays.

Cumberland Bay, South Georgia, 1 specimen, typical, 8 rays.

Heretofore only 3 specimens have been known: two recorded by Koehler (1914, 1923) and one by Grieg (1929), all from South Georgia. The number of rays in these was 8 and 9.

The present collection affords an altered picture of the species. The number of rays varies from 7 to 9 among adult specimens and young large enough to fend for themselves. But a tally of young carried by the mother indicates the astonishing range of from 5 to 10 rays with the greatest frequency 8, then 7, 9, 6, 10, 5.

The typical form as described by Koehler has the thickest skin and most swollen welts around the spines, and the latter do not protrude much if at all beyond the broad collar. It is this swelling of the spine collars which hides the large madreporite that escaped both Koehler and Grieg. The madreporite is subcircular, flat, 5 mm. in diameter, and its inner border is at mid-r. The typical form has the weakest abactinal skeleton, and (in large specimens) the best development of hidden *actinal* plates, the series of which extends far along ray. There is in mature specimens an actinal series of conspicuous papulae, extending nearly three-fourths length of ray measured on side. The skeletal intervals for these papulae alternate with the actinal plates. In this actinal

channel are a few simple lanceolate pedicellariae, which are found also in the inter-marginal channel and abactinally.

From Undine Harbour (including St. 25) and Leith Harbour (St. 1941) are 4 specimens sufficiently different to constitute a well-marked variety, forma *emota*, which is characterized by conspicuously protruding abactinal spines, with narrower collars, an exposed madreporite, a stronger abactinal skeleton, a much shorter series of hidden actinal plates, and actinal papulae which are largely suppressed on rays (Undine Harbour), or are small and form only a short series (St. 1941). There is a variable number of straight pedicellariae, as in typical form (see Pl. XXI, figs. 1, 2). The type, Undine Harbour, has 9 rays; R 100 mm., r 29 mm., br 20 mm.; madreporite circular, 4.5 mm. in diameter, the inner border 16 mm. from centre of disk, hence rather more than half of r from centre.

The largest specimen of the typical form (St. MS 6) has 9 rays; R 130 mm., r 36 mm., br 22 mm. The disk is arched and rays approximated to form a brood chamber around the mouth. In this were 707 young, ranging in diameter from 3.75 to 5 mm.; date, 12 January 1924. Random sampling gives the following counts for the number of rays: 74 have 8 rays; 36 have 7 rays; 16 have 9 rays; 5 have 6 rays; 2 have 10 rays; 1 has 5 rays—surely an astonishing variation. An adult 6-rayed *octoradiata* will give the future systematist something to puzzle over. Except for its mostly monacanthid adambulacrals it could hardly be distinguished from *Diplasterias meridionalis*.

A large 8-rayed specimen from St. 145 (7 January 1927) has the brood chamber filled with young in the same stage of development as those from St. MS 6. These young have been left undisturbed but a considerable number had already shaken loose. Sixty-seven have 8 rays, 34 have 7 rays, 8 have 9 rays, 2 have 6 rays. There is a "Siamese twin" with 2 mouths and 13 rays. Two undeveloped eggs are 3.5 mm. in diameter.

The young from St. MS 6 have 12-14 pairs of tube-feet. There is as yet no mouth, but on the arched abactinal surface of the largest a few tiny papillae have appeared. Many are greatly distorted by mutual pressure due to crowding, and in some cases 1 or 2 rays are larger than the others. The young have long "umbilical" cords proceeding from an interradius by which they are united in clusters to a common small, fleshy, lobed mass, such as I figured for *Leptasterias arctica* (1930, pl. 10, fig. 4). The cord is 0.034-0.17 mm. in diameter and varies in length from two to five times diameter of young. Sometimes a cluster is anchored to a tube-foot by a loop of a cord which has cut into the skin.

A series of specimens from St. MS 10 includes the following graded sizes: R 6 mm. (7 rays); R 7 mm. (8 rays); R 7.5 mm. (9 rays); R 10 mm. (7 rays); R 14 mm. (8 rays); R 15 mm. (8 rays); R 21 mm. (8 rays); R 26 mm. (7 rays); R 30 mm. (8 rays, St. MS 6); R 46 mm. (8 rays). In the smallest specimen the tube-feet are biserial but the second has indications of a quadriserial arrangement. The fourth, with R 10 mm. and 7 rays, would pass for a young *D. meridionalis* but a majority of the adambulacrals are monacanthid, with a scattering of diplacanthid plates. In this the occurrence of diplacanthid plates is about as frequent as in the third specimen with 9 rays which could not be

meridionalis. In 2 series chosen at random the spines counts run as follows from base to tip of ray:¹ 5m, 1d, 1m, 1d, 4m, 1d, 2m, 1d, 1m, 3d, 1m, 1d, 1m, 1d, 1m, 1d, 2m: total 28 plates. Another runs: 7m, 1d, 1m, 1d, 2m, 2d, 4m, 2d, 1m, 2d, 3m: total 26 plates.

In these small specimens the skeleton is arranged as follows: a circle of plates (its radius equal to $\frac{1}{2}r$) on disk bearing 1 or 2 spinelets each, enclosing numerous isolated monacanthid plates; a carinal and 2 superomarginal series of monacanthid plates with a zone of bare skin between, the superomarginals defining the abactinal area; a series of monacanthid inferomarginals and mixed monacanthid and diplacanthid adambulacrals; a few crossed pedicellariae attached to all plates except adambulacrals; a broadly lanceolate straight pedicellaria on each mouth-plate, which carries 1 apical and 1 suboral spine.

Studer's type of *Pedicellaster octoradiatus* from South Georgia in which R is 6 mm. is described as having an irregular calcareous net on the central part of disk, forming on the rays three distinct bands, tube-feet biserial. This would apply to the three smallest specimens listed above.

Koehler did not describe the skeleton, but placed the species in *Lysasterias* (*Anasterias* to him) by reason of the development of the circumspinal collars or pustules. After the type reached the U.S. National Museum I made a dissection and described the skeleton as follows (1922, p. 595): "It has a complete irregularly reticulate abactinal skeleton, consisting of very numerous small, but fairly robust, oval, elliptical oblong, and a few irregularly 3-lobed plates (which latter perhaps represent the primary dorsolaterals). There is an irregular carinal series, of which the plates are no larger than the others. The abactinal plates are joined to the superomarginals by transverse bands of plates which are a little more regular than the others, and between consecutive trabeculae are broad (but short) papular areas which form a zone just above the superomarginal plates. These papular areas, or skeletal meshes, are larger than the other abactinal and the intermarginal meshes. The marginal plates are fairly robust and of the form usually found in the Asteroiinae—namely, 4-lobed. The descending lobe of the superomarginal is the longest and strongly overlaps the ascending one of the inferomarginal. The superomarginals are regularly monacanthid, while most of the inferomarginals are diplacanthid. There is a very inconspicuous series of small spineless actinal plates."

This skeleton is like that of *Diplasterias meridionalis*, even to the obscured actinal plates. I prepared the skeleton of one ray of *meridionalis* from St. MS 10, for comparison with that of *octoradiata* from the same haul. These are more closely similar than is the skeleton of the two formae of *octoradiata*! In *meridionalis* and the typical form of *octoradiata* the actinals extend far along the ray whereas in forma *emota* they stop at about the middle of ray. Pl. XXI, figs. 2-4.

A comparison of alcoholic specimens reveals a striking similarity between the two species except for the number of rays and number of adambulacrals spines. *Meridionalis* has the same broad "pustulate" collars around the spines, not less swollen or fleshy than in *octoradiata*.

¹ This means 5 monacanthid plates, 1 diplacanthid, 1 monacanthid, etc.

If the adambulacral armature is disregarded, a South Georgian specimen of *D. meridionalis* would serve to illustrate a 6-rayed *octoradiata*; or a 7-rayed *octoradiata* would pass for *meridionalis* (of which there are 2 small 7-rayed specimens from St. 140). *Octoradiata* has regularly a variable number of sporadic diplacanthid adambulacrals, as noted in connection with young examples.

The crossed pedicellariae are closely similar in size and form, ranging from 0.34 to 0.39 mm. in length abactinally, and 0.45–0.55 mm. on inferomarginals. In profile the terminal lip in *meridionalis* descends slightly further than in *octoradiata*. The lanceolate straight pedicellariae are usually a little heavier in *meridionalis*.

Diplasterias radiata (Koehler)

(Fig. M, 3–3*b*)

Cosmasterias radiata Koehler, 1923, p. 36, pl. 2, fig. 5; pl. 3, figs. 1, 2.

St. 160. Near Shag Rocks, 53° 43' 40" S, 43° 57' W, 177 m., grey mud, stones and rock, 3 specimens.

Like Koehler's specimens, these are unfortunately young; two have 8 rays and one has 9. R is 16 mm., 13 mm., 7 mm. A few of the proximal adambulacrals are monacanthid and rest diplacanthid.

The crossed pedicellariae are of the rather noncommittal *Diplasterias* form, 0.27–0.33 mm. long and the terminal lip is more like that of *D. meridionalis* than of *octoradiata*—namely, more extensive in profile. Although these specimens are very small, the largest pedicellariae are about the same size as the smallest pedicellariae of a full grown *octoradiata* (0.34–0.55 mm.). In the actinal interradial area of one specimen are 1 or 2 lanceolate straight pedicellariae about 0.85 mm. long, while those on the adambulacral margin are about 0.35 mm. long. In the largest specimen the axillary pedicellariae are no larger than the adambulacral while in the smallest they are absent.

It is unprofitable to hold too strong opinions concerning the generic position of this young form. From its resemblance to *octoradiata* I believe it is better to place it in *Diplasterias* than *Cosmasterias*.

TYPE LOCALITY. Shag Rocks, 160 m.

Genus *Cryptasterias* Verrill

Diplasterias Koehler, part, 1906, p. 19; 1908, p. 574.

Cryptasterias Verrill, 1914, p. 362. Type *Diplasterias turqueti* Koehler.—Koehler, 1920, p. 57; 1923, p. 25.—Fisher, 1923, p. 604; 1930, p. 228.

Cryptasterias turqueti (Koehler)

Diplasterias turqueti Koehler, 1906, p. 19, pl. 2, fig. 17; pl. 4, fig. 39; 1908, p. 574.

Cryptasterias turqueti Verrill, 1914, p. 362.—Koehler, 1920, p. 57, pl. 17, figs. 1–5.—Fisher, 1920, p. 228.

St. 165. Dove Strait, south-east of Queen's Bay, Signy Island, South Orkneys, 10 m., 1 specimen.

The specimen is much smaller than Koehler's type; R 32 mm., r 7.5 mm. Koehler remarks that this species superficially resembles *Lysasterias perrieri*. *Cryptasterias* bears to *Diplasterias* much the same relation that *Lysasterias* does to *Anasterias*.

Diplasterias induta Koehler (1908, p. 575, pl. 7, figs. 68-70) from Scotia Bay, South Orkneys is obviously immature and is probably young *turqueti*.

TYPE LOCALITY. Booth Wandel Island.

DISTRIBUTION. Booth Wandel Island and South Orkneys, 0-36 m.

Genus *Neosmilaster* Fisher

Neosmilaster Fisher, 1930, p. 237. Type *Asterias georgiana* Studer.

DIAGNOSIS. Resembling *Diplasterias* in having diplacanthid adambulacral plates and gonads which open ventrally, but differing in having abactinal pedicellariae scattered among small spinelets rather than in circlets on circumspinal sheaths; in having the inferomarginal spines in oblique, transverse combs of from 2 to 5, as in *Smilasterias*. Actinal plates spiniferous, varying from one-third to one and one-half series; straight pedicellariae conspicuous, not toothed; abactinal skeleton an irregular, close, or medium open net, the small spinelets, with interspersed papulae, either close-set or spaced according to relative compactness of skeleton; superomarginal spinelets similar to and only slightly larger than abactinal; prominent actinal papulae.

REMARKS. This genus was instituted for 2 species which at least superficially resemble one another more than they do typical *Diplasterias*, to which they have been assigned by Perrier and Koehler. It differs from *Smilasterias* in having well-developed actinal papulae and gonads which open ventrally (paedophoric).

Neosmilaster georgianus (Studer)

Asterias georgiana Studer, 1885, p. 150, pl. 1, fig. 3a-d.

Diplasterias georgiana Perrier, 1891, p. 7.

Podasterias georgiana Koehler, 1917, p. 26; 1920, p. 41.

Ctenasterias georgiana Koehler, 1923, p. 40, pl. 3, figs. 3-7, 10.

Neosmilaster georgianus Fisher, 1930, p. 237.

St. 142. East Cumberland Bay, South Georgia, 88-273 m., 1 specimen.

St. 145. Stromness Harbour, South Georgia, 26-45 m., 10 specimens.

St. 159. South Georgia, 53° 52' 30" S, 36° 08' W, 160 m., rock, 1 specimen.

St. 179. Melchior Island, Schollaert Channel, Palmer Archipelago, 64° 20' S, 63° 01' W, 160-335 m., mud, 1 specimen.

St. WS 25. Undine Harbour (N.), South Georgia, 18-27 m., mud and sand, 6 specimens.

St. WS 56. Drygalski Fjord, South Georgia, 2 m., kelp roots, 2 specimens.

St. WS 65. Undine Harbour, South Georgia, kelp roots, 1 specimen.

St. MS 6. East Cumberland Bay, South Georgia, 27 m., 2 specimens.

St. MS 10. Same, 26 m., 15 specimens.

St. MS 12. Same, 25-53 m., 1 specimen.

St. MS 63. Same, 23 m., 5 specimens.

St. MS 64. Same, 15-7 m., 1 specimen.

St. MS 67. Same, 38 m., 3 specimens.

St. MS 71. Same, 110-60 m., 4 specimens.

Cumberland Bay, South Georgia, 6 specimens.

Borge Bay, South Orkneys, fish trap, 1 specimen.

Koehler (1923) has described and figured this species. His fig. 5 (pl. 3) of a dried specimen shows the reticulate skeleton and the larger meshes just above the superomarginal plates. At base of ray there are equally large intermarginal intervals. Both may be wider than in Koehler's figure. The rest of the abactinal reticulum is smaller, irregular, and the skeletal bars are slender—2 or 3 slender secondary plates uniting the mostly 3-lobed primaries. There is no differentiated carinal series. The mostly diplacanthid inferomarginal plates are adjacent to adambulacrals except at base of ray where a short series of inconspicuous actinals is interpolated. These sometimes carry a single spine in line with the 2 inferomarginals (South Georgia), but may be mostly spineless (South Orkneys). In the South Georgia specimens the superomarginal spinelets (usually 1 to a plate) are subequal to the abactinal and conspicuously smaller than the inferomarginals. In the example from South Orkneys (R 50 mm.) they are larger—intermediate between the abactinals and the spatulate truncate inferomarginal spines, of which the proximal plates carry 2 and the distals usually 1. The integument of this specimen is distinctly thicker and more verrucose than in South Georgia examples. In the latter the spinelets are all distinct as shown in Koehler's fig. 3, while in the South Orkney form the intricate folds of skin are flush with ends of spinelets and occupy all the space between. They completely hide numerous crossed pedicellariae. The specimen resembles an *Anasterias* or a *Lysasterias*.

Typical specimens have sporadically triplacanthid adambulacrals.

DISTRIBUTION. Shag Rocks; South Georgia, low tide to about 160 m.; South Orkneys, shallow water; Palmer Archipelago, 160-335 m.

Neosmilaster steineni (Studer)

Asterias steineni (Studer), 1885, p. 152, pl. 1, figs. 4a, b.

Diplasterias steineni Perrier, 1891, p. 84.—Koehler, 1912, p. 20, pl. 1, figs. 4, 7, 10.

Podasterias steineni Koehler, 1917, p. 26; 1920, p. 41; 1923, p. 30, pl. 3, figs. 8, 9.

Neosmilaster steineni Fisher, 1920, p. 237.

St. 159. South Georgia, 53° 52' 30" S, 36° 08' W, 160 m., rock, 1 specimen.

St. WS 824. Falkland Islands, 52° 29¼' S, 58° 27¼' W, 146-137 m., 9 specimens.

St. WS 825. Falkland Islands, 50° 50' S, 57° 15¼' W, 135-144 m., 1 specimen.

The largest specimen (St. WS 824) has R 92 mm., r 22 mm., br 21 mm. Koehler's figures (1912, pl. 1, figs. 4, 7, 10) show the general habit. The species can be readily distinguished from *georgiana* by the closer knit skeleton and the extensive series of actinal plates. These extend far along ray and each carries, oriented in a longiseries, 2 terete spines, as long as, and a little stouter than, the adambulacrals. The largest specimen has a short second series at base of ray, each plate with 1 spine. Outside of the actinal spines, the inferomarginals carry an oblique transverse series of 3 or 4 similar terete

spines, or heavier terminally flattened ones. The superomarginals are intermediate in size between the inferomarginals and the small cylindrical or slightly clavate abactinal spinelets, but are not much larger than the latter. The proximal superomarginal plates carry 2 or 3 spinelets, the distals 1 spinelet.

On the marginal and actinal plates are numerous large conical straight pedicellariae, the largest half as long as the inferomarginal spines. The base is broad, the jaws triangular with a bluntly pointed tip. On the largest specimens they occur also on the lateral parts of the abactinal area. Very numerous crossed pedicellariae are scattered among the abactinal and superomarginal spines, attached to the plates but not to the spine sheaths. They appear to be absent from the actinal and proximal inferomarginal plates. A few are present on the dorsal part of the distal inferomarginal plates, but are not on pads or spine sheaths.

This species differs from *georgianus* in the extensive development of the actinal series of plates, a second series being present proximally; in the absence of crossed pedicellariae from the proximal inferomarginal plates; in having more numerous inferomarginal spines, a less open skeleton, and larger straight pedicellariae.

On account of the oblique series of 3 or 4 inferomarginal spines in addition to at least 2 actinals, large specimens resemble *Smilasterias*, which, however, has gonads opening dorsally, and well-developed actinal papulae.

DISTRIBUTION. Tierra del Fuego; Falkland Islands; south of Cape Horn; South Georgia; 99–160 m.

Genus *Smilasterias* Sladen

Smilasterias Sladen (subgenus), 1889, pp. 562, 578. Type *Asterias scalprifera* Sladen.

DIAGNOSIS. Small, 5-rayed forms with compact, reticulate abactinal and lateral skeleton beset with small spinelets; inferomarginals on ventrolateral border of ray, each with a prominent, oblique comb of 2–6 flattened truncate spines which radiate apart and are without attached pedicellariae; adambulacral plates with 2–4 slender, often flattened, spinelets, devoid of attached pedicellariae; a series of small actinal plates,¹ spiniferous in genotype; abactinal and intermarginal but no actinal papulae; adoral carina comprises first pair of postoral adambulacrals which are longer than second pair; crossed pedicellariae scattered, not in circlets around spinelets; straight pedicellariae lanceolate, scattered on all surfaces; in addition, sometimes, large spatulate unguiculate pedicellariae with curved interlocking tines; tube-feet in 4 series; one madreporite; gonads open dorsally at upper margin of superomarginal plates, near interradius.

REMARKS. The presence of *S. scalprifera* off Marion Island and in the Falkland region seems to indicate that it is a subantarctic species. The records of *triremis* from Heard and the Palmer Archipelago point to an Antarctic distribution. Sladen, however, records *scalprifera* from 75 fathoms off Heard Island, which, to be sure, is shallower water than the record of *triremis* (150 fathoms).

¹ Stated to be lacking in *S. irregularis* Clark, *Records South Australian Museum*, III, No. 4, 1928, p. 102.

Smilasterias scalprifera Sladen

Asterias (Smilasterias) scalprifera Sladen, 1889, p. 578, pl. 100, figs. 4-6; pl. 103, figs. 1-2.

Smilasterias scalprifera Fisher, 1930, p. 239.

St. 1562. Off Marion Island, 46° 52' S, 37° 55' E, 97-104 m., 4 specimens.

St. 1563. Off Marion Island, 46° 48.4' S, 37° 49.2' E, 101-106 m., 1 specimen.

St. 1564. Off Marion Island, 108-113 m., 1 specimen.

St. WS 85. (Specimen adrift in sorting; near this station.) Falkland Islands, 52° 09' S, 58° 14' W, 79 m., sand and shell, 1 specimen.

St. WS 93. West Falkland Island, 51° 51' S, 64° 45' W, 108-109 m., fine dark sand and stones, 1 specimen.

St. WS 99. Falkland Islands, 49° 42' S, 59° 14' 30" W, 251-225 m., fine dark sand.

St. WS 214. North of Falkland Islands, 48° 25' S, 60° 40' W, 208 m., 1 specimen.

St. WS 246. Falkland Islands, 52° 25' S, 61° W, 267-208 m., coarse green sand, pebbles, 1 specimen.

St. WS 824. Falkland Islands, 52° 29.1' S, 58° 27.1' W, 146-137 m., 4 specimens.

St. WS 825. Falkland Islands, 50° 50' S, 57° 15.1' W, 135-144 m., 7 specimens.

This species has heretofore been known only from off Marion and Heard Islands. Its capture in the Falkland region, already fairly well explored by the dredge, indicates the part which chance plays in deep water collecting.

The largest specimen, from St. 1564, measures R 51 mm., r 8-10 mm., br 10 mm. A characteristic of the species is the presence of a series of small actinal plates, extending ordinarily to about the middle of ray, and corresponding to the inferomarginals. Each carries a chisel-shaped spine which is the innermost of the characteristic ventrolateral oblique series. In the specimen from 1564 there are 6 or 7 spines in these combs except near end of ray where there are 5, then 4. In this particular specimen the first 5 or 6 actinal plates carry 2 spines. The first 4 or 5 adambulacral plates carry 2 spines, the next 3 have 3 spines; then over most of the ray there are 4, and near end of ray, again 3. Specimens smaller than the above (Sts. 1562, 1563, WS 825) have 3 adambulacral spines as a rule.

Specimens from the Falkland region, of which the largest measures R 40 mm., r 7 mm., br 8 mm., appear to be typical *scalprifera*.

The scattered crossed pedicellariae which in form and dentation are not peculiar to the genus have small teeth and measure 0.27-0.32 mm. In side view they are rather broadly ovate, the toothed terminal part of jaw occupying one-fourth total length. There are 3 or 4 shank teeth. The lanceolate straight pedicellariae have the tips of jaws slightly crossed and are upward of 0.85 mm. long and 0.35 mm. broad. The great majority are larger than the crossed pedicellariae, whereas in *triremis* the two sorts are subequal. In the actinal interradial areas are 1-4 lanceolate straight pedicellariae similar to the others but larger (1-1.2 mm. long).

DISTRIBUTION. Off Marion Island, 50 fathoms and Heard Island, 75 fathoms; Falkland Islands, 79-267 m.

Smilasterias triremis Sladen

Asterias (Smilasterias) triremis Sladen, 1889, p. 578, pl. 101, figs. 5, 6; pl. 102, figs. 5, 6.

Smilasterias triremis Fisher, 1930, p. 239.

St. 181. Schollaert Channel, Palmer Archipelago, 160–335 m., mud, 2 specimens.

St. 187. Neumayr Channel, Palmer Archipelago, 259 m., mud, 1 specimen.

St. 190. Bismarck Strait, Palmer Archipelago, 93–130 m., rock or stones and mud, 2 specimens.

The smallest specimen measures R 40 mm., r 7 mm., br 8 mm.; the largest measures R 61 mm., r 7 mm., br 8–10 mm. All are therefore larger than the type which has R 35 mm., r 5.5 mm. Treatment with caustic potash reveals a single series of small actinal plates which extend as far as seventh to tenth inferomarginal plate—or about one-fifth length of ray. They are normally spineless but sporadically one of the proximal plates of the series carries a small spinelet. In the largest specimen the first few inferomarginals carry irregularly 2–4 spines; throughout rest of ray, 3 flat, truncate, chisel-shaped spines. In the other specimens there are usually 3, but occasionally 2, spines. The adambulacral plates are diplacanthid as a rule, but here and there a plate with 3 spines occurs. Obviously the actinolateral region is less spiny than in *scalprifera*. Direct comparison of specimens shows that the marginal spines of *triremis* are markedly longer and broader, and the adambulacral spines are longer and more robust than those of *scalprifera*. Dorsally the two species are similar in appearance, actinally very distinct. Attached to the furrow face of the adambulacral plates near base of innermost spine are numerous pedunculate lanceolate straight pedicellariae which, in *scalprifera*, are about 0.6–0.75 mm. long, and, in *triremis*, only 0.25–0.3 mm.

In *triremis* the lanceolate straight pedicellariae which are liberally scattered on the actinal and marginal areas, and more sparingly on the abactinal plates, are subequal in length to the crossed pedicellariae. There are regularly no enlarged pedicellariae in the actinal interradial areas. In *scalprifera* there are conspicuously large lanceolate actinal interradial straight pedicellariae. A definite row of actinal and scattered inferomarginal straight pedicellariae are usually obviously larger than the crossed; very few superomarginal and abactinal straight pedicellariae.

Crossed pedicellariae are similar to those of *scalprifera* and measure 0.27–0.31 mm. in length and 0.18 mm. broad.

The species has heretofore been known only from the type series taken in 150 fathoms, between Kerguelen and Heard Islands, coarse gravel, bottom temperature 35.2 F. Its capture in the Palmer Archipelago indicates that it is an antarctic species, in contrast to *scalprifera* which is subantarctic.

Genus *Cosmasterias* Sladen

Cosmasterias Sladen, subgenus, 1889, p. 576. Type *Asteracanthion sulcifer* Perrier = *A. luridum* Philippi.—Fisher, 1930, p. 227.

Diplasterias Perrier, part, 1891, p. 77.—Meissner, 1904, p. 6.

Comasterias Perrier, 1891, p. 159.

Podasterias Perrier, 1891, p. 160.

Quadraster Perrier, Rés. camp. Prince de Monaco, 1896, p. 27. Type *Stichaster felipes* Sladen.

DIAGNOSIS. Actinal plates in two or more prominent longiseries forming the actinal or the actinal and actinolateral surfaces of ray (and not dominated or overhung by the inferomarginal plates); adambulacral plates diplacanthid, without attached pedicellariae; large unguiculate straight pedicellariae; plates of the abactinal area of ray have the appearance of forming definite longiseries, the carinals and superomarginals being conspicuously regular, and the dorsolateral area generally rather narrow with the plates in discernible longiseries; actinostome sunken, the adoral carina long, consisting of three or more contiguous pairs of adambulacral plates; gonads opening dorsally; not paedophoric.

Southern Hemisphere.

Until this genus is subjected to a revision based upon the study of a thousand or so specimens it will not be possible to determine whether one polymorphic species, or several species inhabit the Magellan-Falkland region.

Cosmasterias lurida (Philippi)

Asteracanthion luridum Philippi, *Arch. Naturges.*, xxiv, 1858, p. 265.

Asteracanthion sucifer Perrier, *Ann. Sci. Nat.*, 1869, p. 235.

Asterias sulcifera Perrier, *Rév. Stell.*, 1875, p. 58.

Asterias (Cosmasterias) sulcifera Sladen, 1889, p. 562.—Leipoldt, 1895, p. 552 (literature list).

Comaterias sulcifera Perrier, 1891, p. 160.

Cosmasterias sulcifera Perrier, 1894, p. 107.

Cosmasterias lurida Ludwig, 1903, p. 40.—de Loriol, 1904, p. 39, pl. 3, figs. 2, 3.—Kochler, 1912, p. 22, pl. 2, figs. 1-7; pl. 5, fig. 8; 1923, p. 39.—Fisher, 1930, p. 227.

To this species Leipoldt, 1895, unites *Asteracanthion clavatum* Philippi, *A. fulvum* Philippi, *A. spectabile* Philippi, *A. mite* Philippi, and *Stichaster polygamus* Sladen.

St. 1902. 49° 48' S, 67° 39' 5" W, 47 m., 1 specimen.

St. WS 78. 51° 01' S, 68° 04' 30" W, 95 m., fine dark sand, 1 specimen.

St. WS 84. 4½ miles south, 9' W of Sea Lion Island, East Falkland Island, 19 specimens.

St. WS 85. 7½ miles south, 9° W of Sea Lion Island, East Falkland Island, 75-74 m., coarse sand, shells, stones, 3 specimens.

St. WS 583. 53° 39' S, 70° 54' W, 14-78 m., 7 specimens.

St. WS 762A. 43° 50' S, 65° 01' 51" W, 67-65 m., 1 specimen.

St. WS 776. 46° 18¼' S, 65° 02½' W, 107-99 m., 5 specimens.

This species has multispinous and paucispinous forms paralleling the behaviour of *Evasterias* and *Pisaster* of the Pacific coast of North America. A very multispinous specimen having an arcuate transverse row of 4 or 5 tubercles on the carinal plates, a similar number on the superomarginals, and consecutive transverse dorsolateral series of 5 or 6, was taken at St. WS 762A. At St. WS 84 were taken paucispinous and intermediate specimens, with 1-3 superomarginal and carinal spines. In one example the spines are small while the unguiculate straight pedicellariae are very numerous. The same variation occurs in *Pisaster brevispinus*, which this specimen superficially resembles (Fisher, 1930, pl. 91, fig. 2, forma *paucispinus*).

It seems to me probable that *Cosmasterias tomidata* Sladen (= *C. germaini* Philippi) is a form of *lurida*.

A specimen from St. WS 78 is labelled "mauve colour dorsally"; while those from St. WS 776 exhibited the following colour range: violet (16), white (7), purple (4), pink orange (3), blue (1).

DISTRIBUTION. Region of the Straits of Magellan and adjacent coasts on both Atlantic and Pacific sides; Tierra del Fuego; South Georgia; low tide to 636 m.

Genus *Granaster* Perrier

Granaster Perrier, 1894, pp. 129, 133. Type *Stichaster nutrix* Studer.—Fisher, 1923, p. 604; 1930, p. 232.

Hemiasterias Verrill, 1914, p. 362, footnote. Type *Granaster biseriatus* Koehler.

Granaster nutrix (Studer)

Stichaster nutrix Studer, *Jahrb. wiss. Anst. Hamburg*, 11, 1885, p. 1554, pl. 1, fig. 5*a-d*; pl. 2, fig. 5*e-l*.

Granaster nutrix Perrier, 1894, p. 129.—Koehler, 1923, p. 53.

Granaster biseriatus Koehler, 1906, p. 11, pl. 1, fig. 6; pl. 4, fig. 42; 1908, p. 565, pl. 5, figs. 48, 49; 1912, p. 29, pl. 3, fig. 2; pl. 6, fig. 1.—Fisher, 1930, p. 233.

Hemiasterias biseriata Verrill, 1914, p. 362.

St. 141. East Cumberland Bay, South Georgia, 17–27 m., 1 specimen.

St. 166. South-east point of Paul Harbour, Signy Island, South Orkneys, shore collecting, 2 specimens.

St. 179. Melchior Island, Schollaert Channel, Palmer Archipelago, 4–10 m., rock, 5 specimens.

St. 1941. Leith Harbour, South Georgia, 55–22 m., 1 specimen.

St. WS 56. Larsen Harbour, Drygalski Fjord, South Georgia, 2 m., kelp roots, 7 specimens.

St. WS 65. Undine Harbour (North), South Georgia, 1 m., kelp roots, 1 specimen.

St. MS 10. East Cumberland Bay, South Georgia, 26 m., 1 specimen.

St. MS 71. East Cumberland Bay, South Georgia, 110–60 m., 1 specimen.

Cumberland Bay. South Georgia, November 1929, 1 specimen.

The largest specimen (St. 166) with R 18 mm. was bright yellow in life.

Koehler (1912) has given good photographic figures. The genus appears to be an isolated one. Possibly it is related to *Calvasterias*.

The species has been reported from South Georgia, South Orkneys, Graham Land, low tide to 250 m.

SPECIES FROM AFRICA AND AUSTRALIA

Astropecten irregularis africanus Koehler

Astropecten africanus Koehler, *Ann. l'Institut Oceanographique*, 11, fasc. 5, 1912, p. 5, pl. 2, figs. 8, 9.

Astropecten irregularis africanus Döderlein, 1917, pp. 47, 73, 168.

St. 299. Tarrafal, San Antonio, Cape Verde Islands, 7–11 m., 1 specimen.

The specimen measures R 28 mm., r 7 mm., R=4r; br at second superomarginal, 7 mm., width of paxillar area 3 mm. Heretofore reported from west coast of Africa 20° to 24° N (Anguin Bank, Cape Blanco, Rio de Oro).

Astropecten irregularis pontoporaeus Sladen

Astropecten pontoporaeus Sladen, *J. Linn. Soc.*, xvii, 1883, p. 259; 1889, p. 210, pl. 35, figs. 1, 2; pl. 38, figs. 10-12.—Clark, 1923, p. 249.

Astropecten irregularis pontoporaeus Döderlein, 1917, p. 75, pl. 1, fig. 5; pl. 7, figs. 9, 9a, 10, 10a.
Astropecten irregularis var. *pontoporaeus* Clark, 1926, p. 6.—Mortensen, 1933, p. 232.

St. 91. Simon's Town, False Bay, South Africa, 35 m., 9 specimens.

The specimens range in size from R 9 mm. to R 45 mm. and are typical since they are from the type locality. Colour note: aboral surface pale apricot with pale mauve, a deeper mauve band along centre of rays.

Apparently both Clark and Mortensen regard this as a valid subspecies, which means a geographic race if it signifies anything. May one suggest therefore that it is time to abandon the term "variety" which is often used to name any one of a number of somatic variations that have no geographic or even ecologic implication. For the subspecies the straight trinomial has been in good standing among zoologists for over half a century.

Genus Luidia Forbes

Luidia Forbes, *Mem. Wernerian Nat. Hist. Soc.*, viii, 1839, p. 123. Type *L. fragilissima* = *L. ciliaris*, designated, Fisher, 1911, p. 105. See Döderlein, 1920, revision.

Subgenus Luidia Forbes

Hemicnemis Müller & Troschel, *Monatsber. Akad. Wiss. Berlin*, April 1840, p. 105. Type *L. ciliaris* (Philippi), designated, Fisher, 1911, p. 105.—Döderlein, 1920, pp. 217, 244.

The citation of a subgenus for the *ciliaris* group of *Luidia* is more to correct an error of Döderlein's than an expression of confidence in the subgenera which he rather lavishly created. When a genus is subdivided, it seems to me axiomatic that the section which includes the original type-species should retain the original name—in this case *Luidia*, and not its obvious synonym *Hemicnemis*.

For the benefit of future workers, and in no way as a criticism of Döderlein's splendid memoir, I wish to record the omission of Goto's¹ two Japanese species, *Luidia yesoensis* (Hokkaido) and *L. moroisoana* (Misaki).

The new species, described below, while resembling *ciliaris* in a general way departs rather radically in having the inferomarginal armature different on alternate plates. The number of rays, 10, is the highest in this section of *Luidia*.

Luidia heterozona sp.nov.

(Fig. M, 4-4c; Plate XXIII)

DIAGNOSIS. Rays 10; rays narrower than in *ciliaris*, the upper inferomarginal spines as long as breadth of abactinal area plus superomarginal plates; inferomarginal spines bristling, 2 and 3 in fairly regular alternation; abactinal, superomarginal, inferomarginal,

¹ Seitaro Goto, A Descriptive Monograph of Japanese Asteroidea, *J. Coll. Sci., Tokyo Imp. Univ.*, xxix, 1914, pp. 301-11.

actinal, and oral bivalved pedicellariae; 3 adambulacral spines in a single transverse series; tube-feet very large; a dark brown superomarginal band; R 115 mm., r 11.5 mm., R = 10r; br 8 mm.

DESCRIPTION. Abactinal area of ray narrow, with 3 regular longiseries of circular spaced paxillae on either side, those of the outermost series representing the superomarginals. These, except at base of ray, are very much larger than the adjacent abactinal paxillae, of which 8-12 can be counted across ray to the other superomarginal series. In the median abactinal area (4 paxillae wide at base of ray and 8 at middle) regular longiserial arrangement is lost. The paxillae are stellate, not squarish, well spaced, and decrease in breadth and height very rapidly along ray. At base of ray, the lateral, with 8-12 slender marginal and 1-3 similar central spinelets are obviously larger than the median paxillae; but the disparity becomes rapidly less and less, the lateral-most paxillae become very small and the longiserial arrangement less obvious. The largest paxillae with 10-12 spinelets (and very low tabulum) are now in the central area, intermingled with smaller ones (5-8 spinelets). Many paxillae of disk and proximal third of ray carry a central or marginal conspicuous bivalved pedicellaria (Fig. 4b).

The first 3 superomarginal paxillae are subequal to the lateral abactinal but they rapidly increase in size and the outer margin fuses with the dorsal margin of the inferomarginal. The free border carries 10-12 spinelets and the surface 3-6, of which one, slightly enlarged, constitutes an incipient superomarginal spine. Some of the plates carry a bivalved pedicellaria larger than the abactinal. Corresponding to first 10 superomarginal paxillae are 14 lateral; to the second 10, also 14 lateral.

The inferomarginal plates are heavy, block-like (with deep, wide fascioles), and form a rounded lateral face to ray; that is, they occupy little of the actinal face of ray. At base of ray, the first 6 or 8 are short and wide; width rapidly diminishes so that it is only twice length, and continues until at middle of ray and distally the two dimensions are equal, or the width is slightly the greater. Inferomarginal spines acicular, sharp, bristling. Beginning with second to eighth plate, each alternate plate carries 3 spines. The longest (6-7 mm.) is on the dorsal end and directed upward; the next (5-6 mm.) is on the middle of plate, directed outward or distad; the third (3 mm.) is near lower end, directed downward. Alternating with these (with some interruptions in regularity) are diplacanthid plates; the uppermost spine (subequal to the dorsal of triplacanthid plates) is set slightly above *middle* spine of other plates, while the second (about two-thirds length of upper) is opposite interval between middle and lower spine of triplacanthid plates. The surface of plates has a sparse covering of very delicate ciliary spinelets which become crowded on the transverse margins to cover the fascioles. There is an occasional inferomarginal pedicellaria, similar to abactinal but larger; and smaller than the actinal pedicellariae.

The small actinal plates, in a single series, overlap the outer margin of the adambulacrals and are so strongly joined to the inferomarginals that they appear to be the lower ends of these plates. Each plate is subconical and carries at apex a prominent, lanceolate, two-jawed pedicellaria.

Adambulacral plates block-like, not compressed, except on disk. Each plate carries a transverse series of 3 slender compressed spines, that in furrow the least robust, and most strongly curved; second spine obviously the most robust and slightly longer than the third or outer spine. One or 2 spinelets usually stand adoral to outermost spine.

Mouth-plates very narrow and convex, so that they arch high above the level of disk adambulacrals. The true furrow margin is a short ridge deep in the furrow at inner end of plate. It carries 2 bivalved slender pedicellariae and a slender spinelet which are close to and may touch the broad junction of radial and ring nerve bands. Along the superficial carina of each plate, bordering suture, are 5 or 6 prominent slender tapering blunt spines, the inner almost as long as the plates. They decrease in size from inner to outer which stands one-third plate length from outer end. The outer third of plate carries 5 or 6 superficial spinelets, 5 or 6 along first adambulacral suture margin, and a variously located bivalved pedicellaria.

Papulae (the usual compound sort) are absent from the median area of distal third of ray but appear everywhere else on the abactinal surface. They form three regular longiseries on either side of abactinal area. In a general way their size is in direct relation to that of surrounding paxillae.

Madreporite concealed in smallest specimen but uncovered in the type, broadly elliptical, 2.5 mm. longest diameter, with fine striae radiating from centre.

Colour in alcohol: abactinal surface light brown; dark brown between marginal plates, which are whitish; bases of marginal spines brown.

YOUNG. From St. 279 are 2 specimens having R 26 mm. and R 55 mm. (both with 10 rays). In the smaller the single central spinelet of each ornate paxilla is quite definitely longer and stouter than the peripheral—long enough to be called “enlarged”—especially on the larger lateral and superomarginal paxillae. The spinelets are very delicate and sharp. This disparity in size is less evident in the second, larger, specimen and is lost in the adult (except on superomarginals). The ancestral form may have had well-developed central paxillar spines. Pedicellariae are very rare on the abactinal surface, absent from the mouth-plates, and are present on only the proximal actinals. In place of the two oral pedicellariae at entrance to ambulacral furrow are two coordinated spinelets which will develop into the valves of a pedicellaria as, in one instance, the differentiation is under way.

The inferomarginal armature lacks the lowest spine of the triplacanthid plates. There are thus 2 spines to a plate on proximal two-thirds of ray but with the differentiation shown on the adult—the dorsal spine of alternate plates is close to the upper margin. Distally the lower spine of the diplacanthid plates of the adult is lost so that the major spines are 2, 1, 2, 1. This is true also of the second specimen.

In the second specimen the first half dozen superomarginals may carry a pedicellaria, the actinal pedicellariae extend to about the middle of ray, and a large oral pedicellaria is present at mouth of furrow, definitely a development of the 2 spinelets of the small specimen. A suboral pedicellaria is present on some but not all plates and there are

three instead of five major suboral spines. The single series is continued from middle to outer end of plate by 5 smaller spinelets, or 3 spinelets and the pedicellaria just mentioned.

TYPE LOCALITY. St. 272. Off Elephant Bay, Angola, 73-91 m., 1 specimen.

SPECIMENS EXAMINED. The type and 2 from St. 279, off Cape Lopez, French Congo, 58-67 m.

REMARKS. This species seems to be definitely in the *ciliaris* group on account of the superomarginal plates abruptly larger than the adjacent lateral paxillae and the squarish block-like inferomarginals. The regular alternation of 2 and 3 long lateral spines is highly characteristic. The mouth-plates, however, are very convex and the presence of 2 pedicellariae near the inner end, deep in furrow, is similar to the condition in *L. avicularia* (subgenus *Integraster* Döderlein, 1920, p. 243, fig. 19).

This species is related to *L. aciculata* Mortensen but not closely to any other in the *ciliaris* group.

Luidia aciculata Mortensen

(Fig. M, 5)

Luidia aciculata Mortensen, *Echinoderms of St Helena*, 1933, p. 425, text-fig. 7, pl. 20, figs. 7-12.

St. 279. Off Cape Lopez, French Congo, 58-67 m., 1 specimen.

This specimen was dredged along with the two smaller examples of *L. heterozona*, and is not fully grown since the dimensions are R 45 mm., r 6 mm., br 7 mm. The longest arm fragment of type is 130 mm. and the broadest, 12 mm. The specimen agrees in most details with Mortensen's description and line figures. The paxillae, devoid of pedicellariae, all have the enlarged central spinelet. There are 1 or 2 conspicuous, conical tri-valved actinal intermediate pedicellariae. The mouth-plates have 2 spinelets at inner end, close to nerve ring, co-ordinated into a simple pedicellaria; there is a very slender spinelet adoral to the outer and smallest of the 3 adambulacral spines; the actinal plates bear a group of usually 3 spinelets.

Mortensen's description reads: "Inferomarginals with 3, in the proximal part some of them with 4 large, erect, cylindrical, pointed spines, the uppermost the longest." In the Discovery specimen the first plate is very compressed with 3 smallish ventral spines, the lowest the largest; second plate with 4 larger spines, the upper very much larger, and equal to the succeeding ones; third plate, 3 spines, the upper normal, the 2 lower larger than the 3 of second plate. From here on there are 2 large spines on each plate; but on alternate plates the pair has moved downward so that the dorsal spine is removed from upper end of plate and stands out of line, as does the lower with the corresponding spine of adjacent plates, precisely as in the diplacanthid plates of the 2 specimens of *L. heterozona* from St. 279.

This difference in the position of spines may be accentuated in young specimens and therefore may have escaped notice in larger examples. The peculiarity points to a closer relationship between *aciculata* and *heterozona* than between either of these species and any other in the *ciliaris* group. Even the mouth-plates with the furrow pedicellaria are

closely similar, while it will be recalled that young *heterozona* have the central paxillar spinelet larger than the peripheral. In *aciculata* the superomarginal paxillae are essentially as in *heterozona* with the outer margin fused with the upper end of the inferomarginal. This takes place, of course, in *ciliaris* also.

Ophidiaster guildingii

Ophidiaster guildingii Gray, *Ann. Mag. Nat. Hist.*, 1840, vi, p. 284.—H. L. Clark, *Echinoderms of Torres Strait*, 1921, pp. 78, 79.

St. 1. Clarence Bay, Ascension Island, 16 November 1925, 16–27 m., 2 specimens.

The larger specimen has R 24 mm., r 4.5 mm. and conforms to Clark's characterization of *O. guildingii*, rather than to *O. ophidianus*.

Genus Patiria Gray

Patiria Gray, *Ann. Mag. Nat. Hist.*, vi, 1840, p. 290. Type *Patiria coccinea* Gray = *Patiria miniata* (Brandt) *vide* Mortensen, 1933, p. 257.—Fisher, 1908, p. 90.—Verrill, 1913, p. 482.

Callopatiria Verrill, 1913, p. 480. Type *Patiria bellula* Sladen.

Not *Patiria* Perrier nor of Sladen. *Asterina*, in part, of authors.

Mortensen's discovery (1933, p. 257) that Gray's *Patiria coccinea* was based upon specimens of *P. miniata* with erroneous label is substantiated by his photograph of one of the types. Even if this type should prove to be the Japanese *P. pectinifera* it will make no difference as the two species are closely related.

This genus contains usually large species characterized by having numerous small secondary plates inserted peg-like in the papular areas. They form a sort of small secondary mesh between the primary plates and serve to isolate the numerous papulae of the areas formed by the primary plates. A good enlarged photographic figure is given in my *Asteroidea of the North Pacific* (1911, pl. 62, fig. 1; see also pl. 56, fig. 8a for plan of primary plates). The primary plates of the papular area overlap by their corners, the amount of imbrication depending upon age of specimen and position of plate, those in the median radial region overlapping less than on the lateral parts of ray.

The secondary plates or ossicles do not extend, as a rule, through to the coelomic surface of the body wall. Each bears a group of spinelets.

In *Patiria* the gonads open dorsally and the eggs develop into a pelagic *Bipinnaria*.¹

Patiria bellula Sladen

Patiria bellula Sladen, 1889, p. 385, pl. 63, figs. 1, 2; pl. 64, figs. 5, 6.—Koehler, 1908, p. 632.

Asterina coccinea Bell (not of Gray), *Marine Investigations S. Africa*, 1905, p. 248.

Callopatiria bellula Verrill, 1913, p. 480.

Parasterina bellula H. L. Clark, 1923, p. 280.—Mortensen, 1933, p. 260.

St. 91. Simon's Town, False Bay, South Africa, 1 specimen, deep orange.

Saldanha Bay, South Africa, 1926, beach, 1 specimen.

¹ Figured by Mortensen, 1921, *Studies of the Development and Larval forms of Echinoderms*, p. 186, pl. 33, figs. 1, 2, *Patiria pectinifera*.

An examination of the skeleton of the larger specimen (R 40 mm.) reveals that it differs from that of *Patiria miniata* only in the presence, on the primary plates, of hyaline convexities. These are the surface ends of what appear to be hyaline cylinders descending into the matrix of the plate. The primary plates overlap by the lobes or corners and the papular areas are occupied by small secondary plates as in *P. miniata*.

NOTE ON *PARASTERINA* FISHER

It is curious that *Patiria bellula* again becomes known by the combination which Sladen originally used. Sladen's *Patiria* was not Gray's. It was a group, originating with Perrier (1875, p. 323), which omitted Gray's type, and comprised 2 species, *P. ocellifera* Gray and *P. crassa* Gray. This genus, not the original *Patiria*, was named *Parasterina* by me (1908, p. 90), with *P. crassa* Gray the type. Justification for the genus lay in Perrier's statement that, in *crassa*, the dorsal ossicles are rounded, nearly circular, and are not imbricated as ordinarily the case in *Asterina*, but touch one another. This statement is repeated in Sladen's key to the genera of Asterinidae (1889, p. 276).

Through the kindness of Dr H. L. Clark I have received a specimen of *Parasterina crassa*, from near Fremantle, Western Australia.¹

This specimen has R 45 mm., r 10 mm., br 11–12 mm., and the abactinal aspect resembles superficially that of *Nardoa variolata*, as the convex primary plates are spaced and the spinelets extremely fine, close-set, and visible only under strong magnification. The species is quite unlike a true *Patiria* but resembles *Nepanthia*. In fact, the actinal surface does not differ from that of *Nepanthia* (e.g. *N. belcheri*) in any important particular. The actinal plates are covered with co-ordinated groups of very numerous spinelets. There are 15–18 similar subambulacral spinelets, and 8 or 9 furrow spinelets. The inner longiseries of actinal plates extends to 3 or 4 inferomarginals short of the end of ray; the next two series nearly as far; the fourth series about three-fifths length of ray measured on side; while a fifth and sixth series constitute a small additional chevron in the interbrachial angle.

The two series of marginal plates are quite regular, and correspond, plate to plate; they are obviously larger than the adjacent abactinals and actinals, which are small.

There are two differentiated areas on the abactinal surface. (1) A lateral triangular area reaching, at interradius, one-half of r toward centre of disk and distally nearly half length of ray; from this point it extends usually as a double series of plates nearly to tip of ray. The plates of this area, in regular longiseries, strongly imbricate, and the upper margin is excavated to accommodate a papula. Around this papular opening are 2–4 small superficial plates. Nearly all the plates carry a spiniform pedicellaria. (2) The other area, that of the convex primary plates, comprises the central part of disk and rays. It broadens distally to include most of the sides of ray also. The roundish and irregular, convex, almost tubercular primary plates for a short distance at base of ray imbricate irregularly but over rest of area are joined by smaller and lower secondary plates. These

¹ Clark, H. L., Echinoderms from Australia, *Mem. Mus. Comp. Zool.*, LV, 1938, pp. 179–181.

are irregular in shape and imbricate irregularly. Sometimes the end of these plates extend under the large primaries, sometimes they slightly overlap their edges—in short, imbricate. Very many small superficial tertiary plates of variable size fortify the joints of the primaries and secondaries and help to define the papular pores. These are the same as the superficial platelets of lateral area.

The exposed surface of the plates is covered by a multitude of very small spinelets with microscopically thorny tips (length 0.22–0.28 mm.) of nearly uniform thickness (0.04–0.05 mm.) on the secondary and tertiary plates, but, more robust (0.08–0.12 mm.) on the centre of the primaries.

The pedicellariae of the lateral abactinal plates are rather remarkable. There is a conspicuous pit usually near or at the upper excavate margin of plate. Extending over this are 5–8 minutely thorny, sharp spinelets tapering from a rather broad base and conspicuously larger than the other spinelets of plate. They form a U-shaped series or sometimes a circle, and resemble the circular spiniform pedicellariae of the Benthoplectinidae. The pits probably contain a sense organ.

I find precisely similar pedicellariae in *Nepanthia variabilis*¹ Clark from Broome, Western Australia. Nearly every plate of the lateral areas is provided with one, and a scattering of the larger crescentic plates of the abactinal area are similarly armed.

The adambulacral, actinal, and the lateral abactinal plates of *Parasterina crassa* are in no way different from those of *Nepanthia*. This leaves only the enlarged plates of the median abactinal area with the numerous intervening secondary plates and superficial tertiary plates upon which to base a new genus. But *Parasterina occidentalis* Clark (1938, p. 180, pl. 21, fig. 5) has no secondary abactinals. It is questionable, therefore, whether we can place too much reliance for generic characters upon these median abactinal plates. The behaviour of the abactinal plates of *Nardoa* furnishes reason for caution. In *N. pauciforis* the plates are numerous, small and most nearly uniform in size. Somewhat larger and progressively more diverse as to size are those of *N. mollis*, *N. tuberculata* and *N. novae-caledoniae*; while in *N. tumulosa* and *N. frianti* the large primary plates are hemispherical and the secondaries small and much more numerous (Fisher, 1919, pls. 108–110). The possibility must be considered that in *Nepanthia* aberrant species exist with over-developed primary abactinal plates. It is not a rare occurrence in the Asteroidea, and in certain species of the Asteriidae (e.g. *Leptasterias polaris*, *Pisaster ochraceus*) is of less than specific value. Both *Parasterina crassa* (Gray) and *P. occidentalis* Clark must be regarded with suspicion. I think the former is an aberrant *Nepanthia*.

Patiria granifera Gray

Patiria granifera Gray, *Proc. Zool. Soc. Lond.*, 1847, p. 82, Synopsis, 1866, p. 17.

Asterina granifera Perrier, 1875, p. 319.—H. L. Clark, 1923, p. 281, pl. 17, figs. 1, 2.—Mortensen, 1933, p. 256.

St. 90. Simon's Town, False Bay, South Africa, 2–10 fathoms, 2 specimens (R 50 and 55 mm.).

¹ Clark, 1938, p. 176, pl. 10, figs. 4, 5; pl. 20, figs. 4, 5.

The skeleton is like that of *P. bellula* and there are the same hyaline beads on the surface of the primary plates. The two forms are so close that I think there is no escaping Mortensen's conclusion that we are dealing with one variable species.

Patiriella exigua (Lamarck)

Asterias exigua Lamarck, 1816, III, p. 554.

Asterina exigua Perrier, 1875, p. 302.—Clark, 1923, p. 285.

Patiriella exigua Verrill, 1913, p. 484.—Fisher, 1919, p. 416, pl. 109, figs. 3, 4.

Asterina (Patiriella) exigua, Mortensen, 1933, p. 252, pl. 12, figs. 4-8.

Saldanha Bay, beach, 1926, 3 specimens.

St. 271. Elephant Bay, Angola, 30 July 1927, shore, 3 specimens.

Henricia ornata (Perrier)

Echinaster ornatus Perrier, *Ann. Sci. Nat.*, sér. 5, XI, 1869, p. 251.—Mortensen, 1933, p. 263.

Cribrella ornata Perrier, 1875, p. 112.—Sladen, 1889, p. 543.—Koehler, 1908, p. 629, pl. 12, figs. 105-106.

Henricia ornata Döderlein, 1910, p. 252, pl. 4, figs. 2, 2a.—Clark, 1923, p. 289.

Saldanha Bay, Cape of Good Hope, beach, 2 specimens.

Mortensen (*loc. cit.*) states: "It is perfectly evident that this species is not a *Henricia* since it has no papulae on the oral side." But *Echinaster reticulatus* H. L. Clark, listed on the following page, has actinal papulae right up to the adambulacral plates (Clark, 1923, pl. 291). *Echinaster* in the restricted sense lacks actinal papulae. *Othilia* Gray, usually merged with *Echinaster*, has actinal papulae.

But *ornatus* resembles *Henricia* more than it does *Echinaster*. Its relationship to typical *Henricia* is that of *Echinaster*, *s.s.*, to *Othilia*. If one recognizes this distinction between the two sorts of *Echinaster* he is probably justified in doing the same for the two categories of *Henricia*.

One of the principal distinctions between *Echinaster* (plus *Othilia*) and *Henricia* (including *ornatus*) is the structure of the adambulacral armature. In *Echinaster* there is an unbroken web along the furrow margin uniting successive *innermost* subambulacral spines (not the spinelets deep in furrow). Sometimes this web is thin and much retracted, especially in dried specimens; sometimes it is thick, almost leathery, as in *E. callosus*. It is emarginate between the spines giving a serrate border to furrow. The spines and membrane may be directed over the furrow, and interlock with the spines of opposite side.

Henricia entirely lacks this web. The marginal spine, or spines, of any adambulacral plate are completely independent of those of adjacent plates.

The gonads of *Henricia* open on the actinal surface—as do those of *Othilia*, at least.

In the two dried specimens of *H. ornata* the gonopores are clearly visible—two in each actinal interradial area.

Coscinasterias calamaria (Gray)(Fig. L, 5, 5*b*)*Asterias calamaria* Gray, 1840, p. 179.*Coscinasterias calamaria* Perrier, 1894, p. 106.—Fisher, 1928, p. 128.—Clark, H. L., 1938, p. 189.

St. 1686. Port Philip, Victoria, Australia (piles of Queen's Cliff Jetty), 1 specimen.

A wide ranging, variable species. The specimen has 9 rays and R 35 mm.

Marthasterias glacialis forma *rarispinga* Perrier*Asterias rarispina* Perrier, 1875, p. 62.*Marthasterias rarispina* Clark, 1923, p. 305.*Marthasterias glacialis* var. *rarispinga* Mortensen, 1933, p. 273, pl. 16, figs. 2, 3.

St. 90. Simon's Town, False Bay, South Africa, 2-10 m., 7 specimens.

St. 91. Same locality, 35 m., 4 specimens.

The largest specimen has R 95 mm. All are the extreme form, without dorsolateral spines, similar to Mortensen's fig. 2.

A colour note to St. 91 reads: "lilac with apricot spines". One wishes for a colour plate!

The multispinous form, *africana*, figured by Mortensen, is not present in the collection, although I have seen it. Such variation in the number of spines is similar to the condition found in *Pisaster giganteus* and *P. brevispinus* of California.

When adequate material has been compared, I believe that a small but constant difference will be found between typical north European specimens and those from South Africa. One distinction may be a small average difference in the size of the crossed pedicellariae. I have followed Mortensen's nomenclature for the sake of stability, but I think the South African form will eventually be *Marthasterias glacialis africana* (Perrier) with forma *africana*, forma *rarispinga*, and probably others if one cares to name them.

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NOTE: All line figures are five-sixths the stated enlargement on account of necessary reduction of original plates.

Fig. A

1. *Perknaster fuscus*, cotype. Spinelets of abactinal paxillae from ray, 0.54 and 0.55 mm., $\times 100$. 1*a*. Abactinal spinelet, base of ray, 0.55 mm., $\times 100$. 1*b*. Actinal intermediate spinelet, 0.65 mm., $\times 100$. 1*c*. Inferomarginal spinelet, 0.54 mm., $\times 100$. 1*d*. Abactinal spinelet from near end of ray, 0.45 mm., $\times 100$.
2. *Perknaster fuscus*, cotype. Profile of abactinal paxillae, pedicel 0.22 mm. high, $\times 50$. 2*a*. Larger abactinal plate, $\times 50$. 2*b*. Small paxilla pedicel 0.18 mm. high, $\times 50$. 2*c*. Side view of abactinal plate with pedicel, 0.22 mm. high, $\times 50$. 2*d*-2*f*. Three adambulacral spines from near proximal end of furrow, 1.7, 1.4 and 0.85 mm. respectively, $\times 40$. 2*g*. Tip of 2*f*, $\times 100$.
3. 3*a*. *Perknaster densus*. Two abactinal plates, base of ray, seen from side, pedicel 0.45 mm. high, $\times 50$. 3*b*. Two abactinal spinelets proximal third of ray (from plates 3, 3*a*), 0.48 and 0.45 mm. long, $\times 100$. 3*c*. Spine from actinal interradial area, 0.58 mm. long, $\times 100$. 3*d*. Adambulacral plate, mouth toward right, and furrow spines on lower side of figure shown extended over furrow, $\times 15$. 3*e*. Four of 8 adambulacral spines of seventh plate, the longer spine from each of the 4 longiseries, $\times 30$: *a*, aboral furrow spines, 2 mm.; *b*, adoral of second row, 1.5; *c*, adoral of third row, 0.93 mm.; *d*, adoral of outer row, 0.8 mm. 3*f*. Adambulacral armature of a seventh plate seen from oral side, the spines erect and closely apposed as is usual in this specimen.
4. *Perknaster fuscus*, cotype. Fourth to sixth adambulacral plates; lowest plate the fourth, $\times 20$.

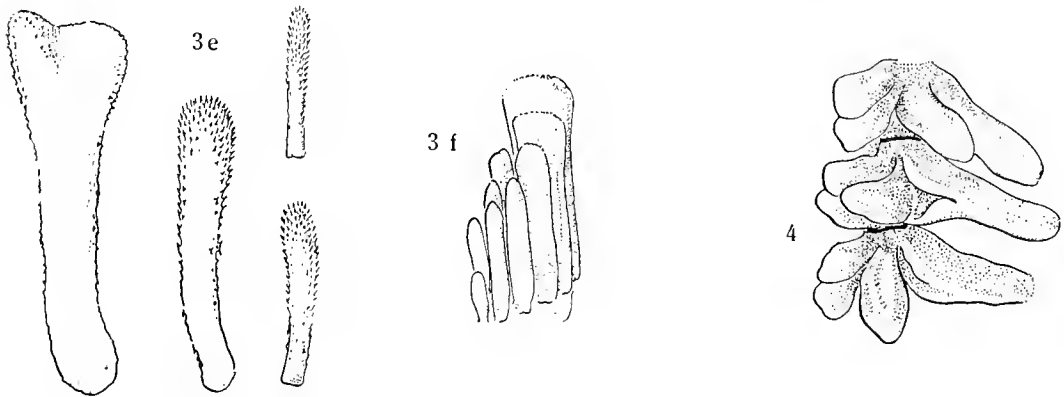
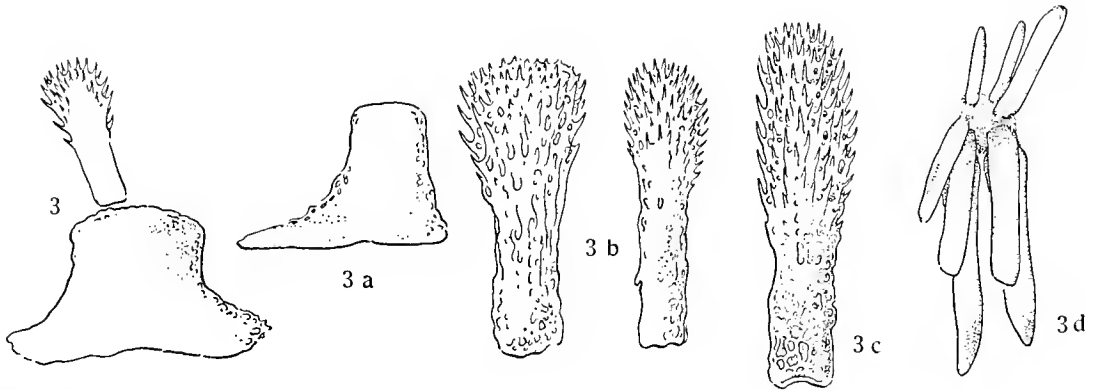
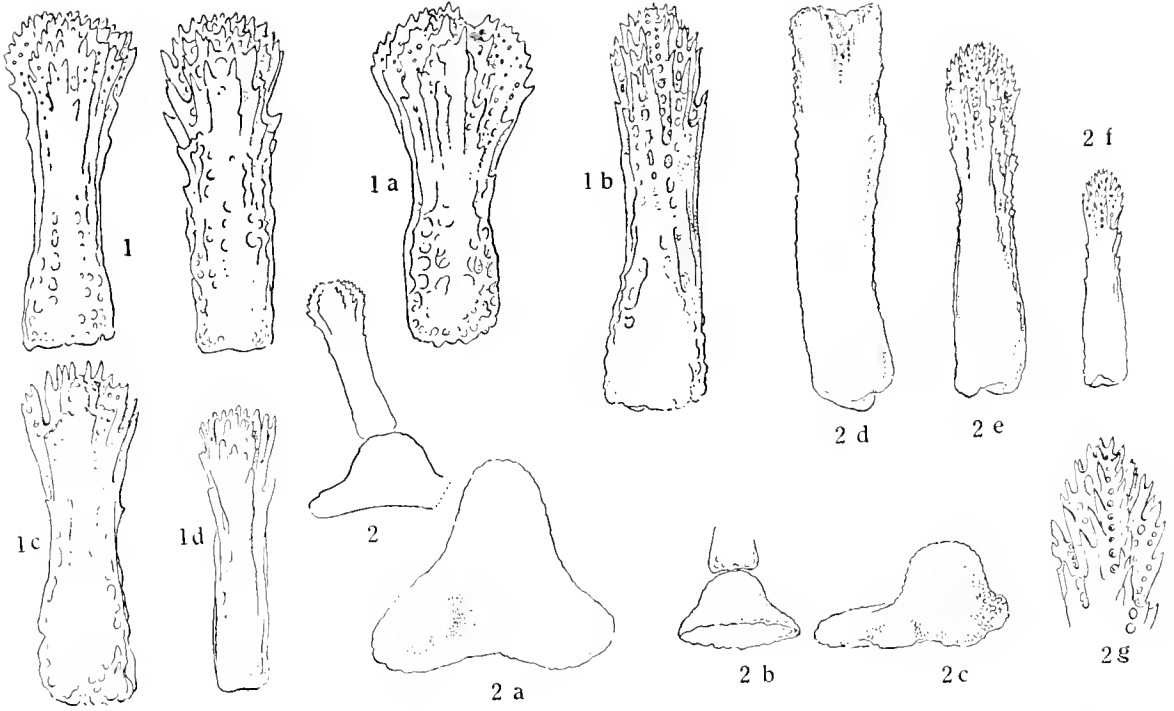


Fig. B

1. *Perknaster fuscus antarcticus*, St. 181. Abactinal spinelet, 0.5 mm. long, $\times 100$. 1*a*. Profile of an abactinal paxilla; pedicel 0.2 mm. high, $\times 50$.
2. *Perknaster sladeni georgianus*, St. 42. Abactinal spinelet, 0.54 mm. long, $\times 100$. 2*a*. Actinal spinelet, 0.72 mm., $\times 100$. 2*b*. Profile of abactinal paxilla; pedicel 0.4 mm., $\times 50$.
3. *Perknaster sladeni*, Shag Rocks. Abactinal spinelet, 0.6 mm. (to 0.7 mm.), $\times 100$. 3*a*. Actinal spinelet, 0.86 mm., $\times 100$. 3*b*. Two adambulacral furrow spinelets, 2.2 and 2.7 mm., $\times 25$. 3*c*. Profile of abactinal paxilla; pedicel 0.54 mm., $\times 50$.
4. *Perknaster sladeni*, St. 182. Two abactinal spinelets, 0.65 and 0.67 mm., $\times 100$. 4*a*. Profiles of 2 abactinal paxillae; pedicels 0.5 and 0.46 mm., $\times 50$. 4*b*. Normal actinal spinelet, 0.8 mm., $\times 100$. 4*c*. One of the 3 valves of an actinal pedicellaria, 0.66 mm., $\times 100$.
5. *Perknaster charcoti*. Profile of paxilla of large specimen C, pedicel 0.62 mm., spinelets 0.74 mm., $\times 50$. 5*a*. Abactinal spinelets of small specimen B, 0.53 and 0.63 mm., $\times 100$. 5*b*–5*d*. Specimen B, profiles of 3 paxillae, pedicels 0.45, 0.36, 0.45 mm., $\times 50$. 5*e*. Actinal spine of large specimen C, 1.7 mm., $\times 50$.

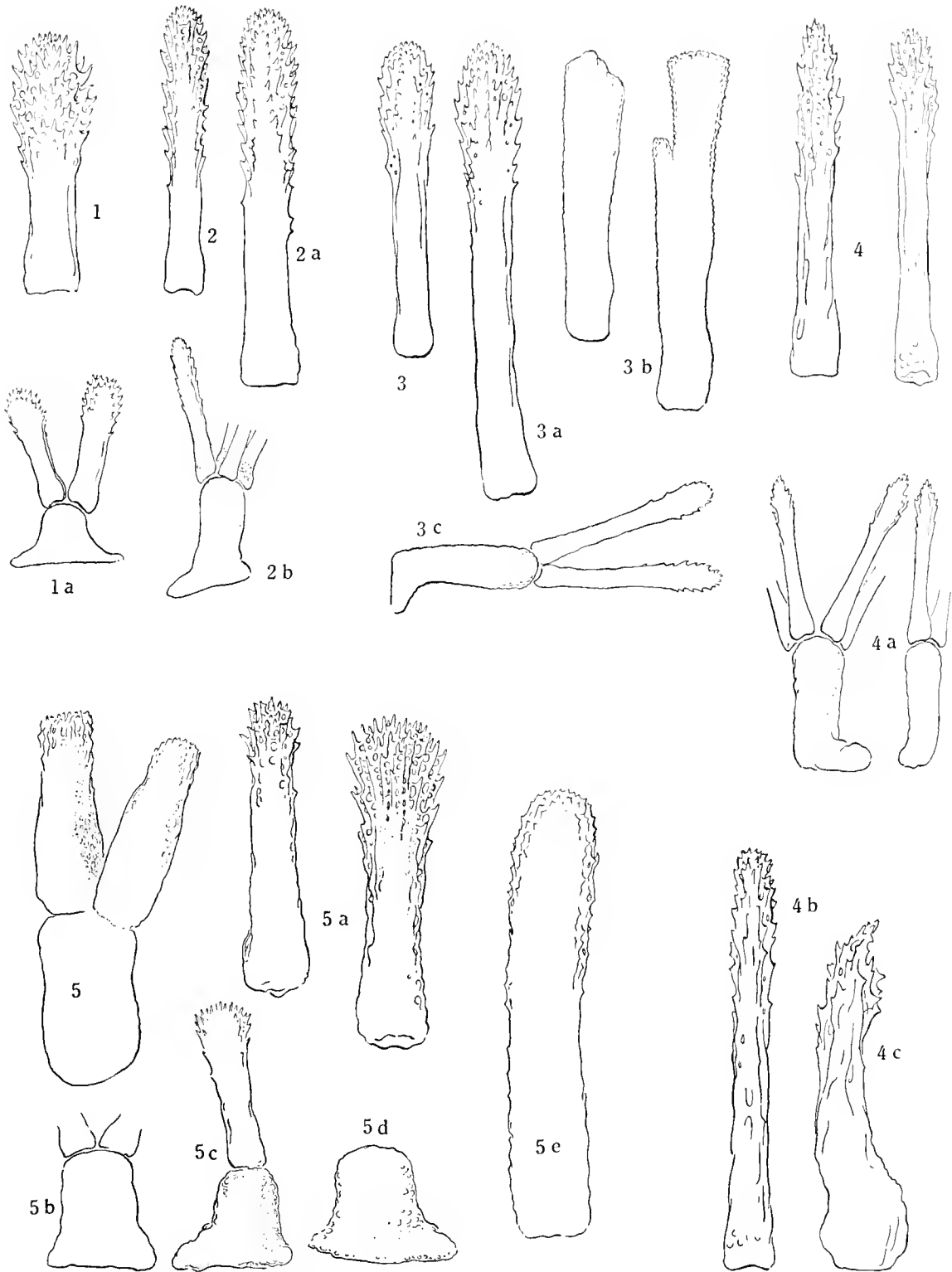


Fig. C

1. *Perknaster aurorae*, small specimen (R 40-50 mm.), St. 371. Abactinal spinelet, 0.63 mm., $\times 100$. 1a. Actinal spinelet, 0.7 mm., $\times 100$. 1b, 1c. Profiles of abactinal paxillae, 0.32 and 0.22 mm. high; 1c is a secondary plate.
2. *Perknaster aurorae*, large specimen, St. 366. Abactinal spinelet, 1.5 mm., $\times 50$. 2a. Enlargement showing spicules beginning to degenerate.
3. 3a. *Perknaster aurorae*, "aberrant" specimen, St. MS 71. Two abactinal spinelets, 0.63, 0.55 mm., $\times 100$. 3b. Actinal spinelet, forming part of a pedicellaria, 0.8 mm., $\times 50$. 3c. Tip of 3b, $\times 100$. 3d. Profile of an abactinal paxilla, pedicel 0.5 mm. (varying to 0.45 mm.); spinelet 0.68 mm., $\times 50$.
4. *Cycethra verrucosa*, abactinal spinelets from various specimens, $\times 100$. 4a. Specimen (R 25 mm.) from St. M 71, South Georgia; spinelet 0.35 mm. 4b. St. 160. Shag Rocks; R 15 mm., 0.27 mm. long. 4c. St. 167. South Orkneys; R 44 mm., 0.45 mm. long. 4d. St. 123. South Georgia; R 75 mm., largest of the Antarctic forms; 0.45 mm. long. 4e, 4f. St. 170. Marginal plates not superficially distinguishable from abactinal or actinal plates; R 41 mm.; spinelets 0.45 and 0.38 mm. long. 4g. St. 55. Falkland Islands; specimen with slender rays and small marginals similar abactinally to Koehler, 1923, pl. 7, figs. 5, 11, but forma *electilis* actinally.
5. *Peribolaster folliculatus*, $\times 10$. Three adambulacral plates, near base of ray with ankylosed inferomarginals, and 3 superomarginals (*S*) on right; *A* 12-*A* 14, adambulacral plates 12-14, the fourteenth divided as happens sporadically; *I*, inferomarginal plates with the single long spine; lowermost plate is cross-lined to show its extent but there is no line of demarcation in the specimen. The broken line crossing the adambulacral marks portion of inferomarginal fused to upper surface of adambulacral, which was identified in a smaller specimen from St. WS 93.

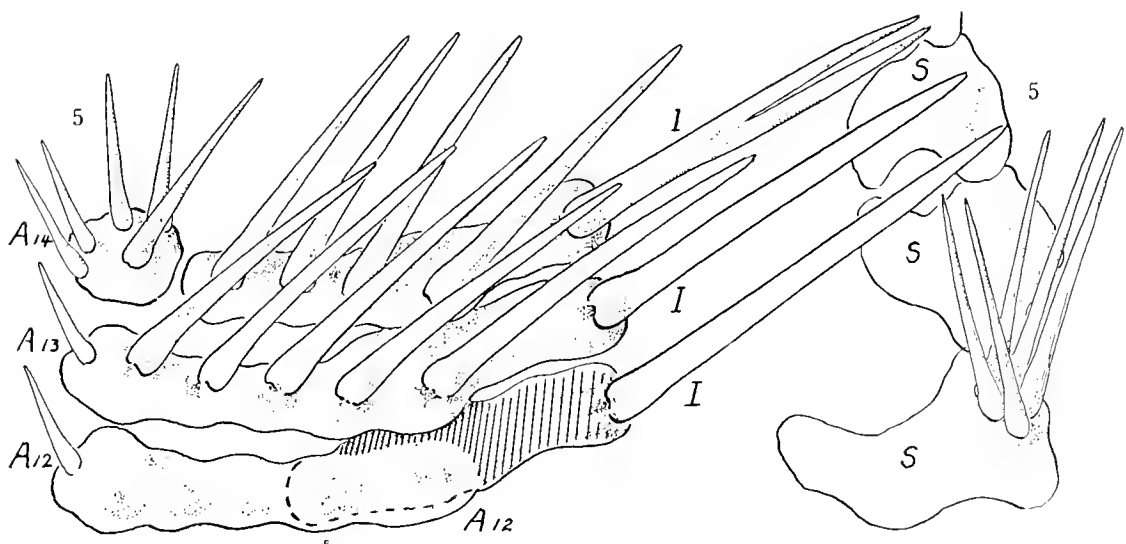
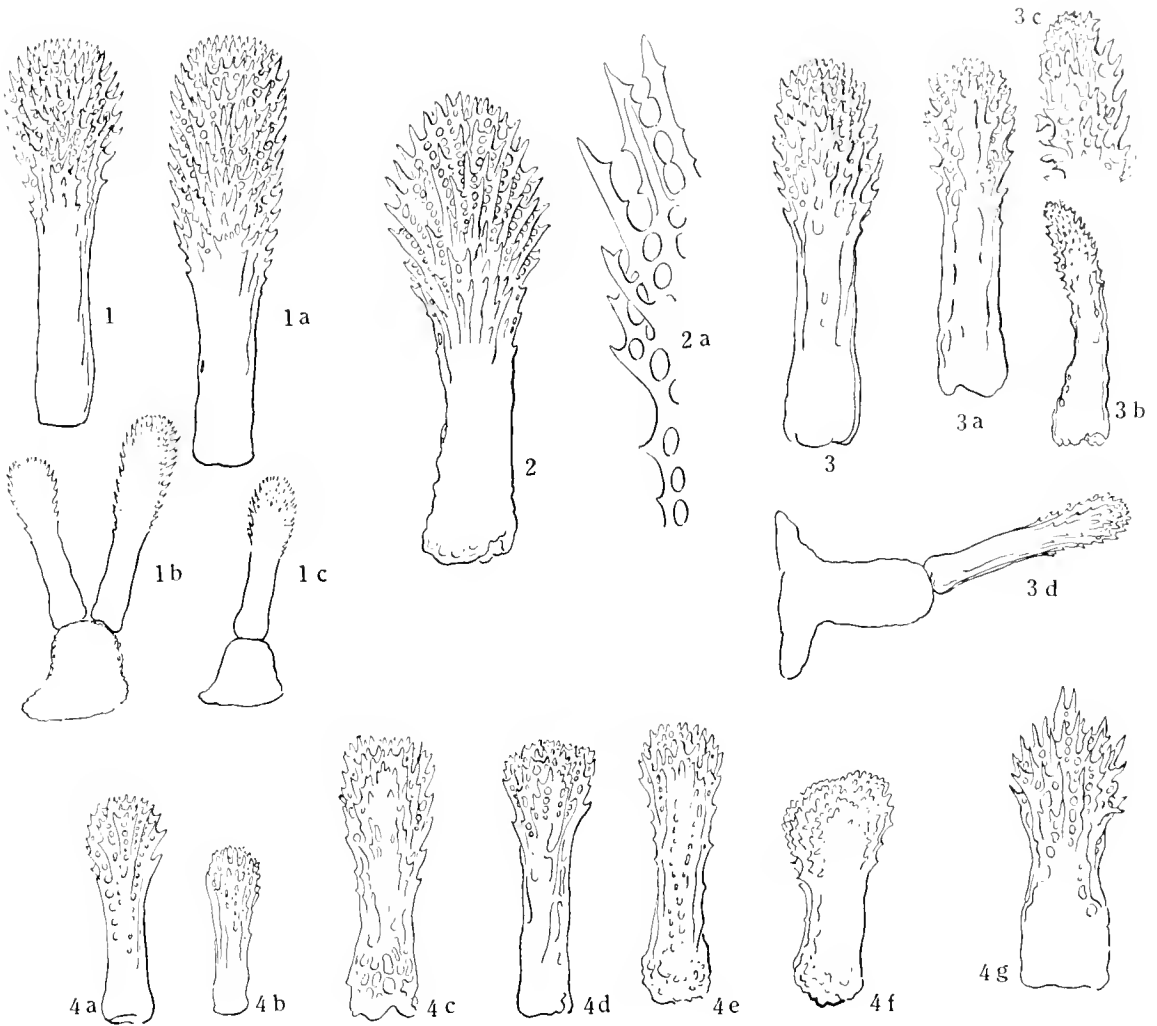


Fig. D

1. *Notioceramus anomalus*, $\times 10$. Plan of abactinal plates of proximal radial region: *C-C*, radial line; papulae shown as large spots. 1*a*. Adambulacral furrow spines, 1.7 mm. long, $\times 25$. 1*b*, 1*c*. First and second subambulacral spines, $\times 25$; 1*b* is 1.5 by 0.85 mm.; 1*c* is 0.85 by 0.5 mm. 1*d*. Three abactinal granules, 0.29, 0.32 and 0.51 mm. high. 1*e*. Second and third (lower) adambulacral plates, and an actinal plate (*AC*) carrying a 3-valved pedicellaria, $\times 15$. The subambulacral spines of second plate are much foreshortened.
2. *Cladaster analogus*, 2 actinal pedicellariae; left open, 1 mm. wide, 0.9 mm. high, $\times 20$; right, closed, $\times 40$.
3. *Kampylaster incurvatus*, abactinal spinelet 0.18 mm. high, $\times 200$. 3*a*. Another spinelet, 0.23 mm., $\times 100$. 3*b*. Abactinal spinelet of young specimen, 0.1 mm. high, $\times 200$. 3*c*. Spinelet from third marginal plate, 0.39 mm., $\times 200$. 3*d*. Actinal spinelet, 0.54 mm., $\times 100$.
4. *Mirastrella biradialis*, side view of ray, $\times 12$, to show plates: *AD*¹, *AD*², adradials; *I*, primary interradials; *IN*, inferomarginals; *R*, primary radial, *r*¹, *r*², the 2 series of radials; *S*, superomarginals; *T*, terminal. 4*a*. Abactinal "granule" or spinelet, 0.15 mm. long, $\times 200$. 4*b*. Inferomarginal spinelet, 0.27 mm. long, $\times 100$. 4*c*. Abactinal spinelet to same scale, $\times 100$. 4*d*. First and second inferomarginals and adjacent adambulacral plates, $\times 30$; *a-a*, 2 groups of 3 actinal spinelets. 4*e*. Map of abactinal plates, $\times 15$, the marginals omitted on lower side; *C*, central plate; *x*, adcentral end of interradian groove; superomarginals dotted.

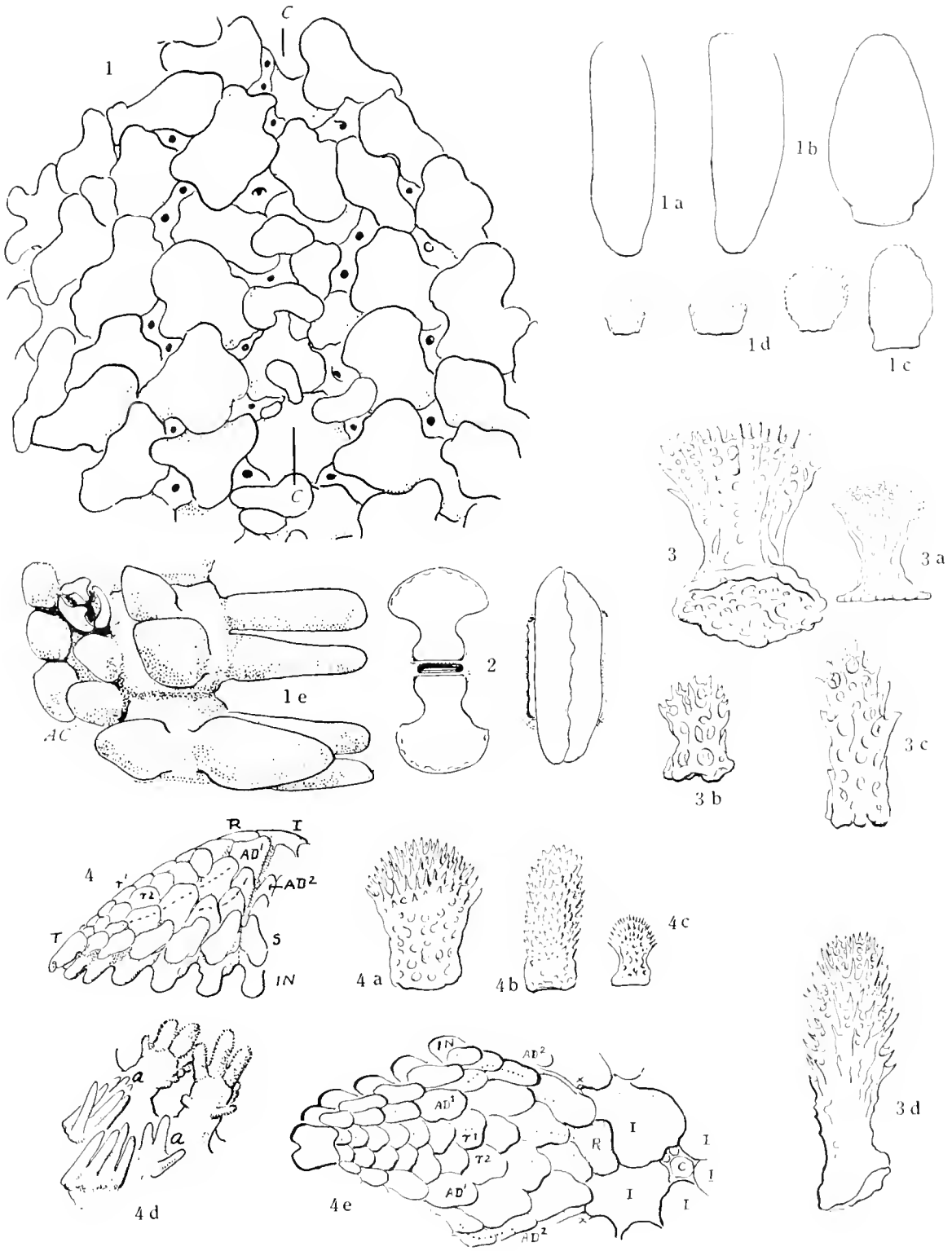


Fig. E

1. *Anseropoda antarctica*; an abactinal granule 0.18 mm. long, $\times 200$. 1a. Dorsolateral plates adjacent to adradials (*AD*) seen from coelomic side, $\times 30$. 1b. One of the dorsolateral plates to show internal process, $\times 40$. 1c. Actinal spinelet, 0.37 mm., $\times 100$.
2. *Rhopiella kochleri*; primary abactinal spinelet, 1.2 mm. long, $\times 50$. 2a. Secondary abactinal spinelet, 0.9 mm. long, $\times 50$. 2b. Terminal part of a primary spine, $\times 100$. 2c. Sixth adambulacral plate of type showing adoral face of web, furrow on right, $\times 20$; *AC*, actinal spine. 2d. Excised adambulacral plate, adoral face showing relation of spines to the web.
3. *Lophaster stellans*, St. 81; superomarginal spinelet 1.25 mm. long, $\times 100$. 3a. Three abactinal paxillar spinelets, 0.85, 0.7, 0.86 mm. long, $\times 100$.
4. *Lophaster densus*; abactinal spinelet 0.34 mm., $\times 100$. 4a. Concave side of tip of an abactinal spinelet, $\times 200$. 4b. Largest and smallest inferomarginal spinelets of same paxilla (0.63 and 0.32 mm.), $\times 100$. 4c. Inner subambulacral spinelet at base of ray, 1.17 mm. long, $\times 50$.

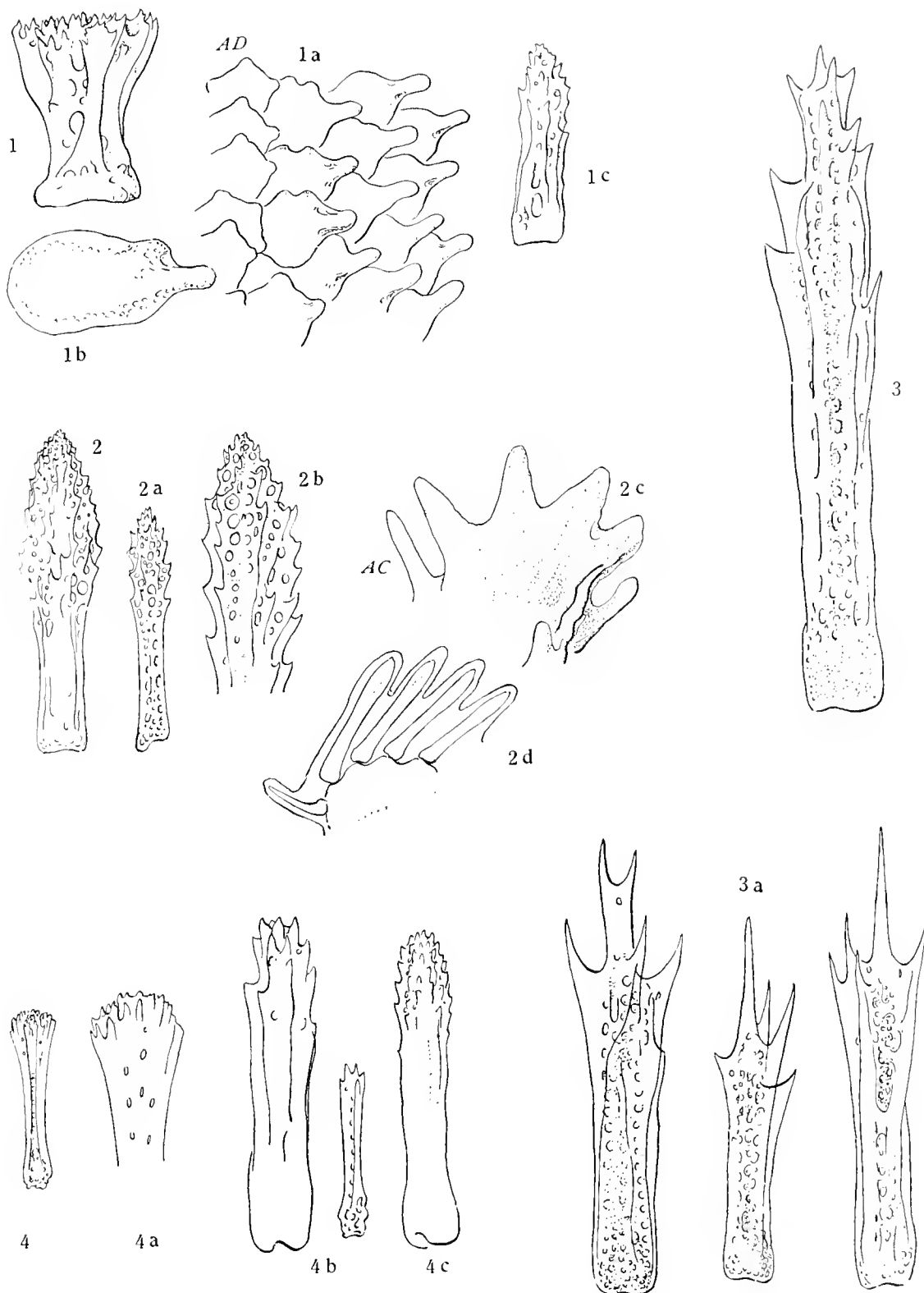


Fig. F

1. *Lophaster marionis*, type; 2 abactinal spinelets, 0.8 and 0.83 mm. long, $\times 100$. 1a. Type, inferomarginal spinelet, 0.9 mm., $\times 100$. 1b. St. WS 81; inferomarginal spinelet, 1.05 mm., $\times 100$. 1c. Inner subambulacral spinelet, base of ray, 1.8 mm., $\times 50$. 1d. Outermost subambulacral, same series as 1c, 1.5 mm. long, $\times 50$.
2. *Paralophaster godefroyi meseres*; 2 abactinal spinelets 0.9 and 1 mm. long and ends of 2 others, $\times 100$. 2a. Inferomarginal spinelet, 1.4 mm. long and tip of another, $\times 50$. 2b. Subambulacral spinelet 1.8 mm. long, and 2 tips, $\times 50$.
3. *Pedicellaster hypernotius*, $\times 200$. An abactinal pedicellaria (0.225 mm. long, St. 160) between single jaws of actinal pedicellariae; left, St. 160, 0.4 mm. long; right, St. 190, 0.38 mm.
4. *Antliaster scaber*, St. 1563; abactinal pedicellaria 0.2 mm. long. 4a. Two abactinal spinelets, 0.38 and 0.31 mm.

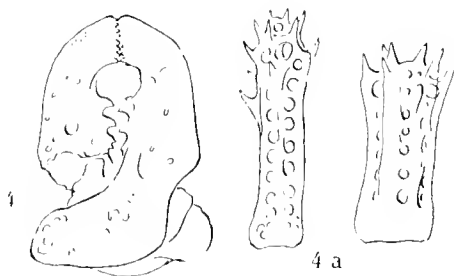
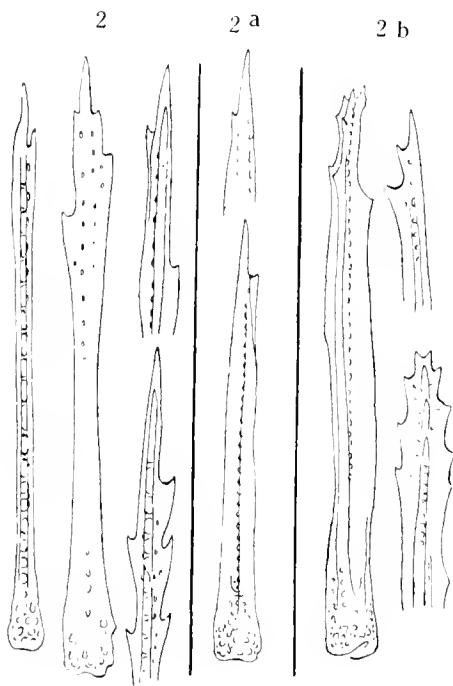
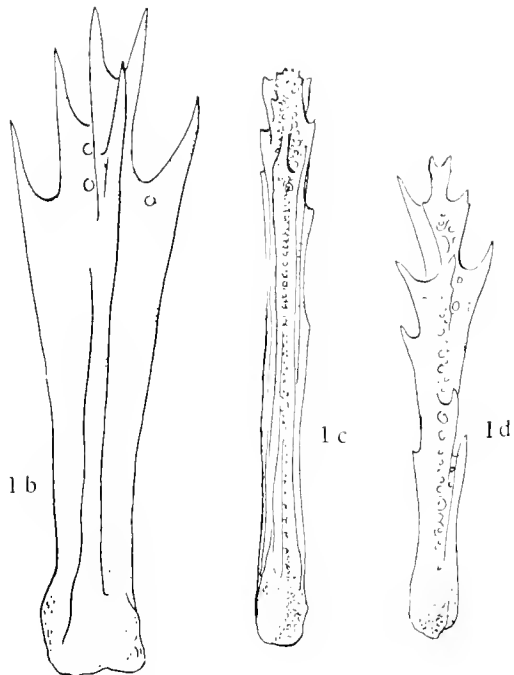
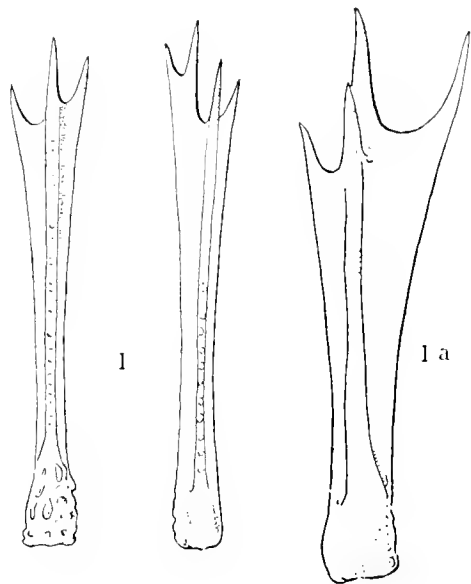


Fig. G

Odinella nutrix

1, 1*a*. Disk spinelets from immature specimen, St. 123 (pl. XVII, fig. 2), having extreme diameter of 34 mm., $\times 100$. Fig. 1, 0.57 mm. long, is one of the long-pronged spinelets found only on disk. 1*a*. 0.6 mm. long. 1*b*. St. WS 766. Disk spinelet of immature specimen, 0.63 mm. long.

2-2*c*. Disk spines of adult specimens $\times 100$; 2, St. 123, 1 mm. long, the same sort being found on the type; 2*a*-*b*, pronged spines from type, St. 39, 1.08 and 0.95 mm. long; 2*c*, tip of spine, type. 2*d*. Abactinal spine from genital inflation of type, 1.53 mm. long, $\times 50$. 2*e*. Sixth inferomarginal spine of type, 2.5 mm. long, $\times 50$.

3-3*c*. Young in stage 4 from brood pouch. 3. Abactinal plate, 0.45 mm. in diameter, $\times 50$; 3*a*, abactinal spinelet, $\times 50$; 3*b*, abactinal spinelet, 0.36 mm. long, $\times 100$; 3*c*, adambulacral spinelet, 0.4 mm. long, $\times 100$.

4-4*d*. Young in stage 1 from brood pouch, St. 123. Fig. 4, abactinal, diameter 2.55 mm., $\times 20$. 4*a*, actinal view of 3 rays, $\times 30$; 4*b*, an embryonic abactinal plate, 0.2 mm. in diameter, $\times 100$; 4*c*, 4*d*, abactinal spinelets, 0.15 and 0.12 mm. long, $\times 200$.

5, 5*a*. Pedicellariae from lateral spine of type, middle of ray, 0.135 mm. high, $\times 300$; 5*a*, inner face of jaw tip; 5*b*, middle piece.

6-6*b*. Pedicellariae from marginal mouth spines of type, $\times 300$; 6, detail of jaw tip; 6*a*, back view to show the flaring "handles" of the blades or jaws; 0.16 mm. high (*mp* = middle piece); 6*b*, profile view showing numerous excessively fine shank teeth, height 0.18 mm.

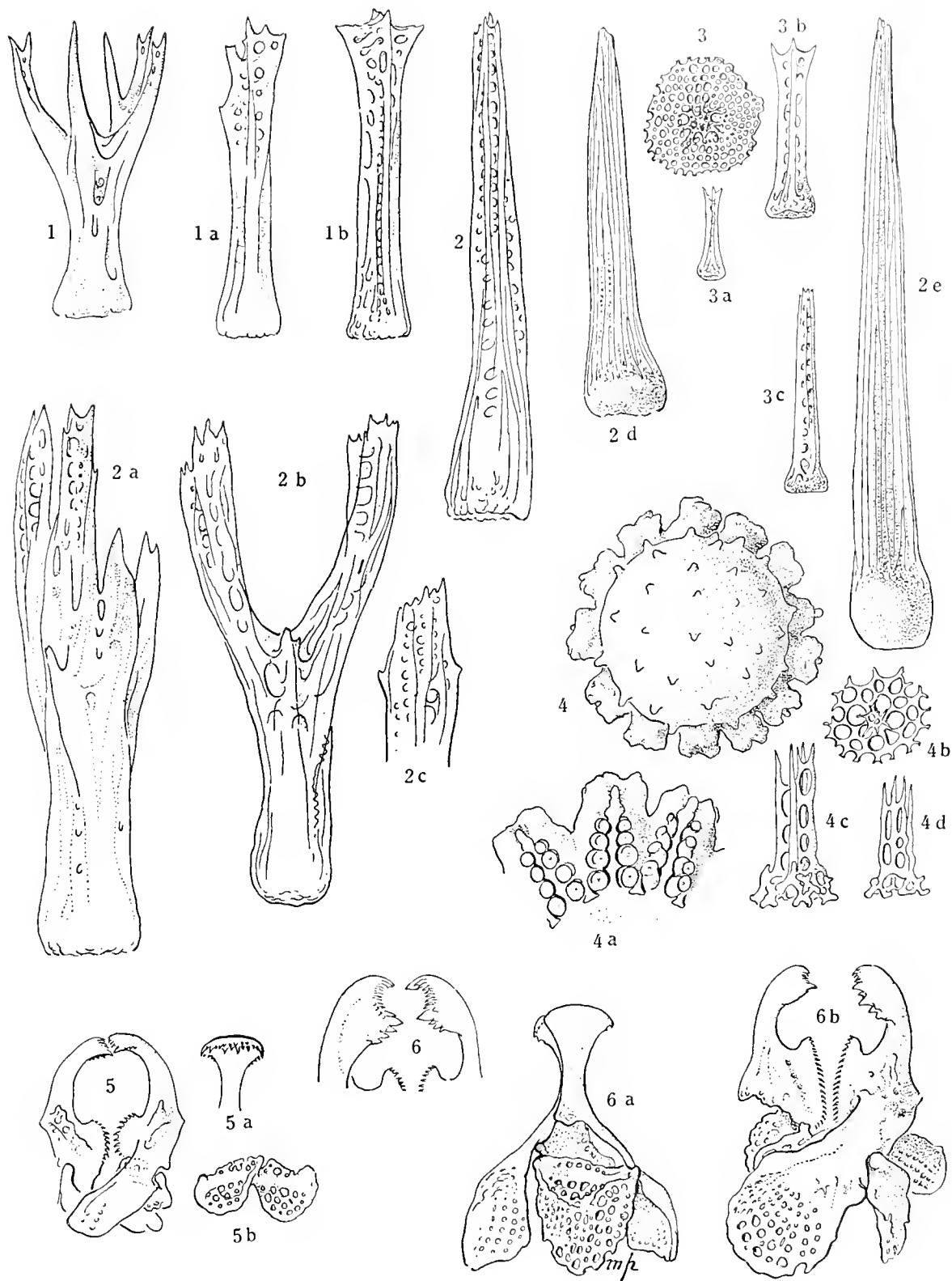


Fig. H

All figures enlarged $\times 20$, except 7 and 8 which are $\times 10$

1. *Odinella nutrix*. Actinostomial ring viewed from outside, showing an interradius and the distal face of second ambulacral and of first adambulacral plates where 2 rays have been detached. a^1 , first ambulacral plates (dorsal surface); a^2 , distal face of second ambulacral plates; ad^1 , distal, articulating face of first adambulacral plates; i , interradiial plate (odontophore); m , first pair of inferomarginal plates, closely apposed, above the first adambulacrals; p^1, p^2 , position of first and second ambulacral pores.
2. *Brisingella pusilla* Fisher (California). Mouth-plate (z, x, y) for comparison with fig. 3. The plate is seen from the furrow face, the actinal surface being in profile below. On the left the odontophore (i), marginal (m), and first adambulacral (ad^1) are shown. In this genus the interradiial angle (on the opposite side of ad^1 and m) is defined by these plates (fig. 8); v , groove of circumoral water tube at point where the radial tube passes to right in groove r ; s , spine-bearing margin of plate; in the groove above is the circumoral nerve; x , lateral wing of plate shown in figs. 7 and 8 viewed endwise; y , shorter ventrolateral wing shown in fig. 7; z , dorsal wing (fig. 8).
3. *Odinella nutrix*. Mouth-plate viewed from furrow face with interradiial plate (i) in position. a'' , articulating surfaces of first ambulacral plate; ad'' , same of first adambulacral; p' , side of first ambulacral pore; r , groove for radial water tube; s , spine-bearing margin of plate, the deep groove above for circumoral nerve; v , groove for circumoral water tube; x , lateral wing of plate which joins that of neighbouring plate across ambulacral furrow; y , portion of plate which forms a ventrolateral wing in fig. 7; z , the dorsal extension of plate (figs. 4, 6).
4. *Odinella nutrix*. Segment of actinostomial ring viewed from the inner or oral face. On the right a pair of mouth-plates, o , is hatched to differentiate them from the first ambulacrals (a^1), one of which has been lifted out. Note x , the lateral wing of each mouth-plate for comparison with figs. 5 and 7, and crossing it, v , the groove of circumoral water canal; o' indicates position of muscles so indicated in fig. 6; z , the dorsal extension of plate which locks with the first ambulacral.
5. *Odinella nutrix*. A pair of mouth-plates seen from below. On either side is the first ambulacral plate a' , the left one is hatched; ad'' , the facet of plate with which the first adambulacral forms a muscular joint; s , spine-bearing margin; v , position of circumoral water tube; x , lateral wing which joins that of opposite side of furrow ($x-x$, fig. 4); y , portion of plate corresponding to y , fig. 7.
6. *Odinella nutrix*. Segment of actinostomial ring viewed directly from above. On right, a single first ambulacral plate is hatched. Note the broad muscular symphyses at o', o'' directly below odontophore, i , in contrast to the same in *Brisingella* (fig. 8). These confer a high degree of flexibility to actinostomial ring. The first adambulacrals are shown in solid black beneath the second ambulacrals. The entire length of the first inferomarginals, m , is shown, whereas in fig. 1 they are greatly foreshortened; z is the dorsal extension of mouth-plate which forms a non-muscular symphysis with the first ambulacral.
7. *Brisingella pusilla*. The ventral aspect of a segment of the actinostomial ring ($\times 10$) for comparison with fig. 5. A pair of mouth-plates is dotted. The lateral extensions $x-x$ (so marked in other figures) are notable for unusual length. Above them passes the radial water tube, r ; the ventrolateral wings, Y' , are not present in *Odinella*. One first ambulacral is hatched. Other letters: a^1, a^2 , first and second ambulacrals; ad , first adambulacrals; m , pair of first inferomarginals defining the interradiial angle; p^1, p^2 , pores of first and second tube-feet.
8. *Brisingella pusilla*. Dorsal aspect of segment of actinostomial ring for comparison with fig. 6. On right the odontophore, i , has been removed and a pair of mouth-plates dotted; behind them as much as can be seen of first adambulacrals, ad' is hatched. The lateral, x , and dorsal, z , wings of the mouth-plates o are conspicuous. Other letters as in fig. 7.
9. *Odinella nutrix*. Ventral aspect of the interradiial plate or odontophore.

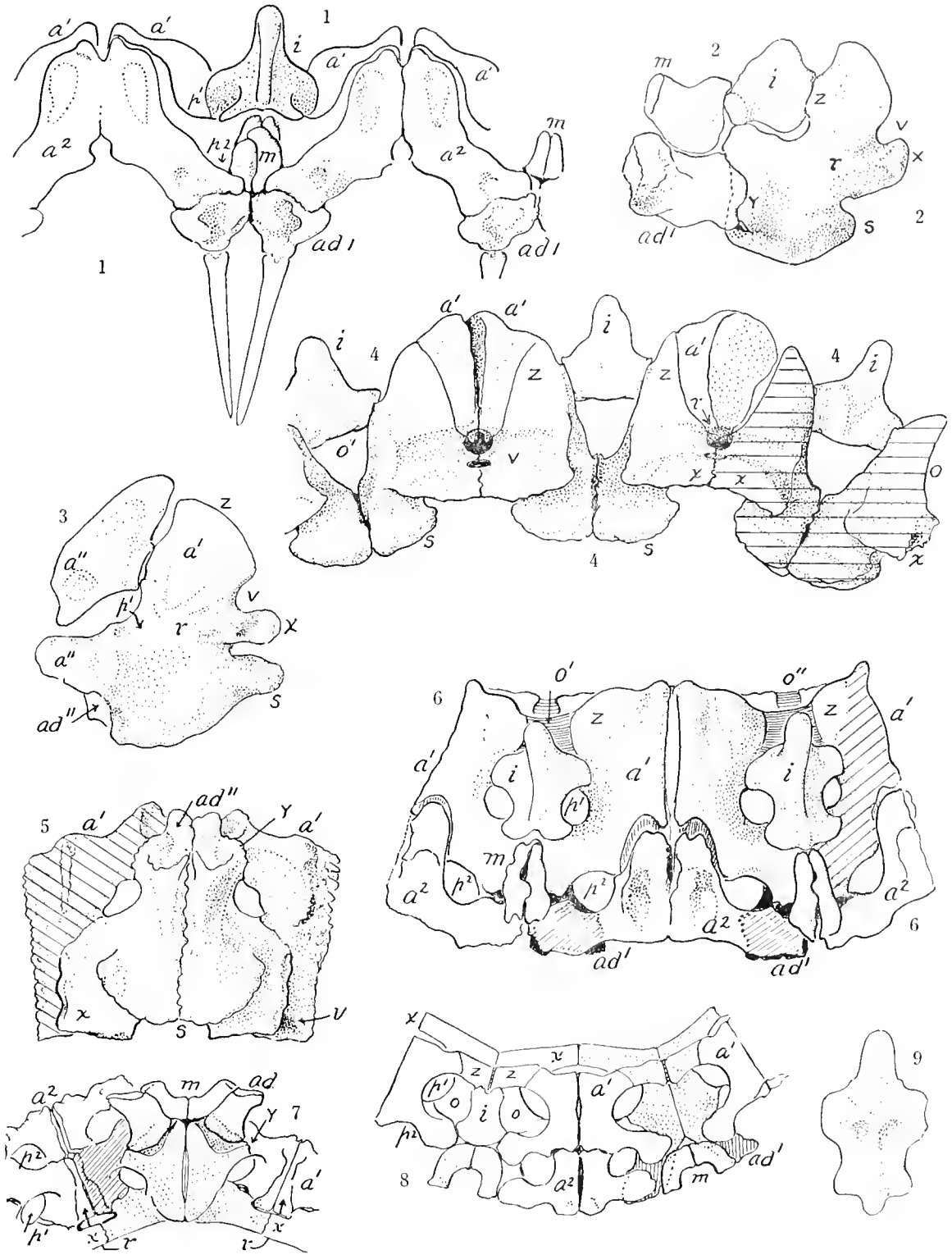


Fig. 1

1. *Anteliaster australis*, type; crossed pedicellaria, 0.4 mm. long, $\times 100$. 1a. St. 246. One jaw, $\times 200$; pedicellaria 0.3 mm. long. 1b. Paratype, inferomarginal spine, 0.5 mm., $\times 100$. 1c. Paratype, carinal spinelet, 0.35 mm., $\times 100$. 1d. Paratype, dorsolateral spinelet, 0.29 mm., $\times 100$.
2. *Labidiaster radiosus*, abactinal pedicellaria from transverse ruff at middle to ray, St. 51; length 0.6 mm., $\times 100$. 2a. Same from St. WS 79, R 105 mm.; length 0.65 mm., $\times 100$. 2b. From outer adambulacral spine, St. 51; length 0.26 mm., $\times 100$.
3. *Labidiaster amulatus*, pedicellaria from abactinal transverse ruff at about middle of ray of large specimen, St. 1955; length 1.4 mm., $\times 100$. 3a. Same as 3, from smaller specimen, St. 1955, length 0.9 mm., $\times 100$. 3b. From outer adambulacral spine, St. 1955; length 0.27 mm., $\times 100$. 3c. One of the small crossed pedicellariae found among the large ones, from smaller specimen, St. 1955, length 0.38 mm., $\times 100$. 3d. Straight pedicellaria from inner margin of mouth-plates, larger specimen, St. 1955; length 1.27 mm., $\times 50$. 3e. Three oral angles showing fusion of mouth-plates; from small specimen with disk diameter 22 mm., St. 371, $\times 15$. Most of the pedicellariae are omitted to show the spines more clearly; NC, neural canal roofed by joined mouth-plates.

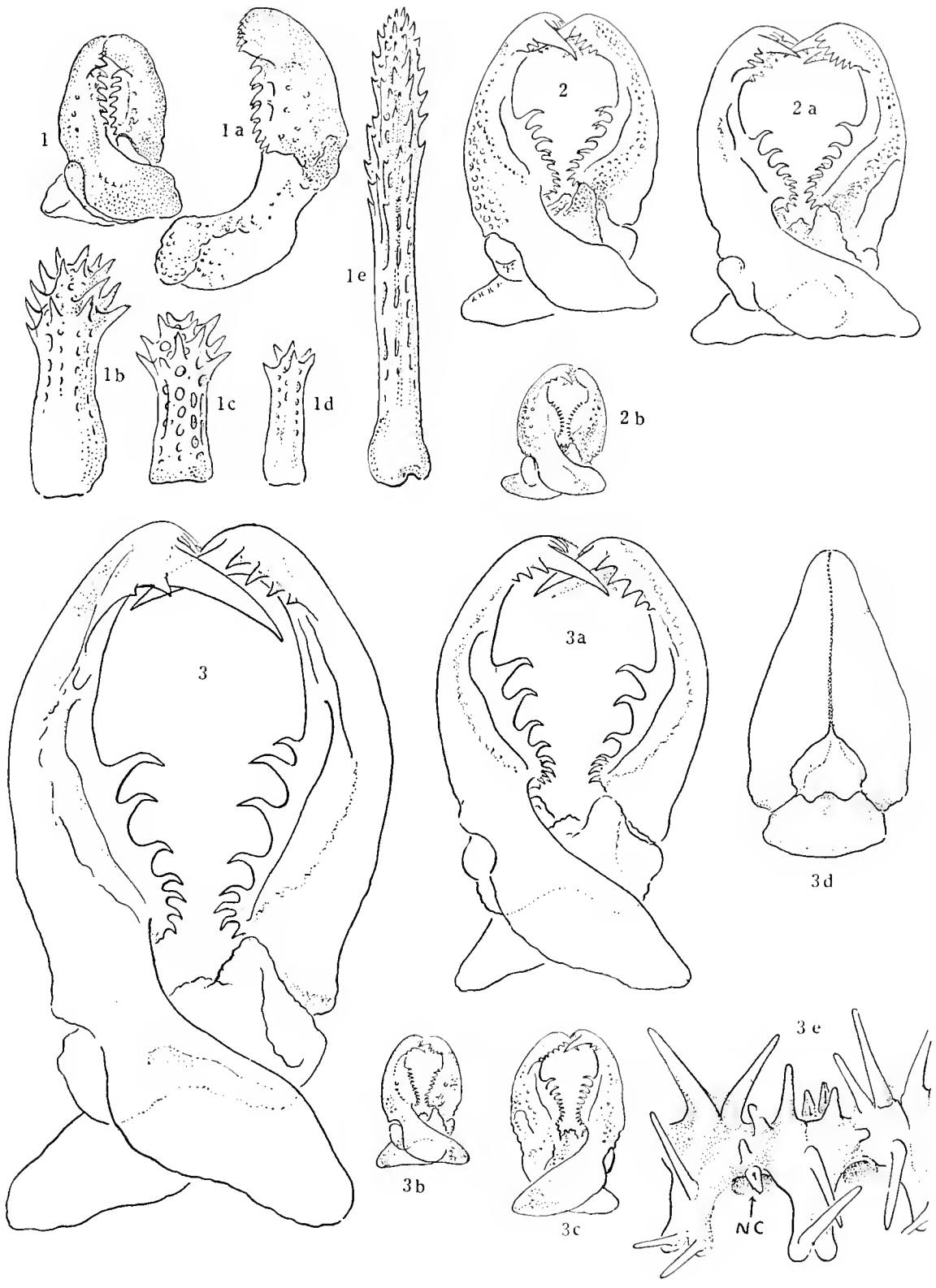


Fig. J

1. *Notasterias stolophora*, pedicellaria from carinal spine, 0.76 mm. long, $\times 100$. 1*a*. From same spine as fig. 1, 0.78 mm. long. 1*b*. From inferomarginal spine, 0.71, $\times 100$. 1*c*. From superomarginal spine, 0.76 mm., $\times 100$. 1*d*. An incompletely developed pedicellaria of the sort shown in fig. 1*b*, from inferomarginal spine, 0.6 mm., $\times 50$. 1*e*. Carinal spine and pedicellaria, $\times 25$.
2. Pedicellariae drawn to scale, $\times 10$: *a*, *N. armata*, carinal; *b*, *N. stolophora*; *c*, *N. bongraini*, carinal; *d*, *e*, *N. bongraini*, normal crossed ped. from inferomarginal spine.
3. *N. bongraini*, from carinal spine, length of ped. 1.87 mm., $\times 100$. 3*a*. From superomarginal spine, 0.62 mm., $\times 100$. The inferomarginal pedicellariae are similar and 0.37–0.5 mm. long.
4. *N. armata*, jaw of a carinal pedicellaria; whole ped. 3 mm. long, $\times 50$. 4*a*. Incompletely developed superomarginal ped., $\times 10$. 4*b*. From inferomarginal and actinal spines, 0.93 mm., $\times 50$.

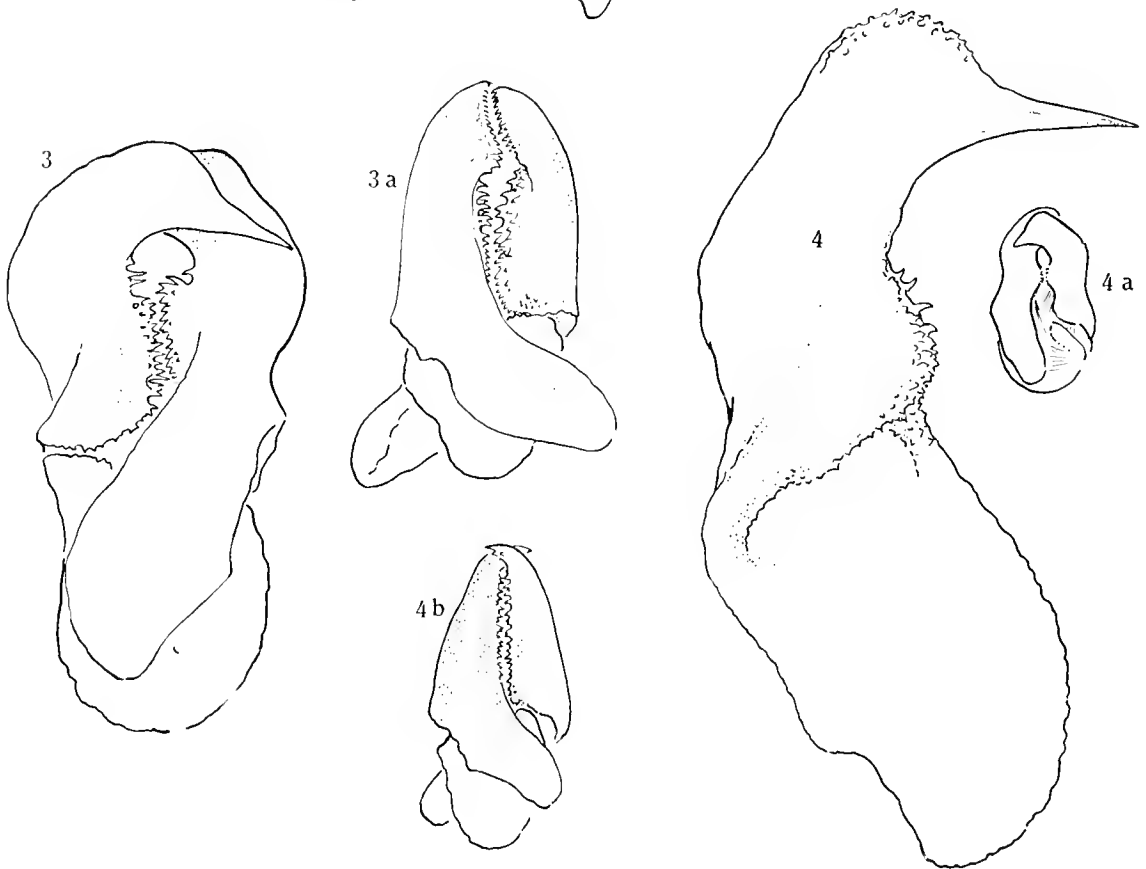
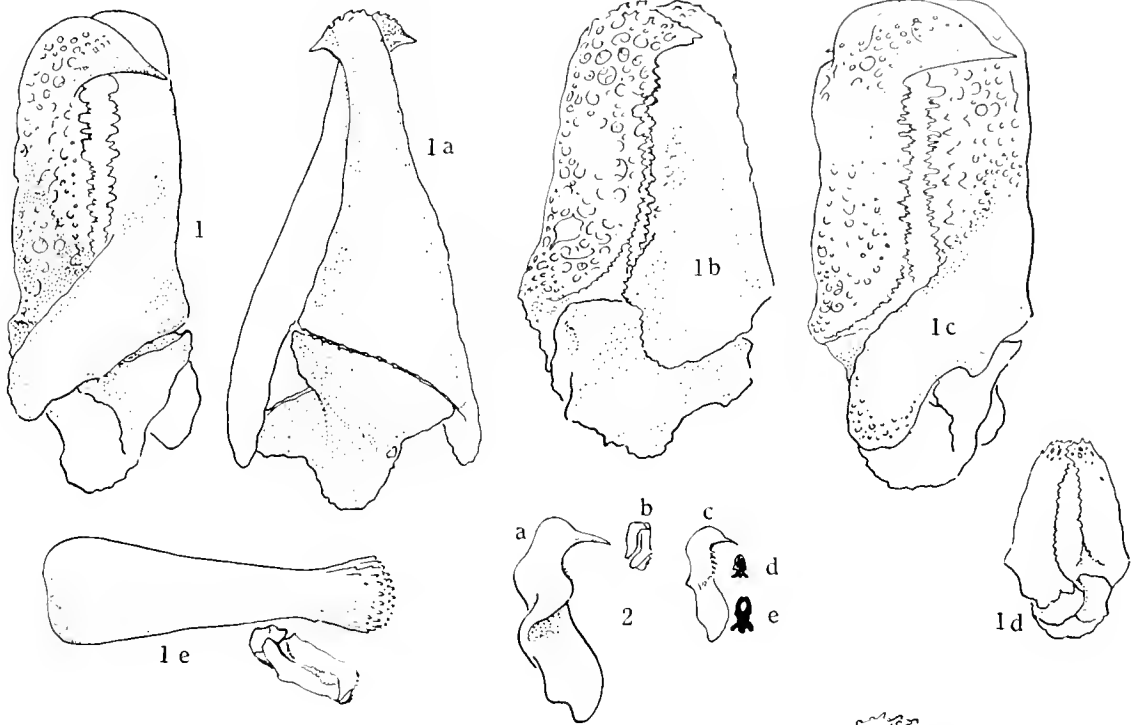


Fig. K

1. *Notasterias armata*. Skeleton of one side of ray, near base (which is to left), $\times 6$; *CC*, carinal series; *DL*, dorsolaterals; *S*, superomarginals; *I*, inferomarginals; *A*, actinals.
2. *Psalidaster mordax*. Typical abactinal pedicellaria, 0.9 mm., $\times 100$. 2*a*. Inner side of one jaw, $\times 100$. 2*b*. Inferomarginal pedicellaria, opposing face of a jaw, $\times 50$. 2*c*. Inner side of a jaw, $\times 100$. 2*d*. Adambulacral straight pedicellaria, 0.68 mm. long, $\times 50$. 2*e*. Opposing face of a jaw showing denticles, 0.5 long, $\times 100$. 2*f*. Back view of inferomarginal pedicellaria (0.93 mm. long) to show flaring handles and basal piece, $\times 50$. 2*g*. Side view of same, $\times 50$.
3. *Psalidaster mordax*. Abactinal spinelet 1.8 mm. long, $\times 50$. 3*a*. Two abactinal spinelets, 1 and 1.5 mm. long, $\times 50$. 3*b*. Portion of lateral and actinal skeleton near base of ray which is at left, $\times 10$. *DL*, dorso-lateral primary plates; *S*, superomarginals; *I*, inferomarginals; *AD*, adambulacrals.

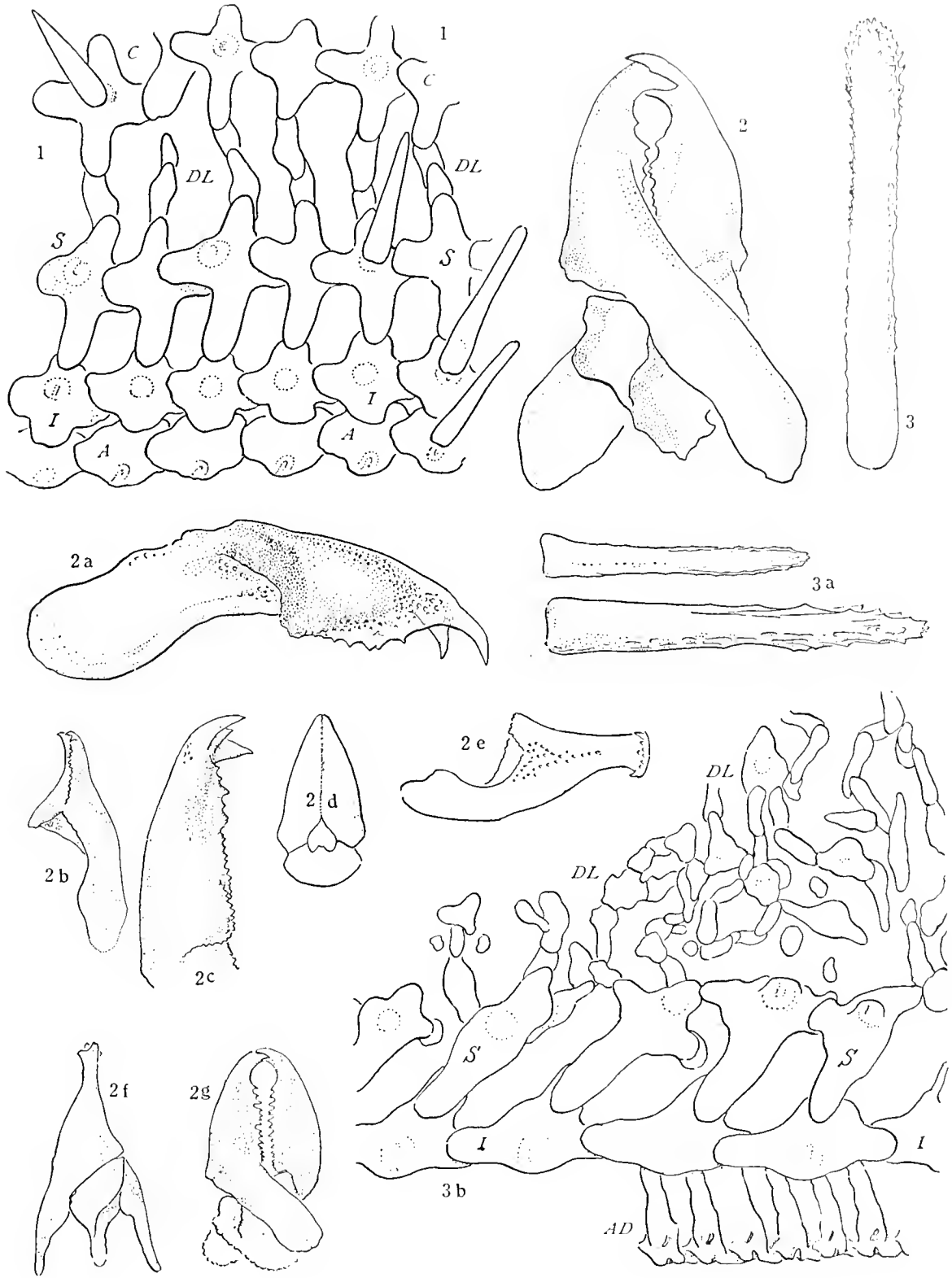


Fig. L

1. *Lethasterias australis*, jaw of inferomarginal crossed pedicellaria, $\times 200$. 1*a*. Carinal spine, 1.53 mm. long, $\times 25$. 1*b*. Dorsolateral spine, 0.85 mm., $\times 25$. 1*c*. Two aspects of a superomarginal spine, 1.6 mm., $\times 25$. 1*d*. Two inferomarginal spines, 1.45 and 1.7 mm., $\times 25$. 1*e*. An adambulacral spine, 1.5 mm., $\times 25$. 1*f*. An abactinal crossed pedicellaria, 0.3 mm., $\times 100$. 1*g*. A marginal crossed pedicellaria, 0.43 mm., $\times 100$.
2. *Lethasterias australis*, plan of plates of one side of ray from fifth to eleventh superomarginals, base of ray to left; C-C, carinal series; DL, dorsolaterals; S, superomarginals; I, inferomarginals.
3. *Lysasterias hemiora*, abactinal crossed pedicellaria, 0.38 mm., $\times 100$.
4. *Lysasterias heteractis*, abactinal pedicellaria, 0.46 mm., $\times 100$. 4*a*. Inferomarginal pedicellaria, 0.74 mm., $\times 100$. 4*b*. Detail of abactinal pedicellaria 0.5 mm. long.
5. *Coscinasterias ealamaria*, St. 1686; abactinal crossed pedicellaria, 0.21 mm., $\times 200$. 5*a*, 5*b*. Straight pedicellariae, 0.20 and 0.30 mm., $\times 200$.

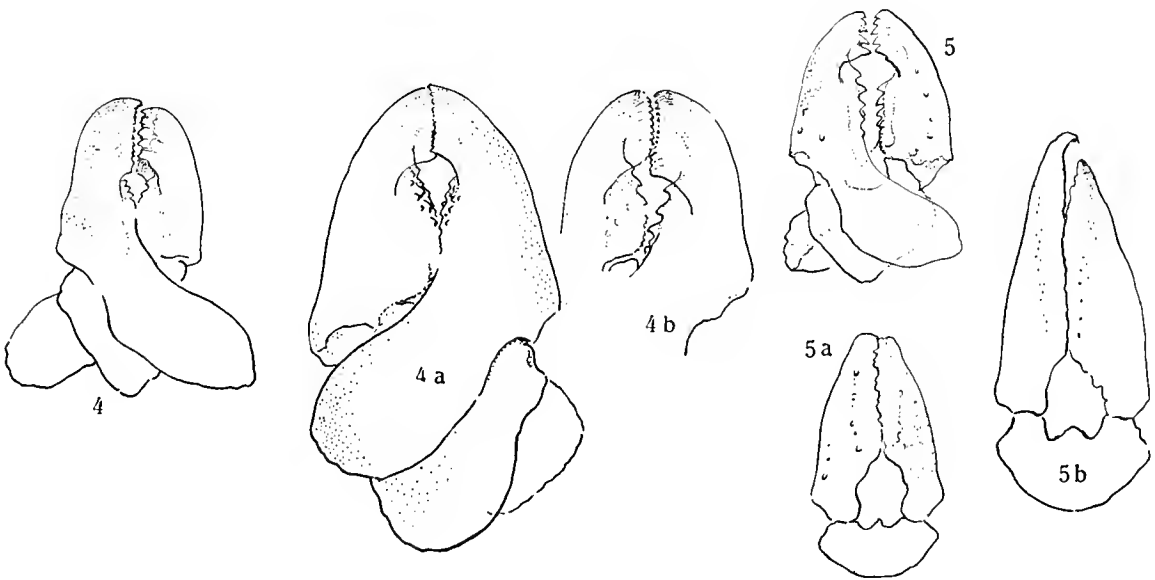
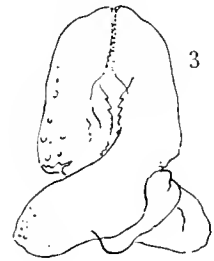
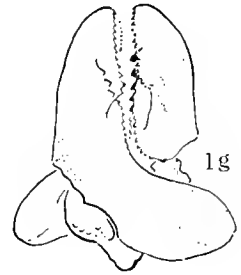
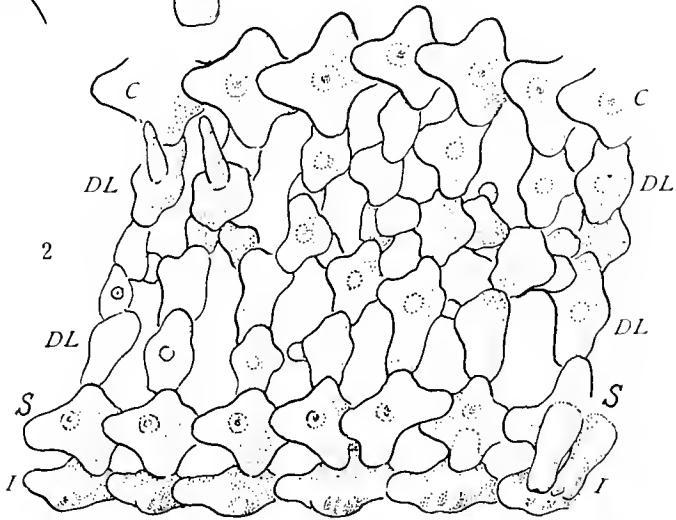
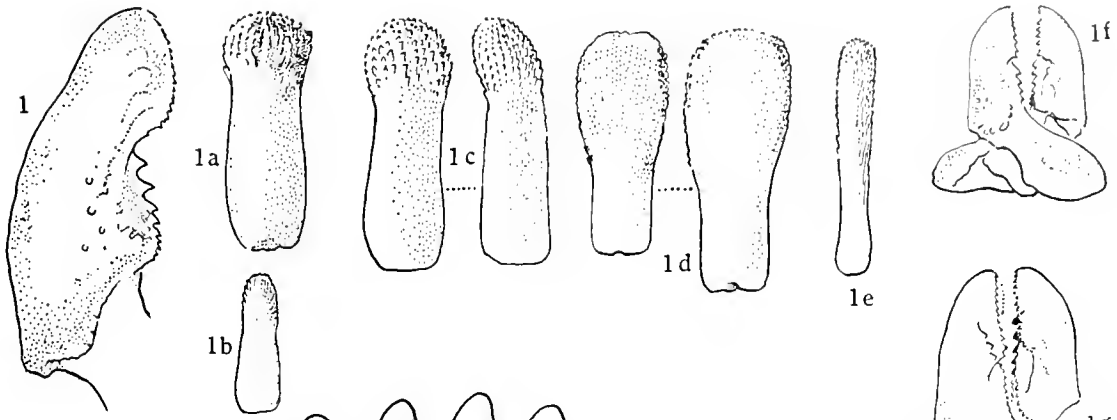


Fig. M

1. *Diplasterias octoradiata*, St. MS 6; abactinal pedicellaria, 0.43 mm., $\times 100$. 1*a*. Profile of 2 jaws, $\times 100$. 1*b*. A straight pedicellaria, 1.27 mm., $\times 50$. 1*c*. Forma *eunota*, profile of 1 pedicellaria jaw.
2. *Diplasterias meridionalis*, St. MS 10, abactinal pedicellaria, 0.37 mm., $\times 100$. 2*a*. Marginal pedicellaria, 0.52 mm., $\times 100$. 2*b*. A straight pedicellaria in profile, and inner face of 1 jaw. 1.02 mm., $\times 50$.
3. *Diplasterias radiata*, 2 abactinal spinelets, 0.85 mm., $\times 50$. 3*a*. Jaw of a crossed pedicellaria, $\times 200$; length range 0.27–0.3 mm. 3*b*. Valve of a straight pedicellaria, $\times 100$.
4. *Luidia heterozona*, 2 inferomarginal plates, proximal third of ray, to show different armature of alternate plates; base of ray is to left, $\times 10$. *a*, abactinal paxilla; *ap*, actinal pedicellaria, *s*, superomarginal, fused to upper end of inferomarginal. 4*a*. A single mouth-plate seen slightly from side, $\times 10$. *a*, apical spine; *n*, nerve; *p*, pedicellariae mentioned in text. 4*b*. Abactinal paxilla of second longiseries, dried, $\times 30$. 4*c*. Disk paxilla, alcoholic specimen, $\times 30$.
5. *Luidia aciculata*. Two inferomarginal plates near base of ray to show different position of spines on alternate plates, $\times 10$. Two superomarginal paxillae (*s-s*) are also shown.

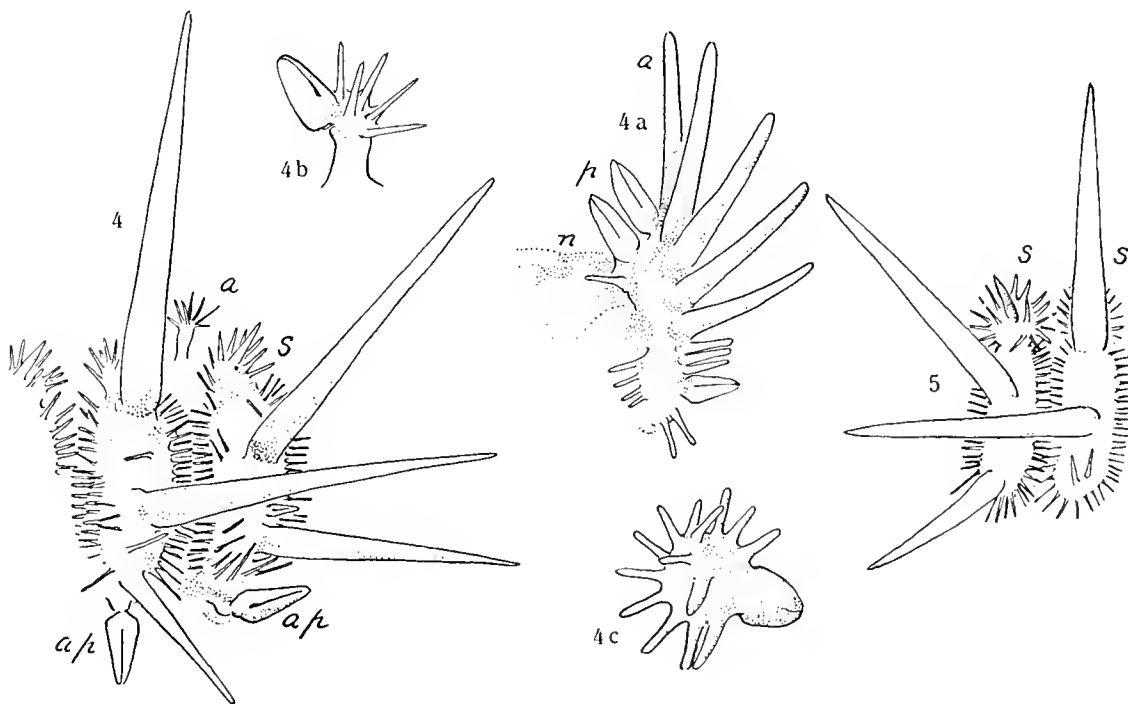
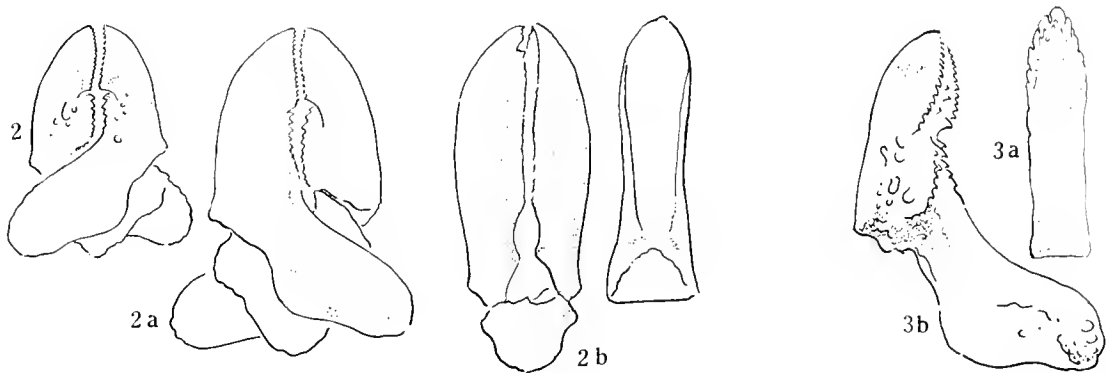
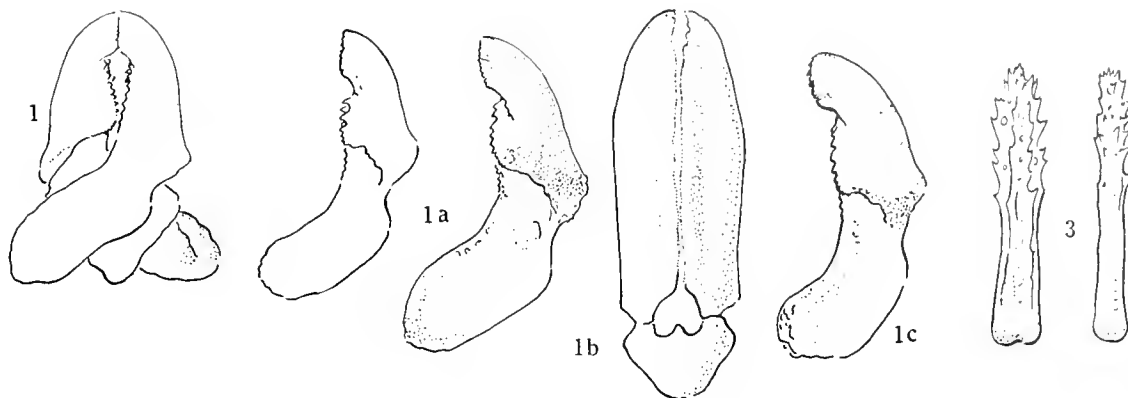


PLATE I

Variations of *Acodontaster elongatus granuliferus*, $\times 0.8$

- Fig. 1. Specimen B, forma *granuliferus*, St. WS 823.
- Fig. 2. Specimen D, forma *granuliferus*, St. WS 804.
- Fig. 3. Intergrade, forma *ceramoideus*, St. WS 83.
- Fig. 4. Specimen G, intergrade, forma *ceramoideus*, St. WS 799A.
- Fig. 5. Specimen J, forma *ceramoideus*, St. WS 652.
- Fig. 6. Specimen K, forma *ceramoideus*, type, St. WS 246.

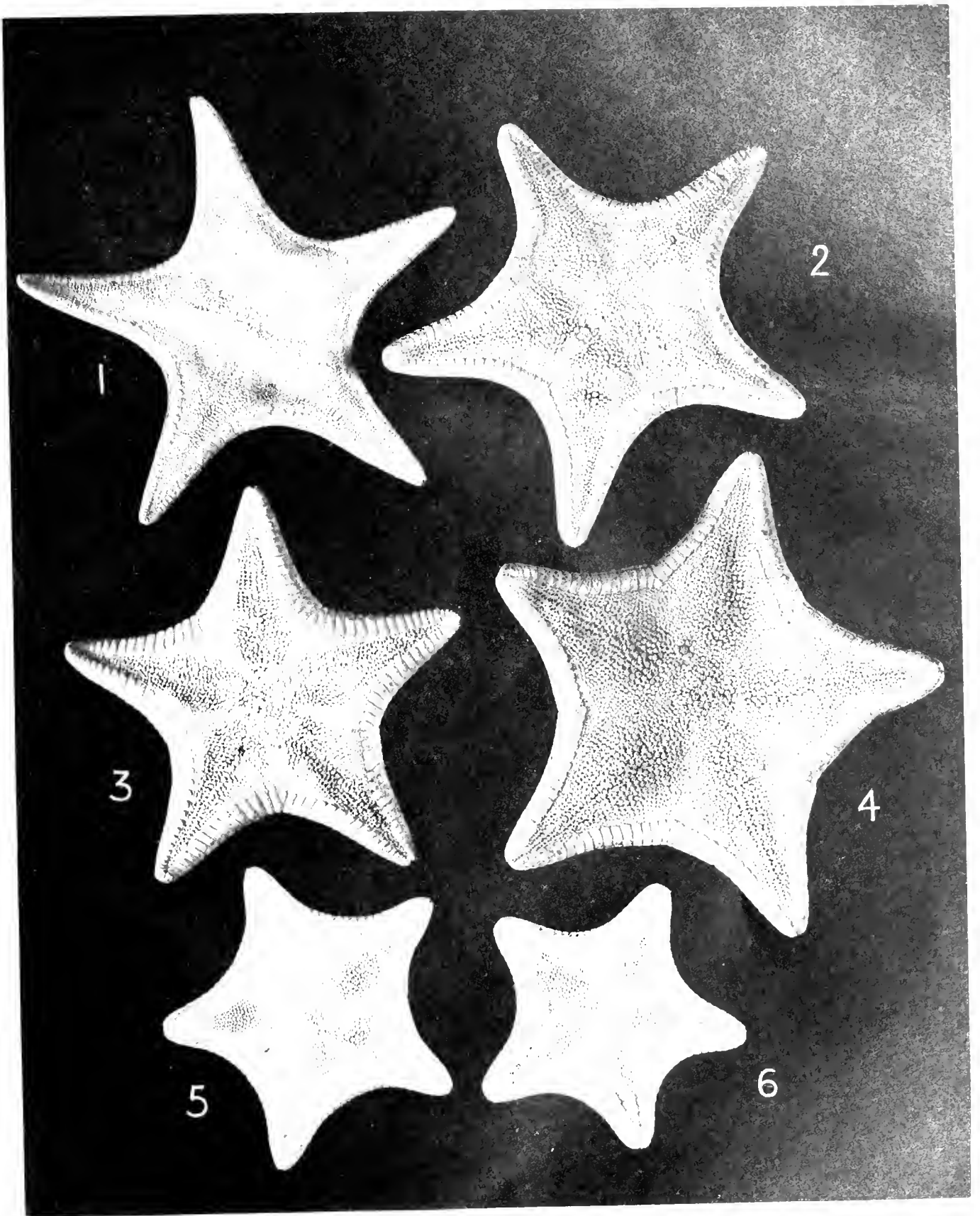


PLATE II

- Fig. 1. *Pergamaster incertus*, abactinal surface of type specimen, B.M.
1907.59.45; R 26-27 mm., r 14 mm.
- Fig. 2. Abactinal view of same specimen, $\times 3$.
- Fig. 3. *Pergamaster synaptorus*, type, actinal view, $\times 1.66$.
- Fig. 4. *Notioceramus anomalus*, type, actinal view, $\times 1.66$.

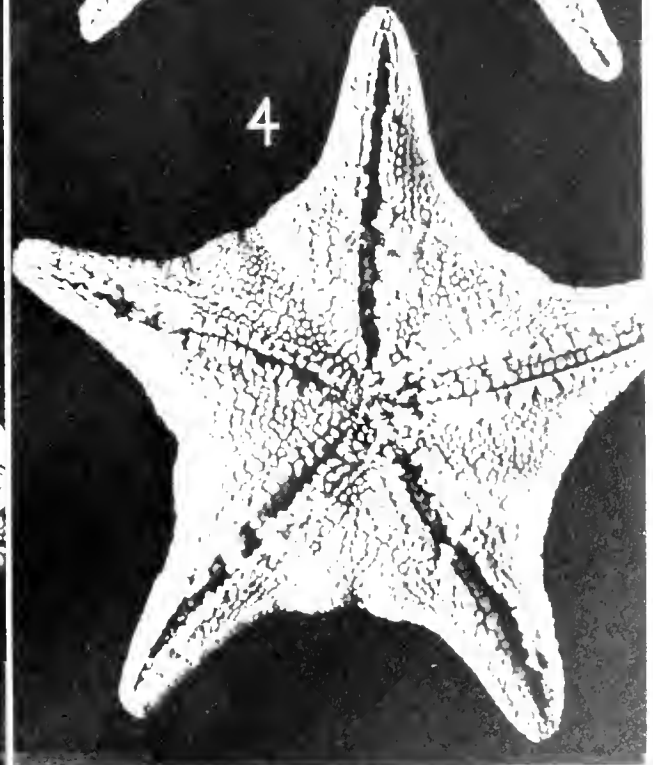
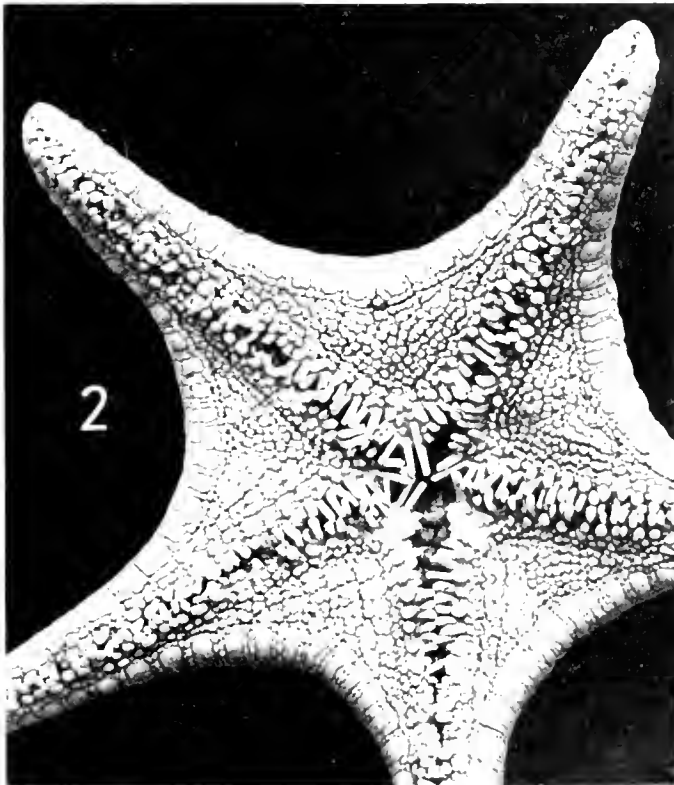
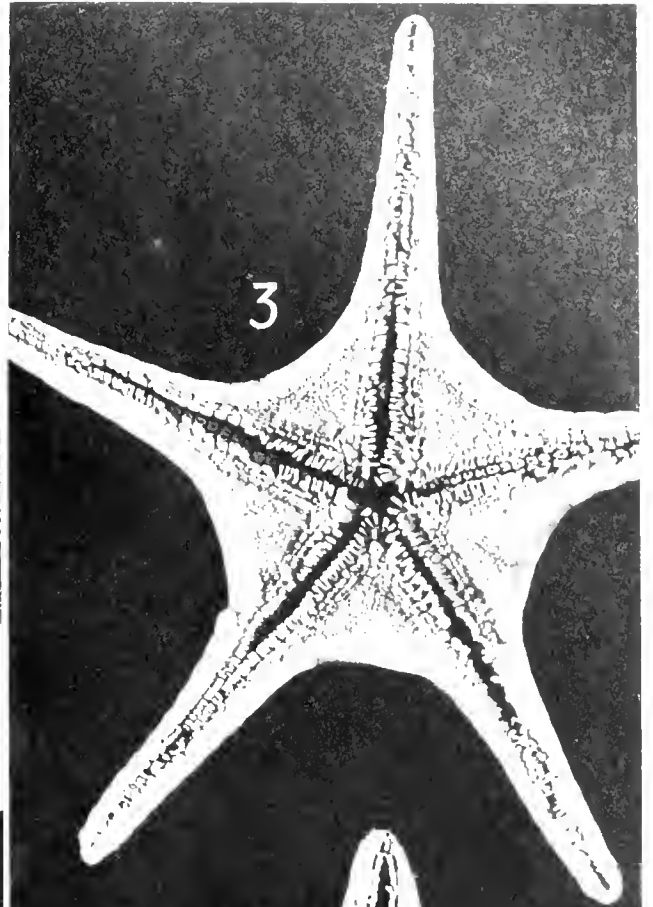
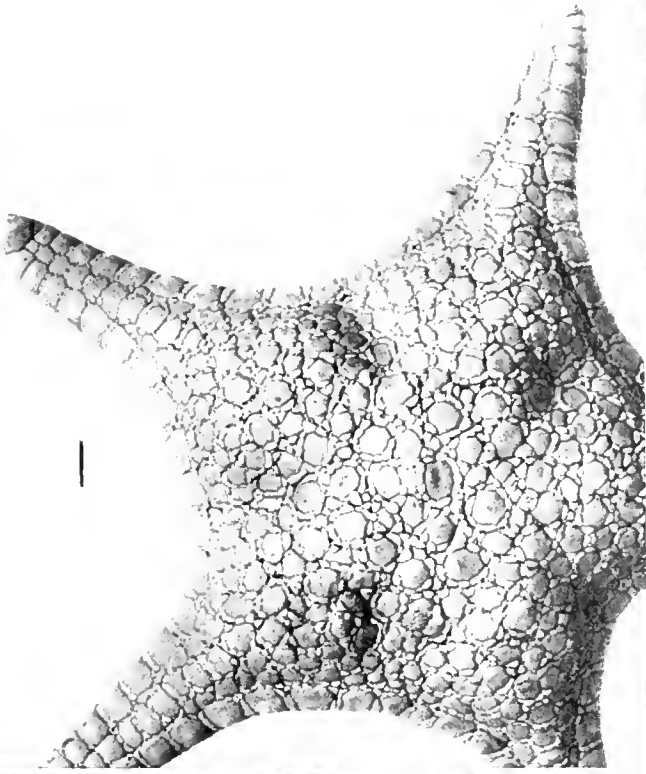


PLATE III

- Fig. 1. *Pergamaster synaptorus*, abactinal surface of type, $\times 2.25$.
Fig. 2. *Hippasteria falklandica*, abactinal, $\times 1.4$.

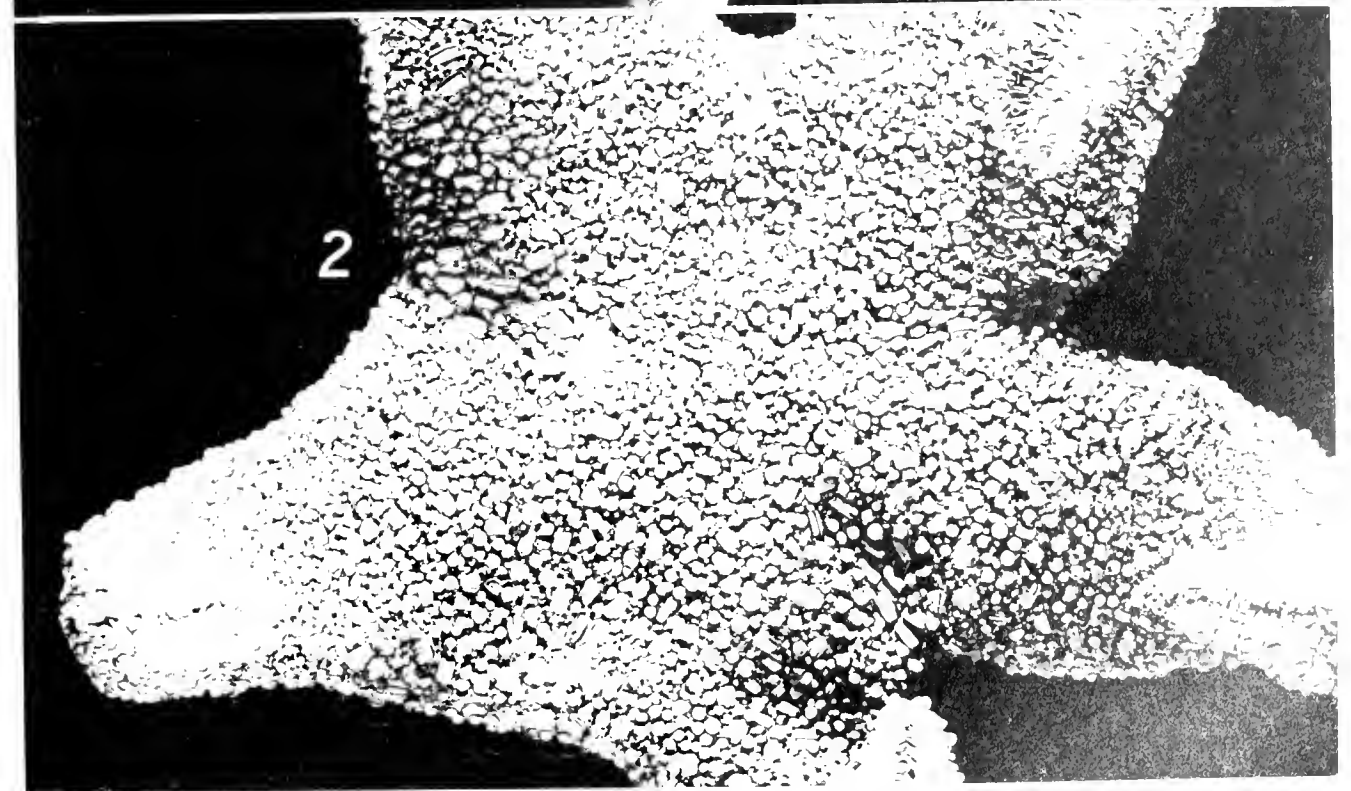
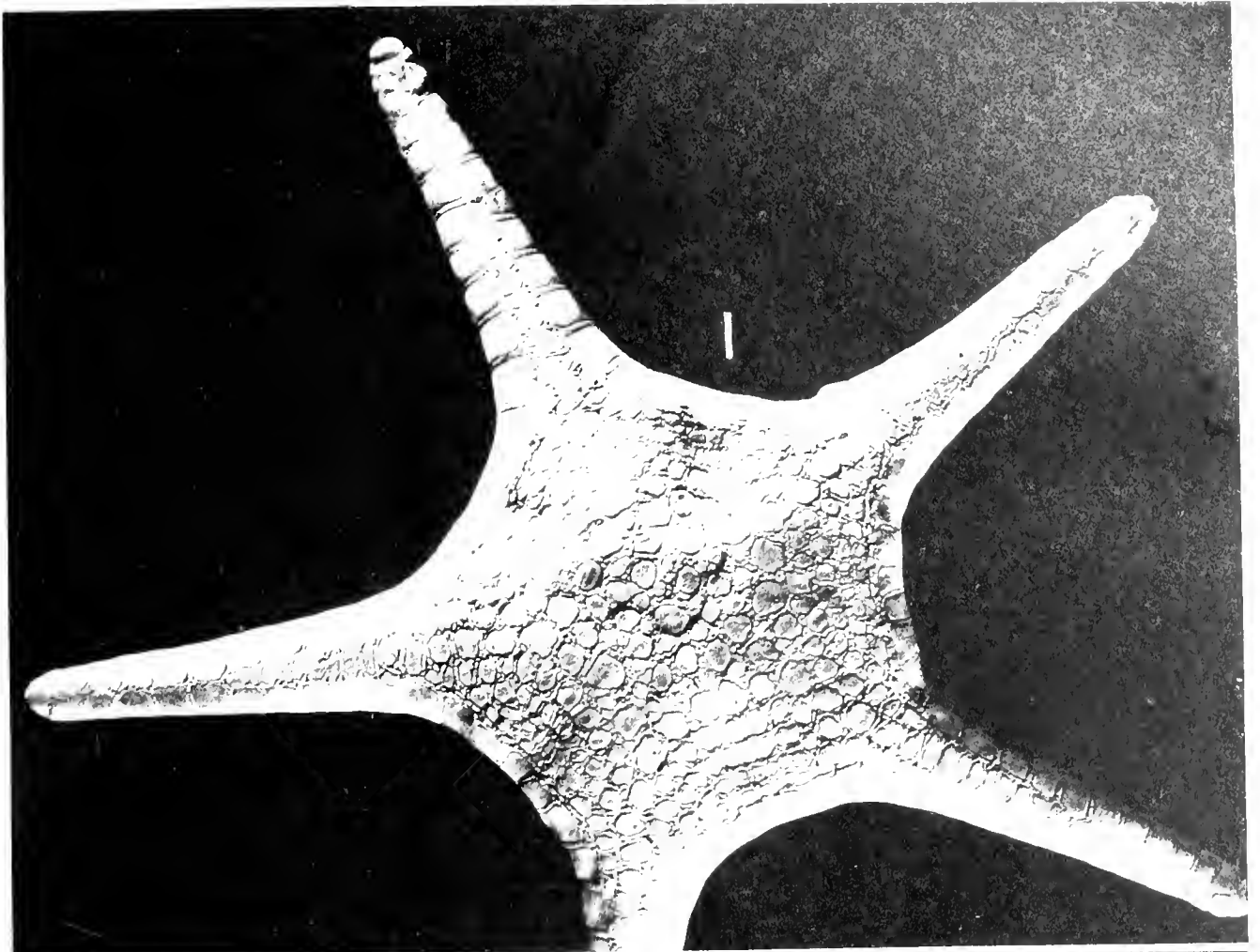


PLATE IV

- Fig. 1. *Cladaster analogus*, type, abactinal view, $\times 1.2$.
Fig. 2. *Cladaster analogus*, type, actinal view, $\times 1.2$.
Fig. 3. *Cladaster analogus*, type, $\times 20$; a plate and pedicellaria of actinal interradial region.
Fig. 4. *Hippasteria falklandica*, type, actinal view, $\times 0.85$.
Fig. 5. *Notioceramus anomalus*, type, abactinal view, $\times 1.66$.

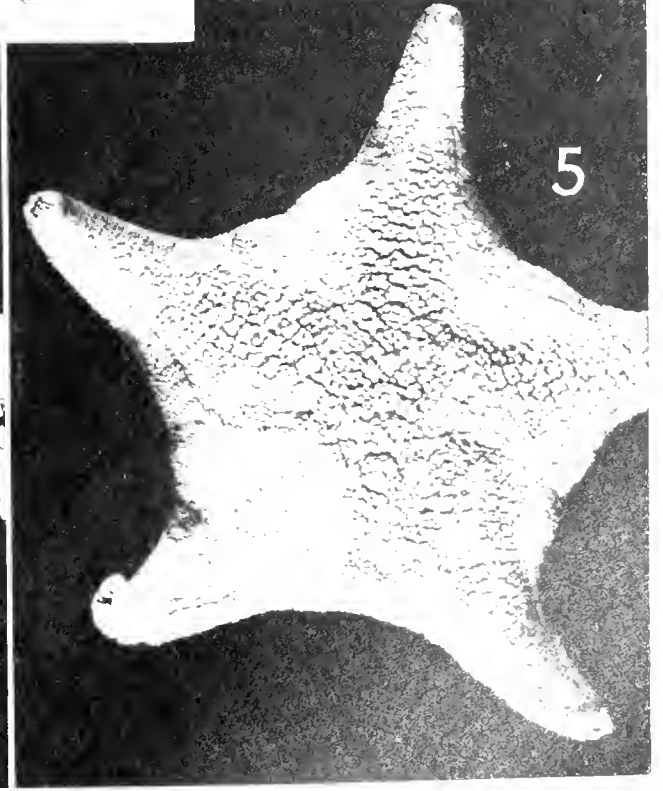
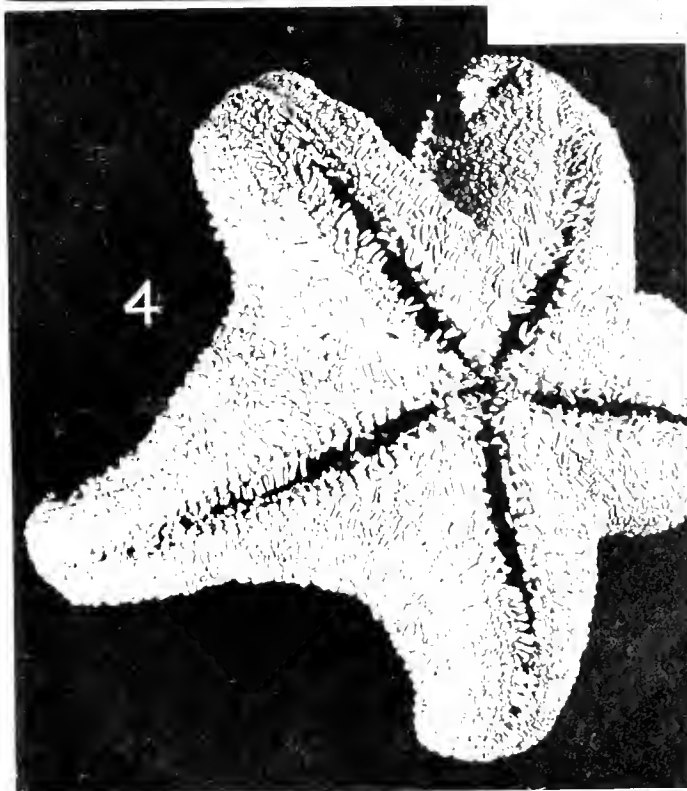
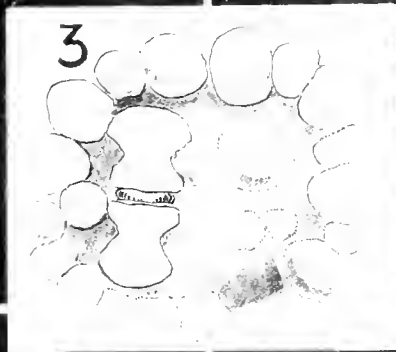
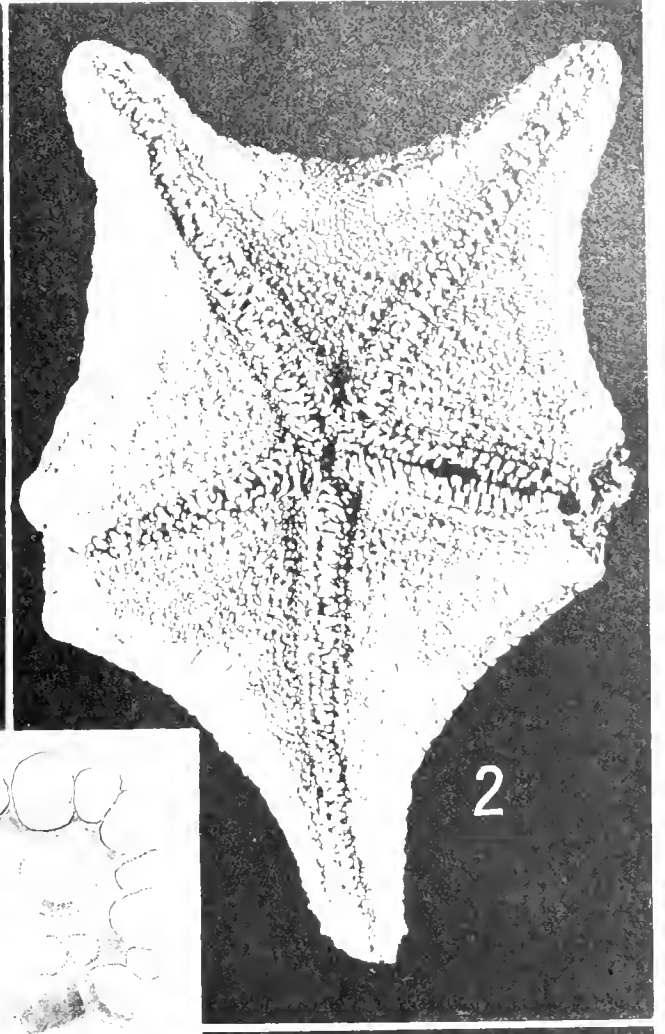
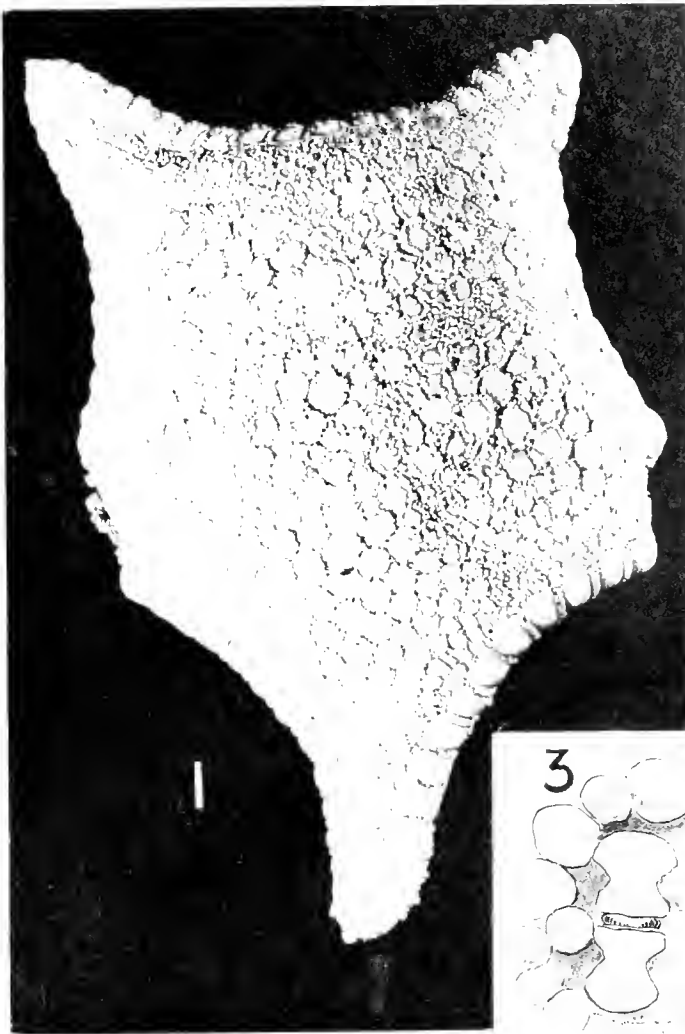


PLATE V

Fig. 1. *Perknaster fuscus*, cotype, 'Challenger' St. 149D, slightly less than $\times 2.5$.

Fig. 2. *P. sladeni georgianus*, type, St. 42, $\times 3$.

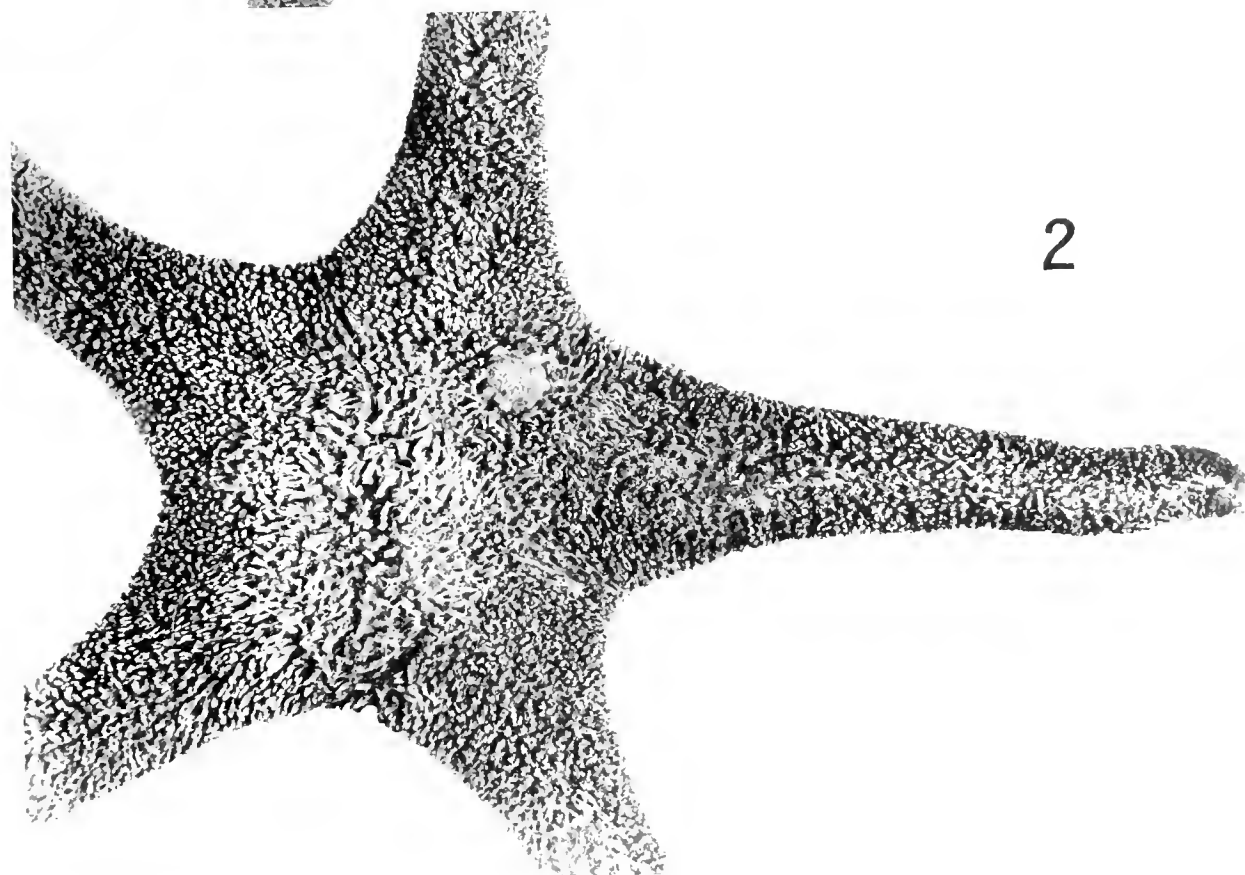
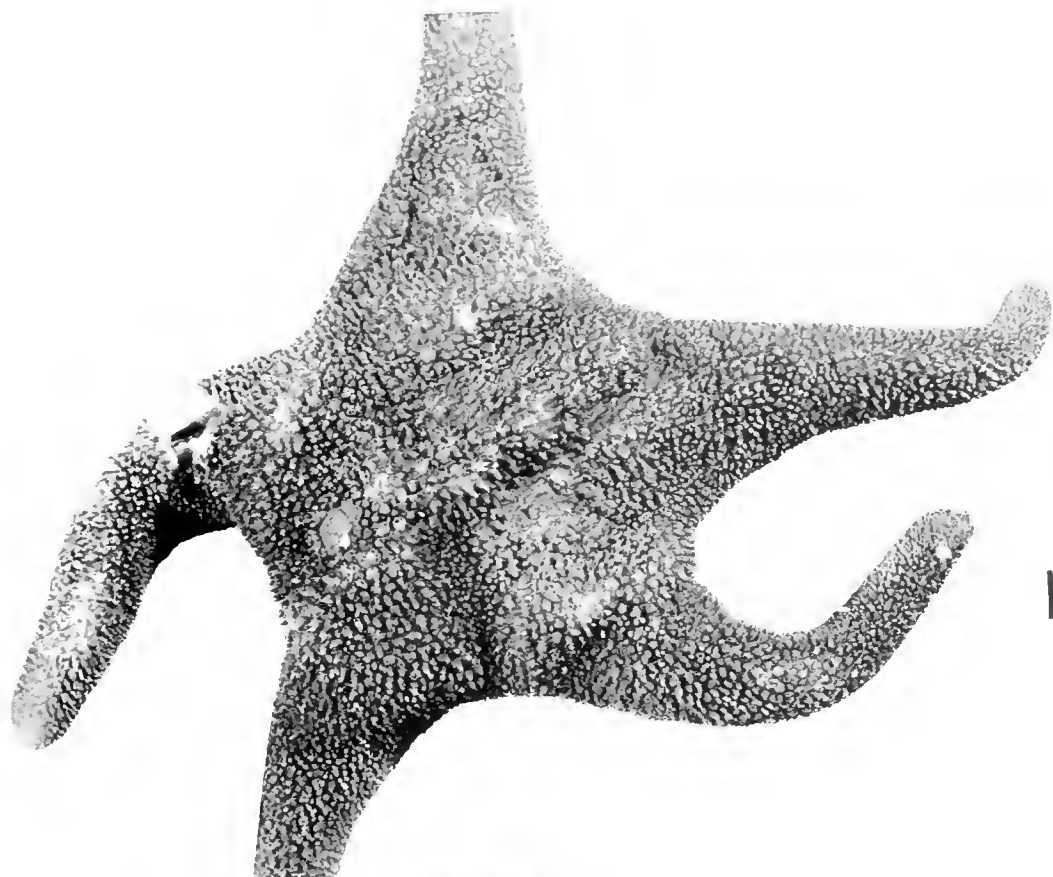


PLATE VI

Fig. 1. *Perknaster fuscus*, cotype, actinal surface, $\times 2.3$.

Fig. 2. *P. fuscus antarcticus*, St. 181, $\times 2.3$.

Fig. 3. *P. sladeni georgianus*, paratype, St. 140, $\times 2.5$.

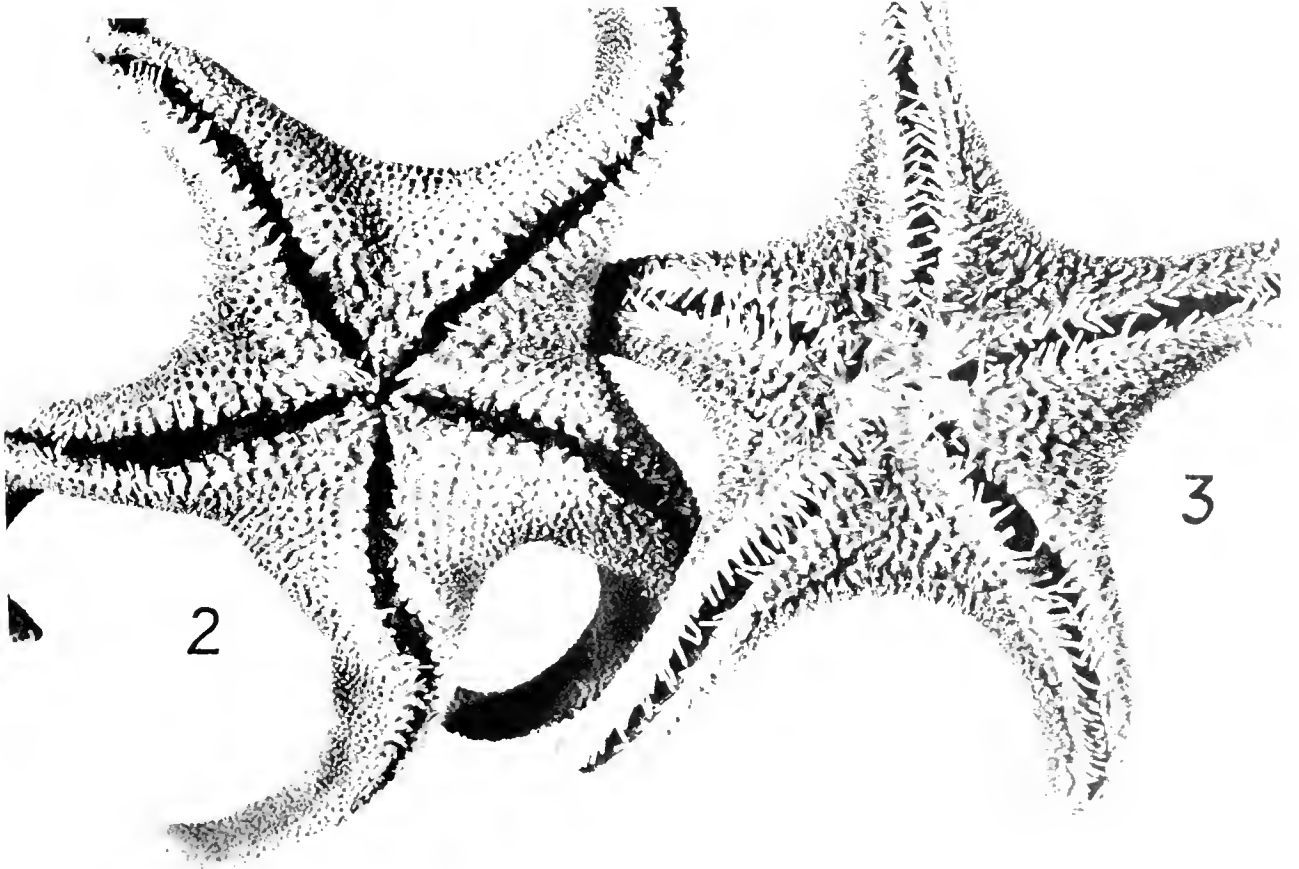
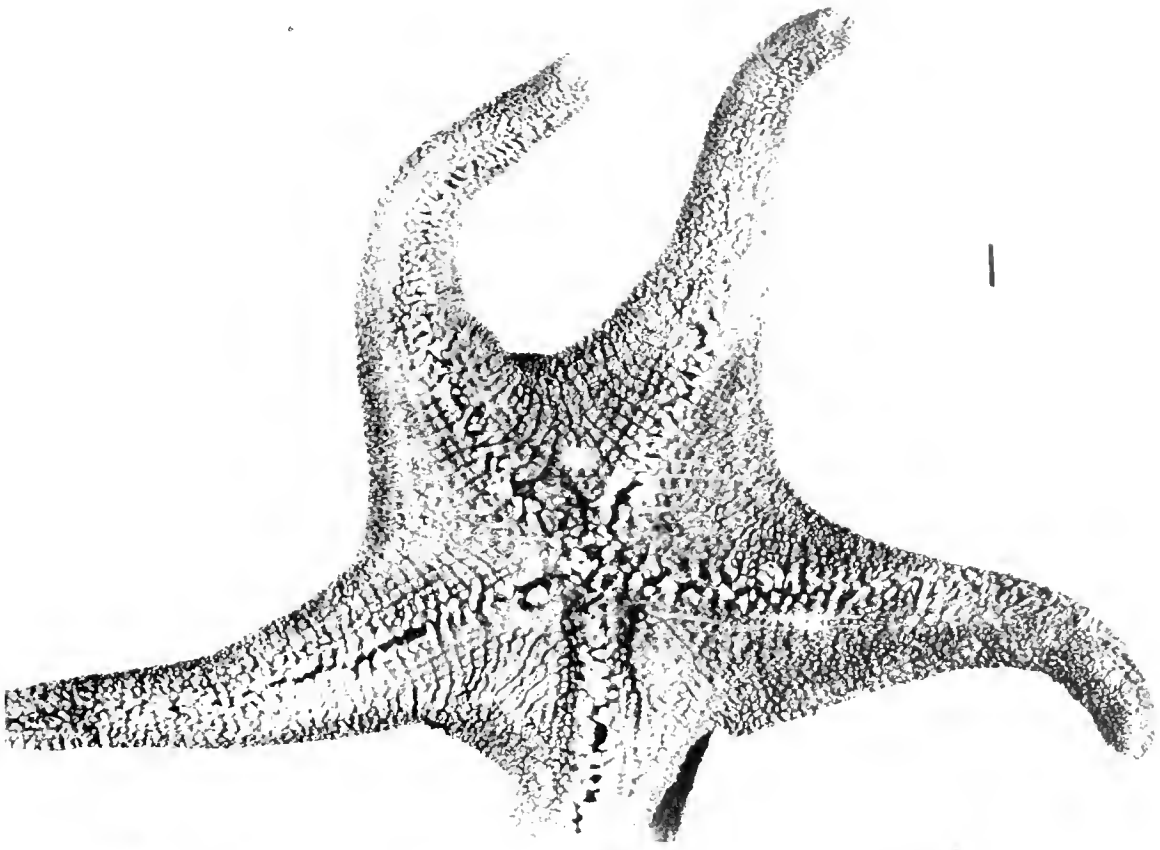


PLATE VII

Fig. 1. *Perknaster sladeni*, St. 474, $\times 2.3$.

Fig. 2. *P. aurovae*, St. 371, $\times 1.5$.

Fig. 3. *P. charcoti*, specimen B, St. 148, $\times 2.3$.

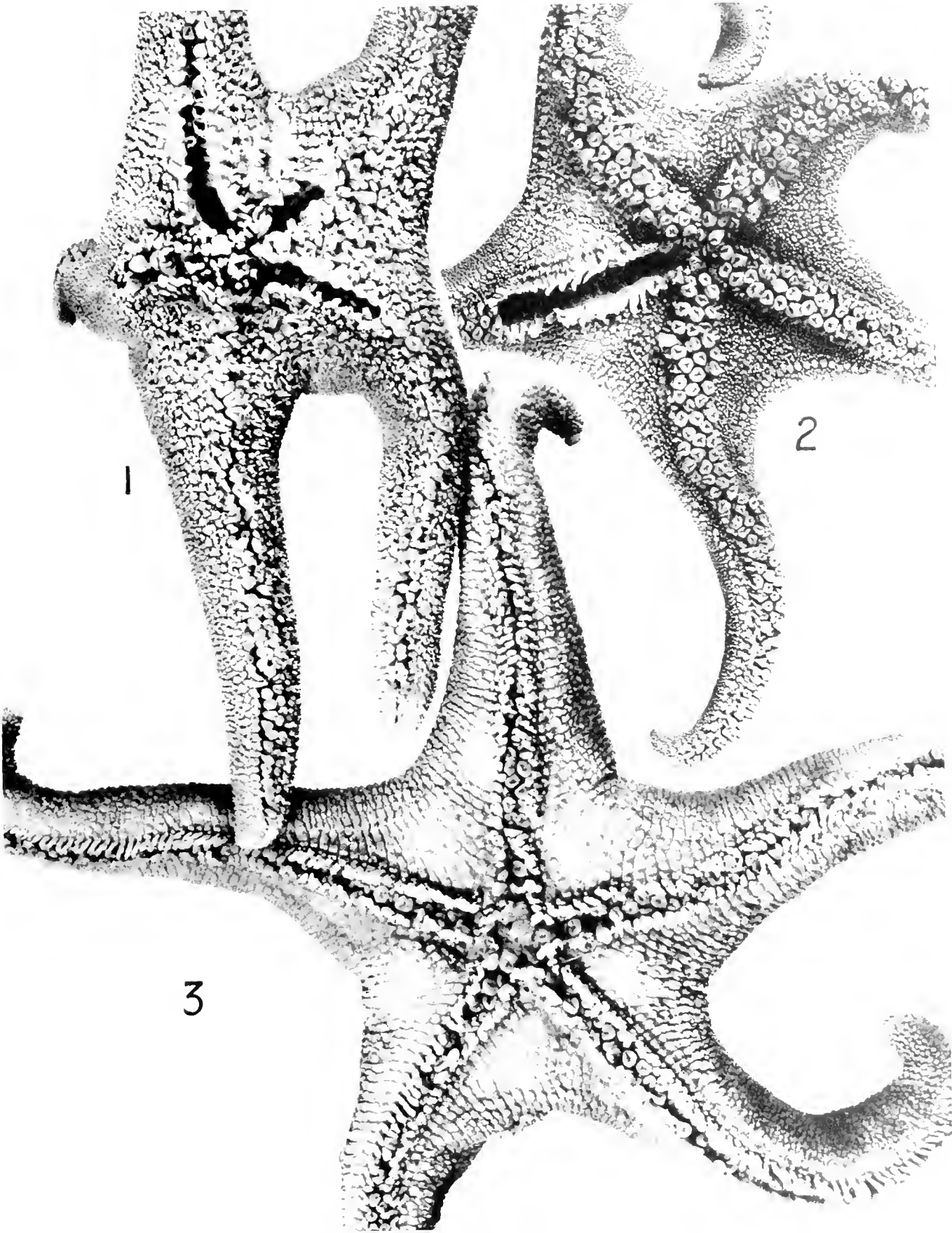


PLATE VIII

Fig. 1. *Perknaster densus*, abactinal view, $\times 3$.

Fig. 2. *P. densus*, portion of actinal surface, $\times 4$.

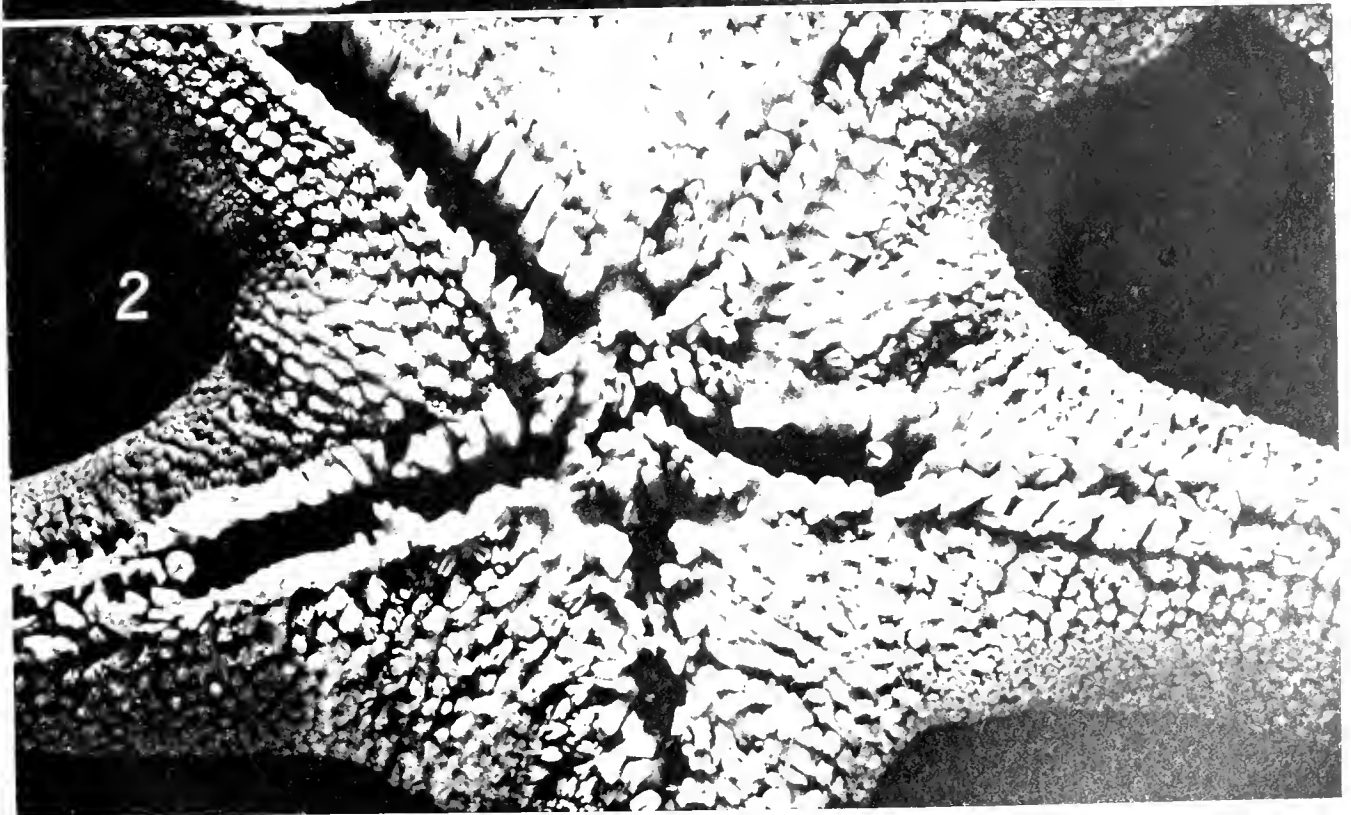
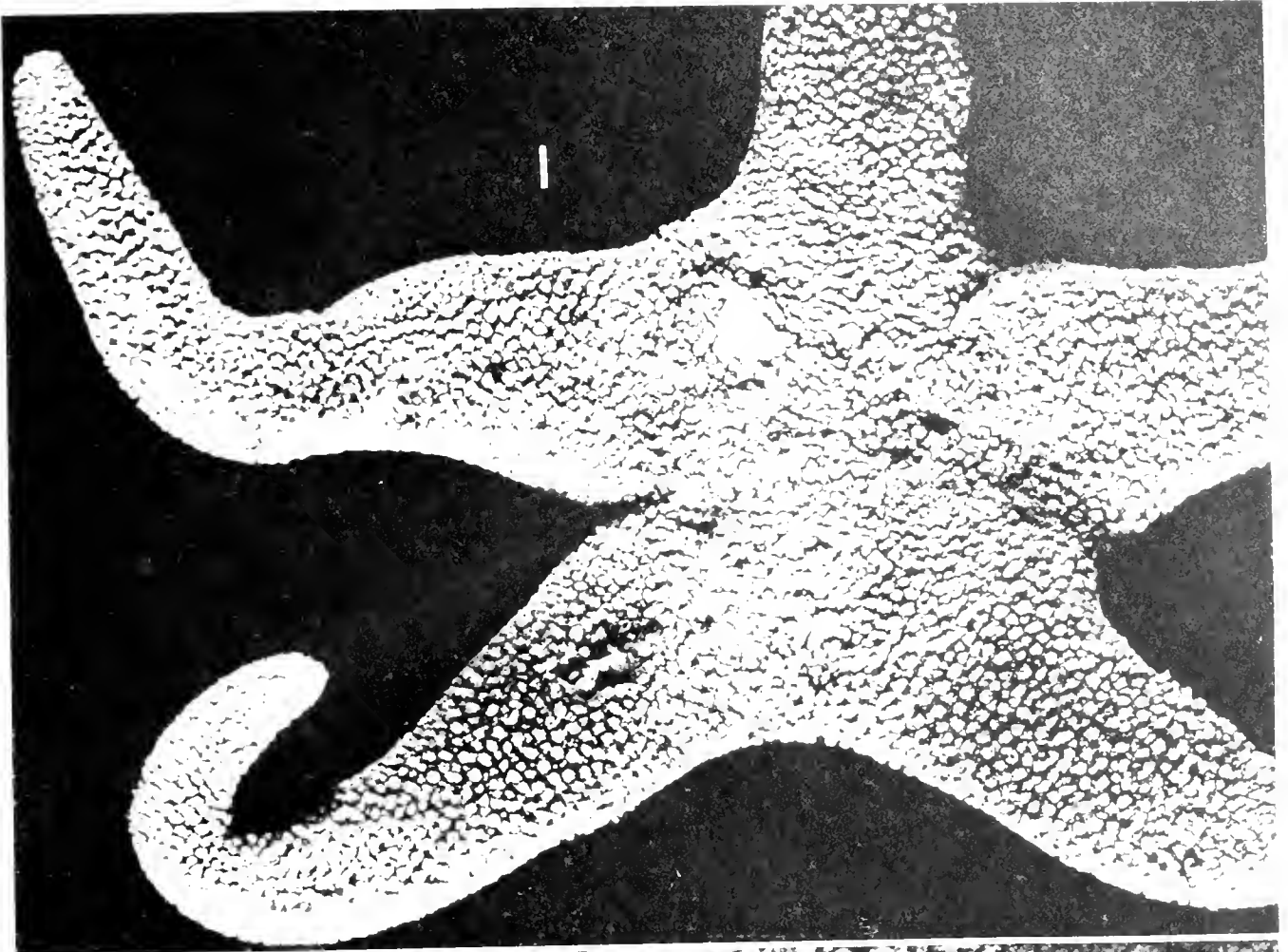


PLATE IX

Fig. 1. *Mirastrella biradialis*, 4 specimens, St. 160, $\times 5$.

Fig. 2. *Anteliaster australis*, abactinal view of type, $\times 2.3$.

Fig. 3. *Anteliaster australis*, actinal view of type, $\times 4$.

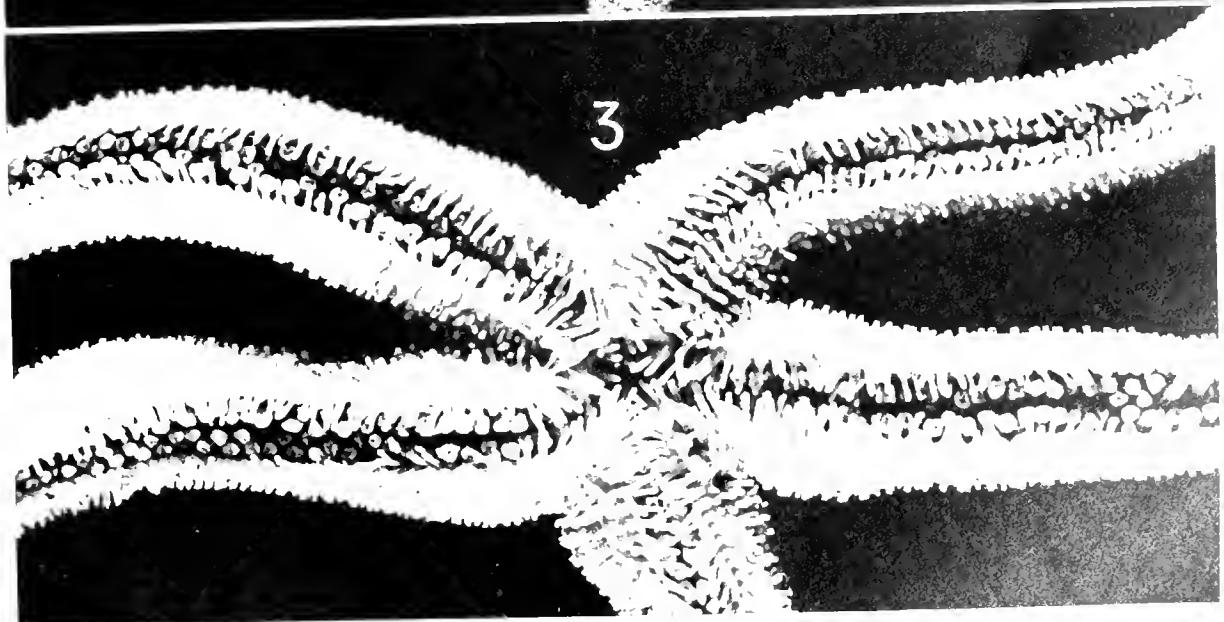
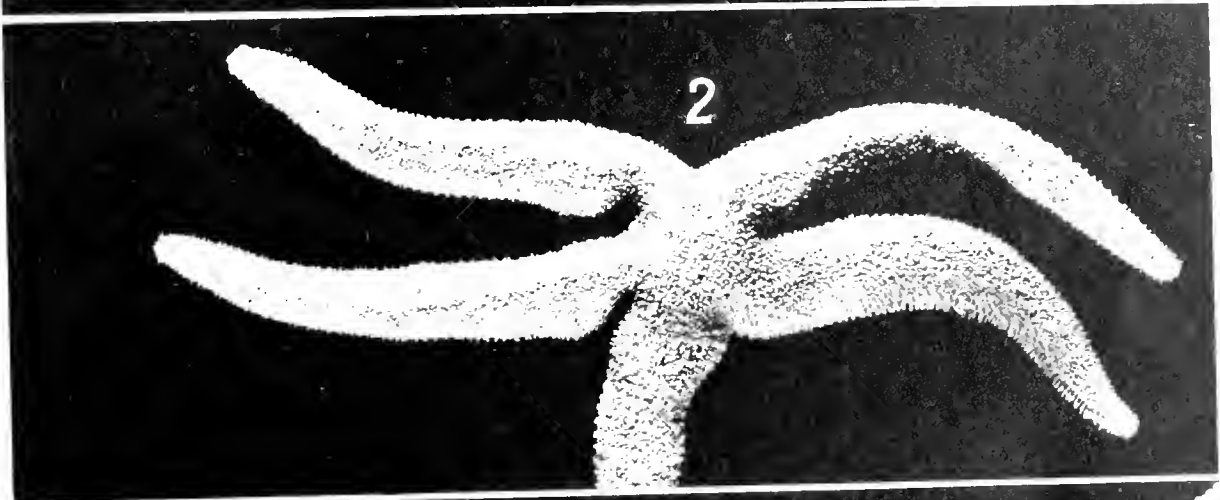
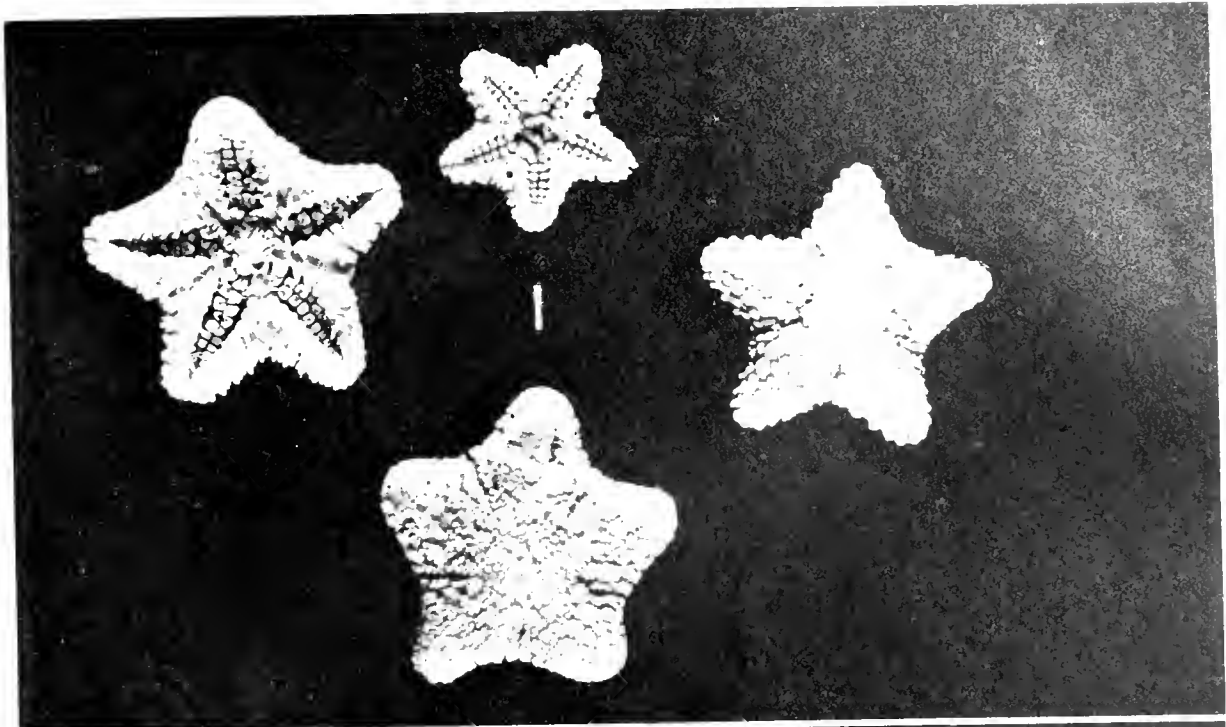


PLATE X

Fig. 1. *Rhopiella koehleri*, actinal view of type, $\times 5$.

Fig. 2. Same abactinal view of type, $\times 2.5$. A part of the gonad shows in the opened ray at right.

Fig. 3. *Anseropoda antarctica*, abactinal aspect of type, $\times 4.3$.

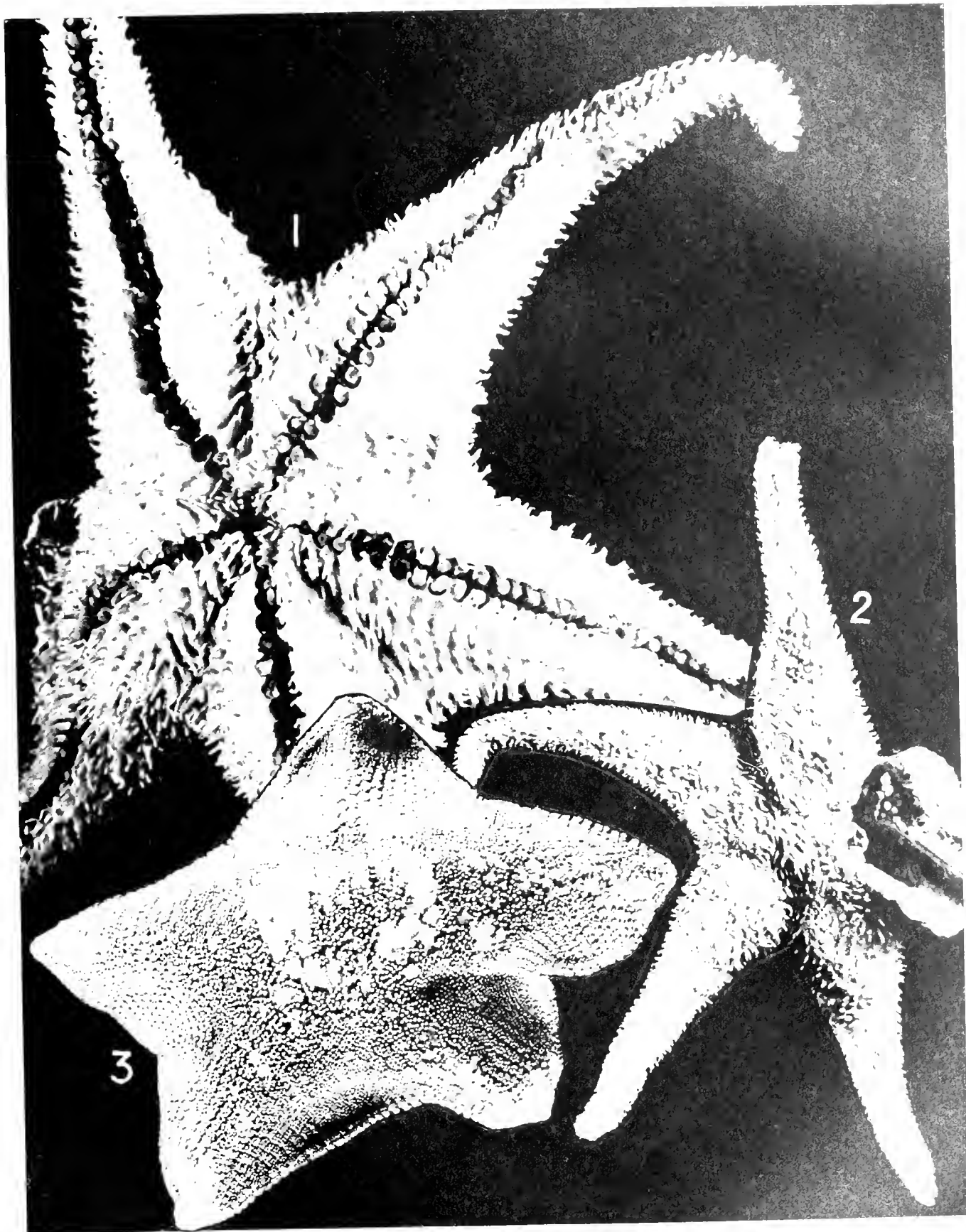


PLATE XI

- Fig. 1. *Henricia studeri*, St. WS 782, $\times 2.5$.
Fig. 2. *Henricia obesa*, St. WS 796B, $\times 2.5$.
Fig. 3. *Henricia simplex*, St. 1564, $\times 2.75$. The dark spots on the actinal surface are shadows of spinelets, not papulae.
Fig. 4. *Henricia pagenstecheri*, St. 39, $\times 5$; *p*, *p* actinal papulae.

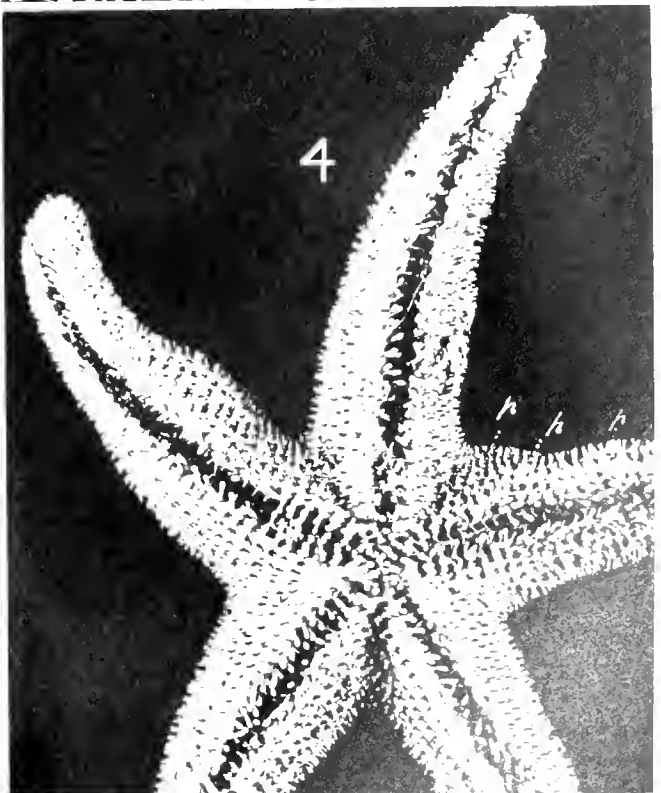
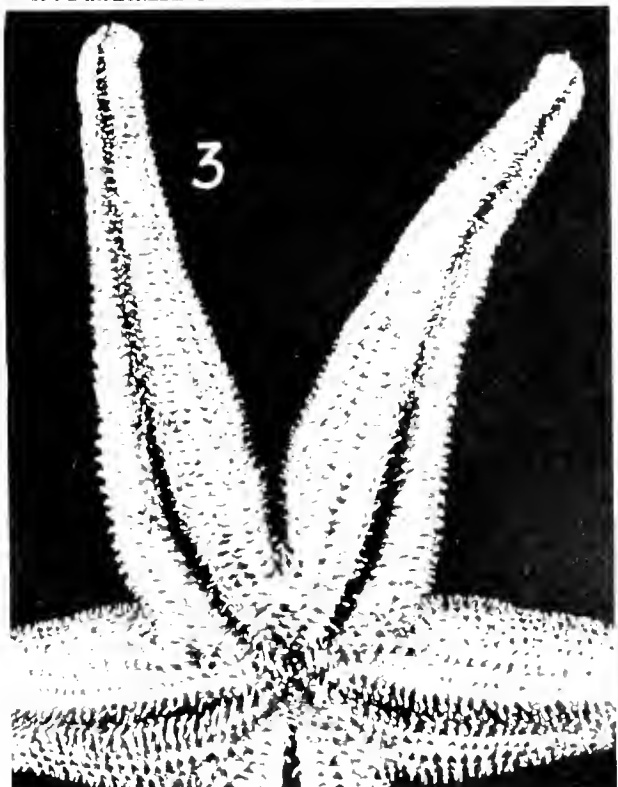
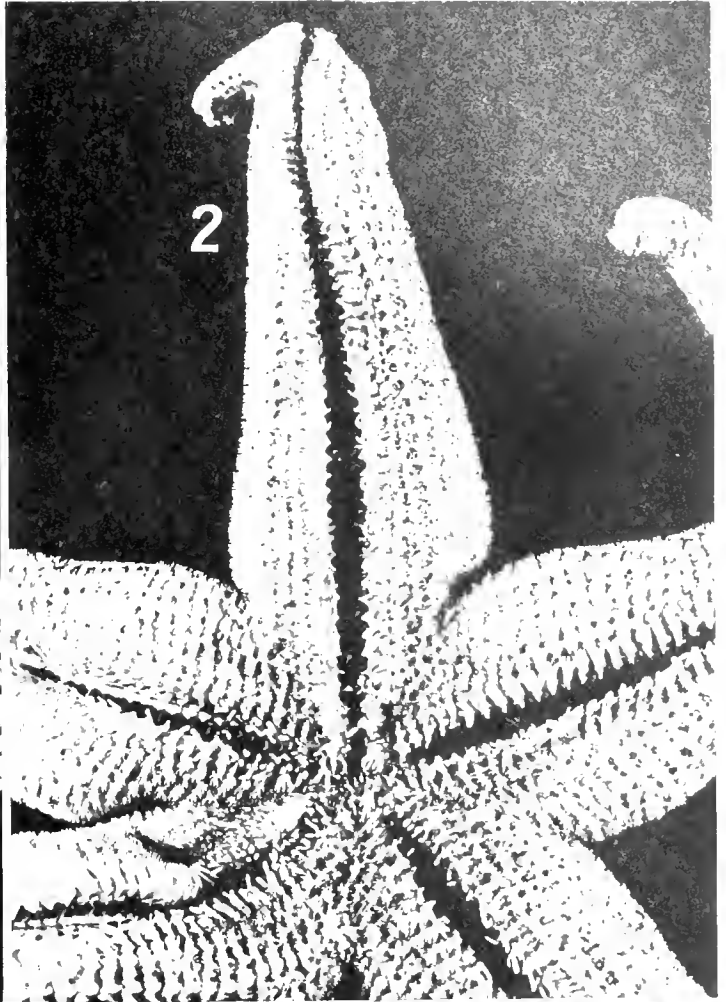
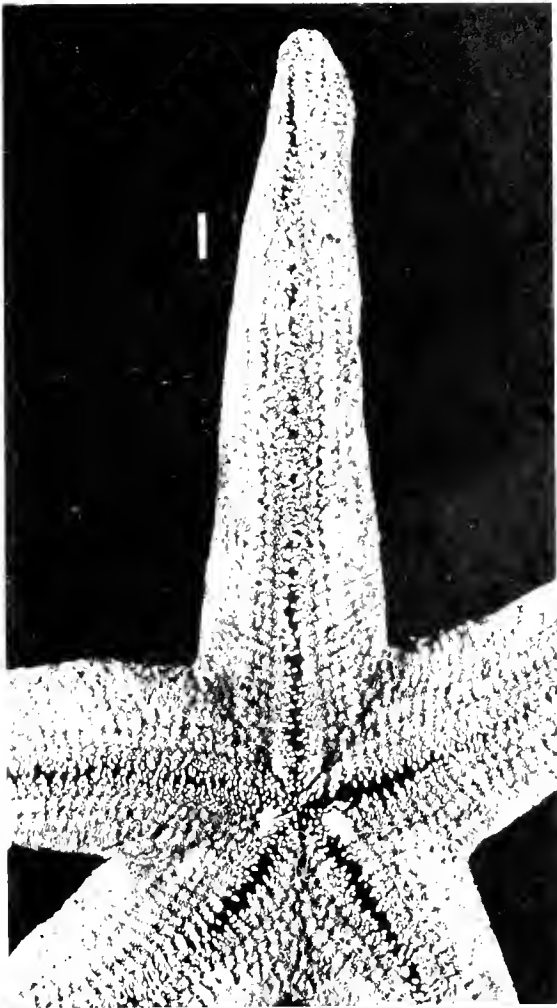


PLATE XII

Fig. 1. *Anseropoda antarctica*, actinal view of type, $\times 8$.

Fig. 2. *Paralophaster godefroyi meseres*, abactinal aspect of type, $\times 2.5$.

Fig. 3. Same, actinal surface, $\times 2.5$.

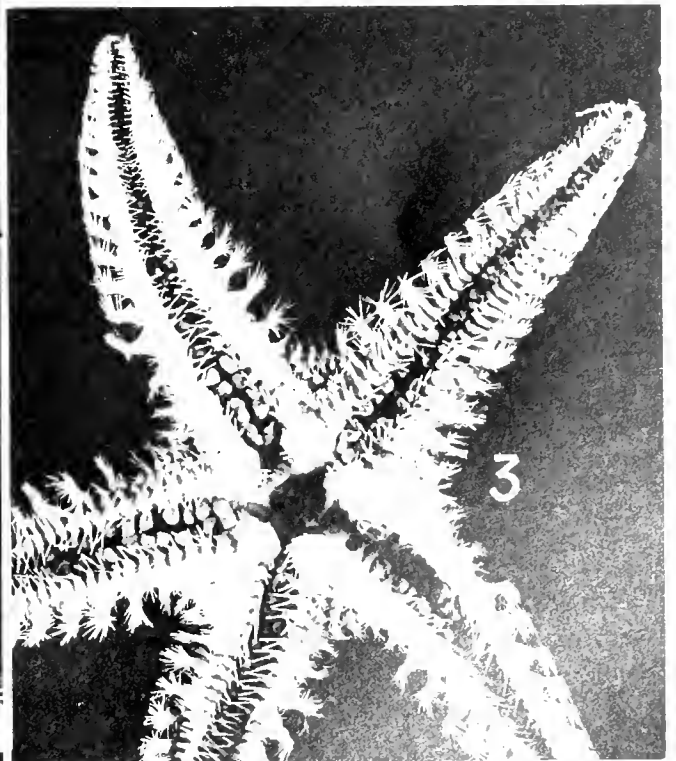
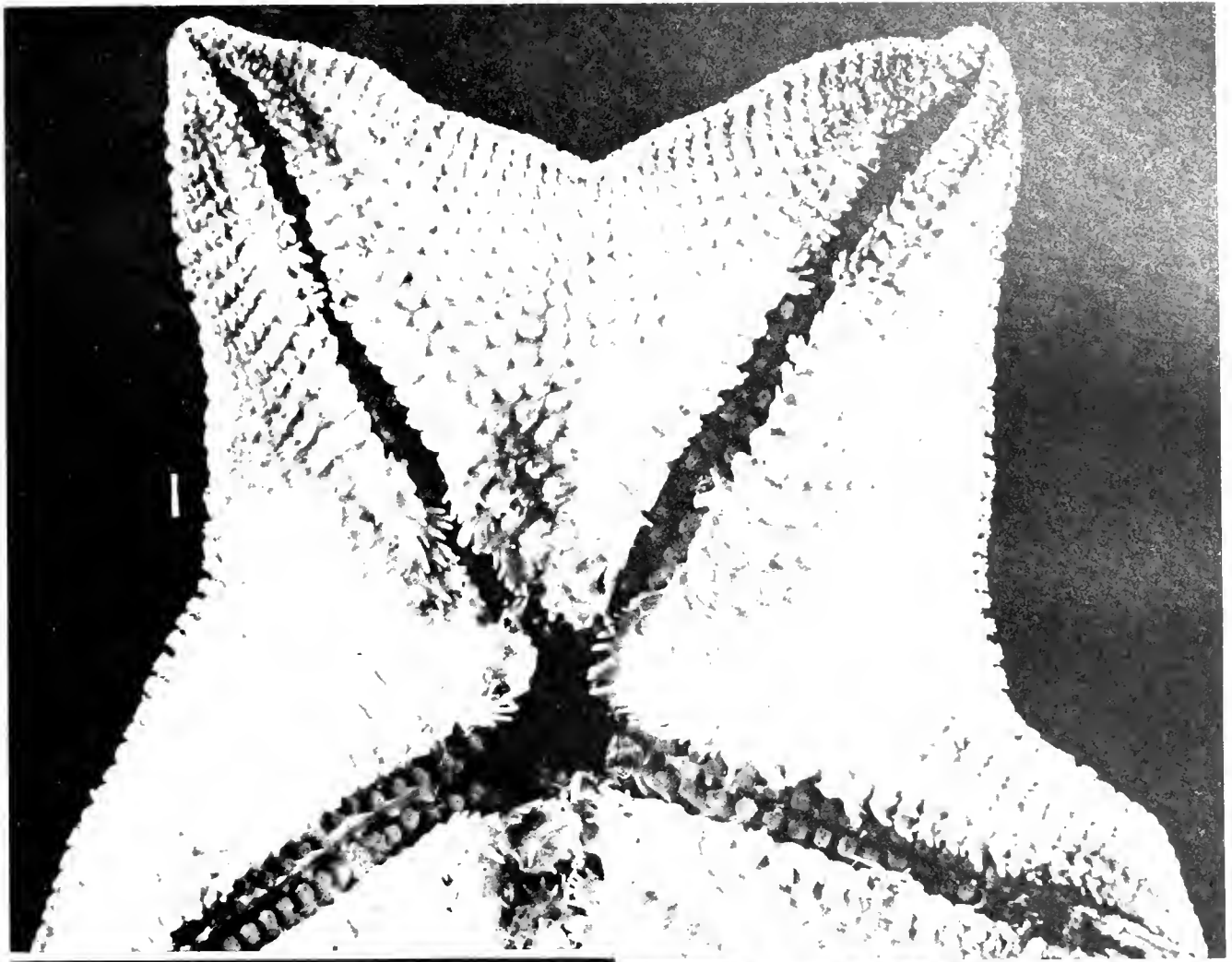


PLATE XIII

Fig. 1. *Lophaster marionis*, type, $\times 4$.

Fig. 2. *Lophaster densus*, abactinal view of specimen from St. 1948,
 $\times 3.5$.

Fig. 3. Same, actinal aspect of type, $\times 3.5$.

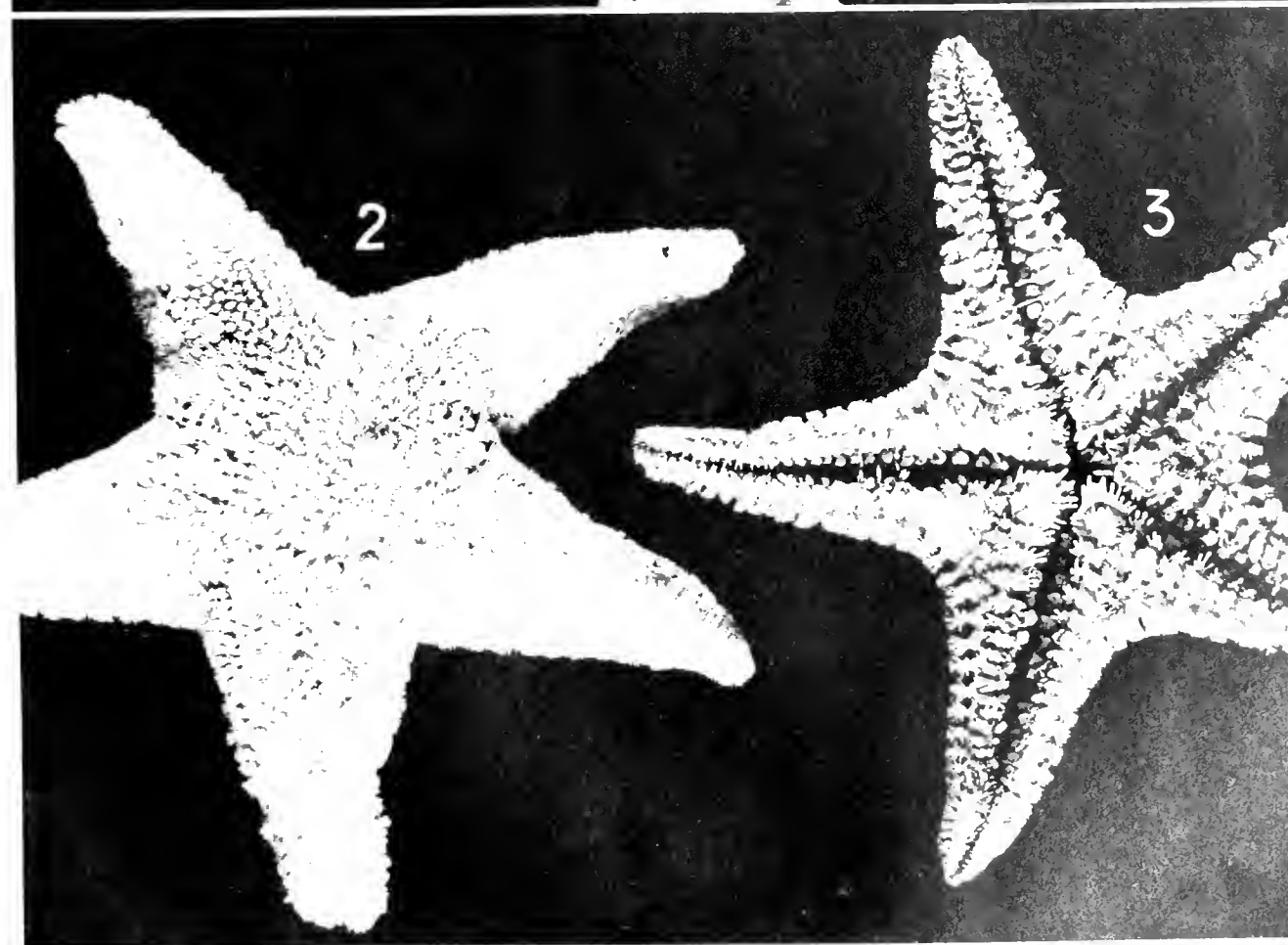
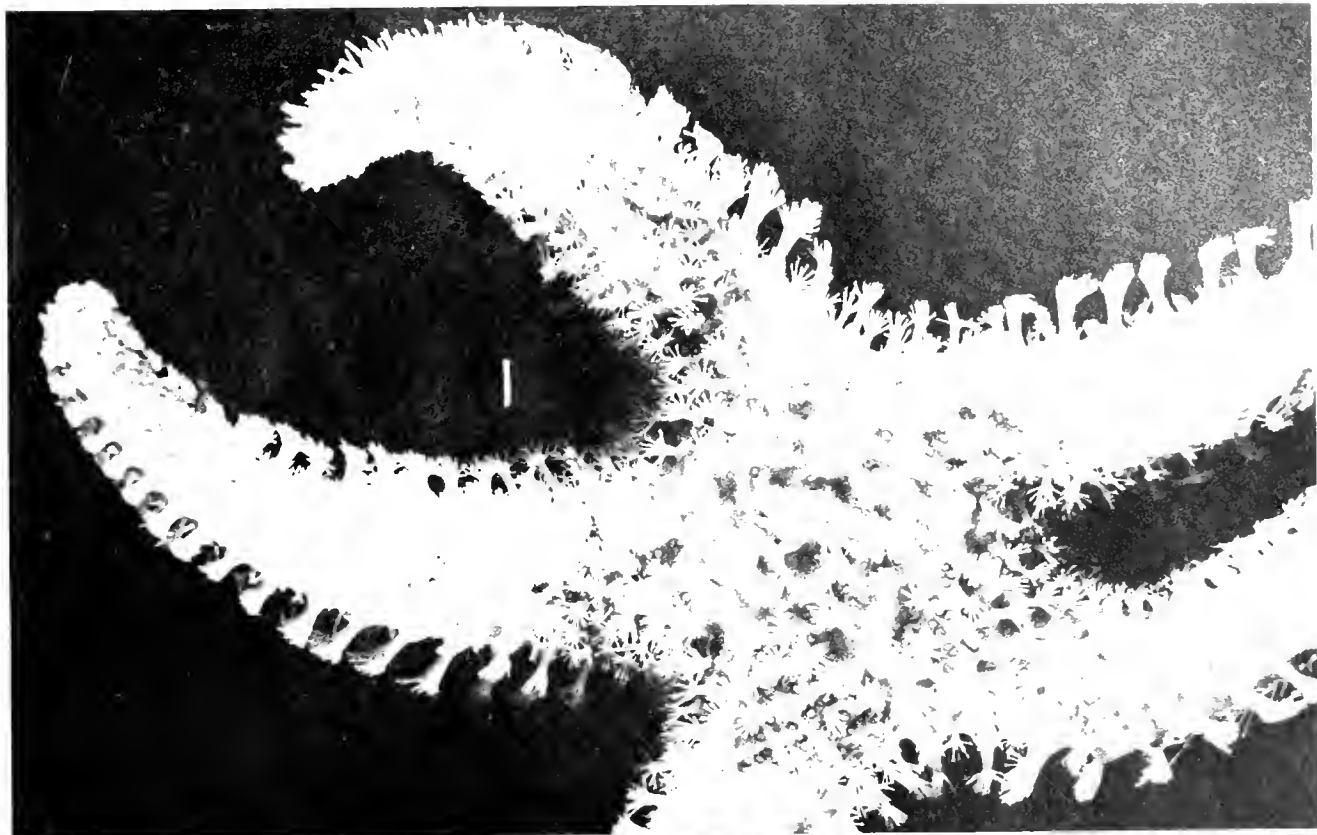


PLATE XIV

Odinella nutrix, female, St. 125, enlarged. This specimen shows well the large sacculi and the interlocking dorsolateral spines of the genital inflation.

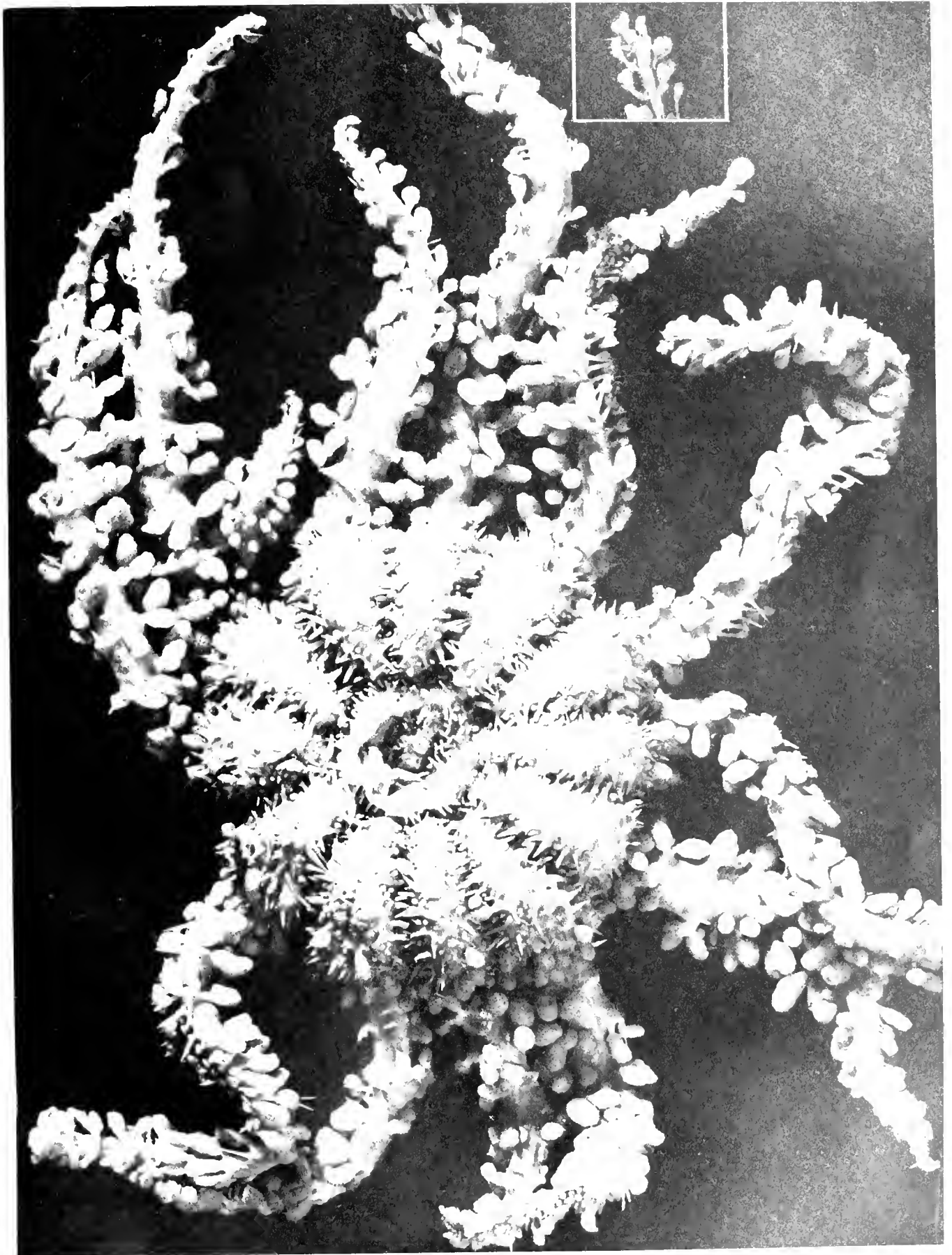


PLATE XV

Odinella nutrix, actinal view of type, enlarged a little less than $\times 3$.

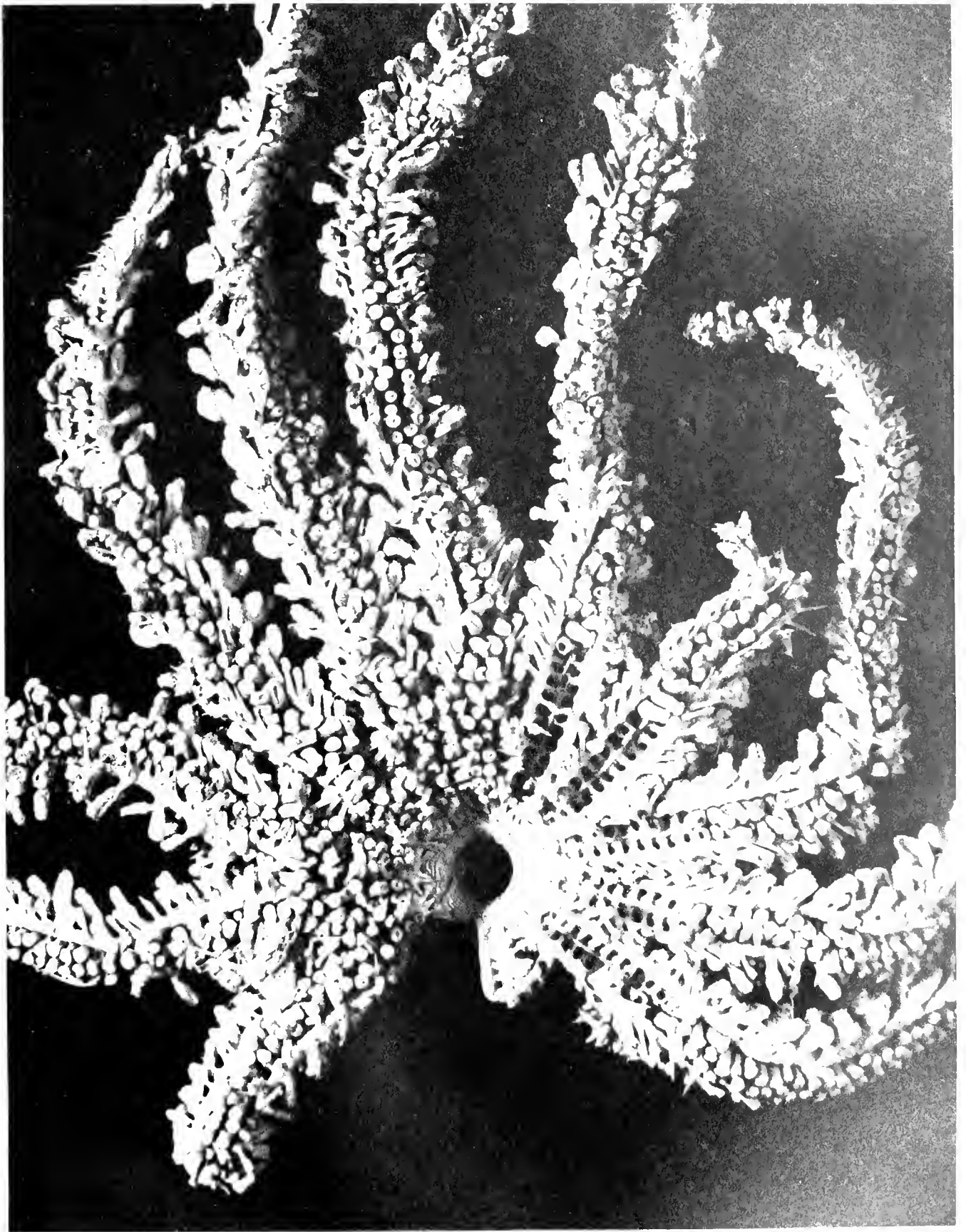


PLATE XVI

Odinella nutrix

- Fig. 1. Lateral aspect of base of ray of type at distal border of genital inflation showing fifth and sixth skeletal arches with their sacculate spines, $\times 10$; *ad*, adambulacral spines; *p*, *p*, papulae.
- Fig. 2. Lateral aspect of ray, about midway between genital inflation and tip, $\times 10$; St. 42. On right the sacculi have been removed and skin cleared to show plates and form of spines; sacculus removed from left inferomarginal spine; midradial pad of pedicellariae on left without a central spinelet. *ad*, adambulacral spines; *d*, dorsolateral spines; *i*, inferomarginal spine, *r*, isolated midradial plate and spine; *s*, superomarginal spine.
- Fig. 3. Lateral aspect of genital region of ray of male specimen, St. 42, to show arrangement of skeletal arches, $\times 5$; I-V, first 5 skeletal arches, *ad*², second adambulacral plate; *g*, male gonopore; the female gonopore is in the position of "II"; *i*², second inferomarginal (enlarged in fig. 5); *p*, lower intercostal papulae.
- Fig. 4. Proximal end of same ray as fig. 3, showing narrow aperture to disk and arrangement of plates, $\times 5$. The aperture is partly occluded by a dorsal diaphragm.
- Fig. 5. Enlargement ($\times 20$) of lower end of arch I of fig. 3, to show the enlarged inferomarginal 2 (*i*²) with a lateral facet by which it is joined to its fellow of the adjacent ray and to inferomarginal 1 (of disk complex) by a small facet at *i*¹. A similar non-muscular symphysis at upper part of second adambulacral (*ad*²) joins it to its fellow of adjacent ray; *a*, ambulacral plate; *s*, superomarginal.
- Fig. 6. Lateral aspect of tip of ray of the type, with sacculus removed, showing the terminal spines of one side, $\times 20$.
- Fig. 7. Lateral aspect of terminal plate of a specimen from St. 123, $\times 20$, showing the terminal organ in place but with rest of integument removed.
- Fig. 8. Ventral aspect of terminal complex of the largest specimen (R 100 mm., St. 123), $\times 10$. The compound terminal sacculus is capable of much greater expansion.
- Fig. 9. Actinal surface of 2 rays of a young specimen in stage 2, from brood pouch of type, $\times 30$.
- Fig. 10. Actinal surface of one ray of a young specimen in stage 5, $\times 20$.
- Fig. 11. Abactinal view of a sector of a young specimen from brood pouch of type, $\times 20$. The dorsal wall is removed from 2 rays to show the ambulacral plates. In the middle ray 3 plates of the first skeletal arch have appeared, the middle one with pedicellariae; *ad*, adambulacral spines; *B*, primary interradial plate; *C*, central plate.

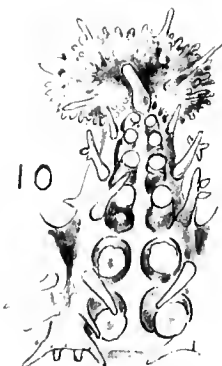
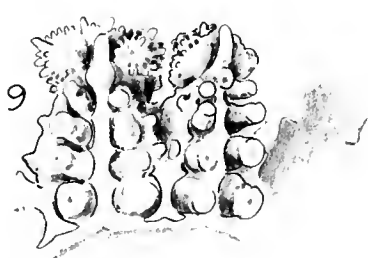
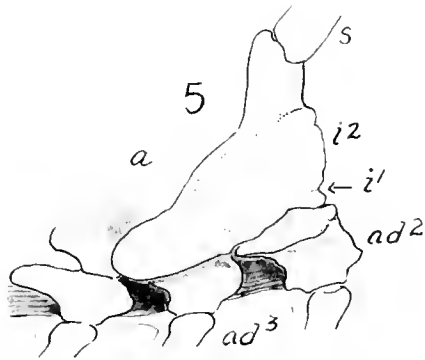
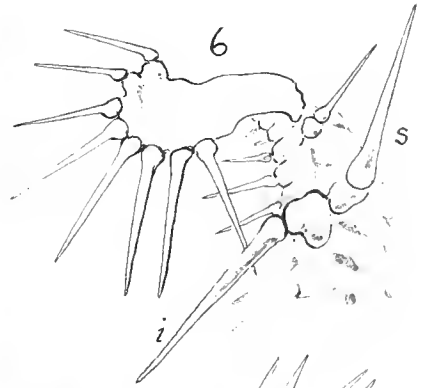
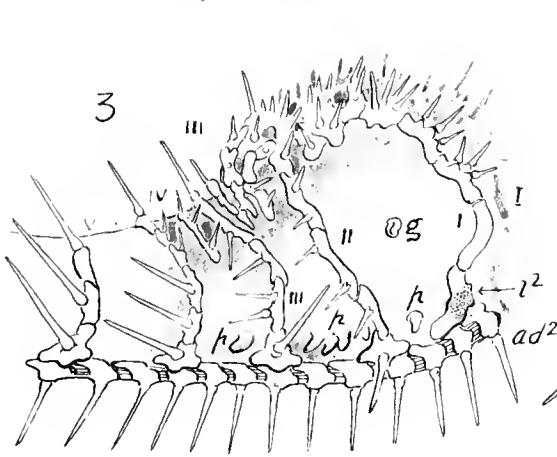
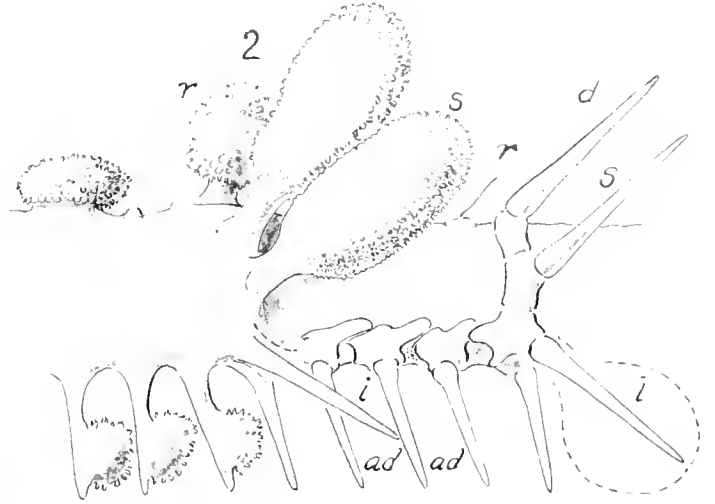


PLATE XVII

- Fig. 1. *Odinella nutrix*, side view of base of ray of type, $\times 6$; I-V, first 5 skeletal arches; *p*, papulae; *s* spines which had pierced the integument of adjacent ray, forming spine bridges as explained in text. The end of these spines was forcibly withdrawn from the sheath which has coalesced with the skin of adjacent ray and remains attached thereto when rays are forcibly separated. The young is in stage 5 and shows abactinal spinelets and well-developed terminal sacculus.
- Fig. 2. Same. Immature specimen, St. 123, $\times 3$, listed under "growth" as 3. Two mysid shrimps are held by pedicellariae which have grasped the numerous delicate bristles of their appendages.
- Fig. 3. Same. Type, base of a ray showing another young in stage 5 (figured pl. 16, fig. 11). Under this were several smaller young (stage 3). The first skeletal arch was destroyed in removing ray; *s'*, sheaths from which spines of adjacent rays have been pulled; other letters as in fig. 1.
- Fig. 4. *Notasterias stolophora*, type, $\times 2.5$.
- Fig. 5. *Lethasterias australis*, type, $\times 2.5$.

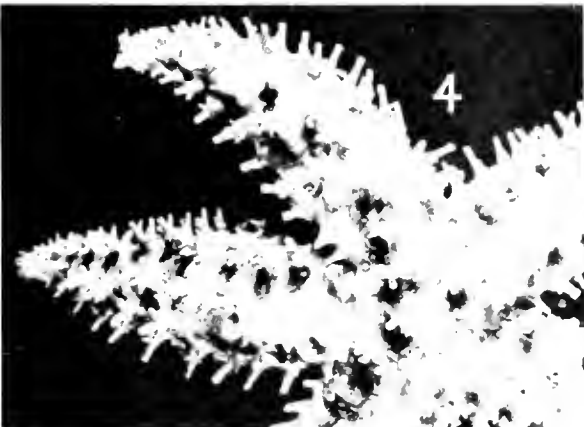
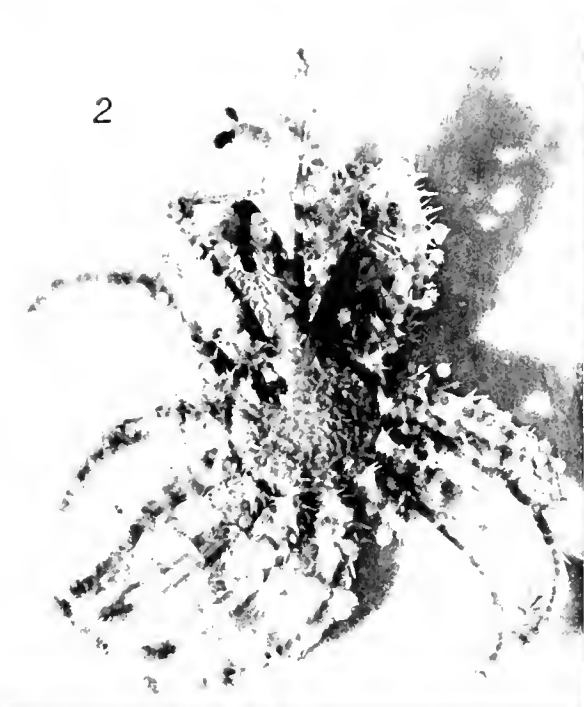
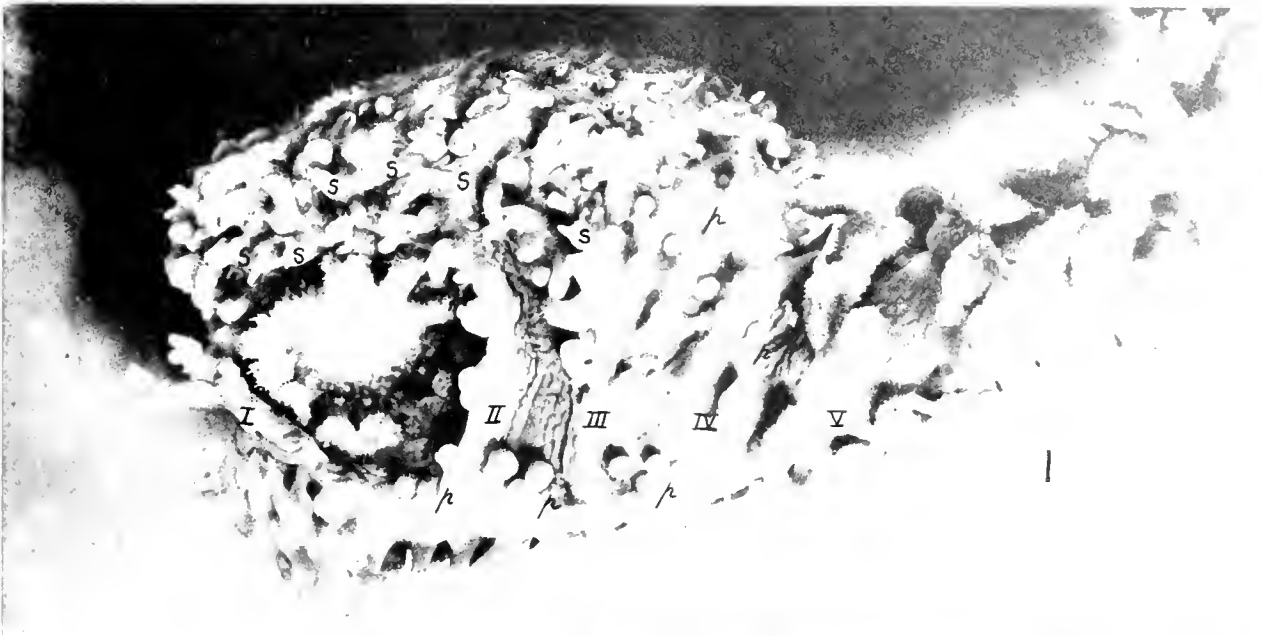


PLATE XVIII

Fig. 1. *Psalidaster mordax*, paratype, abactinal surface, $\times 1.5$.

Fig. 2. Same, portion of actinal surface, $\times 2$.

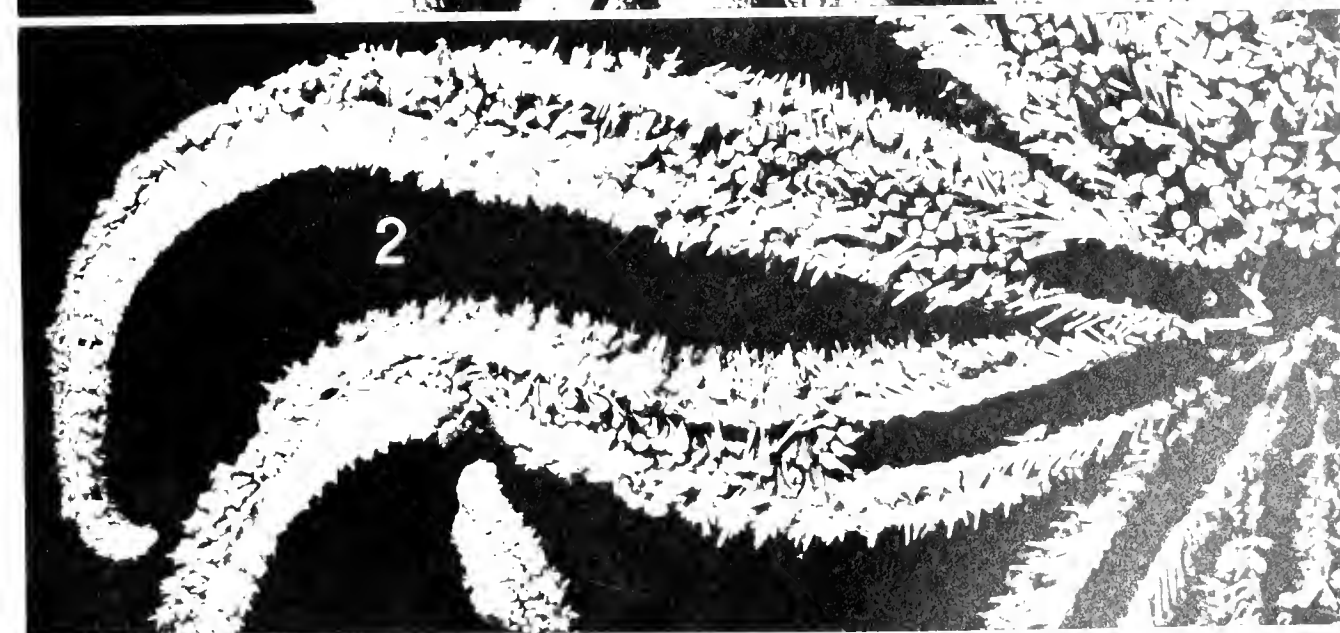
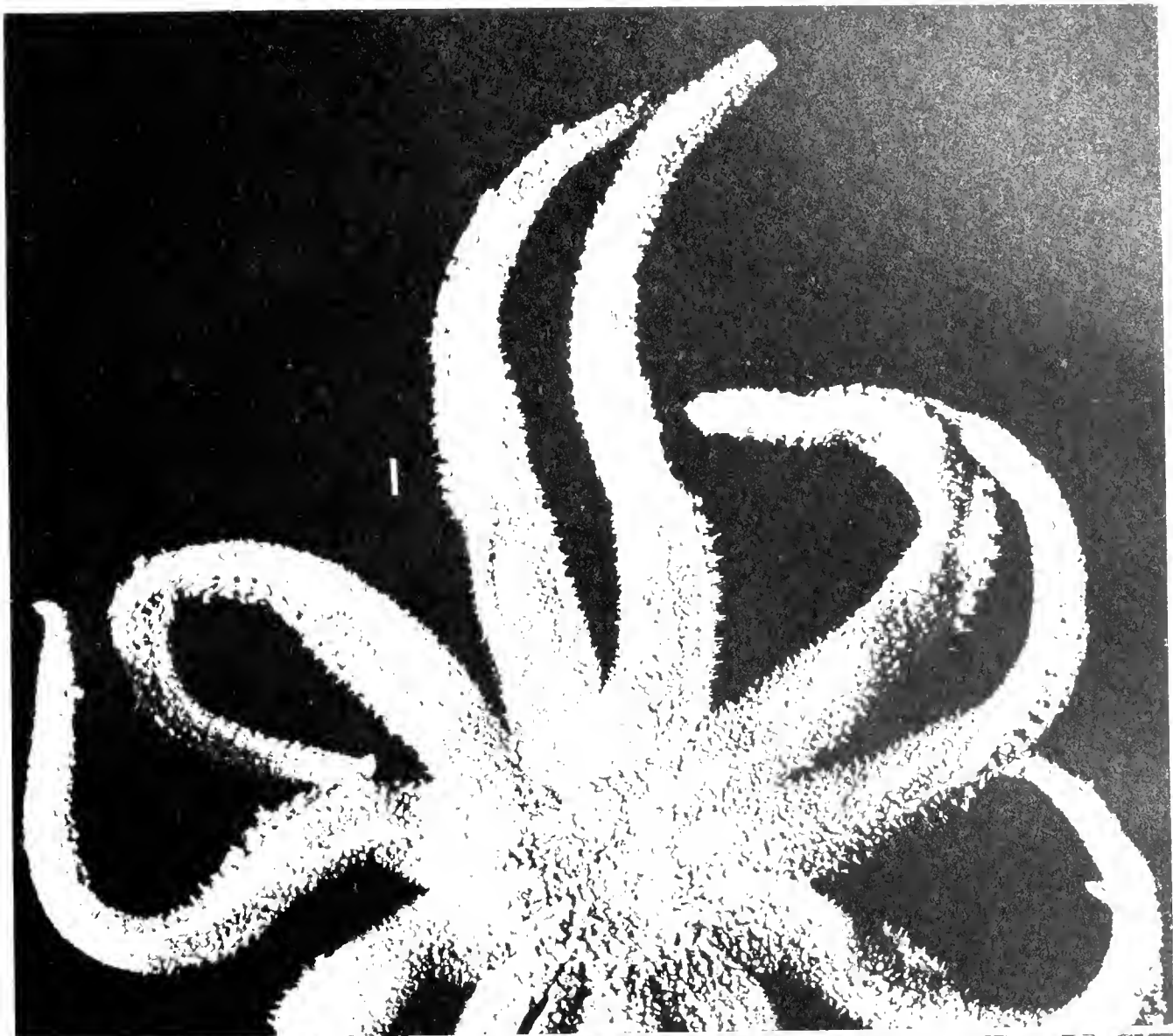


PLATE XIX

- Fig. 1. *Anasterias antarctica*, St. 1902, $\times 1.25$.
Fig. 2. *A. studeri*, St. WS 92, $\times 1.25$.
Fig. 3. *A. pedicellaris*, St. WS 81, $\times 1.25$.
Fig. 4. *A. minuta*, St. 55, $\times 2.5$.
Fig. 5. *A. conferta*, St. 53, $\times 2.5$.
Fig. 6. *A. stolidota* (Sladen), R 46 mm., Messier Channel, 'Challenger' expedition. Photographed by G. A. Smith. Dorsal view to show reticulate skeleton, $\times 2$.

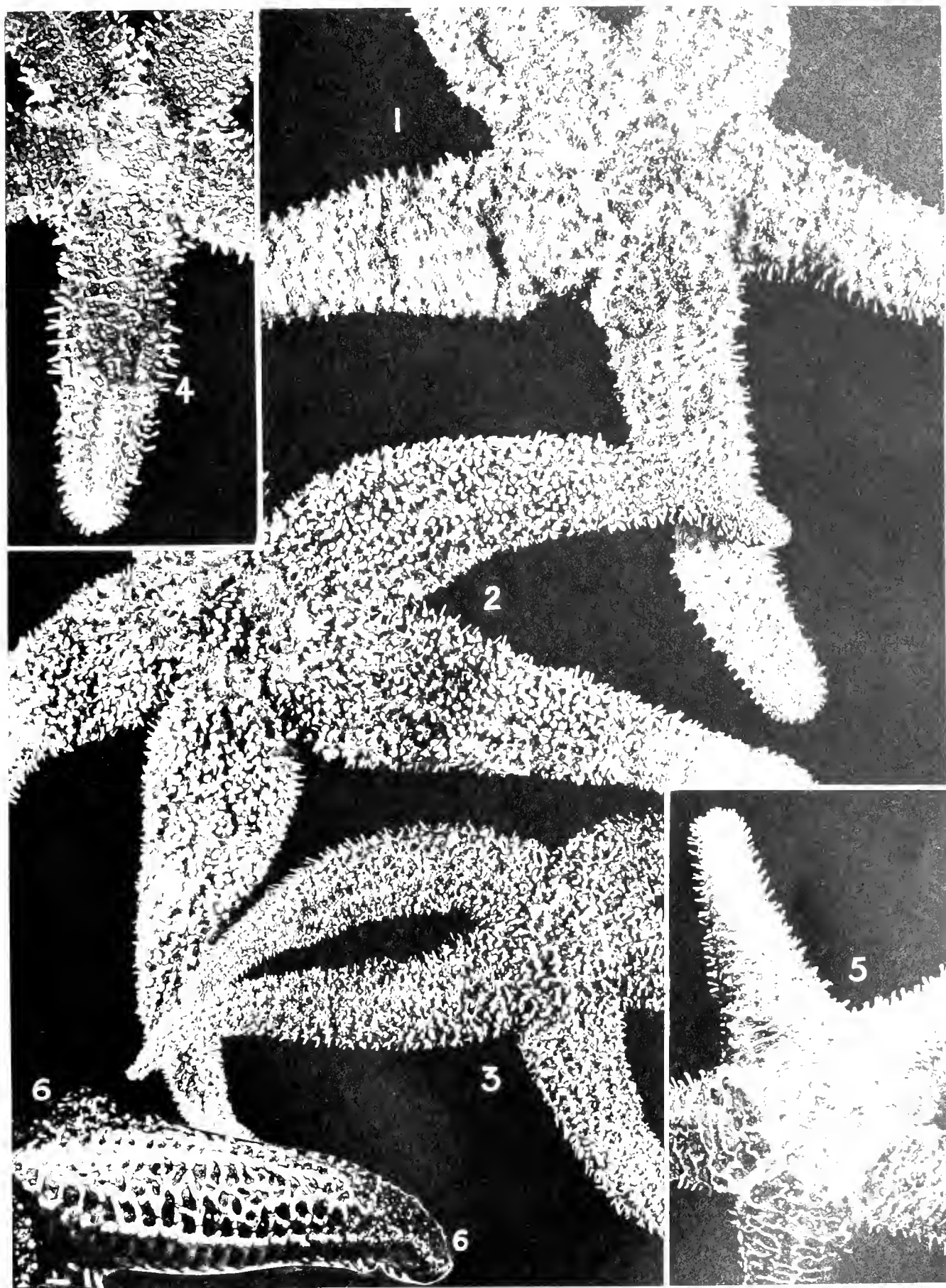


PLATE XX

- Fig. 1. *Lysasterias heteractis*, type, St. 70, $\times 2$.
Fig. 2. *L. hemiora*, type, $\times 1.3$.

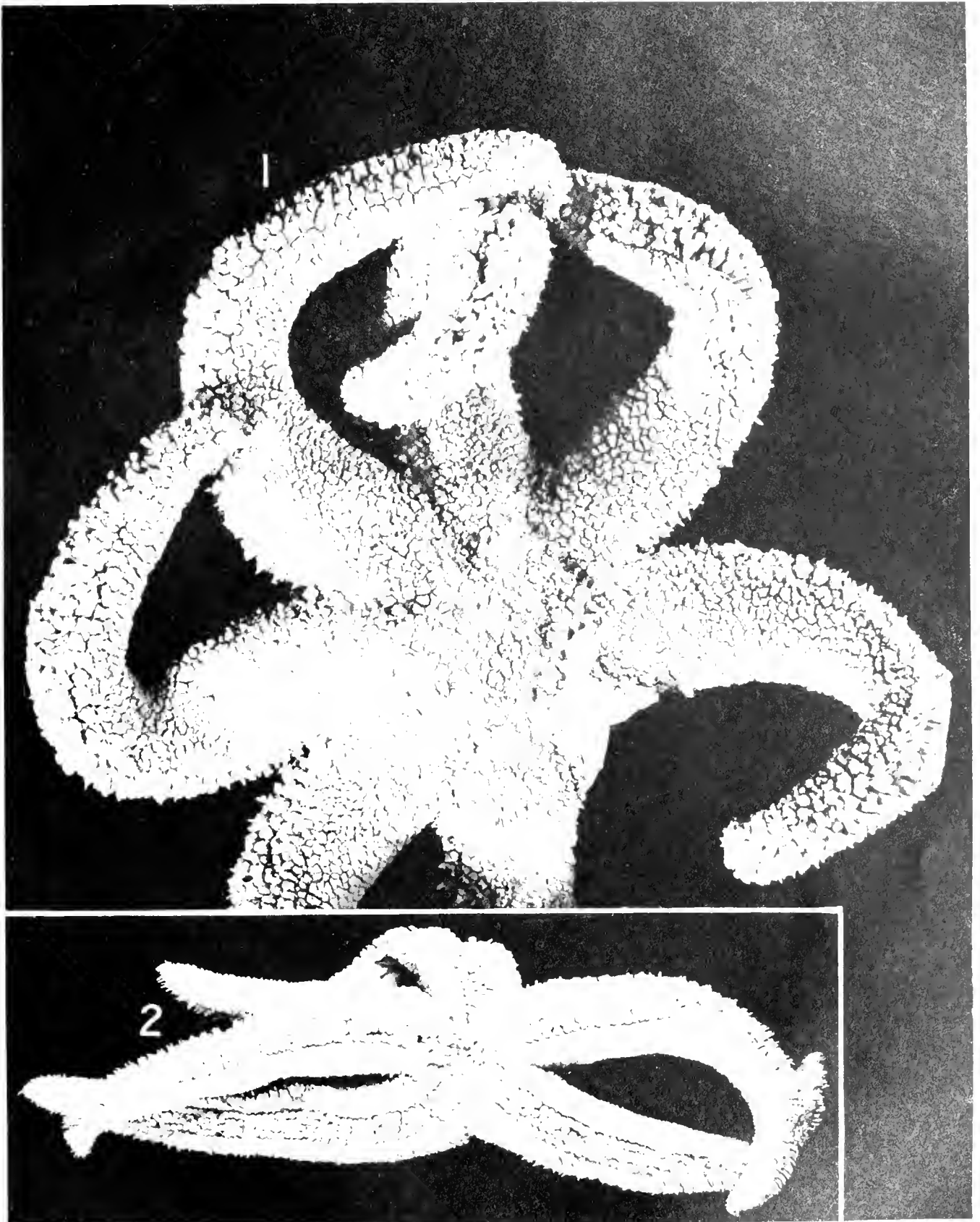


PLATE XXI

- Fig. 1. *Diplasterias octoradiata*, forma *eunota*, type, Undine Harbour, South Georgia, $\times 1.4$.
- Fig. 2. Same, type, $\times 1.3$. Coelomic side of the skeleton of ray which has been opened along ambulacral ridge and spread out.
- Fig. 3. *Diplasterias octoradiata*, forma *octoradiata*, St. MS 10, for comparison, $\times 1.3$.
- Fig. 4. *Diplasterias meridionalis*, St. MS 10, $\times 1.3$; prepared as figs. 3 and 4.

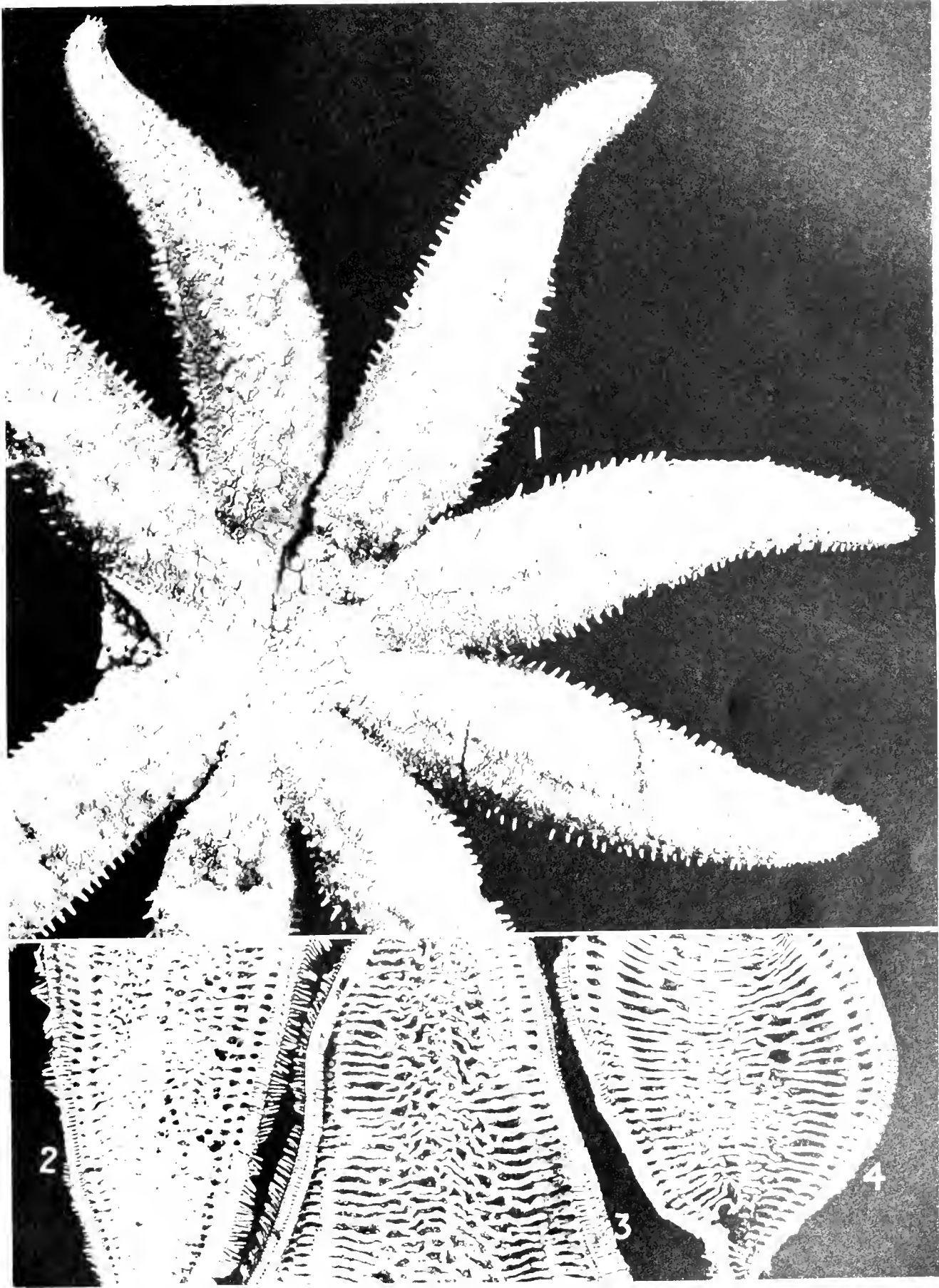


PLATE XXII

Fig. 1. *Diplasterias meridionalis*, St. WS 25, $\times 1.5$.

Fig. 2. *D. octoradiata*, forma *octoradiata*, St. WS 62, $\times 1.5$.

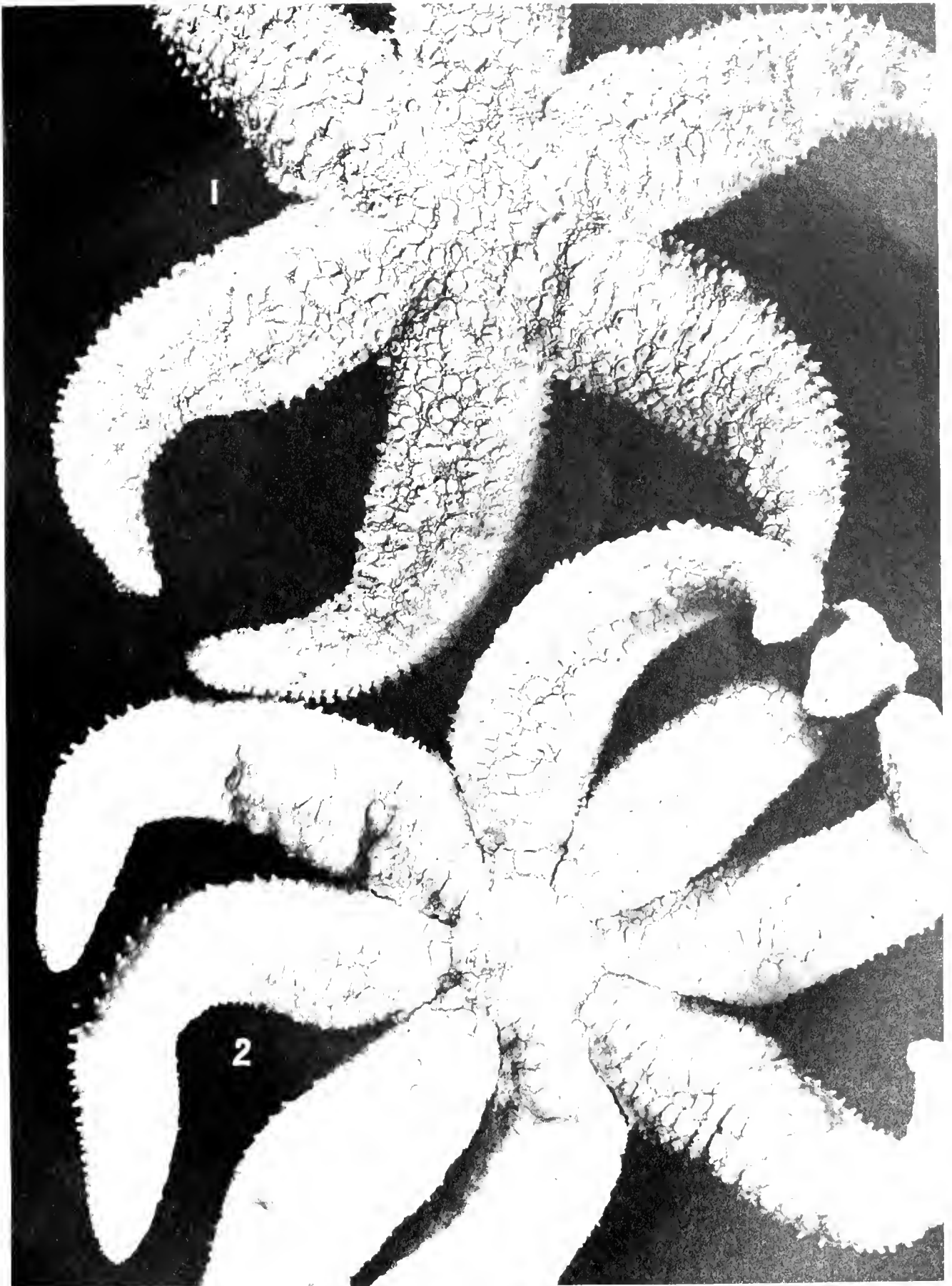
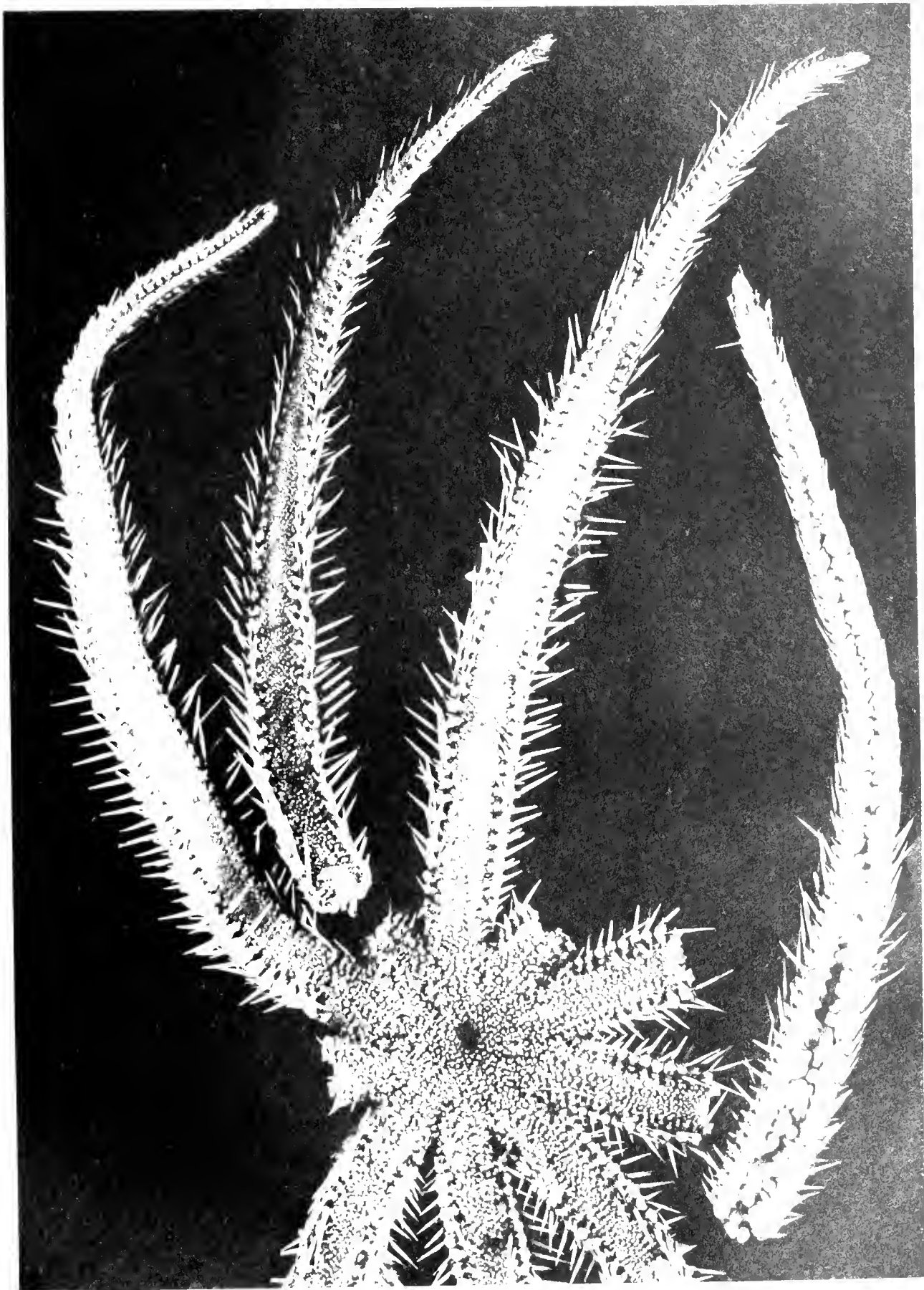


PLATE XXIII

Luidia heterozona, type. × 2.



Discovery Reports. Vol. XX, pp. 307-382, Plates XXII-XXVI, December, 1940.]

ON THE
STRUCTURE OF THE PHOTOPHORES
OF SOME DECAPOD CRUSTACEA

By
RALPH DENNELL, D.Sc.

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ON THE STRUCTURE OF THE PHOTOPHORES OF SOME DECAPOD CRUSTACEA

By Ralph Dennell, D.Sc.

(Plates XXIV-XXVI; Text-figs. 1-31)

I. INTRODUCTION

THE first authentic account of the presence of numerous well-defined photophores in a member of the Crustacea Decapoda appears to have been given by Hansen (1903). In a new species of *Sergestes* obtained by the Challenger Expedition and named by him *S. challengerii* he described the structure of a large number of small dermal bodies equipped with chitinous lenses, and expressed the view that their function was one of light production. It is true that before this, in 1886, Perrier had mentioned the existence of photophores in *Acantheephyra pellucida*, but his account appears to be of doubtful reliability (see Kemp, 1910b, p. 642, and Hansen, 1903, p. 76). Since then further observations on the structural details of Decapod photophores have been made, notably by Kemp (1910b), Terao (1917), and Ramadan (1938), but in general the available information on photophores is scattered throughout the literature relating to taxonomy.

It was with the object of examining the detailed structure of some of the many organs in the Penaeidea and Caridea which have either been suspected or have been definitely shown to be luminous that the present investigation was undertaken at the suggestion of Dr S. W. Kemp. To him I am deeply indebted, not only for the gift of all the material used and for the loan of his notes made on board the 'Discovery' and the 'Discovery II', but for much valuable advice and encouragement during the course of the work. My sincere thanks are also due to Professor H. Graham Cannon for his continued interest and helpful criticism, and for his kindness in photographing for me the sections represented in Plate XXIV, figs. 2-5, and Plate XXVI, figs. 1, 3, 4, and 6. Dr M. D. Burkenroad has kindly described to me the appearance of the liver photophores of living species of *Sergestes* and has given me much valuable information.

The work has been carried out in the Departments of Zoology of the University of Manchester and the Imperial College of Science and Technology.

II. MATERIAL AND METHODS

The material on which this work was begun consisted of a number of specimens from the Discovery Expeditions. They included species of *Sergestes*, one possessing a new type of superficial photophore, and the remainder with organs of Pesta, or luminous liver tubules; a number of specimens of *Parapandalus richardi*, also with

luminous liver tubules; and specimens of *Hoplophorus novae-zealandiae* and *H. grimaldii* with numerous well-differentiated superficial photophores. In some instances either the whole or parts of the animal had been fixed in the Duboscq-Brasil modification of Bouin; otherwise formalin sea water had been used. It was found as the work proceeded that the action of the formalin sea water had been somewhat erratic, fixation occasionally being extremely good, but more usually indifferent or poor. Where possible observations have been made on Duboscq-Brasil fixed material, the formalin-fixed specimens being used for comparison.

Later I received a single specimen of the rare *Systellaspis affinis*, preserved in formalin, from the John Murray Expedition, and one specimen of *Hoplophorus typus* and three of *Systellaspis debilis*, also in formalin, from the Dana Expedition. The specimens of *S. debilis* were beautifully preserved with regard to external appearance, much of the original pigmentation still remaining, particularly in the photophores. These, with the specimen of *S. affinis*, afforded the only instances in which pigmentation of the photophores was observed after varying periods of preservation.

The celloidin-paraffin method of sectioning has been almost exclusively used, and sections were usually cut $10\ \mu$ in thickness, although in some special cases sections as thin as $5\ \mu$ or as thick as $100\ \mu$ were found useful. Of the various staining methods employed Mallory's triple stain, usually with the addition of a mordant for the acid fuchsin (Anderson's modification), was found to be the most generally useful on account of the valuable colour differentiation obtained between the various tissues. For the details of nuclei, however, Heidenhain's haematoxylin was found necessary, and other stains, such as Delafield's haematoxylin and picro-indigo-carmin, have also been used.

In studying the carapace organs of the species of *Hoplophorus* whole mounts, stained in borax carmine or in paracarmine, were found to be of great value.

Most of the drawings are based on a number of similar sections, and have been made with the aid of a squared net micrometer eyepiece, or, in a few instances, by the use of a projection apparatus.

III. PENAEIDEA: SERGESTIDAE

1. THE SUPERFICIAL PHOTOPHORES OF *SERGESTES REGALIS* GORDON

In his notes on Crustacea made on board the 'Discovery' Dr Kemp recorded the positions of a large number of "clearly circumscribed deep purple spots" on the surface of the body of two large female specimens of a new species of *Sergestes*. The specimens have since been described by Dr I. Gordon and the list of numbers and positions of the purple spots quoted (Gordon, 1939). Dr Kemp says in his notes: "These purple spots are probably luminous organs: portions of tissue containing them have been dissected out and fixed in Duboscq together with a few of the appendages." Of these appendages there came into my possession for examination one maxilla and the external ramus of a uropod. The maxilla was described, with regard to the purple spots, as possessing three

on the exopod, while the external ramus of the uropod had "a row of four near the middle and another row of two or three at the distal end, the foremost in line with the tooth of the outer margin".

At the time when I examined the appendages, however, no trace of colour remained in these organs, and it required close examination to determine their position. Although colourless, the organs showed in surface view as small rather opaque areas possessing a faintly mosaic or granular appearance. Both the maxilla and uropod were sectioned for examination.

Study of the sections revealed the presence of well-defined structures (Fig. 1 *a, b*; Plate XXIV, fig. 1) occupying precisely the positions described by Dr Kemp, with the exception that the exopod of the maxilla bears four, not three, of these organs. Three are arranged almost in a longitudinal row, although the second is somewhat lateral to the first and third; while the fourth, which is larger than the other three, is placed on the opposite (morphologically anterior) side of the exopod. This last organ is illustrated in the figures.

The integument overlying the organ is not markedly differentiated from the adjacent surface of the limb, so that there is no lens as in the superficial photophores of *S. challengerii* (Hansen, 1903) and *S. lucens* (Terao, 1917 as *S. prehensilis*). At most, both cuticle and chitin may be somewhat thicker than elsewhere on the limb. The main mass of the organ beneath the integument is composed of fibres arranged in successive parallel sheets (Fig. 1 *a, fib.*), the fibres composing each sheet being interwoven in the horizontal,

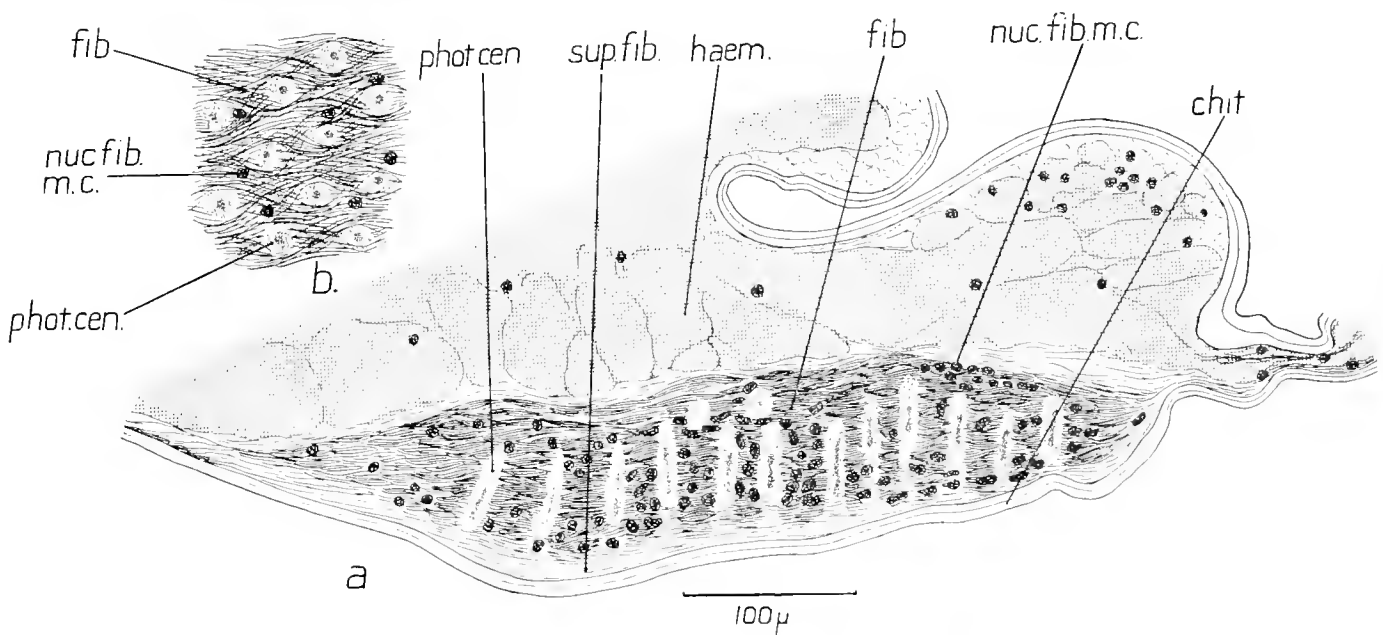


Fig. 1. *a*. Part of a longitudinal vertical section through the maxillary exopod of *Sergestes regalis*, showing one of the photophores. A photograph of the section appears in Plate XXIV, fig. 1. *b*. Part of one of the photophores seen in horizontal section at the level of the photogenic centres, to show the interwoven fibrous tissue. Both fixed Duboscq, Mallory's triple stain. *chit.* chitin; *fib.* interwoven fibrils; *haem.* haemocoel of the limb; *nuc.fib.m.c.* nucleus of fibril mother cell; *phot.cen.* photogenic centre; *sup.fib.* superficial fibres.

though not in the vertical plane (Fig. 1 *b*, *fib.*). The fibrous mass tapers fairly regularly around the periphery of the circular organ, but ceases abruptly at its margin, giving the clearly circumscribed appearance noted by Dr Kemp. Its dimensions are, in the various organs, of the order of $500\ \mu$ in diameter and $100\ \mu$ in thickness, and with Mallory's triple stain it assumes a deep blue colour slightly tinged with purple.

Embedded in the fibrous mass are numerous uniformly scattered small rounded nuclei, about $5\ \mu$ in diameter and staining vividly with acid fuchsin. They are apparently the nuclei of the fibre mother cells. In appearance they differ from the connective tissue nuclei found elsewhere in the limb. Between the deeply staining fibrous mass and the integument of the limb a delicate layer of fibres, staining lightly with aniline blue, may be seen (Fig. 1 *a*, *sup.fib.*). This layer is readily distinguishable from the deeper fibrous mass, but it is not clear whether it is to be regarded as having the same nature and derived from it, or whether it is a connective tissue layer like that on the inner side of the main fibrous mass.

The organ is cut off from the haemocoelic space of the limb on its inner side by a thin sheet of delicate connective tissue fibres, some of which are in connexion with the network of fibres extending across the blood space. Laterally the connective tissue layer extends beyond the organ as a thinner sheet on the inner side of the chitogenous epithelium.

The most remarkable feature of the organ, however, is the presence of rather ill-defined rod-like bodies which stand perpendicularly to the surface of the organ and occupy the centres of cylindrical spaces in the fibrous mass (Fig. 1 and Plate XXIV, fig. 1, *phot.cen.*). These rod-like bodies are rounded at their ends, and are about $15\ \mu$ long and $3\ \mu$ in diameter. With Mallory's triple stain they assume a yellowish brown colour. The cylindrical spaces in which they stand are otherwise filled with a finely punctate substance, which may be a coagulation, staining faintly blue with Mallory. That these spaces with their contained rods are the seat of light production (presuming the organ to be truly a photophore) appears to be indicated by the absence, or at any rate the much more feeble development, of the fibrous mass of the organ over their distal ends. This is clearly seen in Fig. 1. Such an arrangement would permit of the outward passage of any luminescence generated within the "photogenic centres", as I have called these structures. The granular appearance, in superficial view, of the photophores is clearly caused by the absence, at intervals, of the mass of densely packed fibres forming its main body.

Lens-less organs, believed to be luminous, have been recorded in *S. robustus* and related species (Illig, 1914; Hansen, 1919, 1922; Sund, 1920; Burkenroad, 1937).

These observations have been confirmed by Welsh and Chace (1938, p. 371) who, previous to obtaining histological preparations, express the view that the pigmented structures observed by them are actually luminescent in life. It should be mentioned, however, that Hansen (1922, pp. 97, 120) expresses some doubt that this is their function, since they lack a well-defined lens. Later in this paper it will be shown that unquestionable photophores may be without a lens.

Burkenroad (1937, p. 317) describes the structures in freshly caught specimens of *S. richardi* [= *crassus*] as "lenticular transparent structures invested on their inner sides by a layer of vermilion pigment". Further, after receiving information from me on their structure, this author has examined the photophores of *S. regalis*, and informs me in a private communication that their colour in life is caused by the dense pigmentation of the rod-like bodies, the fibrous portion of the organ being translucent. The organs of *S. regalis* and *S. richardi* are therefore different in structure, and a detailed histological examination of all these lens-less organs in the genus *Sergestes* is therefore very desirable.

None of the organs studied in *S. regalis* showed any trace of innervation, but all were in close proximity to the blood space of the limb. This relation of a photophore to a vascular area has been noted several times in the course of the present work.

It would appear that organs of the above type can have no evolutionary relationship with the lensed organs occurring in *S. challengerii* and its allies (Hansen, 1903; Kemp, 1910 *b*; Terao, 1917). Here in *S. regalis* there is no lens, and the source of luminescence is not a regularly arranged cellular mass. The precise significance of the distribution of these two types of superficial luminous organs within the Group I in *S. regalis* of Hansen's scheme is of course a matter for the taxonomist working on a large collection.

In its development the photophore presumably has an ectodermal origin, as its inner sheath of connective tissue continues outwards underneath the general chitogenous epithelium, of which the photophore is probably a specialized portion.

The origin of the rod-like bodies in the photophores of *S. regalis* is not apparent. They are not bounded by any definite limiting membrane which would suggest a nuclear membrane and their staining reactions are not those usually exhibited by nuclei. It is possible, however, that they may be derived from nuclei and that the surrounding cylindrical spaces may represent the cytoplasm of the corresponding cell. We are accustomed to the occurrence of regularly arranged photogenic cells, with definite nuclei, in crustacean photophores (e.g. Euphausiacea, *S. challengerii*, pleopod photophores of *Systellaspis debilis*), but as I shall show (pp. 334, 358) there is strong evidence that in the development of many of the photophores of members of the Hoplophoridae the nuclei of the photogenic cells may undergo very profound changes. The rods and spaces making up the photogenic "units" of the photophores of *Sergestes regalis* may represent a parallel phenomenon.

The mode of functioning of this type of photophore is not very clear. If my interpretation is correct, and the structures I have described as "photogenic units" are truly light producers, then it appears that the organ may be visible from the exterior in two ways. First, the spaces in the fibre mass immediately distal to the rods, acting as windows, would allow of the passage of light to the exterior through the chitin, so that, if this were all, the organ would be visible merely as a group of minute points of light. Second, light emitted laterally, that is, more or less in the plane of the fibres, might undergo successive reflexion and scattering from their surfaces so that they themselves would be illuminated and the organ then appear as an illuminated mass.

As far as I am aware none of the photophores of this type have ever been observed in a state of active luminescence.

2. THE ORGANS OF PESTA (LUMINOUS LIVER TUBULES) IN *SERGESTES CORNICULUM* KRÖYER,¹ *S. SARGASSI* ORTMANN, *S. DIAPONTIUS* BATE, AND *S. EDWARDSI* KRÖYER

The organs of Pesta, or presumed internal cephalothoracic organs which occur in various members of the genus *Sergestes*, are groups of modified liver tubules. They are ventrally directed, and are closely compacted and denser than the normal liver. They are first mentioned by Pesta (1918, p. 10), and an account of their appearance derived from a study of dissections of freshly caught material is given by Burkenroad (1937). The latter author describes the distal (ventral) parts of the tubules as being Antwerp blue in colour in the living animal, the upper parts white, while the normal liver itself is translucent. "That part of the tunic of the gastric gland which covers the dorsal parts of the areas of modified tubules bears a dense layer of carmine chromatophores", so that each photophore is "covered dorsally with a carmine cap". He also describes the variation in number and arrangement of these groups of modified tubules that occur in the genus, and points out that whatever their arrangement an antero-lateral pair situated just above the branchial chamber and immediately behind the base of the mandible is always visible externally through the transparent branchiostegite, while a posterior pair of organs often show "through the gap in the lateral musculature just above the branchial area of the thirteenth somite".

According to Burkenroad, organs of Pesta "appear to be present in all members of the genus other than the *S. mollis*, *S. tenuiremus*, *S. robustus*, and *S. challengerii* super-species of Hansen's 'Group I'". But Welsh and Chace (1938) describe the occurrence in *S. tenuiremus* of organs which closely parallel the structures described by Kemp (1925) in three species of Pandalids from the Indian Ocean. The organs of these Pandalids are almost certainly, from the description given, composed of groups of modified liver tubules, closely similar to those of *Parapandalus richardi* (p. 323), and it would therefore appear that the structures in *Sergestes tenuiremus* are organs of Pesta, in direct opposition to the above-quoted statement by Burkenroad.

Critical examination, however, of Welsh and Chace's account of these structures makes it unlikely that they are truly organs of Pesta. They are described as "large, whitish organs found in the coxae of the last pair of thoracic legs near the opening of the vasa deferentia": each organ is composed of "a cluster of three large photophores with well-developed lenses entirely enveloped by the surrounding tissues". It is perhaps possible that these organs are in reality spermatophores, since they were discovered in a large male specimen: I have seen sections of *Meganyctiphanes norvegica* in which the spermatophores had a very similar staining reaction and superficial appearance to

¹ While this work was in the press specimens identified as *Sergestes corniculum* by Dr Kemp were sent at his suggestion to Dr M. D. Burkenroad for his opinion. Although belonging to the "*corniculum*" group of the subgenus *Sergestes* they are actually specimens of *Sergestes semimudus* Hansen.

the lenses of the posterior thoracic photophores. At all events the account given by Welsh and Chace should be accepted with caution. (I have since received information from Dr M. D. Burkenroad that through the kindness of Drs Welsh and Chace he has been privileged to examine their sections, which show that the supposed photophores are actually "the expanded terminal portion of the vas deferens with its included secretions. This portion of the male genital apparatus of *S. tenuiremus* does not differ particularly from the same structure in males of other species of the genus.")

Dr Kemp made a number of observations on these luminous liver tubules on board the 'Discovery' and has allowed me to consult and quote from his notes. He remarks that the species of *Sergestes* can be separated, according to colour, into two groups, those which are uniformly red, and those which are red anteriorly with the last three abdominal somites, tail fan and limbs colourless. All the specimens of the known Atlantic species belonging to this latter or "half-red" group taken by the 'Discovery' possess two pairs of large organs, one pair anterior and situated above the maxilla, and one above the last gill. These organs may be luminous. In two cases (*S. sargassi* and *S. armatum* (?)) he describes them as having their bases deep purplish black or black, and their upper parts shining red. They are undoubtedly organs of Pesta.

I have had the opportunity of examining specimens of *S. corniculum*, *S. sargassi*, *S. diapontius*, and *S. edwardsi*, all of which possess these organs. Burkenroad (1938, p. 317) states that in *S. corniculum* there are as many as ten distinct groups of modified liver tubules: all of these I have identified and examined. In this species, in addition to the usual large antero-lateral pair, a smaller antero-median organ is situated between and a little behind them, and posteriorly a prominent postero-lateral pair have between them a smaller postero-median organ. Situated between these two groups of organs are a further two pairs, lateral in position, making up the full complement of ten mentioned by Burkenroad.

In both *S. diapontius* and *S. edwardsi* there are five distinct organs; an antero-lateral pair, one single antero-median, and a postero-lateral pair. *S. sargassi* lacks the single antero-median organ, having only the antero-lateral and postero-lateral pairs.

Since the structure of the modified liver tubules in the four species I have examined appears to be identical, the following description is based on the condition found in *S. corniculum*, of which I had most specimens. Fig. 2 indicates the position of the antero-lateral pair of organs as seen in a transverse section of the animal: the antero-median organ occurs some little distance behind the plane of this section. It will be seen that the organs (Fig. 2, *lum.l.*) are borne on the ventral surfaces of two anteriorly directed lateral horns of the liver (Fig. 2, *dig.l.*), the individual tubules projecting forwards and downwards, and coming into close proximity to the roof of the branchial chamber anteriorly. It is true that, as Burkenroad says, they are visible to the exterior through the wall of the branchial chamber, but apart from this any light they may produce must be most intense in the anterior part of the branchial chamber, since they are only separated from it by a delicate sheet of the integument. The lateral and postero-lateral organs also must, if luminous, illuminate the posterior part of the branchial chamber to

a considerable extent. The interest of this situation of the organs of Pesta will be discussed later (p. 371).

Examination of sections of the individual tubules shows that they are composed of columnar cells arranged in well-defined histological groups. In Fig. 3 is seen an oblique section through a tubule, enlarged from the section seen in Fig. 2 (see also Plate XXIV, figs. 2, 4). The obliquity of the section approximates almost to the longitudinal axis of the tubule, the structure of which is therefore clearly seen in both dorsal and ventral regions.

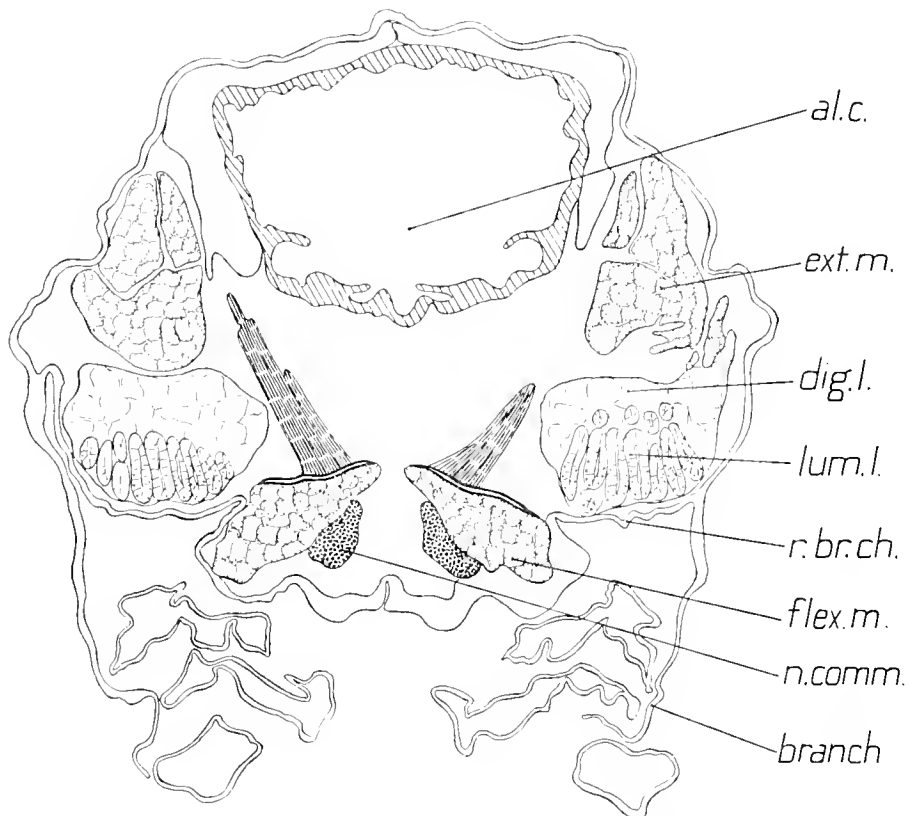


Fig. 2. Transverse section through the cephalothorax of *Sergestes corniculatum* at the level of the anterolateral liver photophores. Fixed Duboseq, Mallory's triple stain. $\times 52$. *al.c.* alimentary canal; *branch.* branchiostegite; *dig.l.* digestive portion of the liver; *ext.m.* longitudinal extensor muscle; *flex.m.* longitudinal flexor muscle; *lum.l.* tubules of the luminous portion of the liver; *n.comm.* commissure of the ventral nerve cord; *r.br.ch.* roof of the branchial chamber.

Ventrally the cells forming the blind tip of the tubule (Fig. 3, *l.c.*) are not remarkable. Their cytoplasm, at any rate after the fixative employed, is homogeneous, there being no inclusions or intracellular structures other than the nucleus, which is situated basally, that is, remote from the lumen of the tubule. The nucleus is about $10\ \mu$ in its greatest dimension, and has its chromatin fairly regularly arranged upon the linin meshwork. These ventral cells are smallest at the tip of the tubule, are sharply differentiated from the cells above them, and form a more or less homogeneous double concave lens-like cap at the distal end of the tubule. It is highly probable that if the tubules prove to be luminous this cap plays the part of a condenser in concentrating the light rays.

Dorsal to the above cells, which may be referred to as lens cells, occurs a zone, seven or eight cells in depth, possessing a pronouncedly different structure. The cells composing it (Fig. 3 and Plate XXIV, fig. 4, *vac.c.*) are columnar, of almost uniform size, and are regularly arranged. Each cell is highly vacuolated, its cytoplasm being distributed in a uniform and well-defined layer around the sides and basal end of the cell, while at the distal end (that nearest the lumen of the tubule) it forms a deeper zone, which is in turn

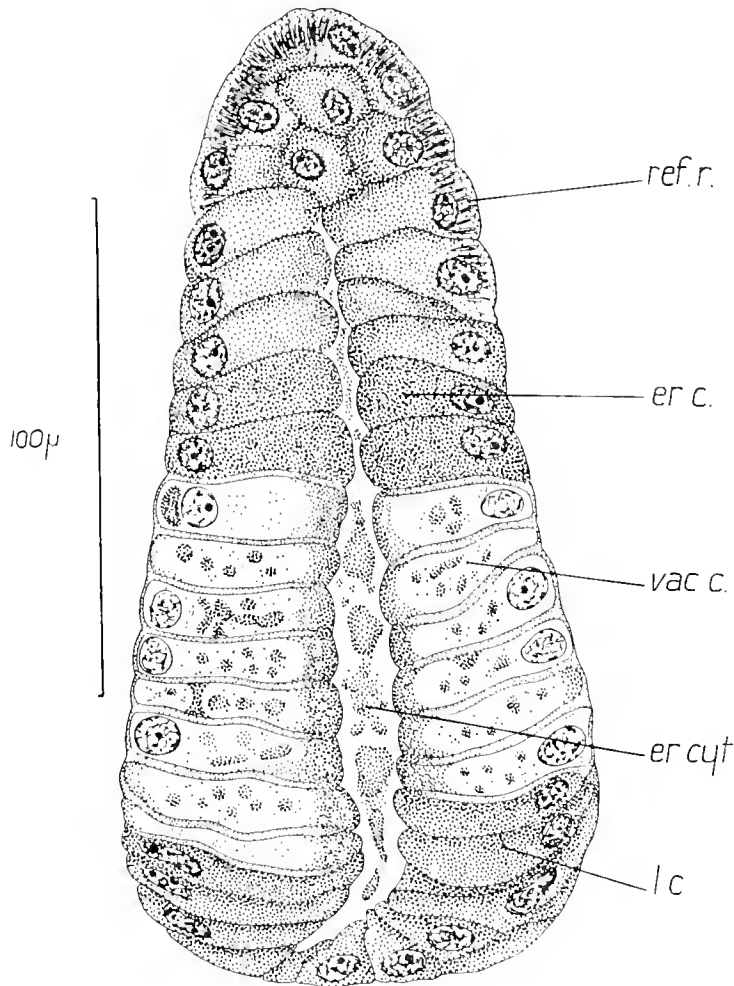


Fig. 3. Oblique transverse section through one of the tubules of the antero-lateral portion of the liver of *Sergestes corniculum*, enlarged from the section seen in Fig. 2. *er.c.* erupting cell of tubule; *er.cyt.* erupted cytoplasm lying within the lumen of the tubule; *l.c.* "lens" cell; *ref.r.* refractile rods; *vac.c.* vacuolated cell.

vacuolated and presents a frothy appearance. This vacuolated distal tip is best developed in the more ventral cells of this zone and progressively disappears in passing to the more dorsal cells, which possess only a uniform distal mass of cytoplasm thicker than that around the remainder of the periphery of the cell. As a result of this arrangement of the cytoplasmic portion of the cell, the greater part of the cell body is occupied by a large vacuole, within which float scattered masses of cytoplasm having apparently the same

structure as the remainder of the cytoplasm. The appearance of this zone of cells suggests considerable secretory activity.

The nuclei of this zone are of the same size as those found elsewhere in the tubule, but do not possess any prominent amount of chromatin, some indeed being conspicuous by their lack of it. On the whole, however, they resemble those of the ventral "lens" zone.

The third zone, beginning immediately above the vacuolated zone, is not very sharply differentiated from the fourth or most dorsal zone, in fact it may not be justifiable to regard these two as constituting separate and distinct zones. They are distinguished from each other by the occurrence in the cells of the fourth zone of spindle-shaped inclusions (Figs. 3, 4, *ref.r.*) which will be described later. The cells of the third zone (Fig. 3 and Plate XXIV, fig. 4, *er.c.*) are very similar in size to those of the preceding zone, but show no trace of vacuolation. Their cytoplasm is dense and almost uniformly distributed, being only very slightly denser at the distal tips of the cells than elsewhere. Furthermore, the cytoplasm of the upper cells of this zone is somewhat less dense than that of the lower cells. Owing to their apparent peculiar behaviour I have called the cells of this zone "erupting cells". In some of my preparations the conditions represented in Fig. 4 are seen. Most of the cells of this zone possess a prominent nucleus with a considerable amount of chromatin, usually condensed into a central chromatin knot. From this knot radiate irregular chromatin strands, and further chromatin is deposited on the inner wall of the nuclear membrane. This may be called the usual condition of the resting nucleus of an erupting cell (Fig. 4, *n.n.er.c.*). Other nuclei, far less numerous however, are remarkably deficient in chromatin, having only small irregular deposits placed on a coiled linin thread, or having merely a small central chromatin mass, the remainder of the contents of the nuclear membrane consisting of a substance with a very finely granular appearance (Fig. 4, *deg.n.er.c.*). There can be little doubt that these are phases in the degeneration of the normal nucleus. In several preparations the cytoplasm of one or more cells of this zone had erupted almost completely into the lumen of the tubule. Fig. 4 shows such a cell, the nucleus of which is almost achromatic (*deg.n.er.c.*). Lying in the lumen of the tubule are two nuclei (*deg.n.*) in a more advanced state of degeneration. The lumen of nearly every tubule examined contained irregular masses (Fig. 3 and Plate XXIV, fig. 4, *er.cyt.*) having the staining properties of the cytoplasm of these cells, and presumably having had their origin in this eruption. It appears probable, then, that the cells of the third zone regularly erupt their contents into the lumen of the tubule, but although special search has been made no indications of proliferation on the part of neighbouring cells, which would result in regeneration of this part of the tubule, has been observed.

The fourth, or most dorsal, zone of the cells composing the tubule shows no essential differences from the previous zone, excepting the presence of the rod-like bodies already mentioned. The cells are of the same size as those of the preceding zone, their staining reactions are the same, and the occasional occurrence of nuclei deficient in chromatin in the more ventral cells of this zone (Fig. 4, *deg.n.ref.c.*) indicates that

perhaps they too may undergo eruption in a similar manner. This would lead to the belief that there is no hard and fast distinction to be drawn between the cells of these two zones.

The rod-like bodies (Figs. 3, 4, *ref.r.*) which alone distinguish the dorsal cells of the luminous portions of the tubules are slightly refractile spindle-shaped bodies, staining deeply in acid fuchsin and arranged perpendicularly at the basal ends of the cells. They do not extend completely to the basal end of the cell, for their tips end some little distance from it, leaving a narrow but clear basal zone of cytoplasm. In haematoxylin-stained preparations the rods are not visible.

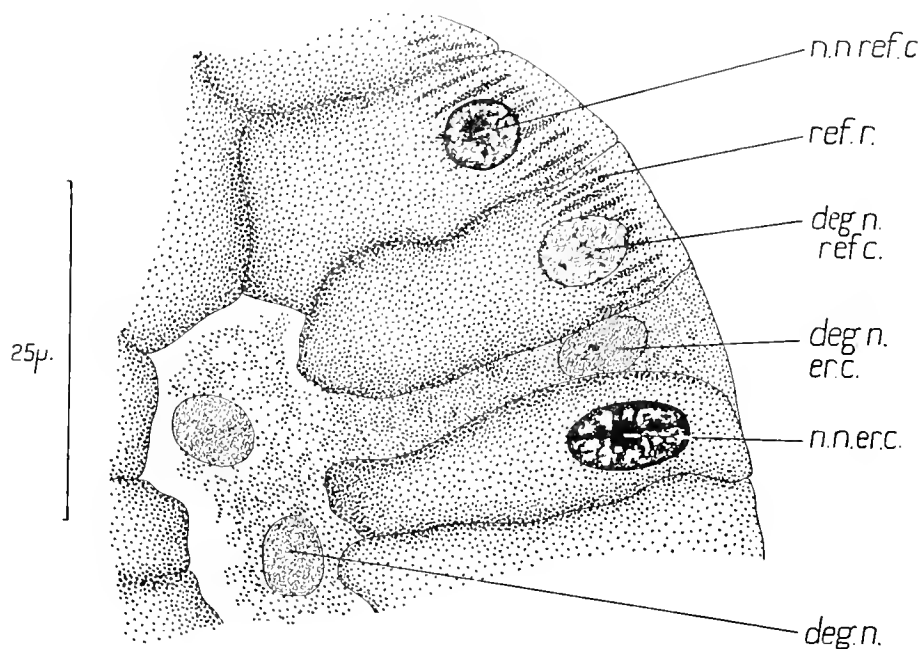


Fig. 4. The dorsal portion of one of the luminous liver tubules of *Sergestes corniculum*. Fixed Duboscq, Delafield's haematoxylin and eosin. *deg.n.* degenerate nucleus lying in the lumen of the tubule; *deg.n.erc.* degenerating nucleus of an erupting cell; *deg.n.ref.c.* degenerating nucleus of a reflecting cell; *n.n.erc.* normal nucleus of an erupting cell; *n.n.ref.c.* normal nucleus of a reflecting cell; *ref.r.* refractile rod.

The cells intervening between the dense luminous tubules and the digestive tubules themselves are not remarkable. It should be stated that the normal liver tubules of *Sergestes* are composed of highly vacuolated irregularly shaped cells whose nuclei are almost completely achromatic. They thus have a very delicate and tenuous appearance, and the organs of Pesta by contrast are very conspicuous. The intervening cells under discussion are denser than those forming the digestive tubules, and their nuclei are rich in chromatin.

The cellular differentiation of the luminous tubules bears a considerable, if not complete, relation to the coloration of the organs of Pesta as seen in fresh material (pp. 314, 315). The lower portion of the organ is described as Antwerp blue (Burkenroad) or purplish black (Kemp), and would appear to be composed of those ventral parts of the

tubules up to the termination of the highly vacuolated zone. The upper erupting and rod-containing zones of the tubules appear to form the upper white portion of the organ in Burkenroad's description (1937). In preserved and sectioned material the limits of the carmine pigment cap cannot be determined.

The optical and physiological qualities of Pesta's organ, if it be truly a luminous organ, can only be suggested. It is possible that the dorsal cells with their contained refractile rods, together with the dorsal external pigment cap, form a reflector; that the ventral lenticular termination of the tubule acts as a lens; and that the intervening zones of cells are concerned in the active production of light. Whether the vacuolated or the erupting zone, or both, form the centre of luminescence, or whether the lumen of the tubule itself may be occupied by a luminous secretion, is of course a matter for speculation, but the tentative suggestion may be offered that it is the lumen of the tubule itself which contains the luminous material.

It was first shown by Dubois and later abundantly confirmed by other workers that the production of luminescence in arthropods results from the interaction of the substances luciferin and luciferase in the presence of oxygen and water. (A convenient review, with a valuable reference list, of work on the physiology of light production in the arthropods is given by Maloeuf (1937).) It is possible that the vacuolated and the erupting zones of cells in the tubules are concerned with the production and discharge into the lumen of the tubules of these two substances, luciferin and luciferase. Certainly the appearance of the cells suggests the active production of two dissimilar substances. If this is correct the lumina of the tubules are the seat of light production. Harvey (1919), however, states that in the ostracod *Cypridina hilgendorfi* the enzyme luciferase alone is located in the photogenic cells, the luciferin being distributed in various tissues. Whether this is so in Crustacea generally is unknown. But until the organs of Pesta have been unequivocally shown to be photophores and their physiology to some extent elucidated further speculation is unwarranted.

3. THE BRANCHIAL CHAMBER PHOTOPHORES OF *SERGESTES CORNICULUM*, *S. SARGASSI*, *S. DIAPONTIUS*, AND *S. EDWARDSI*

While examining the liver photophores of the above species, a glandular streak extending longitudinally in the roof of the branchial chamber was observed in all the specimens. There is considerable reason for regarding this structure, provisionally at least, as a photophore. It occupies precisely the same position as the organs noted by Hansen (1903) on the lateral face of the branchiostegite of *S. challengerii*, and later shown by Kemp (1910*b*) to be internal, facing inwards and downwards on to the gills.

The glandular streak is rather less than 1 mm. in length in a specimen of *S. corniculum* measuring 4.2 cm. It is first seen in a section a little behind the level of the section illustrated in Fig. 2, where it lies on the inner face of the lateral wall of the branchial chamber just below its junction with the body. It runs backwards at this level for some 80 μ , and then, without interruption, turns on to the roof of the branchial chamber, and extends backwards parallel with the body for a further 240 μ . For the

remainder of its length, another 560μ , it slopes obliquely inwards on the roof of the branchial chamber, so that its posterior end lies immediately above the most anterior gill.

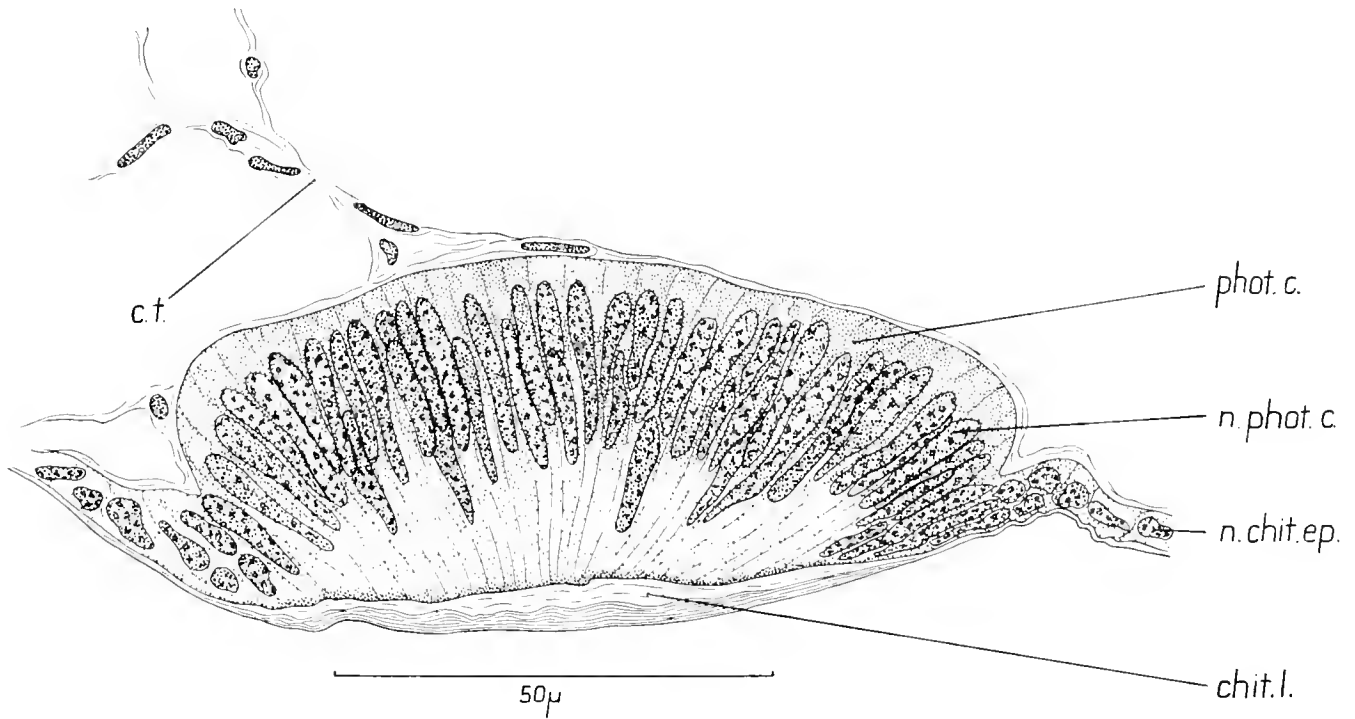


Fig. 5. Transverse section through the photophore in the roof of the branchial chamber of *Sergestes corniculum*, a little behind the level of the section shown in Fig. 2. Fixed Duboscq, Mallory's triple stain. *chit.l.* chitinous lens; *c.t.* connective tissue; *n.chit.ep.* nucleus of chitogenous epithelium; *n.phot.c.* nucleus of photogenic cell; *phot.c.* photogenic cell.

The structure of the streak is indicated in Fig. 5. It is composed of extremely narrow columnar cells (Fig. 5, *phot.c.*), their limits only partially defined, converging on a slight thickening of the integument (Fig. 5, *chit.l.*) forming the roof of the branchial chamber. In conformity with this arrangement the cells are tapered, the elongated nuclei (Fig. 5, *n.phot.c.*) occupying the inner broader ends, which show a denser cytoplasm than the narrower ends. The nuclei, which are in general about half the length of the cells, possess regularly scattered chromatin producing a granular appearance. Some 30–40 cells make up the breadth of the organ. On its inner and outer sides the cells of the organ progressively merge with those of the general chitogenous epithelium (Fig. 5, *n.chit.ep.*), of which they are specialized portions.

The thickening of the integument already mentioned is lens-like in section. It shows two clearly defined layers of equal thickness, the outer of which is closely striated, and the inner only slightly so. These layers are not distinguishable in the much thinner chitin lining the branchial chamber, although this may be merely on account of its delicacy.

Investing the organ on its inner side and separating it from the blood space behind it is a thin layer of connective tissue, occasional strands of which traverse the blood space.

No nerve has been observed actually in connexion with the photophore, although in some sections a small nerve was seen to terminate rather abruptly in its neighbourhood. It may be possible that this is the photophore nerve, the intervening portion not being readily apparent with the methods employed.

The organ just described is clearly very different from those in the branchial chamber described by Hansen (1903) and Kemp (1910*b*) which possess a prominent nerve supply and are identical in structure with those found elsewhere in the body. In view of the fact that the branchial chamber photophores are in structure precisely the same as those scattered profusely over the surface of the body, it may be possible that those species of *Sergestes* having the longitudinal streak in the branchial chamber have also photophores of similar structure in other parts of the body. Although search has been made this has not been confirmed. No colour was retained by these specimens after preservation for a considerable time, and such structures, presumably pigmented in life, would not be readily apparent.

The occurrence of this supposed photophore in the branchial chamber in *S. corniculum*, *S. diapontius*, *S. sargassi*, and *S. edwardsii* may prove to have some taxonomic importance. After mentioning the "complex photophores" of *S. challengerii* and its allies, and the "simple subcuticular bodies" of *S. robustus* and its close relatives, Burkenroad (1937, p. 317) says: "Superficial and presumably ectodermal or mesodermal photophores of these types, which have no structural relation at all to the endodermal organs of Pesta, seem to be absent in all the species in which the latter occur." The branchial chamber organ of *S. corniculum* and its allies, of apparently ectodermal origin, has no relation to the organs of Pesta, and if it should be proved to be truly luminous its presence would call for modification of the above-quoted statement by Burkenroad.

In considering the significance of photophores in the branchial chamber roof, whether several and complex, as in *S. challengerii*, or single and relatively simple, as in *S. corniculum*, the position of the organs of Pesta, also inevitably illuminating the branchial chamber, must not be lost sight of. Whatever may be the various uses subserved by luminous organs in the Decapoda, the presence of these structures emitting light on to the gills adds still further complexities to any speculation.

IV. CARIDEA: PANDALIDAE

Parapandalus richardi (Coutière)

In examining freshly caught specimens of *P. richardi* (Coutière, 1905, p. 18, as *Stylopandalus*) on board the 'Discovery', Dr Kemp noted two groups of structures which in his opinion may possibly be luminous organs. He says in his notes made at the time: "Pleopods colourless, but with a deep red spot at base of endopod in first three pairs only", and also: "The patches of red pigment on the pleopods may be

luminous organs and it appears very probable that the two pairs of large organs on the carapace may have this function. Of the latter, one is situated at the base of the mandible, beneath the carapace, and one pair postero-dorsally underlying both the posterior edge of the carapace and the tegument of the first abdominal somite. In fresh material the organs have the form of rounded cones, their sides shining red, and their bases, which are directed downwards and backwards, dark purplish black. On dissecting out the posterior organs they were found to be attached to the liver and on pulling this from under the carapace it was found that the two mandibular organs were also attached to it anteriorly. Specimens preserved, fixed in Duboscq. No trace of light was observed in the specimens, some of which were alive when brought on board."

Examination of these structures leads me to support the view expressed by Dr Kemp that the liver organs are almost certainly photophores; the pleopod organs are perhaps so, but with less probability.

1. THE LIVER ORGANS

The structure and disposition of the liver of *P. richardi* was first studied in a series of thick sagittal celloidin slices. The main mass of the liver occupies its customary position in the cephalothorax, and is composed of closely packed blind tubules with a characteristic structure. The walls of these tubules are made up of somewhat pyramid-shaped cells, each containing at least one very large vacuole. Their nuclei are basally situated. The bases of the cells are contiguous with each other, and form the outer wall of the tubule, but the sides of the cells are not in contact. The tips of the cells therefore project into the lumen of the tubule, which thus assumes an irregular stellate appearance as seen in transverse section. It may be said at once that the structure of the modified tubules differs profoundly from that shown by the normal tubules just described.

The modified liver tubules do not occur in the main mass of the liver, but constitute two pairs of well-defined outgrowths or horns. The anterior pair, the mandibular organs, arise antero-laterally, and extend downwards and forwards so that their tips come into close relation with the bases of the mandibles. The posterior pair of outgrowths occur dorsally and postero-laterally, and project upwards and backwards from the main mass of the liver. In the borax carmine-stained sections these projecting horns are seen to be of denser and more compact composition than the rest of the liver, and furthermore show a slight but definite yellowish hue.

With the specimens in my possession was a mandible with an adhering mass of liver tubules—the mandibular organ. This is illustrated in Fig. 6, the arrow showing the level of the transverse section seen in Fig. 7 and Plate XXIV, fig. 3. A study of the transverse sections obtained from this structure clearly reveals the composition of the modified tubules. Each tubule of the projecting horn as it leaves the main mass of the liver is composed of the normal vacuolated cells just described. Soon, however, its walls are formed by denser non-vacuolated cells (Figs. 7, 8, *l.c.n.v.*) which are responsible for the denser structure of the organ as compared with the rest of the liver. These denser cells extend almost to the tip of the tubule, which is made up of cells of a very different

character (Figs. 7, 8, *phot.c.*) which I believe are the photogenic cells. In Fig. 7 a tubule is clearly seen on the lower left side of the mandibular organ (*lum.l.*), but is cut across very obliquely, so that the plane of section passes through its tip and then through the wall of the opposite side some distance above it. It therefore shows the two zones of cells composing the tubule. Other tubules in the figure are less clearly defined owing to crowding and the plane of sectioning not being appropriate.

Before describing in greater detail the characteristics of the cells composing a modified tubule, attention may be drawn to its lumen. As already mentioned, this is stellate in cross-section in the normal liver, but it becomes circular and narrow in the denser region of the luminous tubule, expanding again but remaining circular at the extreme tip where it is bounded by the supposed photogenic cells.

Fig. 8 shows part of the tubule referred to in Fig. 7 illustrated in greater detail. The cytoplasm of the cells forming the greater part of the wall of the tubule (*l.c.n.v.*) has an irregular granulated appearance, and stains uniformly with the counterstain employed. No vacuoles or other intracellular structures were observed. The nuclei of these cells are well represented by that indicated as *n.l.c.n.v.*, being usually spherical or ovate and showing a central mass of chromatin with smaller peripherally deposited masses. The central mass appears partially to obscure a nucleolus. The cells enclosing the tip of the tubule, on the other hand, are in distinct contrast to those just described. They are slender and arranged radially in a regular manner, with their rounded and tapered ends projecting into the lumen. Their cytoplasm is of almost uniform density throughout the cell, being perhaps a little denser basally and in some cases along the edge contiguous with the neighbouring cell. Use of an oil-immersion objective shows the presence of delicate longitudinal striae or fibrils, visible more by reason of a slightly different refractive index than by any staining characteristic. These striae are shown in the photogenic cells in Fig. 8, where they are somewhat emphasized. The nuclei of the cells of the tubule tip are entirely characteristic. They are ovate or in many instances kidney-shaped, with a conspicuous chromatin knot lying at one side. From this knot, in which the nucleolus may often be seen, the remainder of the chromatin spreads as a radiating reticulation. The orientation of the nuclei with respect to the position of the tubule tip is constant,

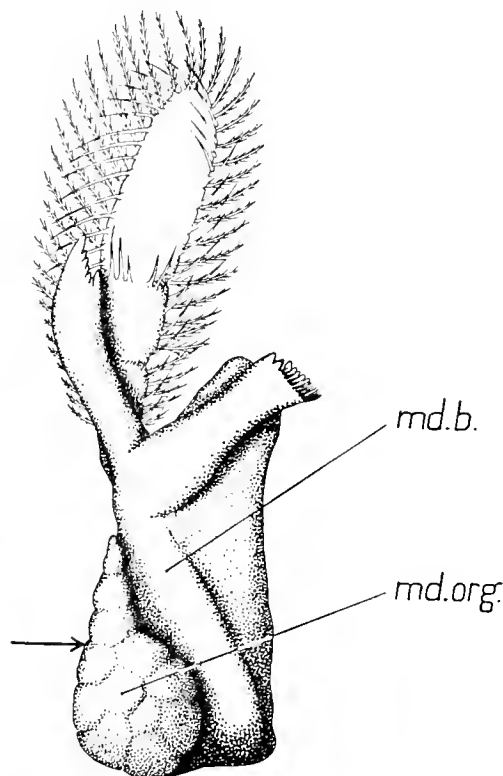


Fig. 6. Mandible of *Parapandalus richardi*, detached from the body, with the "mandibular" luminous organ (modified liver tubules) adhering to its base. $\times 33$ approx. *md.b.* base of the mandible; *md.org.* mandibular organ. The arrow indicates the level of the section in Fig. 7.

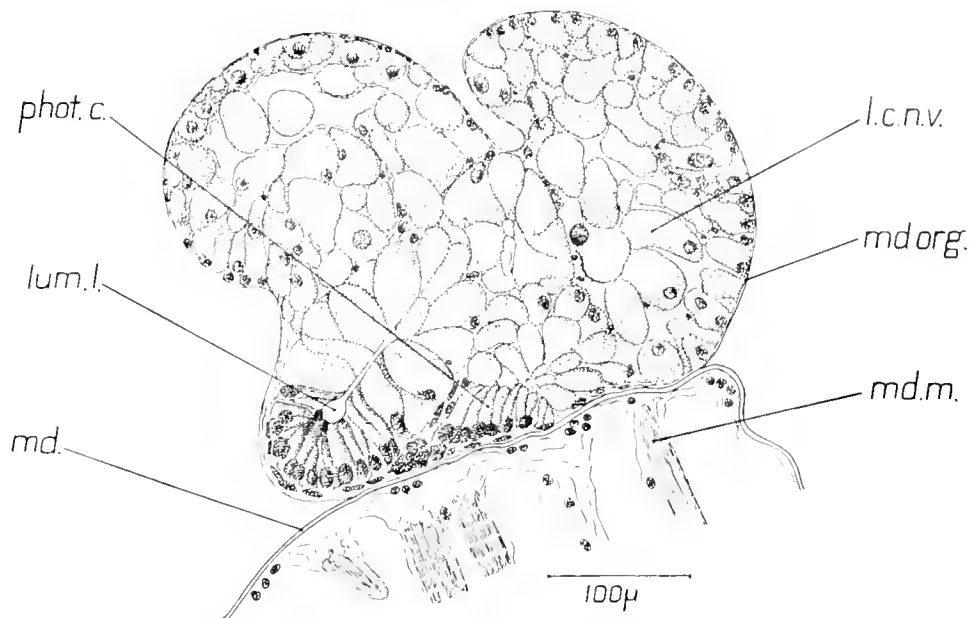


Fig. 7. Transverse section through the base of the mandible and mandibular organ of *Parapandalus richardi* at the level of the arrow in Fig. 6. Fixed Duboscq, Delafield's haematoxylin and eosin. *l.c.n.v.* non-vacuolated liver cell; *lum.l.* lumen of liver tubule; *md.* mandible; *md.m.* muscle of mandible; *md.org.* mandibular organ; *phot.c.* photogenic cell.

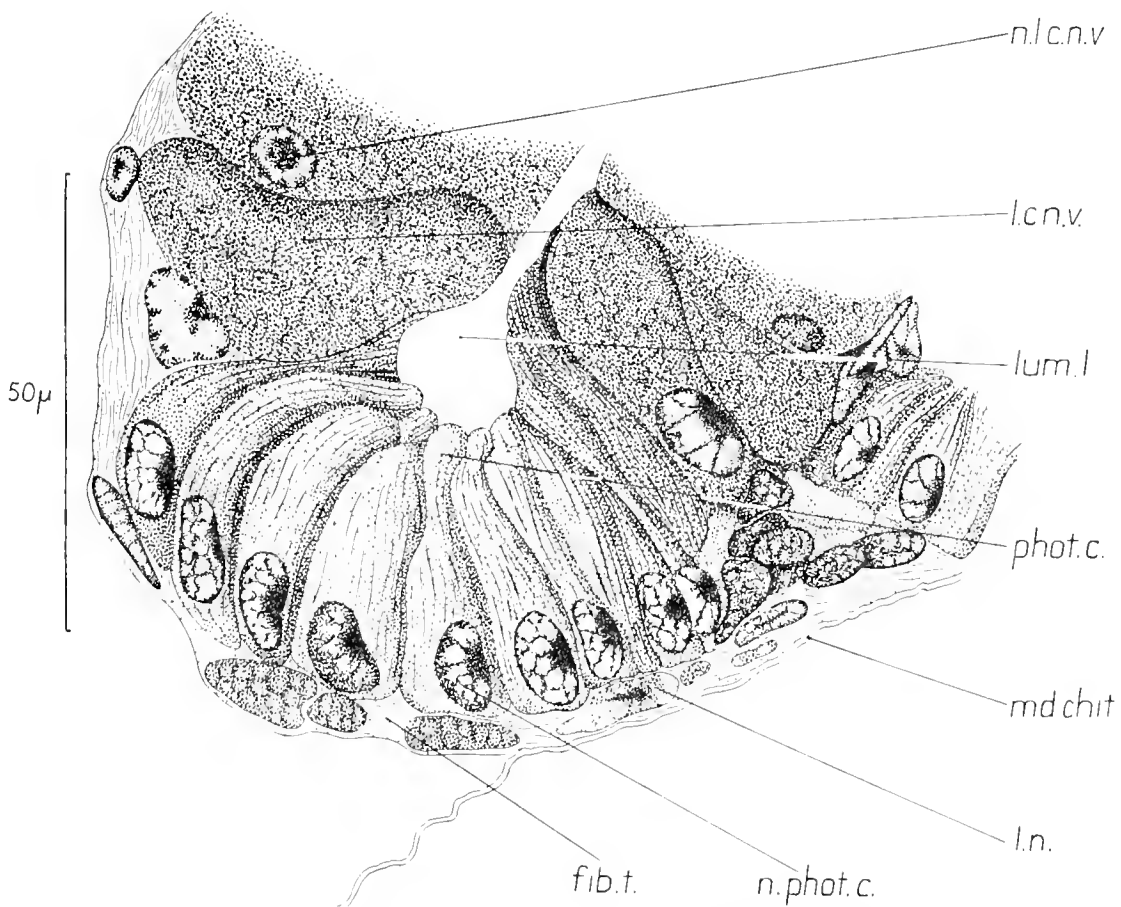


Fig. 8. Enlarged view of the photogenic region of the liver of *Parapandalus richardi* seen on the lower left side of Fig. 7. The liver tubules illustrated are cut obliquely transversely at some distance from their tips at the junction of the two zones of cells described in the text. *fib.t.* fibrous tunic of organ; *l.c.n.v.* non-vacuolated liver cell; *l.n.* lenticular nucleus; *lum.l.* lumen of liver; *md.chit.* chitin of mandible; *u.l.c.n.v.* nucleus of non-vacuolated liver cell; *n.phot.c.* nucleus of photogenic cell; *phot.c.* photogenic cell.

the chromatin knot always being found on the median side of the nucleus. This is clearly illustrated in Fig. 8 and Plate XXIV, fig. 5. In Fig. 7 the modified portion of the liver lies behind and somewhat to the outer side of the mandible (*md.*), and the external face of the liver organ lies to the left of the figure, so that any light which might be emitted by the tubule (*lum.l.*) would be seen from the left. Fig. 8 shows the same tubule in the same relative position, with the chromatin knots all lying on the right side of the nuclei, away from the exterior. This very curious disposition of the nuclei presumably has some bearing on the mode of functioning of this part of the organ, but at present its meaning is entirely obscure.

Surrounding the mandibular organ (and also the posterior organs, whose structure is precisely the same as that just described) is a fibrous tunic (Fig. 8, *fib.t.*) apparently composed of connective tissue. Its nuclei are most plentiful in the neighbourhood of the tubule tips, where they are elongated and lenticular. Elsewhere they are rounded and only sparsely distributed. The elongated nuclei are of two kinds. One type (Fig. 8, to right and left of the guide line *fib.t.*) shows a regular vacuolated appearance, while the second type (Fig. 8, *ln.*) has a central knot and radiating strands of chromatin. It would appear possible that if the tubules are indeed engaged in the active production of light these nuclei may function in some measure as minute lenses. The fibrous tunic probably carries the red pigment mentioned by Dr Kemp in his account of the colour of the organs and so forms a dorsal pigment cap like that of the organs of Pesta of *Sergestes*. It will be realized that these liver organs, like the organs of Pesta, must, if they are actually luminous, illuminate the branchial chamber.

Other members of the family Pandalidae possess organs, probably luminous, which occupy a similar position in the body to those of *Parapandalus*. In the genera *Chlorotocoides* and *Thalassocaris* Kemp (1925, p. 272) mentions them as being conspicuous in the living animal on account of the colour of the investing membrane, and in his description of *Chlorotocoides spinicauda* (1925, p. 277) describes the position of the organs as follows: "One of these organs is close to the base of the maxilla under the branchiostegal wall and one is situated on a slight prominence behind the posterior pleurobranch and above the coxa of the last leg. In shape each organ is nearly spherical and rather less than 0.5 mm. in diameter. The upper part was completely invested with bright red pigment, while the lower part, which in living specimens seemed to be slightly flattened, was glistening white." The author then states that similar organs are found in *Thalassocaris crinita* and *T. lucida*, quoting Dana as remarking that the latter species is "very brilliantly phosphorescent". He gives a brief description of the organs of *T. crinita* (p. 278), and leaves little doubt that the organs he describes are groups of modified liver tubules.

The occurrence of tracts of modified liver tubules, probably functioning as photophores, in members of the Caridea presents an interesting and inexplicable parallel with the organs of Pesta in some species of *Sergestes*. In each we have organs of endodermal origin, derived from tubules of the digestive gland, and occupying similar positions in the body. The colour in life is closely similar, purplish black, blue, or white

below, and red above. But, as may be seen from the description of the organs in *Parapandalus*, the minute structure of the organs of the Penaeid and the Carid show divergences which might be expected from the systematic position of these forms and which can only indicate physiological differences, probably profound, in the mode of effecting whatever function, production of luminescence or not, the organs subserve. The independent acquisition of such organs, so closely similar in their grosser features, in unrelated Decapods is truly remarkable, and may be taken to indicate that they are of some profound significance in the life of the animals. That this significance is the production of light is suggested by their coloration, which resembles that of known Decapod photophores, by their position with respect to the branchial chamber, and by Dana's remark concerning the phosphorescence of *Thalassocaris lucida*.

2. THE PIGMENTED SPOTS ON THE PLEOPODS

When the first three pairs of pleopods of *Parapandalus* were examined with the object of discovering whether any organ was associated with the deep red spot at the base of the endopod, referred to in Dr Kemp's notes, no trace of pigment remained, and in superficial view no unusual structure could be detected. Accordingly, two of the pleopods were sectioned, and careful search revealed the presence, in the precise position described as occupied by the red spot, of the organ illustrated in Fig. 9.

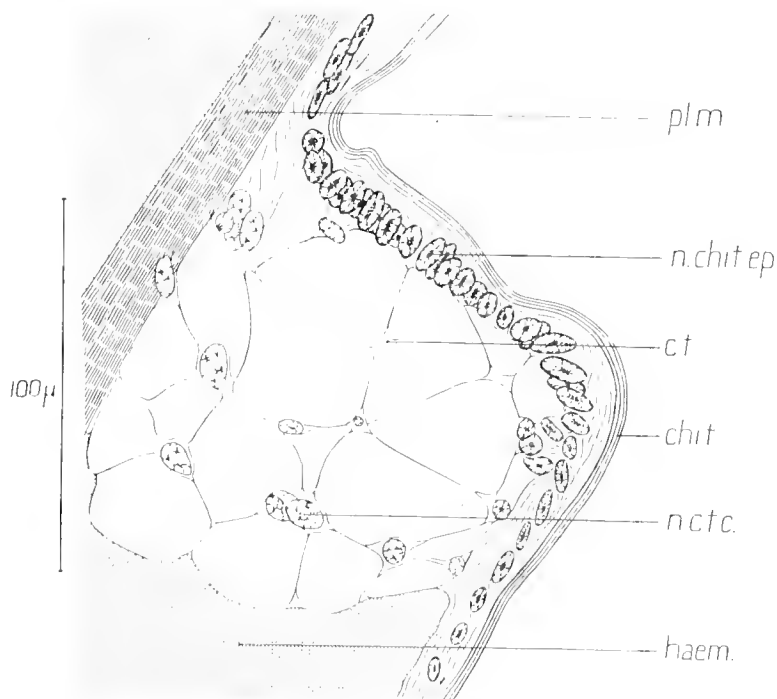


Fig. 9. Longitudinal section through the base of the endopod of the first left pleopod of *Parapandalus richardi*, showing the structure corresponding with the position of a deep red pigment spot in the living animal. Fixed Duboscq, Delafield's haematoxylin and eosin. *chit.* chitin of the limb; *c.t.* connective tissue; *haem.*, haemocoel; *n.c.t.c.* nucleus of connective tissue cell; *n.chit.ep.* nucleus of chitogenous epithelium; *pl.m.* pleopod muscle.

It consists, as may be seen from the figure, of a reticulum of connective tissue strands (Fig. 9, *c.t.*) in some nodes of which are lodged its nuclei. The chromatin content of these differs from that of adjacent nuclei. The chromatin is sparse and disposed within the nuclear membrane as a thready reticulation. The connective tissue reticulum lies between the integument of the limb (Fig. 9, *chit.*) and one of the muscles of the pleopod (Fig. 9, *pl.m.*), and is bathed by the body fluid in the haemocoelic space of the limb (Fig. 9, *haem.*).

The only other feature of interest in this simple structure is to be found in the arrangement of the nuclei of the chitogenous epithelium in its neighbourhood. These nuclei (Fig. 9, *n.chit.ep.*), which exhibit a central chromatin mass with radiating strands, are fairly uniformly distributed beneath the integument except in the neighbourhood of the connective tissue structure, where they are larger and are closely crowded. It must be admitted, however, that other areas are to be found on the limbs, remote from the structure under discussion, where the nuclei are rather irregularly crowded. I am inclined to believe that the crowding of the nuclei shown in Fig. 9 has no relation, therefore, to the network of connective tissue beneath them.

Whether the organ described above is a photophore I must leave entirely in doubt. There is no nerve supply and no chitinous lens associated with it, and its appearance in section is not instructive, there being no resemblance to any other photophore studied in the course of this work.

V. CARIDEA: HOPLOPHORIDAE

I. THE PHOTOPHORES OF *HOPLOPHORUS NOVAE-ZEALANDIAE* DE MAN, II. *TYPUS* A. MILNE-EDWARDS, AND II. *GRIMALDII* COUTIÈRE

Photophores appear to have been first described in a species of *Hoplophorus* by Coutière (1905, p. 3) when he published a description of a new species which he named *H. grimaldii*. He mentions them as occurring on a number of the thoracic limbs, as a long transverse streak at the base of the fifth thoracic limb, as a series of five to six organs on the carapace and as lenticular bodies on the basal joints of the pleopods and uropods. No description is given of the structure of these organs. Kemp (1910b, p. 646), after describing the photophores of *Systellaspis* (as *Acanthephyra*) *debilis*, remarks that the photophores of *Hoplophorus grimaldii* do not differ from them in any essential feature, and that they occur in the usual positions on the pleopods and uropods, and behind the bases of the last pair of legs. No mention is made in this work of the structure of the photophores borne on the carapace, the first observations on which appear to have been made by Dr Kemp in his notes made in the 'Discovery', in which he refers to the presence in *H. grimaldii* of "four very small circular organs arranged in a curved row near the lower border of the carapace and one other, immediately behind the eye and situated about one-third the length of the carapace from the anterior margin". Similar organs have also been observed by Dr Kemp in *H. novae-zealandiae* and by me in *H. typus*.

That all these structures in *Hoplophorus* are truly luminous organs was proved beyond any possibility of doubt by Dr Kemp. On placing a living female specimen of *H. grimaldii* in fresh water all the photophores emitted light, described as feebler than that of *Euphausia longirostris* taken in numbers at the same time. This appears to be the first occasion on which luminescence, apart from the production of clouds of a luminous secretion, has actually been observed in any Carid.

In the following account attention has been concentrated on the structure of some of the photophores rather than on their number and position in the different species.

(a) *The pleopod photophores of Hoplophorus novae-zealandiae*

The pleopod photophores of *Hoplophorus*, like those of *Systellaspis debilis* (Kemp, 1910b, p. 643) and *S. affinis* (this paper, p. 346) are situated at the distal end of the coxopodite on a slight downwardly facing projection borne externally and antero-laterally. Their position is well shown in the figure of *Hoplophorus grimaldii* given by Coutière (1905, fig. 1). They are overlapped by the extensive pleura of the abdominal somites, and would be unseen in lateral view if the pigment of the pleura were uniform. Although I have discovered no reference to any lack of pigment in those parts of the pleura immediately overlying the photophores, such as occurs in *Systellaspis debilis* (Kemp, 1910b, p. 645), I have no doubt that in the species of *Hoplophorus* a similar transparent window-like area, through which light emitted by the photophores may shine, is also present.

Pleopod photophores are present and are closely allied in structure in all three species of *Hoplophorus* examined. They are found on all five pairs of pleopods, and similar organs are found at the base of the uropods. In his 'Discovery' notes on *H. grimaldii* Dr Kemp remarks that the pleopod photophores appear to resemble those on the carapace. Actually the pleopod organs consist basically of radially arranged photogenic cells, while those on the carapace show a linear grouping of very closely similar cells (p. 339). Specimens of *H. grimaldii* and *H. typus*, preserved in formalin, and pleopods and other portions of *H. novae-zealandiae*, fixed in Duboscq, were available for examination, and the following description is therefore chiefly based on the better fixed material afforded by *H. novae-zealandiae*.

The organs are, as Kemp (1910b, p. 646) stated, closely similar in all essential respects to those of *Systellaspis debilis*, but show an even greater structural complexity, notably in their possession of a well-developed musculature capable of moving the whole organ with respect to the limb, and in the details of their innervation. The double convex lens of the photophore, made up of thickened and differentiated chitin, shows, like that of *S. debilis*, three well-defined layers (Fig. 10, *l.o.*, *l.m.*, *l.i.*). Of these the middle layer appears densest, showing closer striations than the inner and outer layers, but unlike them it is not uniformly dense. Its greatest density is progressively reached at its surfaces, contiguous with the inner and outer layers, so that additional middle layers, one of which is indicated in Fig. 10 by the guide-line *l.m'*., may be distinguished. The lens may thus be regarded as built of five layers of varying density, forming a distinct

optical combination. Such an elaboration of structure must have a marked effect on its functional properties. The cuticle of the limb is continuous over the outer face of the lens (Fig. 10, *cut.*).

An annular depression surrounds the lens near its periphery and is seen clearly in Fig. 10. It is produced by folding of the integument which is very thin and delicate in this region and resembles an arthroal membrane. A similar folding of the integument was observed by Kemp (1910*b*, p. 644) in *S. debilis*, and led him to suggest that the photophores might thereby be permitted some degree of movement, although no related musculature was found. In *Hoplophorus* a well-developed musculature is present, and will be described later.

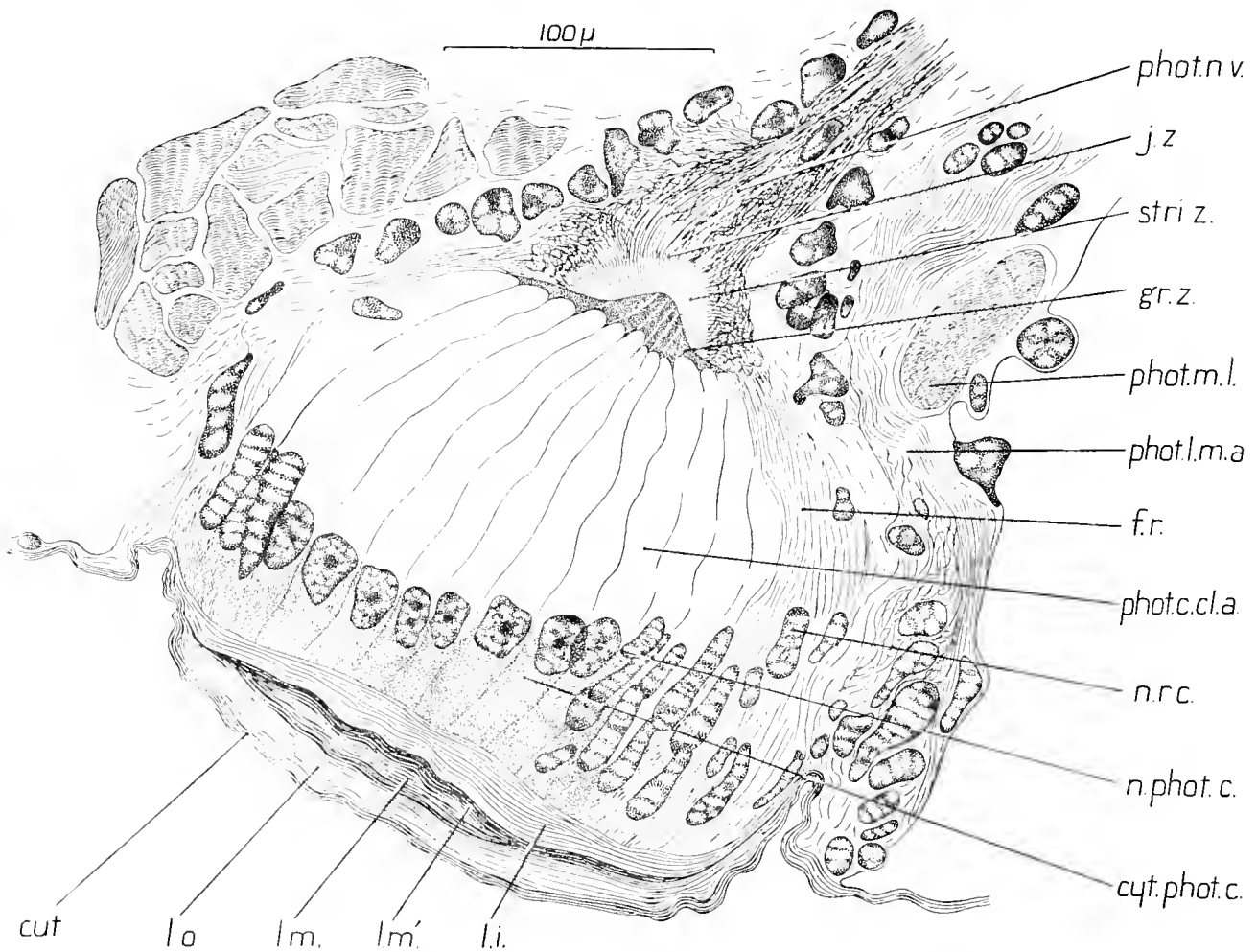


Fig. 10. Section cut diametrically through one of the boss-shaped photophores borne on the bases of the pleopods of *Hoplophorus novae-zealandiae*. A similar section is seen in Plate XXV, fig. 1. Fixed Duboscq, Delafield's haematoxylin and eosin. *cut.* cuticle; *cyt.phot.c.* cytoplasm of photogenic cell; *f.r.* fibrous reflector; *gr.z.* granular zone at bases of photogenic cells; *li.* inner layer of lens; *lm.* middle layer of lens; *lm'.* subsidiary intermediate layer of lens; *lo.* outer layer of lens; *n.phot.c.* nucleus of photogenic cell; *n.r.c.* nucleus of reflector tissue; *j.z.* junction zone between the fibres of the photophore nerve and the striated zone; *phot.c.cl.a.* clear area of photogenic cell; *phot.l.m.a.* attachment of longitudinal photophore muscle; *phot.m.l.* photophore muscle loop (seen clearly in Fig. 12) cut transversely; *phot.nv.* photophore nerve; *stri.z.* striated zone.

Behind the lens occur the radially arranged photogenic cells, which are lacking in cytoplasm at their inner or proximal ends (Fig. 10 and Plate XXV, fig. 1, *phot.c.cl.a.*). The distal cytoplasmic portions (Fig. 10, *cyt.phot.c.*) never occupy more than a third of the length of the cell, and are most extensive in those cells near the periphery of the organ. The cytoplasm is regularly and finely granular, and shows only a slight increase in density at the edges of the cell. No vacuoles or other structures have been observed in the cytoplasm. The nuclei of the photogenic cells (Fig. 10, *n.phot.c.*) lie at the proximal ends of the cytoplasmic portions of the cells, so that a cytoplasmic zone lies immediately inside the lens between it and the zone occupied by the nuclei. The nuclei show to some extent the gradation in size described by Kemp (1910*b*, p. 644) in *Systellaspis debilis*, being regularly larger towards the periphery of the lens than at its centre, and this, together with and mainly due to the variation in extent of the cytoplasmic portions of the cells, results in a concave inner surface being presented towards the vacuous zone of the photopore caused by the absence of cytoplasm proximally. This arrangement of the nuclei is not so well defined here as in *S. debilis*, for the nuclei are merely oval and the difference in size is not great, whereas in *S. debilis* the nuclei are squarely and abruptly truncated and show a marked difference in size, but it must nevertheless exert some optical effect. That the characteristic shape of the nuclei of *S. debilis* has some significance is indicated by the fact that it is again encountered in the carapace organs of *Hoplophorus* (p. 339) and in photophores in other parts of the body in *Systellaspis affinis* (p. 355) and *S. debilis* (p. 365). The nuclei of the photogenic cells of the pleopod photophores of *Hoplophorus novae-zealandiae* possess one or two dense chromatin masses, the remainder of the nuclear contents being uniformly vacuolated (Fig. 10, *n.phot.c.*).

The slender proximal ends of the photogenic cells are in close association with a conical mass of granular material (Fig. 10 and Plate XXV, fig. 1, *gr.z.*), which has a characteristic staining reaction. Unlike the granules which occupy the same position in *Systellaspis debilis* (Kemp, 1910*b*, p. 644) they are readily stained with eosin. The apex of the cone is directed towards the entrant nerve bundle (Fig. 10 and Plate XXV, fig. 1, *phot.nv.*), and the cone itself is seen to be made up of individual columns varying in length and of a number corresponding with the number of photogenic cells. The distal end of each column is markedly concave and receives the proximal end of the corresponding photogenic cell, so that the column forms a proximal cap to the cell. The whole cone is in close association with the entrant nerve fibres through an underlying striated zone.

The photophore nerve (Fig. 10 and Plate XXV, fig. 1, *phot.nv.*) runs down the base of the pleopod and expands somewhat on reaching the centre of the proximal surface of the organ. Within this expansion lies a clearly defined striated zone (Fig. 10, *stri.z.*) which stains more lightly than the nerve fibres, and is composed of very delicate fibrils or striae regularly arranged. The central bundle of fibres in the photophore nerve comes into immediate and direct communication with the apex of this cone of striae, but the peripheral fibres on reaching the neighbourhood of the striated zone become

exceedingly coiled and confused. Some of them make contact with the striated cone, while others appear to extend peripherally around the photophore to its distal surface. A distinct junction zone (Fig. 10, *j.z.*) exists between the nerve fibres and the striated zone. The precise mode of innervation is thus more complex than in *S. debilis*.

The fibrils which extend around the photophore enclose it in a fibrous cup (Fig. 10, *f.r.*) which is no doubt pigmented in life and acts as a reflector, or at any rate as a screen preventing the inward passage of light. Numerous small, dense, and deeply staining nuclei grouped around the photophore nerve bundle and basal part of the reflector may be those of chromatophores and sheathing tissue. Superficially, on a level with the photogenic cells, greatly elongate nuclei (Fig. 10, *n.r.c.*) lie among the fibres of the reflector. On account of their position I have called them the nuclei of reflector cells, but I am unable to offer any suggestion concerning their function, unless they are responsible for the secretion of one of the active principles of luminescence. I do not think that they are necessarily concerned with the production of the reflector fibres. They are curiously distinct from the nuclei of the photogenic cells, being not only long and narrow, but less rich in chromatin content and showing a linear sequence of vacuole-like areas. Similar nuclei appear in a corresponding position in the pleopod photophores of *S. affinis* (p. 349) and *S. debilis* (my observations, p. 363 and the photograph given by Kemp (1910*b*, Pl. lii, fig. 1)).

It has already been mentioned that the annular depression of the integument around the lens (p. 330) suggests the possibility of orientation of the photophore as a whole, and that muscles capable of effecting this movement are present. Parallel with the photophore nerve a longitudinal muscle (Fig. 10 and Plate XXV, fig. 1, *phot.l.m.a.*, Fig. 12, *phot.l.m.*) extends to the integument of the limb just outside the annular depression.

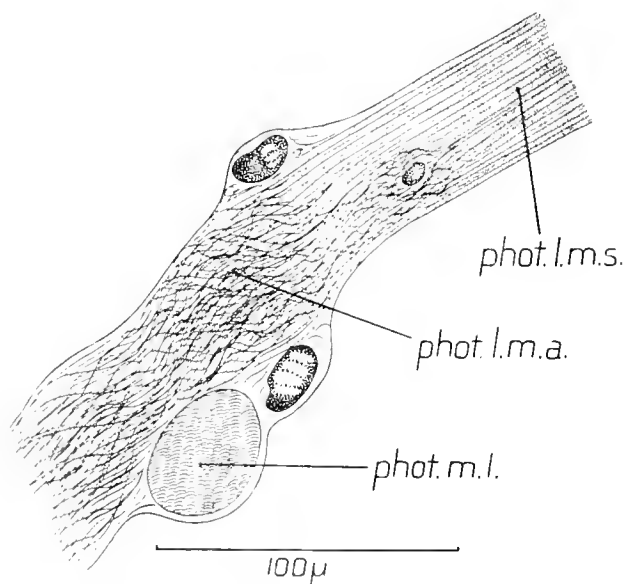


Fig. 11. Section through the longitudinal photophore muscle of the pleopod photophore of *Hoplophorus novae-scalandiae*. *phot.l.m.a.* attachment of longitudinal photophore muscle; *phot.l.m.s.* striated portion of longitudinal muscle; *phot.m.l.* photophore muscle loop.

This muscle is definitely though faintly striated at some distance from the photophore (Fig. 11, *phot.l.m.s.*), but nearer to it the striae progressively disappear and the fibres become sinuous and twisted. This unstriated portion I have called the attachment of the longitudinal photophore muscle (Figs. 10, 11, *phot.l.m.a.*), although it is true that it has little of the normal appearance of crustacean muscle attachment. It clearly functions as a tendon of the muscle. Although the main portion of the longitudinal muscle lies in the situation described there extends from it a mass of connective tissue forming an incomplete sheath around the organ. In the connective tissue lie a number of muscle strands, some of which are condensed into a smaller secondary longitudinal muscle on the opposite side of the photophore (Fig. 12, *phot.l.m'*). This can be clearly seen in a photophore carefully dissected out from the surrounding tissues. In addition, in both the serial sections and the isolated photophore, a loop of muscle (Figs. 10-12 and Plate XXV, fig. 1, *phot.m.l.*) encircles the organ almost completely. It lies equatorially

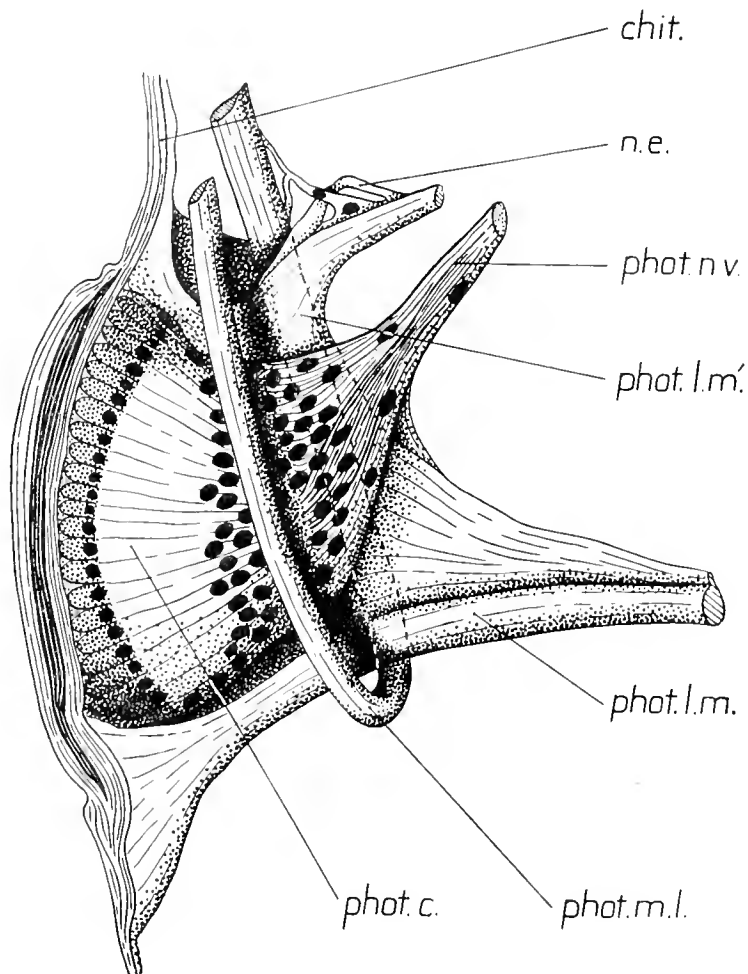


Fig. 12. A pleopod photophore of *Hoplophorus grimaldii*, dissected from the limb and seen in whole view, showing the arrangement of the musculature. *chit.* chitin; *n.e.* nerve ending on photophore muscle; *phot.c.* photogenic cell; *phot.l.m.* longitudinal photophore muscle; *phot.l.m'*. secondary longitudinal photophore muscle; *phot.m.l.* photophore muscle loop; *phot.n.v.* photophore nerve.

but at a level just proximal to the nerve ending. Both ends of the muscle loop are attached to the integument of the limb on the side of the photophore remote from the longitudinal muscle. Furthermore, in the preparation of the isolated photophore a characteristic nerve ending can be seen on the secondary longitudinal muscle and the muscle loop (Fig. 12, *n.e.*). It is clear that the individual components of the photophore musculature are so placed as to work in opposition to each other, and that they are capable of producing quite complex movements of the whole structure, permitted by what amounts to an arthroal membrane around the lens.

The organs at the base of the uropods of *Hoplophorus* are very similar to those found in a corresponding position in *Systellaspis affinis* (p. 350 and Fig. 23), and are therefore not described in detail. The photogenic cells, however, as may be seen by reference to Fig. 13, possess a prominent squarely truncate nucleus, and a basal cap, situated at the proximal end of the cell, appears to consist of a finely granular substance. The photogenic cells are precisely similar to those of the carapace photophores of *Hoplophorus* (p. 339 and Figs. 17, 18). The proximal granular mass found at their bases, and forming there a reflecting surface, is not as in *Systellaspis affinis*, white and opaque, but is translucent and appears colourless by transmitted light. These organs possess no tegumental lens and no special musculature.

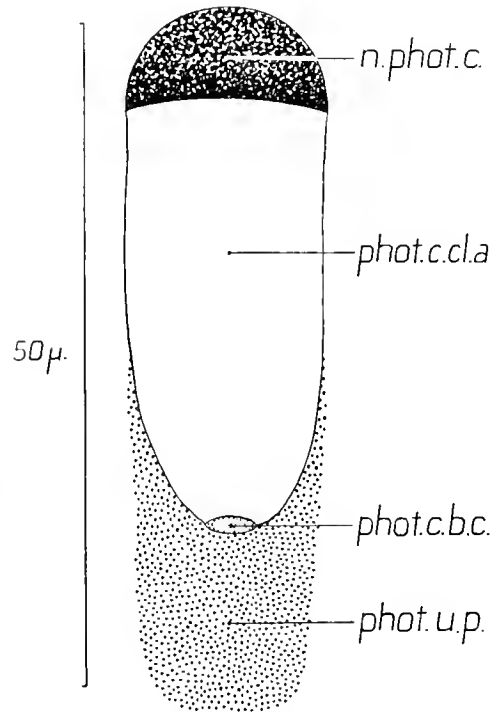


Fig. 13. One of the photogenic cells of the photophore at the base of the uropods of *Hoplophorus typus*. *n.phot.c.* nucleus of photogenic cell; *phot.c.b.c.* basal cap of photogenic cell; *phot.c.c.l.a.* clear area of photogenic cell; *phot.u.p.* proximal granular mass at base of photogenic cell.

(b) *The organs on the fifth thoracic limb of Hoplophorus novae-zealandiae*

The fifth thoracic limb of this species bears a luminous patch at the proximal end of the carpus, and a short proximal and a long distal patch on the propodus. With a view to discovering whether these organs followed the same basic structure as those of the pleopods, differing only in the obvious absence of a lens, longitudinal sections of the limb were cut. It was at once apparent that here we have to consider an entirely new type of photophore. The following description is that of the organ on the carpus of the limb, but the other organs are precisely similar.

The mass of the photophore is made up of a group of cells, presumably the photogenic cells, which show entirely peculiar features and which give every indication of being cells in various phases of differentiation. Dealing first with the innermost mem-

bers of the group, there is little doubt that the structure under discussion is truly a cell. Its limits are defined by a definite membrane within which is the nucleus. The cell immediately to the left of the guide-line, *phot.c. 1* in Fig. 14, shows a complete and normal nucleus, but apart from a finely granular, lightly staining substance on the cell wall remote from the nucleus no other contents are visible. This substance may be cytoplasmic, but for reasons which will be given later this is unlikely. In the neighbouring cell (Fig. 14, *phot.c. 1*) the nucleus shows signs of degeneration, being irregular and with apparently an incomplete nuclear membrane. In the next most superficial layer the cells (Fig. 14, *phot.c. 2*) have the appearance of being products of the continuation of the process. The nucleus is either absent, or is reduced to a deposit of nuclear material at the proximal end of the cell, while at the opposite end lies a deposit of the granular material seen in the cells of the previous layer. In the most superficial

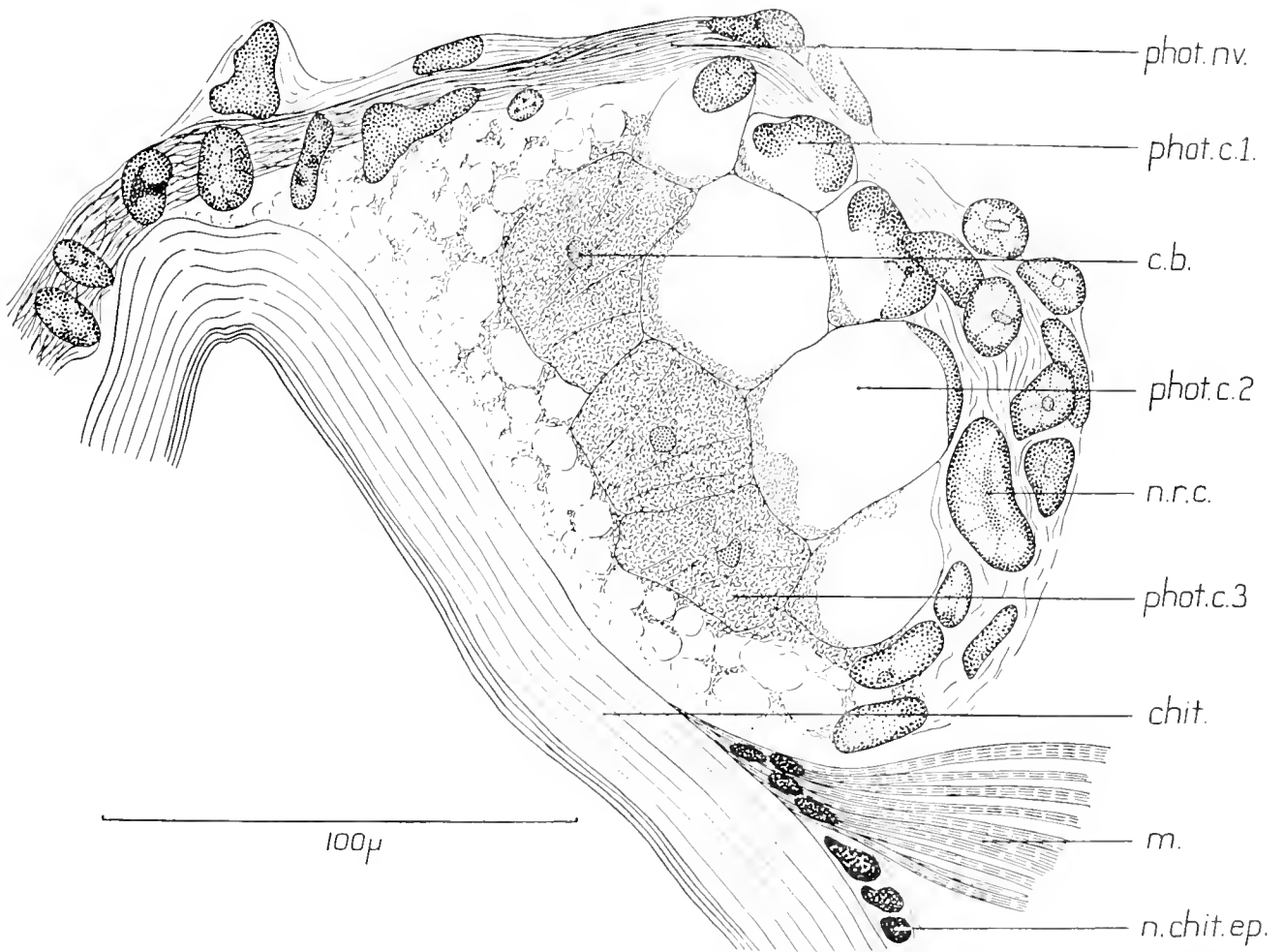


Fig. 14. Part of a longitudinal section through the right fifth thoracic limb of *Hoplophorus novae-zealandiae*, showing the luminous organ at the proximal end of the carpus. Fixed Duboseq, Delafield's haematoxylin and eosin. A similar section is seen in the photograph in Plate XXV, fig. 3. *c.b.* central body; *chit.* chitin; *m.* adjacent striated muscle; *n.chit.ep.* nucleus of chitogenous epithelium; *n.r.c.* nucleus of reflector cell; *phot.c. 1*, *phot.c. 2*, *phot.c. 3*, three successive phases in the appearance of the photogenic cells; *phot.nv.* photophore nerve.

cells (Fig. 14, *phot.c.* 3), if the term "cell" may now be properly used, no nuclei are to be seen, and the granular material occupies the limits of the cell membrane completely. It presents the appearance of having faintly defined fibrils which run more or less perpendicularly to the outer surface of the organ. From a comparison of this organ with that next to be described, however, I believe that these are not fibrils, but are an indication that the granular substance is segmented into a number of blocks. Disposed within the "cells" of this layer is a central body (Fig. 14 and Plate XXV, fig. 3, *c.b.*) of entirely obscure origin. Nothing which could be described as representing possible stages in its differentiation have been observed. It is well defined, apparently granular, and stains more deeply than the surrounding substance. It has, however, none of the appearance or staining reactions of a nucleus, and it closely recalls the granular zone of the pleopod photophores (p. 331) and the basal cap of the photogenic cells of the carapace photophores (p. 340).

Reasons for supposing that stages in progressive differentiation are exhibited by the group of cells described, and also that the granular substance they contain is not cytoplasm, are afforded by the existence of parallel phenomena in the photophore behind the last thoracic limb of *H. grimaldii* (see later p. 337), and in those on the fifth thoracic limb of *Systellaspis affinis* (see later p. 356). In both these instances the granular material is radially and segmentally arranged, and in *S. affinis* it is beyond doubt not cytoplasm.

The group of cells described above are almost certainly the photogenic cells, and in life are probably yellow in colour. Dr Kemp in his notes describes the organ as golden yellow when viewed from beneath, and otherwise surrounded by deep red pigment. The red pigment, acting as a screen or reflector behind the luminous cells, is almost certainly carried by the tissue represented by the cup-shaped group of nuclei (Fig. 14 and Plate XXV, fig. 3, *n.r.c.*) on the inner side of the photogenic cells. Although I have designated all these nuclei as belonging to the reflector, it is possible that some belong to very early and undifferentiated photogenic cells or to other tissues such as sheathing or supporting fibres of the nerve bundle which innervates the photophore. This nerve bundle (Fig. 14 and Plate XXV, fig. 3, *phot.nv.*) leaves the main trunk of the nerve running down the limb (Plate XXV, fig. 3, *lnv.*) as a branch at the distal end of the merus, and its neurofibrils are seen among the nuclei of the reflector layer. The precise mode of communication of the neurofibrils with the photogenic cells could not be discovered with the methods it was possible to employ.

The whole photophore is separated from the integument by the highly vacuolated zone seen in Fig. 14. No trace of differentiation of the chitin in the form of a lens exists in connexion with the organ, and no muscles are associated with it. But although simpler in structure than the pleopod photophores, it presents considerable difficulties in its cytological interpretation. These are mentioned later (p. 374) in this paper.

(c) *The transverse luminous streak behind the base of the fifth thoracic limb of
Hoplophorus grimaldii*

The linear photophores behind the bases of the fifth pair of thoracic limbs of *Hoplophorus* are placed transversely and almost meet in the mid-ventral line. Laterally they curve somewhat upwards and forwards, so that their outer ends are visible in surface view on the posterior face of the limb base. In life these organs are deep violet-blue on the surface, with a layer of shining orange-red pigment underlying the blue. After preservation for some considerable time the organs were only visible as slightly raised tracts of the integument with a more opaque appearance than the surrounding area owing to the density of the underlying tissue.

These photophores have been examined in detail, and it is found that they show a strong resemblance to the organ on the fifth thoracic limb of *H. novae-zealandiae* which has just been described. The same phases of differentiation of the photogenic cells are apparent, but they show a complete inversion of position compared with the similar cells in *H. novae-zealandiae*. Whereas in the thoracic limb of the latter the recognizable photogenic nuclei and early phases of their differentiation are on the side of the organ remote from the integument, here they are superficial and adjacent to it. The inversion of the photogenic tissue is very surprising, and cannot be readily explained. A study of the photophores of *Systellaspis affinis* and *S. debilis* has, however, revealed comparable examples of the reversal of photogenic cells.

The linear photophore of *Hoplophorus grimaldii* is illustrated in transverse section

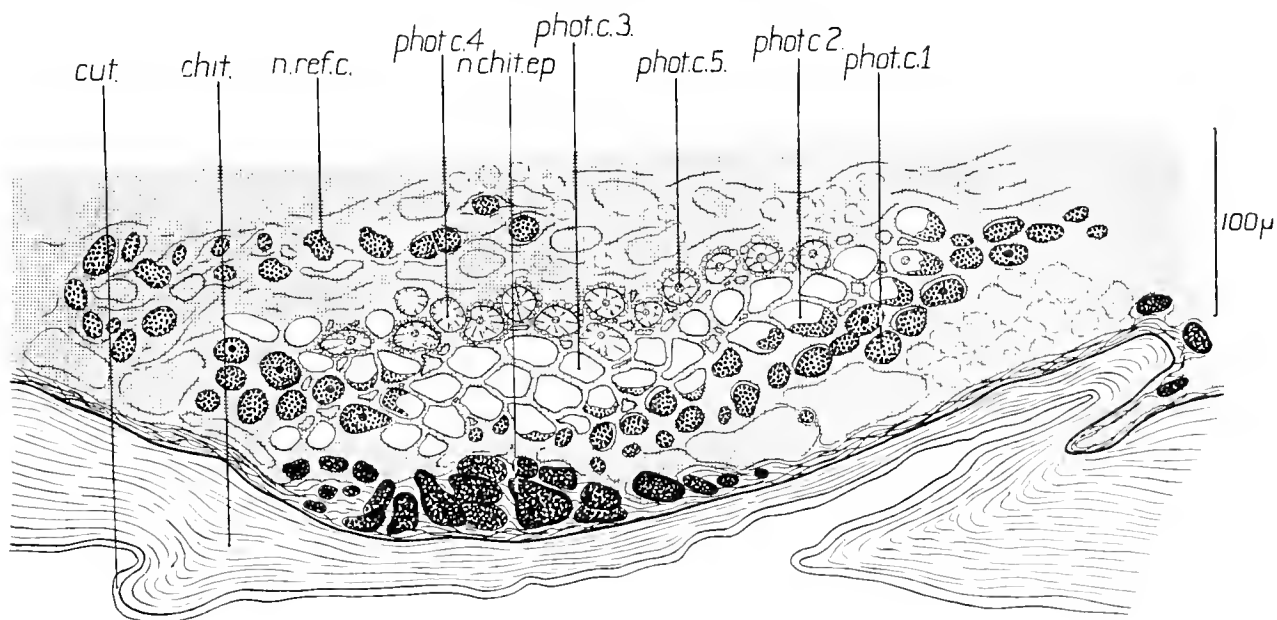


Fig. 15. Transverse section through the luminous streak behind the base of the fifth thoracic limb of *Hoplophorus grimaldii*. The haemocoel is indicated by mechanical stippling. Mallory's triple stain. *chit.*, chitin; *cut.*, cuticle; *n.chit.ep.*, nucleus of chitogenous epithelium; *n.ref.c.*, nucleus of reflecting cell; *phot.c. 1*, *phot.c. 2*, *phot.c. 3*, *phot.c. 4*, *phot.c. 5*, successive phases in the appearance of the photogenic cells.

in Fig. 15. The integument overlying it shows the usual differentiation into cuticle and chitin (Fig. 15, *cut.* and *chit.*) and is not markedly developed to produce a lens-like formation. It appears to carry in life a violet-blue pigment similar to that noted by Kemp (1910*b*, p. 644) in *Systellaspis debilis*, and which is found in the photophores of Decapoda generally (1910*b*, p. 640). Underlying it the chitogenous epithelium is very thin for the most part and with only scattered nuclei. Here and there, however, occur closely packed groups of larger nuclei, one of which (Fig. 15, *n.chit.ep.*) is found in the proximity of the photophore, but has no functional connexion with it. Its presence, however, may perhaps be taken as indicating that whatever the origin of the photophore it is not derived from the ectoderm.

As in the previously described photophore (Fig. 14) the main mass of the organ consists of the photogenic cells in various stages of differentiation (Fig. 15, *phot.c.* 1, 2, 3, 4, and 5) and nuclei which probably belong to the reflector layer (Fig. 15, *n.ref.c.*). The reflector layer in all likelihood carries a red pigment similar to that found in *Hoplophorus novae-zealandiae* (p. 336); this, together with the yellow colour which may be supposed to be associated with the actual photogenic cells, would give rise to the underlying shining orange-red pigment already mentioned (p. 337).

Stages in the presumed growth and differentiation of photogenic cells are illustrated in detail in Fig. 16. On the extreme right of the figure at *a* is illustrated a photogenic nucleus (Fig. 16, *n.*) of the type found lying near the surface of the organ. It almost completely occupies a space bounded by a membrane which may reasonably be interpreted as a cell membrane (Fig. 16, *c.m.*), but no trace of cytoplasm has been found enclosed by it. The nucleus shows a reticulate pattern in the distribution of its chromatin, and in most instances a prominent nucleolus has been observed. At *b* is shown a later stage wherein the nucleus (*d.n.*) gives every indication of degeneration, but still often

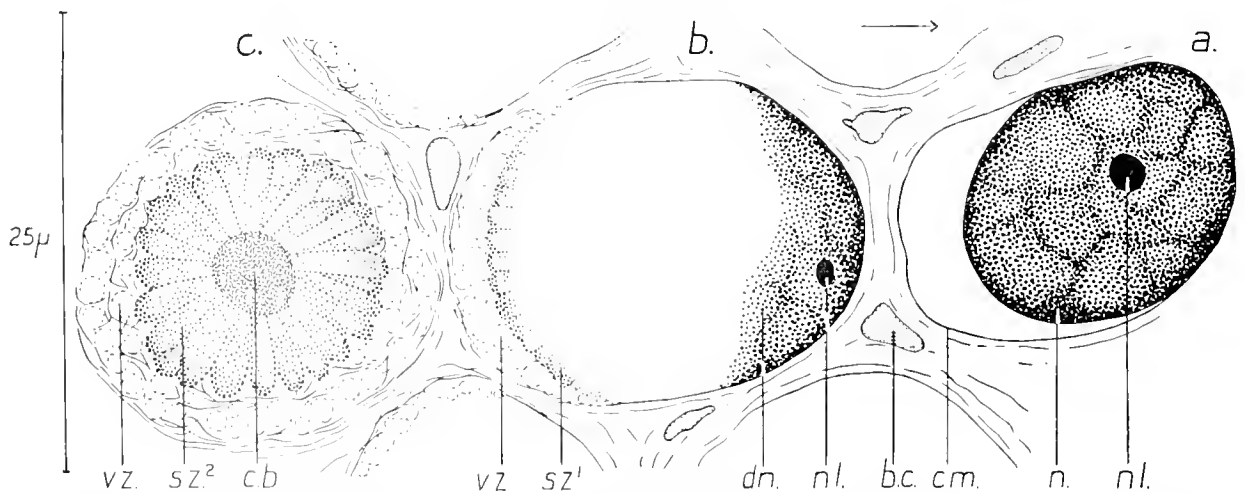


Fig. 16. Part of the preceding section enlarged to show the details of the photogenic cells. The arrow points to the external surface of the photophore. Blood channels are indicated by mechanical stippling, but the remainder of the haemocoel is left white. *b.c.* blood channel; *c.b.* central body; *c.m.* cell membrane; *d.n.* degenerating nucleus; *n.* nucleus; *nl.* nucleolus; *s.c.*¹ early stage in the production of the radially segmented zone; *s.c.*² later stage of the segmented zone; *v.z.* vacuolated zone.

contains a recognizable nucleolus (*nl.*). At the opposite end of the cell to that occupied by the remains of the nucleus, however, new structures begin to appear. A very delicate vacuolated zone (*v.z.*) has on its inner side a layer, segmentally arranged (*s.z.*¹), which corresponds precisely in structure and staining reactions to the substance occupying the superficial cells in the photophore of *H. novae-zealandiae* (Fig. 14, *phot.c.* 3).

At *c* (Fig. 16) the vacuolated zone (*v.z.*) has extended completely around the inner face of the cell membrane, which now has a fibrous appearance, and the segmented zone (*s.z.*²) is also peripherally complete and its segments have extended centripetally. The centre of the "cell" is now occupied by a central body (*c.b.*) precisely like that seen in *H. novae-zealandiae* (Fig. 14, *c.b.*). The similarity of this "cell" to that shown in Fig. 14 (*phot.c.* 3) is unmistakable, and the radially segmented pattern of the substance of the segmented zone, whether cytoplasm or not, would indicate that the striae seen in the cell in Fig. 14 are in reality indications of segmentation.

The photogenic cells are separated from each other by walls of connective tissue, in which fine blood channels (Fig. 16, *b.c.*) are visible. Further strands of connective tissue are seen between the nuclei of the reflector layer (Fig. 15), and the whole region of the photophore is highly vascular. Unlike the condition in the photophore on the fifth thoracic limb of *H. novae-zealandiae* no indications of innervation were observed.

The essential similarity of this with the preceding organ is undeniable, and renders more perplexing the inversion of the photogenic tissues already mentioned. Also it may be said in anticipation that the photophores of *Systellaspis affinis* (p. 354) and *S. debilis* p. 364), which occupy a similar position behind the base of the last thoracic limb, show an entirely different structure from that in *Hoplophorus*, being composed of long slender photogenic cells with basal nuclei.

(d) *The carapace photophores of Hoplophorus novae-zealandiae*, *H. typus*,
and *H. grimaldii*

Well-developed photophores on the outer surface of the branchiostegite of *H. novae-zealandiae* and *H. grimaldii* have been observed by Dr Kemp, and their appearance in freshly caught specimens has been recorded in his notes. They are described in *H. novae-zealandiae* as follows: "On carapace two organs on branchiostegal carina not far from antero-lateral angle, and further back, in posterior half, a curved row of four organs. The foremost of these is situated above the base of the third legs and the hindmost in the blunt projection on the middle of the posterior margin. These six photophores are all directed downwards and appear to be well developed structurally. Lower portion (? lens) deep violet blue, succeeded by pale yellow (? photogenic) layer, then by white layer (? reflector), and above all a thick mass of deep red pigment in which dark pyriform bodies, six in a transverse series, can be detected." With regard to *H. grimaldii* Dr Kemp says: "Luminous organs precisely similar in position and coloration to those of *Hoplophorus* n.sp. (= *H. novae-zealandiae*), but the foremost on the lower border of the carapace behind the branchiostegal spine is missing."

Examination of a specimen of *H. typus*, preserved in formalin, from the Dana Expedition, has also revealed the presence there of similar photophores, arranged in a curved row of five near the ventral margin of the carapace. Presumably the photophores have in life a similar coloration to those described by Dr Kemp.

The carapace organs of the above-mentioned three species are all very closely similar in structure, and discussion of the significance of their pigmentation is postponed until this structure has been described. The photophores have been studied both from whole mounts of the carapace and from serial sections, and their similarity makes it possible to give a basic description of their composition, the slight differences between them being pointed out in proceeding.

The organization of the photophores is best appreciated from the figures of the transverse section of the branchiostegite of *H. novae-zealandiae* (Fig. 17 and Plate XXV, fig. 2). The robust chitin of the outer surface of the branchiostegite is overlain by a well-developed cuticle (Fig. 17, *cut.*), and in the neighbourhood of the photophore it is thickened to form a distinct lens (Fig. 17, *l.*) which is double convex in section. In surface view the lens is semilunar (Fig. 18, *l.*). It is not of uniform constitution, for a middle layer (on which the guide-line *l.* in Fig. 17 terminates) is more heavily striated and deeply stained than those adjacent to it, and presumably it has different optical qualities. The position of the middle layer within the thickness of the chitin is somewhat variable; in some of the photophores examined it was centrally situated, while in others it occupied a position between the centre and the surface of the chitin. But whatever the precise disposition of the middle layer of the lens its presence must exert some influence on the optical qualities of the lens as a whole.

Underlying the integument of the outer surface of the branchiostegite is seen the chitogenous epithelium, from localized areas of which the photophores appear to be differentiated. Over the greater part of the branchiostegite the epithelium consists of flattened densely staining nuclei (Fig. 17 and Plate XXV, fig. 2, *n.chit.ep.*) surrounded by ill-defined cytoplasm, resting on a basement membrane.

On the inner side of the area occupied by the lens, however, well-differentiated structures appear. The most conspicuous of these are the pyriform bodies noted in surface view by Dr Kemp. They are with little doubt the photogenic cells, and show strong similarities to the photogenic cells of the pleopods (Fig. 10 and Plate XXV, fig. 1), having a portion of the cell entirely devoid of cytoplasm (Fig. 17 and Plate XXV, fig. 2, *phot.c.cl.a.*). The dense distally disposed nucleus lies close against the chitin of the branchiostegal wall, and its inner surface is smoothly concave. Owing to its breadth being somewhat greater than that of the clear area of the cell the nucleus has the appearance of constituting a massive distal cap to the cell. The distal position of the nucleus corresponds with that seen in the pleopod photogenic cells, but unlike these the carapace photophores show no distal cytoplasm in their photogenic cells. It will be recalled that the pleopod photogenic cells terminate proximally on the base of a conical granular zone (Fig. 10, *gr.z.*) which is segmented in conformity with the number of photogenic cells and is intimately concerned with the innervation of the photophore.

Similarly the photogenic cells of the carapace organs bear at their basal ends small hemispherical masses of a precisely similar granular material (Fig. 17, *phot.c.b.c.*) showing the same staining reactions and having an equally intimate relation with the

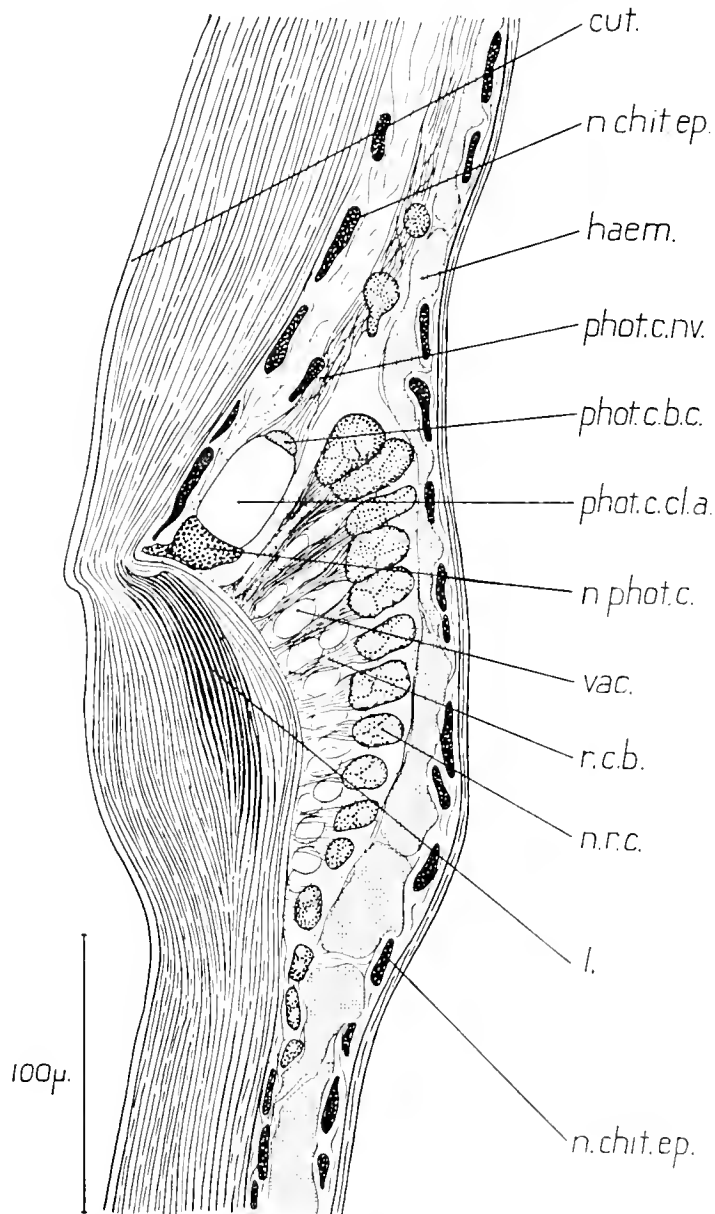


Fig. 17. Part of a transverse section through the branchiostegite of *Hoplophorus novae-zealandiae*, showing one of the lateral carapace photophores. The outer wall of the branchiostegite is on the left, the inner on the right, and between them a haemocoelic blood space is indicated by mechanical stippling. A section through a similar but more anterior organ appears in Plate XXV, fig. 2. In each the plane of section corresponds to a section passing through *ab* in the whole view in Fig. 18. Fixed Duboscq, Delafield's haematoxylin and eosin. *cut.* cuticle; *haem.* haemocoel; *l.* lens; *n.chit.ep.* nucleus of chitogenous epithelium; *n.r.c.* nucleus of reflector cell; *phot.c.b.c.* basal cap of photogenic cell; *phot.c.cl.a.* clear area of photogenic cell; *n.phot.c.* nucleus of photogenic cell; *phot.c.nv.* fibres innervating photogenic cell; *r.c.b.* reflector cell body; *vac.* vacuoles in reflector layer.

nerve fibres of the photophore nerve supply (Fig. 17 and Plate XXV, fig. 2, *phot.c.nv.*). The granular zone of the pleopod organs and the basal caps of the carapace organ may therefore be homologous. The photogenic cells of the pleopod and carapace organs are, then, very closely similar in structure.

It is noteworthy that not all the nerve fibres terminate on the basal cap of the photogenic cells; on the contrary, only the central fibres of the bundle do so, while the peripheral ones extend for some little distance down the walls of the photogenic cells. This is clearly seen in the illustrations (Figs. 17, 18 and Plate XXV, fig. 2). The arrangement of the nerve supply will be further discussed in describing the superficial view of the photophores.

Immediately ventral to the photogenic cells the chitogenous epithelium is profoundly modified. Whereas its normal nuclei are flattened and densely staining, and are closely applied to the inner surface of the chitin, here they are larger, ovate, and removed from the chitin (Figs. 17, 18 and Plate XXV, fig. 2, *n.r.c.*). They show less chromatin than the normal nuclei, being almost uniformly lightly granular. Extending from the distal ends of these nuclei to the inner surface of the chitin constituting the lens are bundles of fibres (Fig. 17, *r.c.b.*) corresponding in number with the nuclei. The fibrous bundles taper progressively as they approach the chitin, and their distal tips spread on to its inner surface in a manner reminiscent of muscle attachment. These bundles may possibly represent the cell bodies of the nuclei with which they are contiguous, and I have provisionally identified them in this manner.

Between the fibrous bundles are numerous spaces, having the appearance of vacuoles (Fig. 17, *vac.*) entirely devoid of contents. For reasons given later (p. 344) I believe that, although they do not contain coagulated blood, they may be fine blood channels observed in transverse section.

The tissue just described progressively merges with the general chitogenous epithelium ventral to the lens. The nuclei become smaller and denser and the fibrous bundles shorter and more diffuse in passing ventrally, until the normal appearance of the chitogenous epithelium is regained at about the level of the ventral margin of the lens. The function of this mass of tissue underlying the lens is uncertain. I am inclined to believe that it is a reflector, and have accordingly named the ovate nuclei as being those of the reflector cells. The possibility remains, however, that the fine fibrous bundles are composed of secretion fibrils lying within the general cytoplasm of a syncytium, or that the vacuole-like spaces are truly vacuoles and are indicative of secretory activity. In this event the function of this zone may be complementary to the activity of the photogenic cells in the mechanism of light production, each producing an essential secretion. Further investigation is clearly required before these questions can be answered.

The integument lining the branchial chamber and forming the inner wall of the branchiostegite is exceedingly delicate, and has beneath it a chitogenous epithelium of the form already described. Enclosed between the inner and outer faces of the branchiostegite is a haemocoelic space (Fig. 17, *haem.*) traversed by occasional strands of connective tissue.

The foregoing information elicited from a study of serial sections renders intelligible the appearance of the carapace photophores in superficial view. In all three species studied the organs are readily visible in specimens stored in formalin, and since those of *H. typus* were most clearly defined in my specimens in this view they will be described as a typical example of the organs. In this species the organs have the form of five short amber-coloured streaks, two of which are situated anteriorly and three posteriorly on a line curving upwards and backwards from the antero-ventral margin of the carapace. The whole carapace is lightly dotted with contracted carmine chromatophores, but these are most numerous around the photophores, where they form a loose dorsal cap to the photogenic cells. The lens is seen as a white bar ventral to the photogenic cells, and is most apparent in the anterior pair of photophores, which are more highly differentiated than the posterior three. Using a moderately high power, a faint white cloudiness was seen in the basal parts of the clear areas of the photogenic cells. This was not seen in the other species examined, nor in the sections. It is not easy to say at this stage whether this was due to a precipitate caused by fixation and preservation in formalin, or whether on the other hand the emptiness of the photogenic cells previously stressed is evidence of imperfect fixation and preservation.

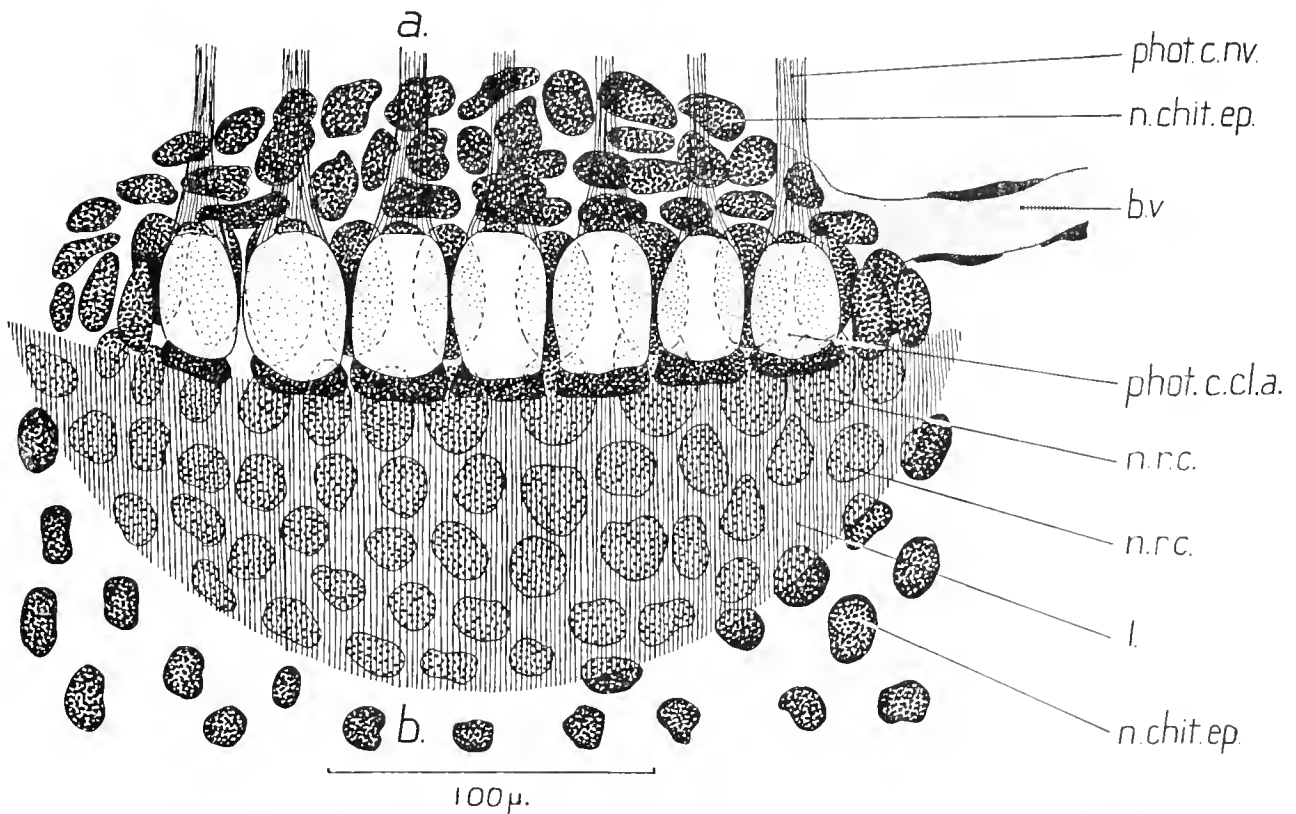


Fig. 18. Semi-diagrammatic external view of the most anterior left carapace photophore of *Hoplophorus typus*. *ab* represents a plane of section corresponding to that of Fig. 17. The vertically striated area is the lens; the remainder of the integument is assumed for the purpose of the figure to be entirely transparent and is not shown. *b.v.* blood vessel; *l.* lens; *n.chit.ep.* nucleus of chitogenous epithelium; *n.r.c.* nucleus of reflector cell; *phot.c.cl.a.* clear area of photogenic cell; *phot.c.nv.* fibres innervating photogenic cell.

In borax-carmine-stained whole preparations details of the photogenic cells are discernible, and Fig. 18 represents such a preparation in surface view. The general surface of the integument is omitted from the figure, but the local thickening forming the lens is indicated by vertical hatching to represent the striated appearance seen in this view. Underlying the chitin are seen the nuclei of the chitogenous epithelium (Fig. 18, *n.chit.ep.*), among which, but difficult to distinguish from them, are the nuclei of contracted chromatophores. Above the lens the longitudinal row of photogenic cells is clearly seen. Their nuclei are still more flattened and denser than those seen in *H. novae-zealandiae* and *H. grimaldii*, but the cells again possess basal caps and associated nerve fibres. Behind and below the photogenic cells lie the nuclei of the reflector tissue (Fig. 18, *n.r.c.*).

It has not been found possible to trace out the further course of the nerve supply to the photogenic cells. As seen in Fig. 18 the nerve bundles extend dorsally and lie parallel with each other in the branchiostegite. Presumably they are all branches from a single nerve, but this has not been observed, either in whole preparations or in sections. Furthermore, it is not clear whether or not all the carapace organs are innervated by branches from a single main nerve trunk. Further investigation, employing suitable methods on properly fixed material, is necessary to elucidate fully the innervation of these and other photophores.

A constant feature of the carapace organs of the three species studied is their close association with a prominent blood channel which runs horizontally in the branchiostegite from the posterior to the anterior end. On reaching each photophore, this breaks up into a number of smaller channels, which, as far as can be seen in the whole mounts of portions of the carapace, form a plexus in the tissues of the organ. It is possible that these fine vessels, appearing in section, may give rise to the vacuolar appearance noted between the fibrous bundles of the reflector tissue (p. 342 and Fig. 17, *vac.*). The fine vessels of the plexus reunite at the anterior end of the photophore to pass on as a single channel to the next most anterior organ, where the same arrangement is observed. The horizontal channel terminates at the most anterior photophore. This distribution of the photophore blood supply has been most clearly seen in *H. typus* (Fig. 18, *b.v.*), but is apparent also in *H. novae-zealandiae* and *H. grimaldii*, and is a further illustration of the copious vascularization of photogenic tissues noted during the course of this work.

The absence of a definite chitogenous epithelium between the photophores and the integument seems to indicate that they are of ectodermal origin.

2. THE PHOTOPHORES OF *SYSTELLASPIS AFFINIS* (FAXON) AND *S. DEBILIS* (A. MILNE-EDWARDS)

The existence of photophores in a member of the genus *Systellaspis* appears to have been first noted by Perrier in 1886 in *S. pellucida* (Kemp, 1910*b*, p. 643, as *Acantheephyra pellucida*). Perrier's account, however, is of somewhat uncertain reliability, and the first dependable account of the presence of photophores in a member of this genus was

given by Coutière (1905, p. 7) in his re-description of *Systellaspis debilis*. This account he amplified the following year (Coutière, 1906, p. 4), and Kemp (1910*a*, p. 67) later compared the positions occupied by the photophores of the two species. A detailed description of the structure of the elaborate pleopod photophores of *S. debilis*, together with some observations on the remainder of the photophores, is also due to Kemp (1910*b*, p. 643). As far as I am aware no other account of the structure of the photophores found in this genus has appeared.

The rare *S. affinis*, like *S. debilis*, possesses luminous organs in considerable profusion, and is of considerable interest in presenting features not found in the latter species. In the following account the photophores of these two species will be described and compared.

(i) *Systellaspis affinis*

The single specimen of *S. affinis* which I have been able to examine was one of forty-five specimens obtained by the Murray Expedition from the Zanzibar area. These specimens have already been described by Dr W. T. Calman (1939, p. 190), who quotes Dr Kemp's notes on the photophores.

My examination has given no considerable support to the view that the pigment spots still visible on the first abdominal segment, at the articulation points of the 4th/5th and 5th/6th abdominal segments, and dorsally at the base of the telson (Calman, 1939, p. 191), are truly luminous organs, although their position is marked in the epithelial tissues by well-defined structures.

The known photophores correspond in position in general with those of *S. debilis*. On continued preservation their pigmentation, which in my specimen consisted of a faint red coloration, has now disappeared, and in its absence a dense white pigmentation is now apparent. It is most prominent on the ocular peduncle, the carapace margin, and behind the base of the last thoracic limb, but is present in many other parts of the body, where it appears to reveal the presence of photophores hitherto unrecorded. In addition to the positions occupied by photophores recorded by Dr Kemp, I am able to mention provisionally the following as indicated by further white opaque spots:

Branchiostegal wall: three scattered spots.

Anterior border of abdominal somite 2: one spot.

Anterior border of abdominal somite 3: one spot.

Posterior border of abdominal somite 3: one spot.

Pleura of abdominal somites 1 and 3: two spots.

Antenna: a fine transverse streak behind the base.

Mxpd. 1: on exopod one spot.

Mxpd. 3: at distal and proximal ends of dactylus one spot.

Pleopods 1, 3, 4 and 5: at base of exopod one spot.

Uropod: at base of protopodite one complex boss-shaped photophore.

The total number of photophores apparent on the specimen I examined would appear to be in the neighbourhood of 125, although due to the fact that some of the

organs are not very clearly defined it is unwise to state a precise number until more specimens have been carefully examined. On the other hand, however, some of the organs, particularly those on the ocular peduncles, the transverse streak behind the bases of the last thoracic limbs, and those on the inferior margin of the carapace, stand out prominently as white streaks and dots against the now dull yellow of the integument. The ocular peduncle photophores (Fig. 19, *oc.p.phot.*) appear as an irregular, somewhat raised white bar, placed on the inner ventral face of the peduncle, and a pear-shaped similar mass borne on a small ventrolateral tubercle. Any light produced by these photophores would be shed mainly downwards from the inner side of the peduncle.

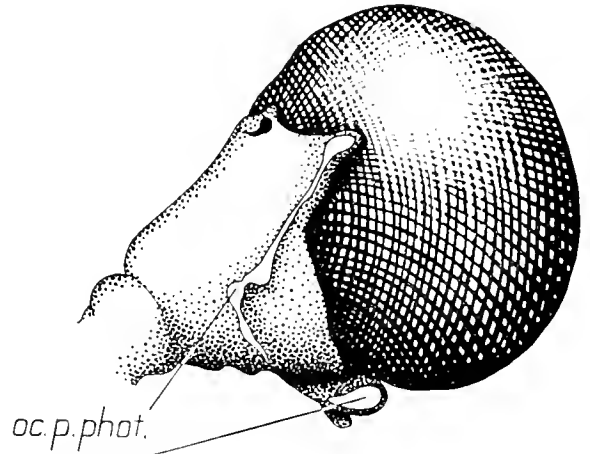


Fig. 19. The left ocular peduncle of *Systellaspis affinis*, viewed from the side and slightly below, showing the photophores in the form of somewhat raised opaque white masses. $\times 140$. *oc.p.phot.* ocular peduncle photophores.

The transverse streak at the bases of the last pair of thoracic limbs (Plate XXVI, fig. 2, *phot.t.s.*) is also raised from the surrounding integument, and extends laterally, curving upwards and somewhat forwards on the ventral side of the body. The right and left streaks almost meet in the middle line. They thus occupy precisely the same position as those in the species of *Hoplophorus* (p. 337).

The branchiostegal photophores (Plate XXVI, fig. 2, *phot.c.m.*) consist, in this specimen at any rate, of a long posterior streak, with fourteen short bars of varying length extending from its anterior end to the anterior end of the lower margin of the carapace, extending in fact to the base of the prominent branchiostegal spine. Although only fourteen streaks are visible superficially, a cleared and mounted portion of the branchiostegite shows that between them occur numerous very small patches of similar tissue, so that the inferior branchiostegal organs may almost be regarded as constituting a potentially continuous band of photogenic tissue, strongly developed in localized areas.

The nature of the deposits of white opaque pigment in the photophores of *S. affinis* will be considered in detail in the discussion at the end of this paper (p. 374).

(a) *The pleopod photophores*

The pleopod photophores of *Systellaspis affinis* (Fig. 20, e.g. *phot.pl.* 5) are borne in the manner which appears typical of the Hoplophoridae and which has already been described in *Hoplophorus* (p. 329). Here too they are overlapped by the pleura of the abdominal somites, in which there is little doubt that a window-like zone free from pigmentation occurs. (It must be admitted, however, that in a water-colour sketch of

the actual specimen I examined, made on the Murray Expedition by Lt.-Col. R. B. Seymour-Sewell, no such absence of pigmentation is indicated. It is possible that such a transparent area of small size might perhaps be overlooked in the preparation of such a figure intended to show the general pigmentation.) The pleopod photophores are readily observed, even in the preserved specimen, on account of the distinct nature of the lens, which appears as a sharply circumscribed shining elevation.

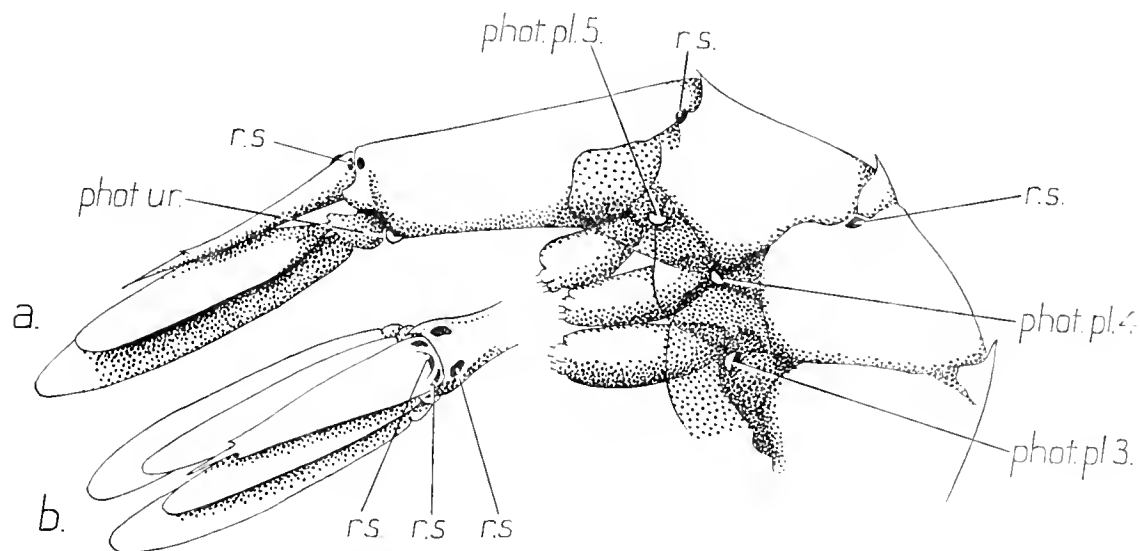


Fig. 20. *a*, the last four abdominal somites and telson of *Systellaspis affinis* in lateral view. *b*, the telson, uropods, and posterior portion of the last abdominal somite in dorsal view, to show the position of the uropod and pleopod boss-shaped photophores and of certain pigment spots. $\times 3.5$. *r.s.* pigment spots; *phot.pl. 3*, *phot.pl. 4*, *phot.pl. 5*, photophores borne on the protopodites of the third, fourth and fifth pleopods; *phot.ur.* photophore just anterior to the base of the uropod.

An essential similarity of structure is readily apparent between these photophores and those similarly situated in *Hoplophorus* and *Systellaspis debilis* (Kemp, 1910*b*, p. 643), but at the same time there exist noteworthy differences which will be mentioned in passing. Apart from these differences the photophores require little description.

The lens of these organs has the same structure as has been seen in *Hoplophorus* (p. 329) and differs but little from that of *Systellaspis debilis*. It shows inner and outer layers, and a middle layer with again a less dense central layer (Fig. 21, *l.o.*, *l.i.*, *l.m.*), whereas in *S. debilis* the middle layer appears to be uniform. The peripheral depression around the lens, noted in *Hoplophorus* (p. 330) and in *Systellaspis debilis* (Kemp, 1910*b*, p. 643), is not very well marked, but this may be due to the condition of preservation of the specimen. The longitudinal photophore muscle (Fig. 21, *phot.l.m.*; cf. *Hoplophorus*, p. 333) has been distinguished, but no circumferential muscle loop like that of *Hoplophorus* could be discovered. A study of carefully fixed material would in all probability reveal this muscle loop, as it is also present in the pleopod photophores of *Systellaspis debilis*.

On the inner side of the lens and contiguous with it lie the radially disposed photogenic cells (Fig. 21, *n.phot.c.*, *cyt.phot.c.*). Their nuclei are distally situated and are of the form and appearance already noted in *Hoplophorus* (p. 331), differing conspicuously

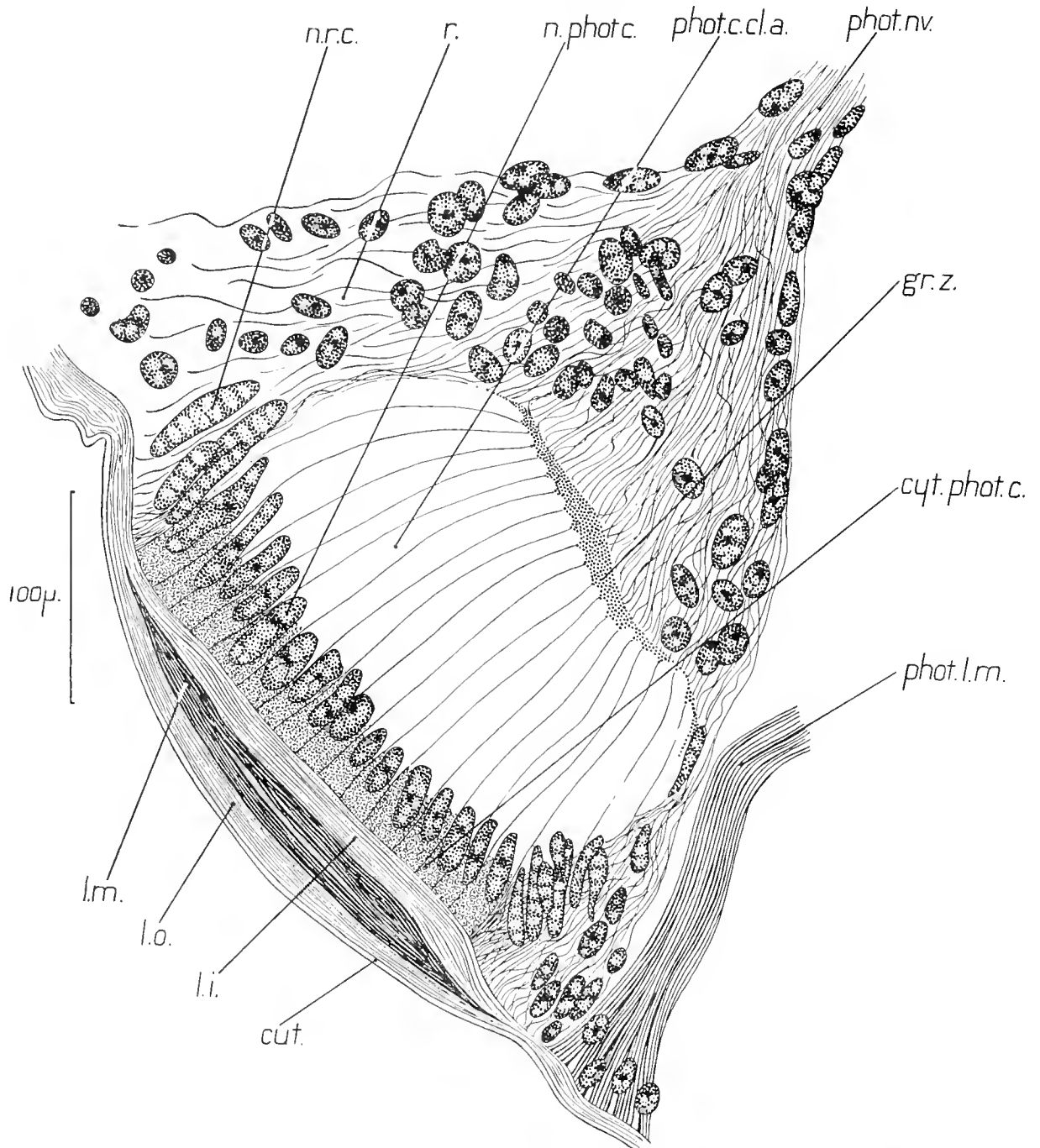


Fig. 21. Section illustrating the structure of the pleopod photophore of *Systellaspis affinis*. Mallory's triple stain. *cut.* cuticle; *cyt.phot.c.* cytoplasm of photogenic cell; *gr.z.* granular zone; *l.i.* inner layer of lens; *l.m.* middle layer of lens; *l.o.* outer layer of lens; *n.phot.c.* nucleus of photogenic cell; *n.r.c.* nucleus of reflector cell; *phot.c.cl.a.* clear area of photogenic cell; *phot.l.m.* longitudinal muscle of photophore; *phot.nv.* photophore nerve; *r.* reflector.

from those in *Systellaspis debilis*. The curious gradation in size and abrupt truncation characteristic of *S. debilis* is not apparent. The uniformly dense cytoplasm of the photogenic cells (Fig. 21, *cyt.phot.c.*) is concentrated distally in the now familiar manner, and again the greater part of the proximal portion of the cells appears to be completely without contents (Fig. 21, *phot.c.cl.a.*). The smoothly rounded narrow proximal ends of the photogenic cells rest on a plate-like granular zone (Fig. 21, *gr.z.*) which has the same appearance and staining reactions as in *Hoplophorus*. On its inner surface this granular zone shows a slight conical elevation corresponding with the more pronounced cone of *Hoplophorus*, but no indication of any segmentation corresponding with the number of photogenic cells is seen.

The granular zones of *Hoplophorus* and *Systellaspis affinis* agree not only in being conical, but in having the apex of the cone basally directed, whereas in *S. debilis* it is distally directed, pointing towards the photogenic cells. Furthermore, in *S. debilis* not all the photogenic cells make contact with the granular zone, the most peripheral ones apparently lying against the fibrous reflector (Kemp, 1910*b*, pl. lii, fig. 1; pl. liv, fig. 1).

Innervation of the photophore is carried out by a bundle of nerve fibres (Fig. 21, *phot.nv.*) which approaches the granular zone directly, without the intervention of a striated zone as in *Hoplophorus*. Peripheral elements of this bundle, presumably non-nervous, do not impinge on the granular zone but diverge to form a funnel-like fibrous capsule, enclosing the organ, which probably acts as a reflector. Numerous small, dense, and rounded nuclei are scattered throughout the fibres of this reflector, as they are in *Hoplophorus* and *Systellaspis debilis*, and probably represent chromatophores. Superficially and peripherally in the same plane as the nuclei of the photogenic cells occur greatly elongate nuclei of uncertain significance. They are clearly distinguishable from the neighbouring photogenic nuclei on account of their delicate vacuolation. Similar nuclei are present in the pleopod photophores of *Hoplophorus* (p. 332), and also, as far as can be seen from Kemp's observations (1910*b*, pl. lii, fig. 1), which are confirmed by my own examination, in those of *Systellaspis debilis*. For convenience I refer to them as nuclei of reflector cells without denying the possibility of their subserving some other function, such as the secretion of an active principle of luminescence.

It would appear improbable that the above-mentioned differences can exercise any significant influence on the precise mode of functioning of the photophores, but in the absence of any extended observations on their luminescence or of any detailed investigation into their physiology it would be premature to assume this. In structure the pleopod photophores of *S. affinis* occupy a position somewhat intermediate between those of *Hoplophorus novae-zealandiae* and *Systellaspis debilis*. In *S. affinis* the truncation and well-marked gradation in size of the photogenic nuclei seen in *S. debilis* is absent, but the full complexity of innervation and musculature of *Hoplophorus novae-zealandiae* is not attained.

(b) The uropod photophores

Complex photophores of the same basic pattern as that shown by the pleopod photophores, but presenting a curious condition of the photogenic cells, occur immediately in front of the bases of the uropods of *Systellaspis affinis* (Figs. 20, 22, *phot.ur.* and Plate XXVI, fig. 1). They are elevated on slight but definite protuberances which face downwards and backwards, and, being without any trace of a controlling musculature or peripheral depression circumscribing the lens, appear to be immovable. They are innervated by a pair of massive nerves (Fig. 22, *phot.nv.*) which arise from the ventral

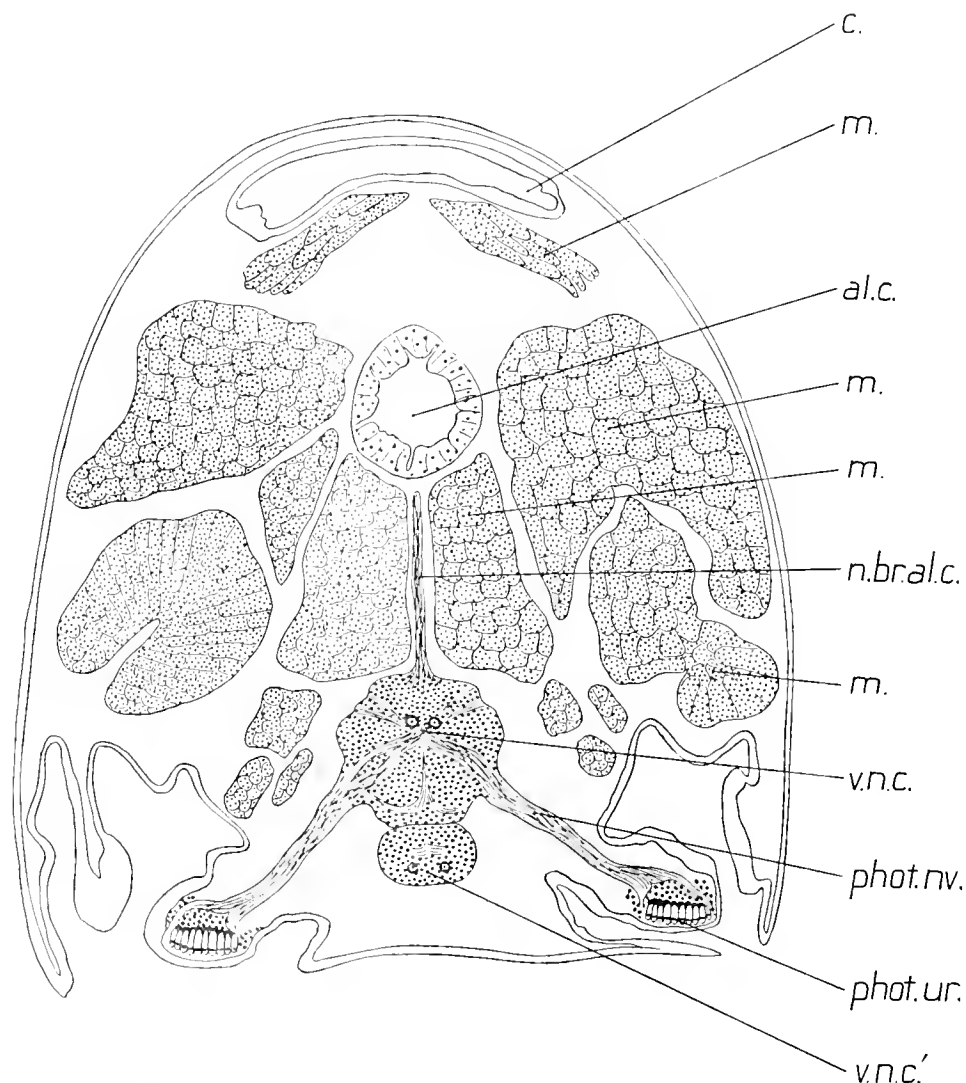


Fig. 22. Transverse section through the junction of the sixth abdominal somite and telson of *Systellaspis affinis* to show the position and innervation of the uropod photophores. $\times 33$. *al.c.* alimentary canal; *c.* cavity appearing in the section due to the slight overlapping of the telson by the sixth abdominal somite at their junction; *m.* abdominal muscles; *n.br.al.c.* nerve from ventral cord to alimentary canal; *phot.nv.* nerve to photophore; *phot.ur.* photophore immediately in front of uropod base; *v.n.c.* ventral nerve cord; *v.n.c.'* tip of a posteriorly directed fold of the ventral nerve cord appearing in the section.

nerve cord immediately anterior to and independently of the nerves supplying the uropods.

The lens of the organ is only relatively feebly developed, and is in fact thinner than many parts of the neighbouring chitin, from which it is mainly distinguished by its possession of an inner and outer layer. The inner layer (Fig. 24, *l.i.*) is more compact and densely striated than the outer (Fig. 24, *l.o.*) and stains more deeply. As a whole the lens is not sharply delimited from the surrounding integument. The reduction of the lens is, I believe, closely correlated with the peculiar condition of the photogenic cells, each of which possesses its own lens.

The photogenic "cells" exhibit no structure which can be interpreted as a nucleus, and for this reason I have preferred to refer to them as "photogenic units". They do not show the pronounced radial disposition of the pleopod organs already discussed, but lie almost parallel with each other beneath and perpendicular to the lens. Like the photogenic cells of the pleopod organs the greater part of their volume is entirely unoccupied by any cytoplasmic content (Figs. 23, 24, *phot.u.cl.a.*). Distally the nucleus is replaced by an aggregation of structures, the most obvious of which is a lens-like septum (Fig. 23, *l.s.*) extending across the photogenic unit at some distance from its distal tip. This lens septum is plano-concave, its concavity facing the clear area of the photogenic unit. It appears to be composed of a number of laminae, and stains an intense red with Mallory's triple stain. That it is a relatively rigid and definite structure is shown by the fact that in the process of sectioning it may be displaced bodily as seen in Plate XXVI, fig. 1.

Immediately distal to the lens occurs a structureless zone (Fig. 23, *st.s.* 1) staining a uniform light Cambridge blue. The distal surface of this zone merges with the next zone, which is highly vacuolated (Fig. 23, *vac.s.*). Its vacuoles are minute proximally, but progressively increase in size towards the distal surface of the zone, where they cease abruptly. Succeeding the vacuolated zone occurs a second structureless zone (Fig. 23, *st.s.* 2), again assuming a blue coloration with Mallory, but not uniformly. Staining is most intense at the proximal boundary, becoming progressively lighter towards the distal tip of the photogenic unit, which is in addition finely granular (Fig. 23, *gr.t.*). There are thus recognizable five zones, including the lens, at the distal end of the photogenic unit.

Proximally the units are in close association with a dense granular mass (Fig. 23, *pr.gr.m.*), which is indifferent to any of the constituents of Mallory's triple stain, and which appears golden brown by transmitted light but a pure opaque white by reflected light. Similar granular substance appears in photophores in other parts of the body of *S. affinis* (p. 356), although laid down according to a different pattern, and it is clearly the presence of this substance which causes the organs to remain visible as white marks after the loss of the original pigmentation.

In the uropod photophores the proximal granular mass occupies about one-quarter of the total length of the photogenic unit, and is densest at its proximal end. Fine striae are discernible in some instances near its distal border (Fig. 23, *str.l.*). At first sight

this granular mass appears to correspond closely with that seen at the base of the photogenic cells of the pleopod photophores of *Hoplophorus* and *Systellaspis affinis* itself, and even more closely with the non-staining granular zone of *S. debilis* (Kemp, 1910b, p. 644). For the reasons which follow, however, I do not believe that this is so.

Close examination of the uropod organs of *S. affinis* shows the presence of minute lenticular bodies resting in the distal concavities of the granular masses (Fig. 23, *phot.c.b.c.*). They stain readily with acid fuchsin, and present a finely punctate appearance, strongly recalling the basal cap of the carapace photophores of *Hoplophorus* (Fig. 17, *phot.c.b.c.*), with which I believe them to be homologous. Earlier (p. 342), I gave reasons for my belief

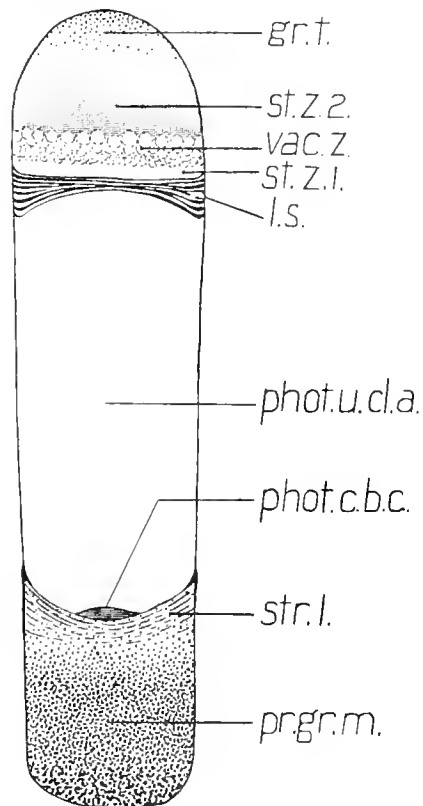


Fig. 23. Diagram of a single photogenic unit of the uropod photophore of *Systellaspis affinis*. *phot.c.b.c.* basal cap of photogenic cell; *gr.t.* granular tip; *l.s.* lens-like septum; *phot.u.c.l.a.* clear area of photogenic cell ("unit"); *pr.gr.m.* proximal granular mass; *st.z. 1.* first structureless zone; *st.z. 2.* second structureless zone; *str.l.* striated layer; *vac.z.* vacuolated zone.

that the basal cap of *Hoplophorus* is homologous with the granular zone of the pleopod organs of *Hoplophorus* and *Systellaspis*. It would therefore appear that the basal cap, and not the granular mass of the uropod photogenic units, corresponds with the granular zone of the pleopod photophores mentioned.

The proximal granular mass, then, is a structure of an entirely new type and is additional to those already seen in the pleopod organs. It forms a compact reflector behind the photogenic units, where its efficiency is no doubt enhanced by the possession by each block of granules of a distal concave surface.

The pattern of arrangement of the photogenic units within the organ leaves little doubt of their homology with the photogenic cells of the pleopod photophores, although the relation between the nucleus of the pleopod photogenic cell and the distal structures of the uropod photogenic unit is far from clear. It is difficult to see in these distal structures any representative of a nucleus, and in the absence of further information I do not intend to speculate on the fate of the nucleus which the photogenic cell undoubtedly once possessed. Only an investigation into the development of the photophores, for which a supply of material would be difficult to obtain, can elucidate the problem. The position of the lens, within the distal tip of the "cell", is to some extent paralleled by the condition seen in the eye of the serpulid worm *Braichiomma* (Dahlgren and Kepner, 1908, p. 241).

Here the elongated hypodermal cells secrete a lens in their distal cytoplasm, but a lens-shaped nucleus is retained. It will be shown later (p. 358) that some cells of other photophores of *Systellaspis affinis*, like those of *Hoplophorus*, also lose their nuclei.

Immediately behind the reflector formed by the proximal granular masses of the photogenic units is situated a conical mass of nuclei (Fig. 24, *n.*) which differ from all other adjacent nuclei. They are closely crowded and are deeply staining, showing a prominent nucleolus, and being larger than the nuclei of the chitogenous epithelium, which in my preparations show no obvious nucleolus, they are readily

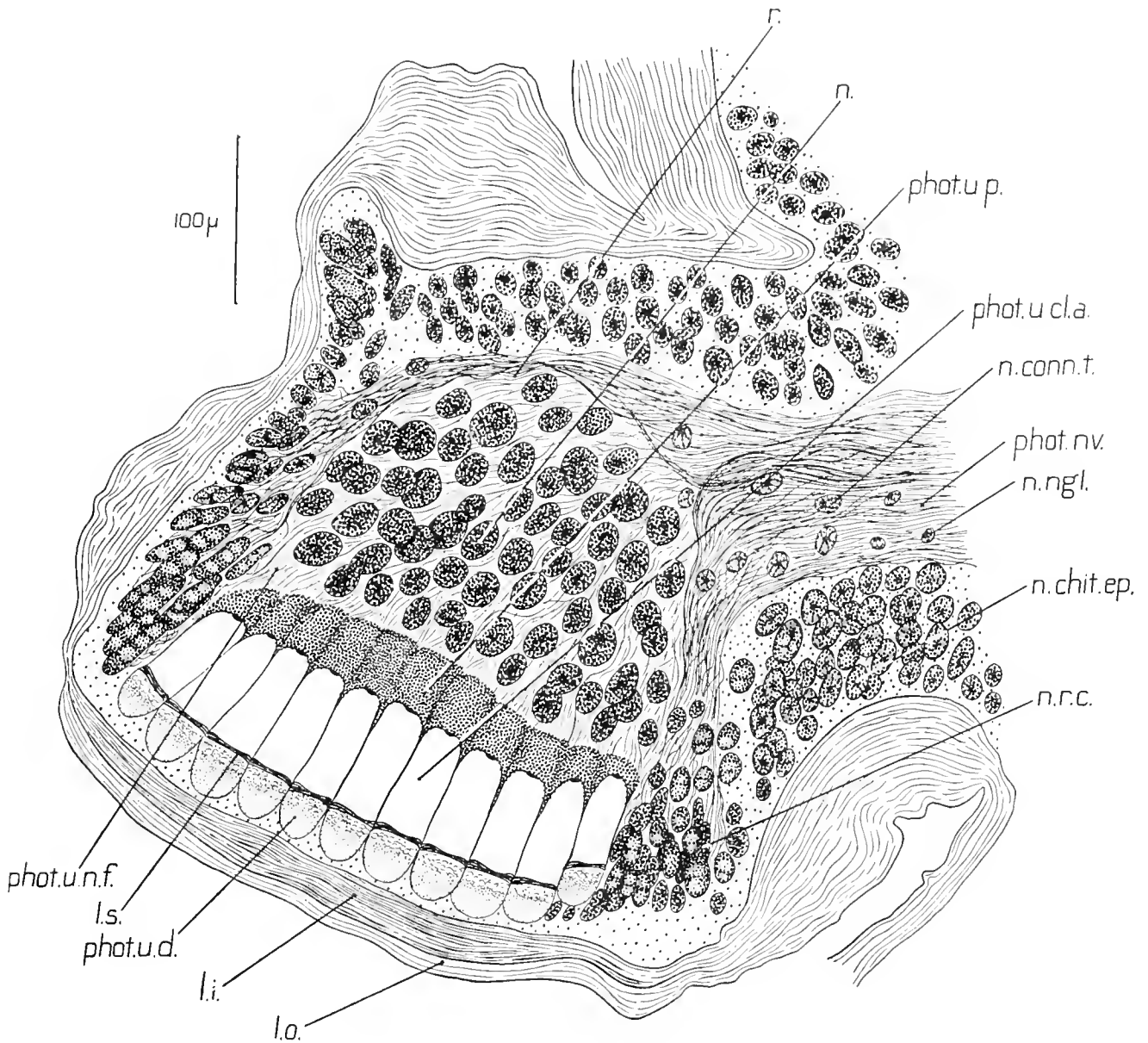


Fig. 24. Part of a transverse section through the abdomen of *Systellaspis affinis* to show the structure of the uropod photophore. Mallory's triple stain. *l.i.* inner layer of lens; *l.o.* outer layer of lens; *l.s.* lens-shaped septum extending across photogenic unit; *n.* one of a large number of densely packed nuclei lying within the fibrous reflector; *n.chit.ep.* nucleus of chitogenous epithelium; *n.conn.t.* connective tissue nucleus; *n.ngl.* neuroglia nucleus; *n.r.c.* nucleus of cell producing reflector layer; *phot.nv.* nerve to photophore; *phot.u.c.l.a.* clear area of photogenic unit; *phot.u.d.* distal mass of photogenic unit; *phot.u.n.f.* nerve fibrils to photogenic unit; *phot.u.p.* proximal mass of photogenic unit; *r.* reflector.

distinguishable from them. On the other hand, they are quite different from both the nuclei of the connective tissue sheath of the photophore nerve (Fig. 24, *n.conn.t.*) and its neuroglia nuclei (Fig. 24, *n.ngl.*), both of which are highly distinctive. The connective tissue nuclei have a much more diffuse chromatin arrangement, and their coagulated nuclear fluid stains lightly with aniline blue, whereas the neuroglia nuclei are small, with very densely packed chromatin. I believe that the cone of nuclei represents a mass of chromatophores still further serving as a screen preventing the inward passage of light.

The massive nerve branch to the photophore (Fig. 24, *phot.nv.*) shows in the neighbourhood of the ventral nerve cord some of its constituent elements—nerve fibres, connective tissue sheath and its nuclei, and neuroglia nuclei. The neuroglia fibres are not discernible with the fixative and stain employed. In the region of the photophore, however, these elements are not so clearly distinguishable, and the nerve shows a greater development of its connective tissue sheath. At the apex of the cone of chromatophore nuclei, on the inner side of the photophore, the connective tissue sheath of the nerve expands to form a cup-like investment of the organ (Fig. 24, *r.*). Since this structure occurs in the position occupied by the fibrous reflector of the pleopod photophores I have retained for it the term “reflector”, although as far as can be seen its function is largely usurped by the massive granular reflector. Just as in the pleopod photophores, elongate vacuolated nuclei are found in the reflector at the level of the photogenic cells (Fig. 24, *n.r.c.*).

As far as I can ascertain, the nerve fibres do not expand with the fibrous sheath and become involved in the reflector, but pass through the cone of chromatophore nuclei and impinge on the proximal granular masses of the photogenic units. The precise mode of entry of the nerve fibrils to the photogenic units has not been discovered.

To recapitulate briefly, the distinctive features of the uropod photophores are their possession of intracellular lenses and a reflector of an entirely novel type.

(c) *The transverse streak behind the coxa of the fifth thoracic limb*

As has been previously stated, the transverse luminous streak behind the base of the fifth thoracic limb of *Systellaspis affinis* occupies the same position as in *S. debilis* and *Hopliphorus*. In my specimen it consisted of a somewhat raised white opaque band, extending laterally and dorsally and slightly anteriorly. It is indicated in the photograph in Plate XXVI, fig. 2, in which it did not show very clearly, as a white streak (*phot.t.s.*). On cutting out and sectioning the strip of tissue it proved, contrary to expectations, to have an entirely different structure from the similar organs of *Hopliphorus*, and also from the photophores on the fifth thoracic limb itself. As will be seen from Fig. 25 it has the same basic structure as the pleopod, and particularly the uropod, photophores. It may be said at once that the proximal granular mass of white opaque substance mentioned in the description of the uropod organs is present here, and accounts for the external appearance of the organ.

The elevation of the luminous streak above the adjacent integument is accounted for

mainly by the thickening of the chitin above the photogenic cells. As seen in Fig. 25 the chitin (*chit.*) in this region is about 60μ in thickness, whereas elsewhere it is only about 15μ thick. In transverse section the thickened band has the form of a plano-convex lens, and is seen to be made up of two layers. It is overlain by the non-striated cuticle (Fig. 25, *cut.*).

The photogenic cells lie immediately beneath the integument, and are disposed for the most part in a double or a treble row. They exhibit the now familiar clear area, devoid of cytoplasmic contents (Fig. 25, *phot.c.cl.a.*) and are as usual so orientated that their nuclei are situated at their distal ends. The nuclei are extremely dense and their chromatin appears to consist of closely packed granules. No trace of cytoplasm is apparent either distal to the nuclei or anywhere else in the cells. The shape of the nuclei strongly recalls that seen in the corresponding nuclei of the carapace photophores of *Hoplophorus* (p. 340), their distal surfaces being smoothly and convexly rounded, while their proximal surfaces, facing the clear areas of the cells, are markedly concave. Each nucleus has the form of a thick concavo-convex lens.

Proximally prominent granular masses (Fig. 25, *pr.gr.m.*), of precisely the same material and form as those seen in the uropod photophores, occupy the bases of the cells, and so constitute a massive reflecting layer behind them. Again the layer is

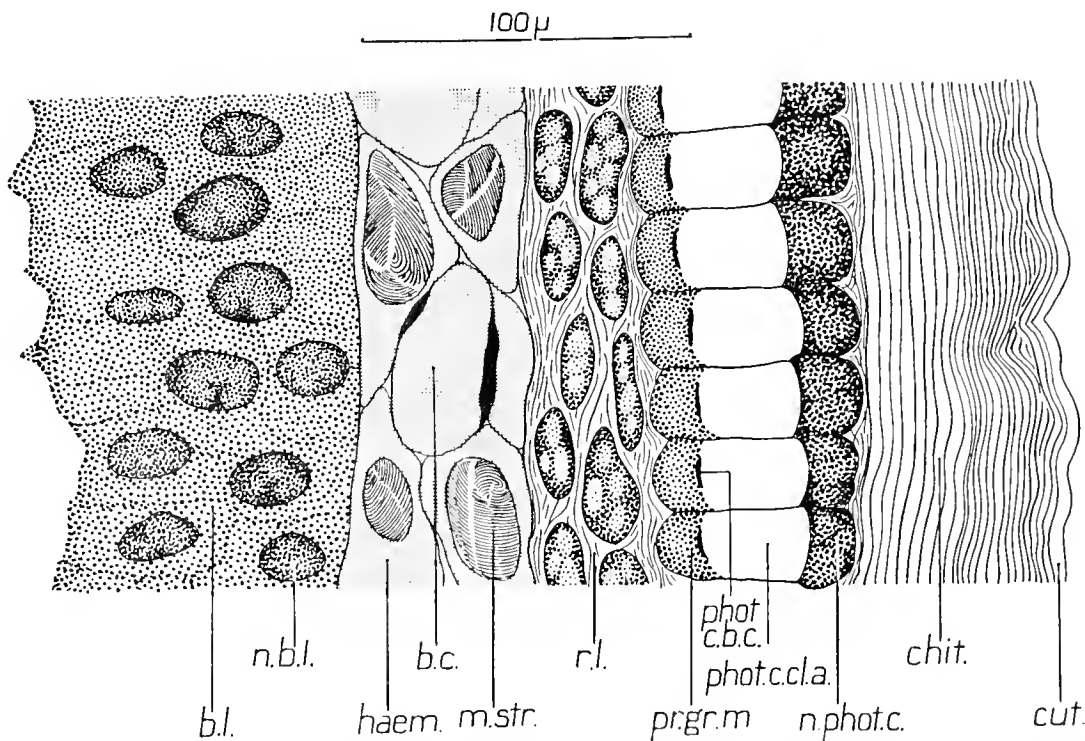


Fig. 25. Part of a section passing vertically through the length of the transverse photogenic streak behind the last thoracic limb of *Systellaspis affinis*. Mallory's triple stain. *b.l.* basal layer; *b.c.* blood channel; *chit.* chitin; *cut.* cuticle; *haem.* haemocoel; *m.str.* muscle strand; *n.b.l.* nucleus of basal layer; *n.phot.c.* nucleus of photogenic cell; *phot.c.b.c.* basal cap of photogenic cell; *phot.c.cl.a.* clear area of photogenic cell; *r.l.* reflector layer; *pr.gr.m.* proximal granular mass.

indifferent to any of the stains used, and appears brilliant white by reflected light. Resting within the distal concavity of each proximal granular mass is a basal cap, corresponding precisely with those observed in the carapace organs of *Hoplophorus*. The basal caps are thin, with almost plane distal, and proximal convex, surfaces. As has been pointed out earlier (p. 352) these basal caps correspond to the granular zone of the pleopod photophores of *Systellaspis* and *Hoplophorus*.

Lying beneath the photogenic cells is a tissue layer, corresponding with the fibrous reflector of the pleopod photophores, and consisting of a fibrous sheet in which lie large vacuolated nuclei elongated in a plane parallel to the surface of the photophore. It will be recalled that the fibrous reflector of the pleopod photophores is apparently derived from the connective tissue sheath of the photophore nerve, or at any rate is continuous with it (p. 354), and that the nerve fibrils impinge directly on to the granular mass (p. 354). With this in mind, careful search has been made in the neighbourhood of the fibrous layer of the photophore under discussion for any indications of nerve supply. Possibly owing to the fact that the fixation of this specimen is not as good as might be desired, no definite indications of such supply were recognized. I believe, however, that a study of specially preserved material will reveal that these photophores possess their own special innervation in relation to the basal caps in much the same manner as has been seen in the carapace organs of *Hoplophorus*.

Underlying the fibrous reflector layer occurs a zone of scattered connective tissue in which muscle strands (Fig. 25, *m.str.*), fine blood channels (Fig. 25, *b.c.*) and larger haemocoelic spaces (Fig. 25, *haem.*) are recognizable.

Lastly, the basal layer (Fig. 25, *b.l.*) of the excised strip of tissue is that lining the main ventral haemocoelic space of the posterior part of the thorax. It shows ill-defined cell boundaries and possesses nuclei which are quite different from any observed in the photogenic streak.

It will be appreciated that a photophore of this type differs fundamentally in structure from that found in the corresponding position in the three species of *Hoplophorus* examined.

(d) *The photophores on the fifth thoracic limb*

For the purpose of description of the photophores occurring on the thoracic limbs, the proximal spot on the propodus of the last thoracic limb has been selected. All other photophores on the thoracic limbs that have been examined are identical, and from the point of view of their structure do not require further attention.

These photophores present an extraordinary appearance which is only paralleled by the organ behind the base of the last thoracic limb, and perhaps by that in the limb itself, of *Hoplophorus* (p. 337). The main mass of the organ is, however, quite unlike those of *Hoplophorus* just mentioned, being composed of the white opaque granular substance mentioned in describing the uropod photophores (p. 351) and the streak at the base of the fifth thoracic limbs (p. 355). It is present in such quantity that the photophores are readily visible in the sections, even without the use of a microscope, as white masses (see Plate XXV, figs. 4, 5).

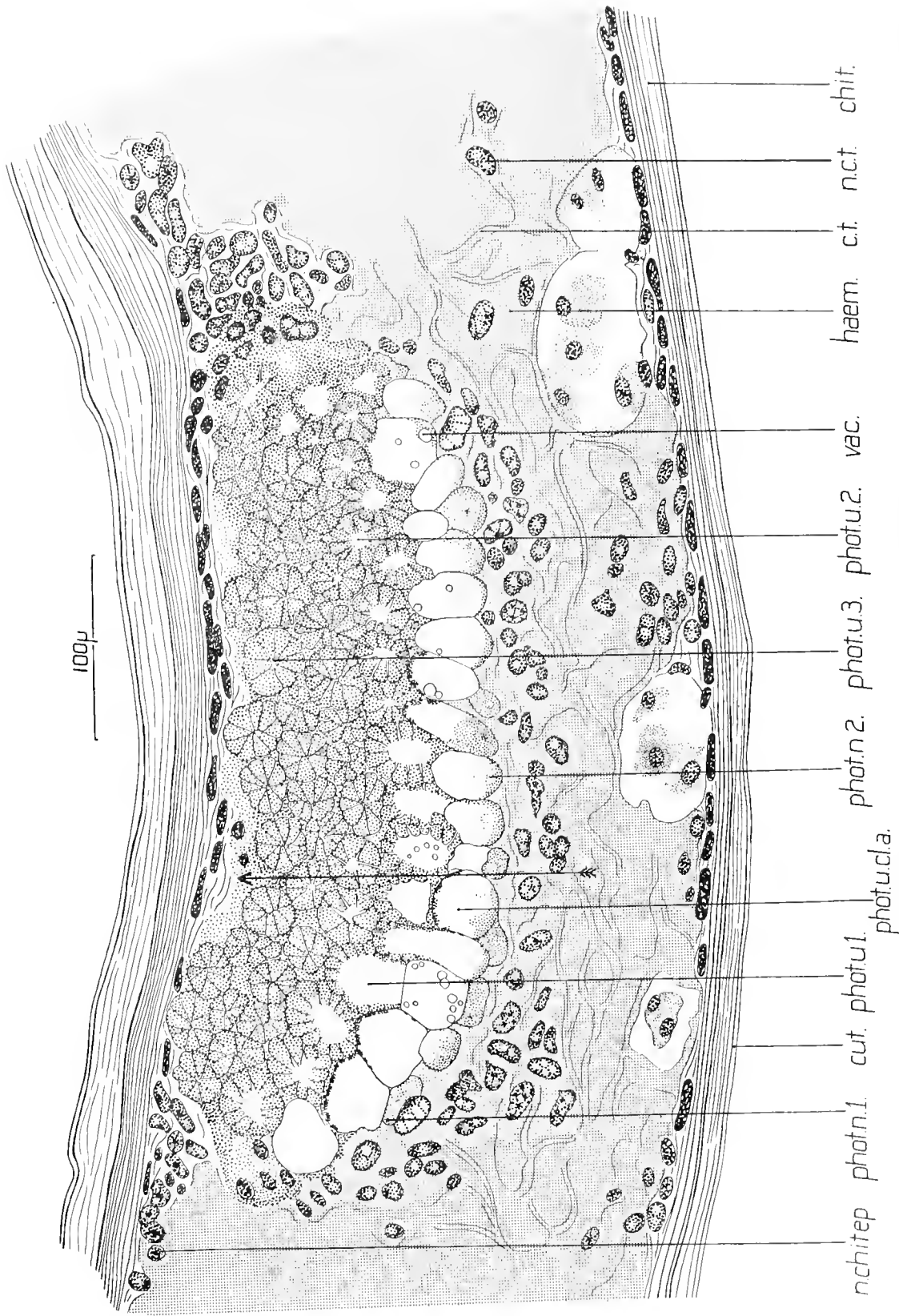


Fig. 26. Longitudinal section through the propodus of the left fifth thoracic limb of *Systellaspis affinis*, showing the structure of its proximal photophore. The haemocoel of the limb is indicated by mechanical stippling. Mallory's triple stain. *c.t.* connective tissue; *chit.* chitin; *cut.* cuticle; *haem.* haemocoel; *n.c.t.* connective tissue nucleus; *n.chit.ep.* nucleus of chitogenous epithelium; *phot.u.* 1, 2, stages in differentiation of photogenic nuclei; *phot.u.* 1, 2, 3, stages in differentiation of photogenic units; *phot.u.cla.* clear area of photogenic unit; *vac.* vacuole within developing photogenic unit.

Microscopic study of the photophore shows that this substance is deposited in a very regular manner. It occurs in the form of radially segmented spherical masses, which appear in the sections as rosette-shaped structures (Fig. 26 and Plate XXVI, fig. 6, *phot.u.* 2) most of which show no central cavity. On the inner side of the organ, however, most of the spherical masses do show a cavity (Fig. 26 and Plate XXVI, fig. 6, *phot.u.* 2), and a close study of this part of the organ suggests that it is a growing zone exhibiting, in passing towards the outer surface of the organ, successive phases in the differentiation of the segmented spheres of granular material. A similar condition was suspected in the organs behind (p. 337) and actually on (p. 334) the fifth thoracic limb of *Hoplophorus*. The organ under discussion will be described on the assumption that such intermediate phases are truly represented, although without a study of developmental stages of the animal it is difficult to form a really definite conclusion.

It appears that the precursors of the spherical granular masses are represented by certain large nuclei on the inner side of the organ (Fig. 26 and Plate XXVI, fig. 3, *phot.u.* 1) which differ from their neighbours in being as much as three or four times larger and in showing a less dense chromatin disposition. I refer to these nuclei as photogenic nuclei without wishing to imply that I am aware of their precise role in the mode of functioning of the organ, but because there appear to be no other structures in the organ capable of interpretation as photogenic structures. In no case has it been possible to detect the cell membrane of any corresponding cell with certainty.

The nuclei appear to increase in size until they are of about the same diameter as the spherical granular masses, and at the same time their chromatin forms a uniform and delicate reticulum (Fig. 27 *a, b*). Intense degeneration of the nucleus, resulting in its complete disappearance, then follows (Fig. 27 *c, d.u.*), being often foreshadowed by the appearance of an ill-defined central cavity. The degeneration of the nucleus appears to leave the nuclear membrane intact (Fig. 27 *c, d, e, f, l.m.*), but whether this is truly the nuclear membrane, or in reality a cell membrane, as would be suspected from a comparison of the organ with that of the photogenic streak and organs on the fifth thoracic limb of *Hoplophorus*, I am unable to say. Whatever the nature of the membrane, it forms the boundary of a space empty but for the inclusion of certain structures shortly to be described (Fig. 26, *phot.u.cl.a.*). This space strongly recalls the clear areas encountered in the photogenic cells of *Hoplophorus* and in the pleopod photophores of *Systellaspis affinis* itself. A noteworthy feature in the degeneration of the nuclei is that their last remnants are always to be found within the limiting membrane on the side remote from the external surface of the photophore (Fig. 26, e.g. *phot.u.* 2).

Small vacuoles (Fig. 27 *c, vac.*), usually apparently empty, but sometimes appearing to contain a coagulated fluid, are scattered within the limiting membrane, and may be sometimes observed in the nucleus at an early stage of degeneration (Figs. 26, 27, *vac.*). The first appearance of the granular substance, which forms the main mass of the organ, has been noted as minute deposits, segmentally disposed, on the inner side of the limiting membrane opposite the degenerating nucleus (Fig. 27 *c, gr.d.*).

With continued reduction of the nucleus (Fig. 27 *d*) these deposits increase in size.

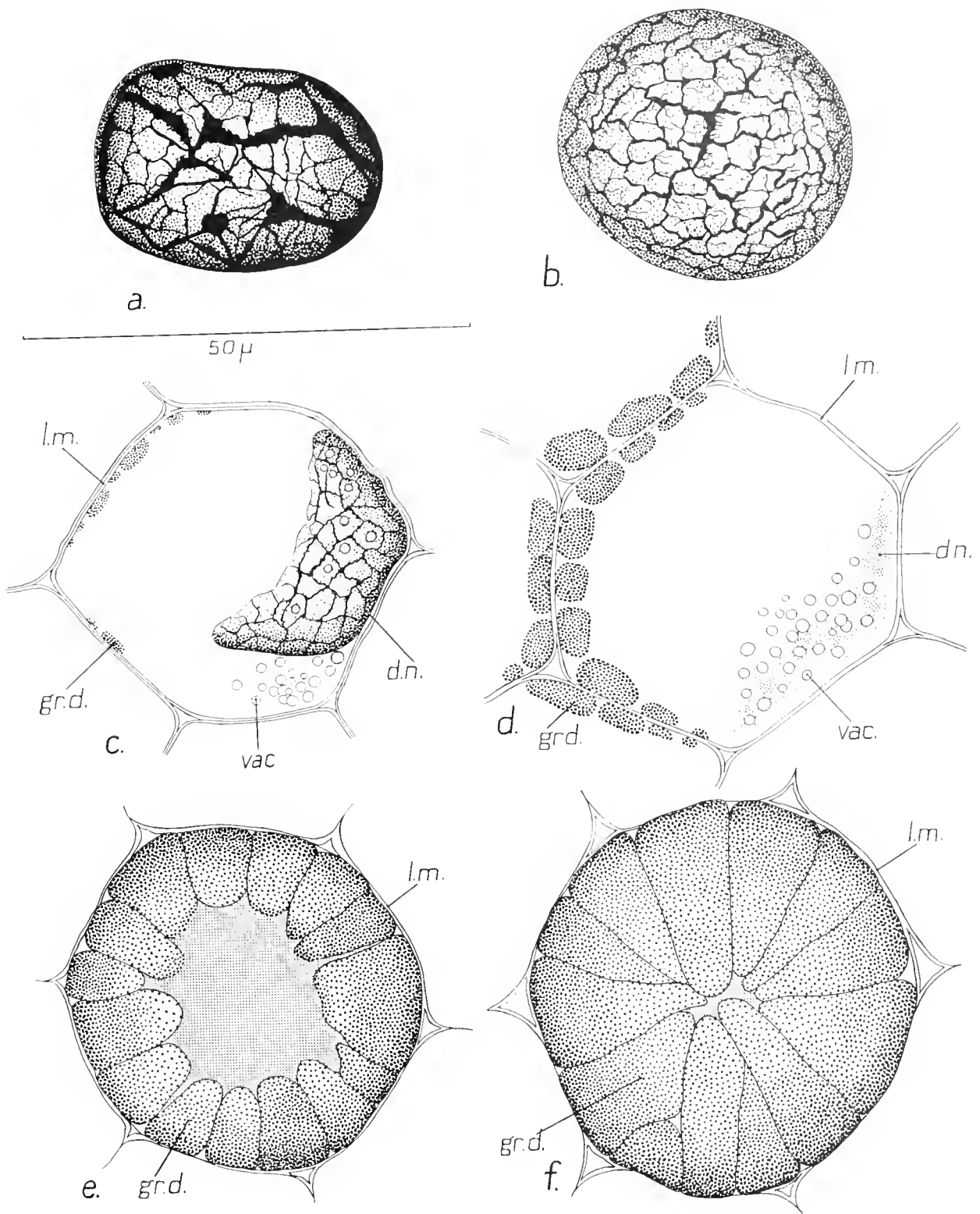


Fig. 27. The successive phases in the appearance of the photogenic units in the photophore on the carpus of the left fifth thoracic limb of *Systellaspis affinis*. The figures are taken in order from the appearance of the structures seen in passing in the direction indicated by the arrow in Fig. 26.

- a. Large nucleus, precursor of photogenic unit.
- b. Nucleus with chromatin becoming less dense and forming a more uniform reticulum.
- c. Nucleus degenerating, vacuoles appearing within the limiting membrane, and the first deposits of granular substance occurring on the inner side of the limiting membrane.
- d. Nucleus almost disappeared, vacuoles still present, and granular deposits larger and more numerous.
- e. Only the granular deposits now remain, regularly arranged and extending centripetally.
- f. Enlargement of the regularly arranged granular masses almost obliterating the central cavity, which finally disappears completely.

gr.d. granular deposit; *l.m.* limiting membrane; *vac.* vacuole; *d.n.* degenerating nucleus.

Finally, the last traces of the nucleus and the vacuoles disappear, and the segmental granular deposits are laid down around the complete periphery of the limiting membrane (Fig. 27 *e*), and continue to increase in size centripetally. Fig. 27 *f* shows the last trace of the cavity within the limiting membrane before its entire elimination by the expanding granular segments.

With reference to Fig. 26, I have used the term "photogenic nucleus" to indicate one of the large nuclei referred to, whether complete or degenerating, and the term "photogenic unit" for the limiting membrane with its granular deposits. There is no morphological indication, however, as to which of these structures is concerned in light production. The difficulty in the way of regarding the large nuclei and their phases of degeneration as being photogenic is, of course, that they are separated from the surface of the limb by the heavy granular deposit, which although it would form an efficient reflector is not adapted to allow of the passage of light.

Apparent phases in the development of the granular spheres, similar to those described above, are found in addition around the periphery of photophores of this type, and lend support to the belief that we are here considering a zone of active growth in the developing photophore.

The significance of the nuclear changes described above, and the nature of the granular substance, will be considered later in this paper (p. 374).

The photophore is bounded internally by loose and scattered strands of connective tissue (Fig. 26, *c.t.*) with small deeply staining nuclei (Fig. 26, *n.c.t.*), and is bathed by the body fluid within the haemocoel of the limb (Fig. 26, *haem.*). No special vascular supply has been observed. On its outer side the organ is cut off from direct contact with the chitin of the limb (Fig. 26, *chit.*) by the chitogenous epithelium (Fig. 26, *n.chit.ep.*) which passes uninterruptedly over it. This would suggest that the organ is not of ectodermal origin. No local lens-like thickening of the integument has been noted.

It is of some interest that the white granular substance which is laid down in a regular manner on the inner surface of the limiting membranes already mentioned is also found irregularly deposited to a far less extent among the connective tissue fibres at the periphery of the organ. Here it is extranuclear, and perhaps even extracellular, suggesting that the limiting membranes around the photogenic nuclei are at least not nuclear membranes. At any rate it is clear that the secretion of this substance is not the especial prerogative of the photogenic nuclei.

(*e*) *The carapace organs*

It has already been mentioned (p. 346) that *Systellaspis affinis* possesses carapace photophores in the form of a long posterior streak and a number of more anterior shorter streaks situated near the lower margin of the branchiostegite. These photophores have been examined, and it was expected that they would prove to have a similar structure to those in the same position in the three species of *Hoplophorus* examined. Actually they have the same form as the organs on the thoracic limb just described. They

therefore require no detailed description. The segmented spheres are of about the same size as those in the thoracic limb, and in the shorter streaks are arranged in a single or a double row, with occasional regions where three or more rows or a confused area may be seen. In general the segmentation of the spheres is not quite so clearly defined as in the thoracic limb organs, and in addition, just as in that organ, the white substance is also irregularly deposited in the neighbourhood of the spheres.

That photophores of this type, differing so much from those in the corresponding position in *Hoplophorus*, should be found in *Systellaspis affinis* is a surprising fact in view of the similarity between the pleopod photophores of these two forms and the resemblance between the carapace and pleopod photophores of *Hoplophorus*. Still more surprising is the observation (p. 366) that the carapace photophores of *Systellaspis debilis* are essentially different from those of *S. affinis*; although simpler they have the same basic structure as those of the three species of *Hoplophorus* examined.

(f) *The pigmented spots on the telson and sixth abdominal somite*

Red-pigmented spots on the telson of *Systellaspis affinis* (Fig. 20, *r.s.*) are mentioned by Dr Kemp in his notes (Calman, 1939, p. 191) and also in a letter to me which accompanied the specimen I examined. Three spots are placed in line dorsally above the base of the telson, but close examination revealed the presence, confirmed by sectioning, of an additional pair of spots placed dorso-laterally at the rear of the last abdominal somite immediately in front of the outer spots of the telson. The pigment spots continued to be visible during the preservation of the specimen in the original alcoholic fluid of unknown composition. On transference to fresh 70% alcohol in preparation for sectioning they completely disappeared, and in their absence no trace of the opaque white substance characteristic of all the photophores other than those of the pleopods was visible. Transverse sections through the pigment spots show that they are associated with simple but well-defined structures.

In the neighbourhood of the pigment spots the integument and chitogenous epithelium present a normal appearance. The chitin (Fig. 28, *chit.*), consisting of two layers differing in density of striation, stains a light Cambridge blue with Mallory's triple stain, and is overlain by the delicate cuticle (Fig. 28, *cut.*) which stains with acid fuchsin. The nuclei of the chitogenous epithelium (Fig. 28, *n.chit.ep.*) are elongated perpendicularly to the integument, and may reach $30\ \mu$ in length. Cell limits are only slightly apparent, and the cells rest on a definite basement membrane (Fig. 28, *b.m.*), beneath which the fibres of a connective tissue sheet lie horizontally. Spindle-shaped and vacuolated connective tissue nuclei (Fig. 28, *n.c.t.*), differing greatly from the nuclei of the chitogenous epithelium, are prominent among the fibres.

The position of each pigment spot is occupied by a dense convex mass of nuclei projecting into the body space. This nuclear mass is formed in part by the nuclei of the chitogenous epithelium, but mainly consists of nuclei of quite different appearance (Fig. 28, *n.m.*). Whereas the nuclei of the chitogenous epithelium are rounded and densely and uniformly packed with chromatin, those constituting the greater part of

the nuclear mass have a prominent nucleolus and show an irregular chromatin reticulation. The mass of nuclei is bounded on its inner side by a continuation of the connective tissue sheet (Fig. 28, *c.t.*), and connective tissue fibres, continuous with those of the sheet, penetrate the mass and are found among its nuclei.

The basement membrane underlying the chitogenous epithelium can be traced for some distance into the mass of nuclei, and although it becomes very tenuous and confused with connective tissue fibres it appears to cut off those nuclei derived from the chitogenous epithelium from the inner nuclei of different appearance. It would therefore appear that these inner nuclei are of mesodermal and not of ectodermal origin, but it is not possible to state what is their precise derivation.

No thickening of the integument in the shape of a lens-like structure is apparent over the mass of nuclei, and nothing in the appearance of the whole organ when compared with the appearance of known photophores definitely suggests that it too may be luminous. It can only be said that if these structures are truly luminous organs then they are of an essentially different form and are simpler than those found elsewhere in the body. It is possible that they are merely dense masses of chromatophores with no power of light production, but this can only be verified by future observations on living animals.

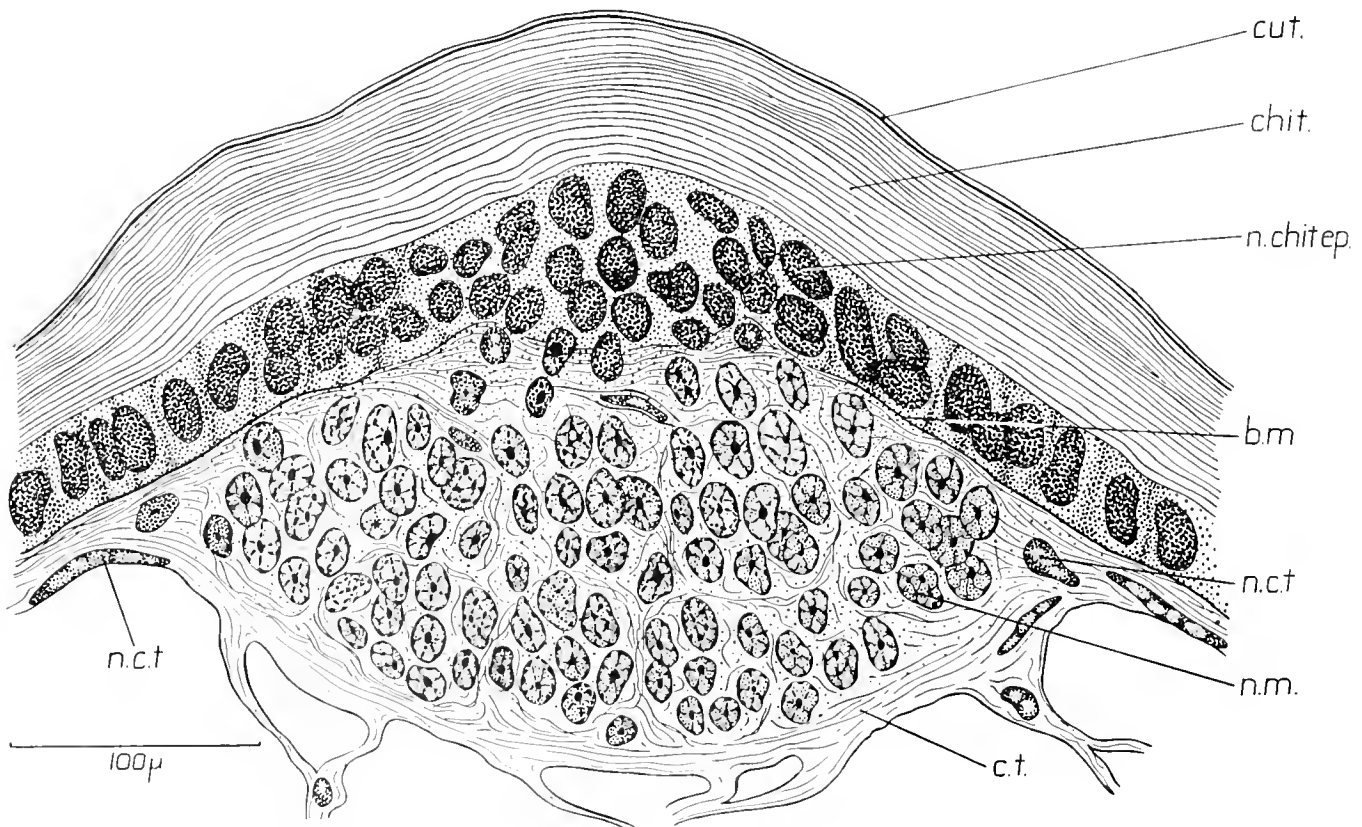


Fig. 28. Part of a transverse section through the base of the telson of *Systellaspis affinis* to show one of the structures associated with red pigment spots during life. Mallory's triple stain. *b.m.* basement membrane; *chit.* chitin; *c.t.* connective tissue; *cut.* cuticle; *n.c.t.* connective tissue nucleus; *n.chit.ep.* nucleus of chitogenous epithelium; *n.m.* nucleus of subintegumental mass.

(ii) *Systellaspis debilis*

The structure of most of the photophores of *S. debilis* has already been described by Kemp (1910*b*, p. 643, as *Acanthephyra*), and the following notes deal only with some additions and corrections based on an examination of formalin preserved material from the Dana Expedition.

In these specimens the photophores are clearly visible as purplish red streaks and spots, but all other pigmentation has been lost. Accounts of the number and distribution of the photophores have already been given by Coutière (1906) and Kemp (1910*a*), and will not be added to here.

(a) *The pleopod and uropod photophores*

After examination of the pleopod photophores of *Systellaspis debilis* I am able to endorse fully the description of them given by Kemp (1910*b*, p. 643) and to give additional observations.

It was suspected by Kemp that the photophores were possibly free to undergo a certain amount of movement with respect to the limb, but it was stated that no trace of any controlling musculature could be found. A thick (100 μ) Mallory-stained section of a photophore shows clearly that it possesses a musculature identical with that of *Hoplophorus grimaldii* (p. 333 and fig. 12), consisting of a longitudinal muscle and a circular muscle loop anchored on the outer side of the limb. In the photograph given by Kemp (1910*b*, pl. lii, fig. 1) the longitudinal muscle appears to be visible parallel to and on the outer (left) side of the photophore nerve, but no trace of the muscle loop is apparent.

A further point of interest concerns the lens, which after Mallory staining does not show clearly the three layers mentioned by Kemp (1910*b*, p. 644). The whole lens stains an almost uniform light blue in thin sections, and the layers can only be distinguished with difficulty by their differing densities of striation. The outermost layer is very dense and closely striated, the middle has a comparatively loose appearance and coarse striation, while the inner layer, although not as dense as the outer, is very closely striated. The staining reactions of the lens, however, are very capricious, for in thick sections it often readily takes up acid fuchsin in preference to aniline blue.

Whereas the photophores situated at the bases of the uropods in *Systellaspis affinis* differ markedly from the pleopod organs in their lack of photogenic nuclei, in *S. debilis* they more closely resemble them. They possess a feebly developed lens derived from the integument, although no special muscles are seen. The nuclei of the photogenic cells show the gradation in size and abrupt truncation characteristic of the pleopod photophores. The organs closely resemble those in the same position in *Hoplophorus*. The discrepancy between the structure of the uropod organs of these two species of *Systellaspis* is very curious, and is not readily accounted for.

(b) *The photogenic streak behind the fifth thoracic limb*

Kemp (1910b, p. 644) describes the transverse photogenic streak behind the last thoracic limb of *S. debilis* as consisting of elongated epithelial cells lying beneath a lens-like thickening of the integument. The epithelial cells usually, though not always, have their nuclei placed close behind the lens. No granules similar to those at the bases of the photogenic cells of the pleopod organs are mentioned. It is not clear from the description whether the elongated epithelial cells, "as in the photophores on the pleopods", have actually the same curious structure as those of the pleopod photophores, or whether they are merely elongated but otherwise normal epithelial cells.

Whereas the sections studied by Kemp were cut transversely to the photogenic streak, those I have examined were cut longitudinally in order to include as much of the photogenic tissue as possible in the section. My sections show that the photogenic elements consist of cells resembling those of the pleopod photophores and almost identical with those of the corresponding transverse streak of *S. affinis* (p. 354 and Fig. 25). The identity of the cells with those of *S. affinis* is so marked as not to require illustration. Their nuclei are distally placed, and lie close beneath the lens. They are characteristically truncate, presenting a plane or slightly concave inner surface. No cytoplasmic contents are apparent, but basally each cell rests in a cup of non-staining granular substance (compare with Fig. 25, *pr.gr.m.*). No basal cap, as in *S. affinis*, was, however, apparent at the basal tip of the cells. The photogenic cells are disposed in a number of closely parallel linear series, about four rows of cells usually forming the width of the streak.

I believe that the discrepancy between the account given by Kemp and my statements above is not a serious one, however, and that they can be reconciled in the following manner. A careful study of the photograph submitted by Kemp (1910b, pl. lii, fig. 2) reveals the presence of two nuclei whose shape is characteristic of the photogenic nuclei I have described above and also of those seen in the pleopod photophores. They are the sixth and seventh nuclei from the left-hand margin of the lens, and are considerably broader than those surrounding them. On their inner side there is a clear area not seen elsewhere in the same plane. I am of the opinion that these nuclei are those of the photogenic cells so numerous in my sections, and that the clear space beneath them represents that part of the cells which is devoid of cytoplasm. All adjacent nuclei appear to be those of the normal chitogenous epithelium lying to right and left of the photogenic streak. This view is supported by measurement of the photogenic nuclei: both those in Kemp's photograph and in my sections appear to be about 10μ in breadth. Additionally, the relation between the length of the photogenic nuclei and the thickness of the lens is about the same in each case. Further than this it is not possible to go on the information given by Kemp, but the different views obtained from sections cut transversely and those cut longitudinally may well account for the difference between the two accounts.

The presence in the transverse streak of photogenic cells of the type found in the

pleopod organs is interesting as bringing *S. debilis* into agreement with the condition found in *S. affinis*. It is also noteworthy that similar cells are found in the organs on the fifth thoracic limb of *S. debilis*.

(c) *The photophores on the fifth thoracic limb*

The photophores on the fifth thoracic limb of *S. debilis* present a striking contrast to those found in the similar position in *S. affinis*. There, it will be remembered, the photophores consist of segmented spherical masses of a white granular substance (p. 356), and differ essentially from those behind the base of this limb, but in *S. debilis* the photophores of the limb have a very similar structure to that at its base.

For the purpose of description the organ borne by the propodus is selected (Fig. 29). It consists of photogenic cells of the now familiar type, showing a cup-shaped nucleus (Fig. 29, *n.phot.c.*), a large area of the cell devoid of cytoplasm (Fig. 29, *phot.c.cl.a.*),

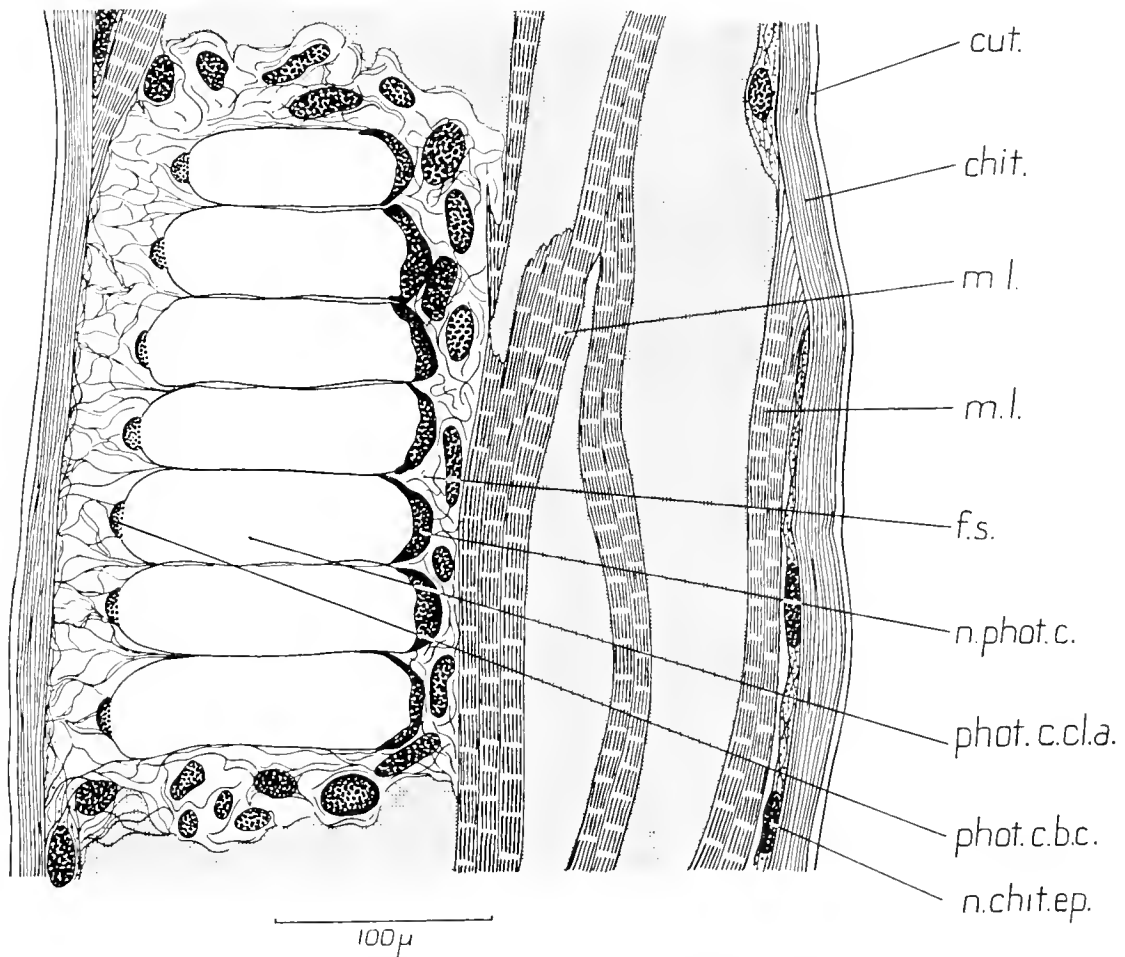


Fig. 29. Longitudinal section through the fifth thoracic limb of *Systellaspis debilis*, to show the structure of the photophore on the propodus. The haemocoel is indicated by mechanical stippling. Mallory's triple stain. *chit.* chitin; *cut.* cuticle; *f.s.* fibrous sheath; *m.l.* muscles of the limb; *n.chit.ep.* nucleus of chitogenous epithelium; *n.phot.c.* nucleus of photogenic cell; *phot.c.b.c.* basal cap of photogenic cell; *phot.c.cl.a.* clear area of photogenic cell.

and a "basal cap" (Fig. 29, *phot.c.b.c.*) at the end of the cell remote from the nucleus. The photogenic cells are arranged parallel to each other and form the units of which the organ is built up. Their disposition, however, differs in a constant and surprising manner from that found in the transverse streak both of *S. affinis* and of *S. debilis* itself, and in fact in all the photophores so far encountered which are composed of similar cells. *The photogenic cells are so disposed that their nuclei occupy the basal, and not the distal, ends of the cells, which are thus completely inverted with respect to the limb.* This is a most astonishing and inexplicable feature, indicating strikingly the need for great caution in any speculation regarding the optical properties of any particular pattern of photogenic cells.

No granular deposits such as have been observed in other organs have been discovered at the ends of the cells occupied by the basal caps, or indeed anywhere else in the organ. Investing the whole photophore is a loose fibrous layer, most strongly developed at the superficial ends of the photogenic cells. Among the fibres of this layer numerous compact nuclei lie behind and at the sides of the photophore, but no nuclei have been observed between the photogenic cells and the integument, indicating the probable origin of the organ as a specialized portion of the chitogenous epithelium. The connective tissue layer is no doubt pigmented during life and acts as a reflector or at any rate as a screen.

No nerves have been found in association with this photophore, but this failure may be perhaps due to the somewhat indifferent fixation of these specimens. There is no thickening of the integument in the form of a lens above the organ.

(d) *The carapace photophores*

The carapace photophores of *S. debilis* are disposed near the lower margin of the branchiostegite (Kemp, 1906) in a pattern much like that formed by the organs of *S. affinis* (Calman, 1939), and from this it might be expected that they would possess the same structural peculiarities. Actually they are basically similar to the carapace organs of *Hoplophorus*, differing only in their greater simplicity.

They consist of a number of photogenic cells arranged in a single linear series, the number of cells in a row varying from three to twenty-nine in the specimen I examined.

The nuclei of the photogenic cells (Fig. 30 A, B, *n.phot.c.*) are finely reticulate and are smoothly ovoid in shape, thus differing markedly from those of the carapace organs of *Hoplophorus*, which possess concave proximal surfaces. No trace of cytoplasm or contents other than the nucleus have been observed in the cells, which therefore show the clear area (Fig. 30 A, B, *phot.c.cl.a.*) characteristic of photogenic cells of this type. No "basal cap" nor any trace of nerve fibres have been discovered in connexion with the cells, which are clearly much simpler than those mentioned in *Hoplophorus*.

The integument is slightly raised by the underlying photogenic tissue (Fig. 30 A), but there is no marked thickening or differentiation of the chitin in the form of a lens. Beneath the integument forming the outer surface of the branchiostegite and that lining the branchial chamber lie normal nuclei of the chitogenous epithelium (Fig. 30 A, B,

n.chit.ep.), but behind the photogenic cells are situated large flattened and somewhat rectangular nuclei which I have called on account of their position "reflector nuclei" (Fig. 30, *n.r.*).

Lying close against the lower ends of the photogenic nuclei occurs a slight granular deposit (Fig. 30, *gr.*). It appears a light golden yellow by transmitted light, but is almost invisible by reflected light, and is apparently of a different nature from the white opaque substance so prominent in the photophores of *Systellaspis affinis*. It provides the only instance known to me of granules situated at the distal end of cells of this type, for it will be recalled that elsewhere any granules associated with similar photogenic cells are basally situated and are intimately related to the nerve fibres supplying the organ.

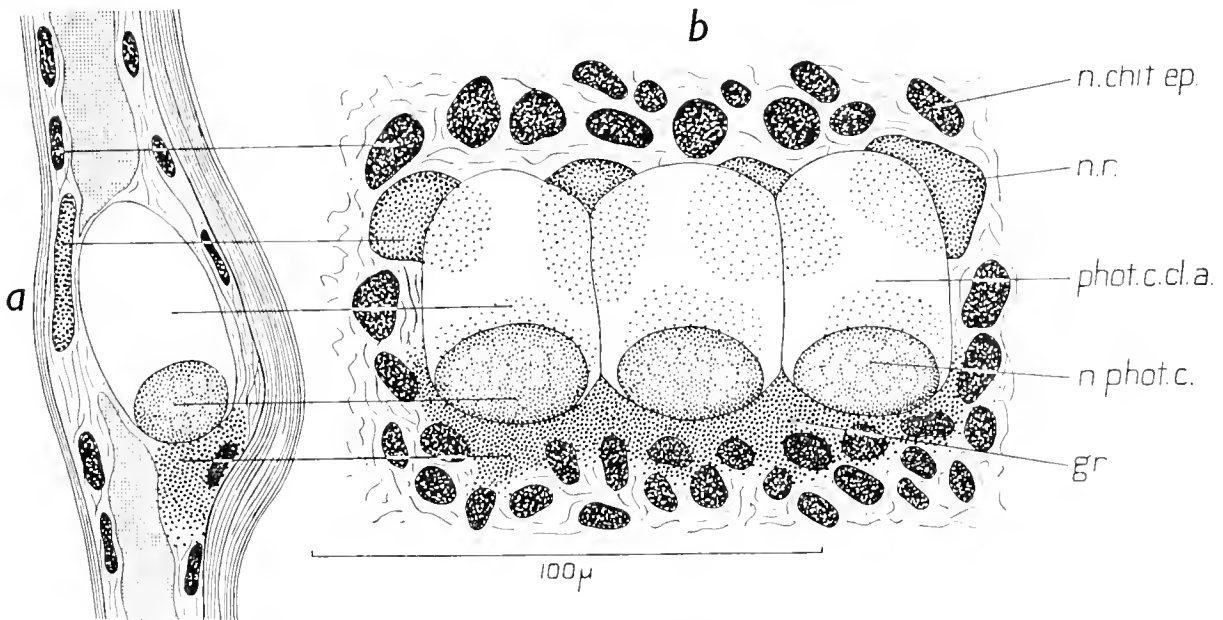


Fig. 30. One of the smaller carapace photophores of *Systellaspis debilis*; *a*, in vertical section, the external surface being to the right; *b*, in surface view. The haemocoel is indicated by mechanical stippling. *gr.* granules; *n.chit.ep.* nucleus of chitogenous epithelium; *n.phot.c.* nucleus of photogenic cell; *n.r.* reflector nucleus; *phot.c.cl.a.* clear area of photogenic cell.

The contrast between the carapace photophores of *S. affinis* and those of *S. debilis* adds still further to the divergence of these two species with regard to their photophores.

(e) *The photophores on the telson*

The photophores on the telson of *S. debilis* consist of two pigmented spots placed dorsally in the median line. The anterior spot is situated not far behind the base of the telson, just between the posterior points of attachment of the pair of telson extensor muscles, and the posterior rather smaller spot is placed near the apex at the level of the anterior limit of the posterior armature of six pairs of articulated lateral spines (cf. Kemp, 1906, pl. ii, fig. 7). Although occupying a dorsal position rarely encountered in

the distribution of crustacean photophores, these pigment spots, like those on the telson of *S. affinis*, will be ventrally directed whenever the telson and uropods are brought into play during the escape reaction of the animal, and will thus be visible from below together with the other photophores of the body.

The pigmented spots mark the position of clusters of radially segmented granular deposits (Fig. 31) of the same pattern as those in some of the photophores of *S. affinis* (p. 356 and Figs. 26, 27). They do not consist, however, of the same material as far as can be judged, for by reflected light they are transparent and almost invisible. By transmitted light they are seen in formalin-preserved material to be somewhat yellowish

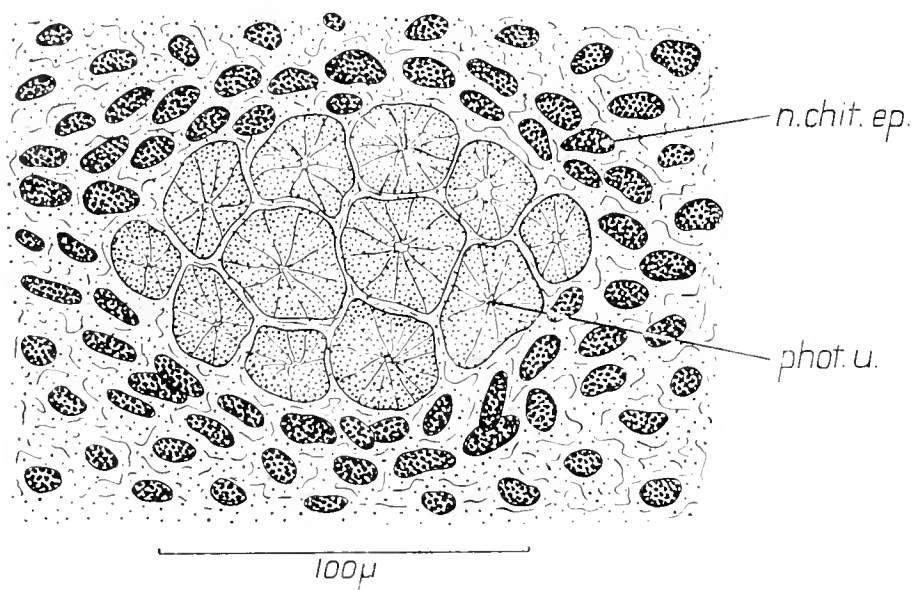


Fig. 31. The posterior telson photophore of *Systellaspis debilis* in surface view. The integument is transparent and is not represented in the figure. *n.chit.ep.* nucleus of chitogenous epithelium; *phot.u.* photogenic unit ("rosette").

when unstained. Even when stained with carmine, which they take up readily, they still possess a yellowish hue. The rosette-like spheres are grouped in a horizontal sheet, ten to twelve spheres forming the posterior and about twenty spheres the anterior photophore. Underlying them are apparent phases in their differentiation as in *S. affinis* (p. 358, Fig. 27), and the whole organ is closely surrounded by a mass of closely packed small dense nuclei resembling those of the chitogenous epithelium.

No lens is present over the surface of these organs, and I have not been able to discover any trace of innervation.

It will be realized that the telson photophores of *S. debilis* possess the structure which might have been expected to be shown by the carapace organs. Their similarity to some of the photophores of *S. affinis* renders the relations between the two species still more obscure.

The variety of photophores encountered in various situations on the body and limbs in the members of the family Hoplophoridae which have been examined in the course

of this work makes some means of ready comparison between them a necessity. The following tabular view, having reference only to some of the photophores occupying a common position in the different members will, it is hoped, be of some assistance.

	Pleopod base	Uropod base	Streak at 5th thoracic limb base	5th thoracic limb	Carapace
<i>Hoplophorus</i> species*	E., L. (p. 329)	E., L. (p. 334)	R. (C.B.) (reversed) (p. 337)	R. (C.B.) (p. 335)	E. (p. 341)
<i>S. affinis</i>	E., L. (p. 346)	E., W. I.C.L. (p. 350)	E., L. (p. 354)	R., W. (p. 356)	R., W. (p. 360)
<i>S. debilis</i>	E., L. (p. 363)	E., L. (p. 363)	E., L. (p. 364)	E. (reversed) (p. 365)	E. (p. 366)

* *Hoplophorus novae-zealandiae*, *H. grimaldii* and *H. typus*. E. Elongated photogenic cells, with basal nucleus and area devoid of cytoplasm. L. External lens. I.C.L. Intracellular lens. R. Radially segmented granular spheres ("rosettes"). W. White granular substance. C.B. "Central body" present, white granular substance absent.

VI. DISCUSSION

The discovery of small subcuticular structures, almost certainly luminous in function, in *Sergestes regalis* adds to the variety of photophores found in members of this genus. In his notes made on board the 'Discovery', Dr Kemp records the positions of about 230-240 purple spots which mark the situation of these presumed photophores, and it is interesting to observe that, as in *S. challengerii* and its close allies, as well as in *S. corniculum*, *S. sargassi*, *S. diapontius*, and *S. edwardsi* (p. 320), some, in this case a row of seven to eight, are found in the roof of the branchial chamber. The peculiarity of this situation will be mentioned again later in this discussion. It is evident that the photophores described by Kemp (1910b) in *S. challengerii*, and in *S. lucens* (Terao, 1917, as *S. prehensilis*, see Gordon, 1935, p. 308), although showing some differences from each other, are actually fundamentally similar. The differences noted by Terao, such as the presence in *S. lucens* of a basement membrane beneath the photogenic cells and of a distinct lens epithelium, and their absence in *S. challengerii*, may perhaps be accounted for by the differences in fixation and preservation of the specimens employed by these two authors. Terao admits that some disintegration had taken place in his specimens before fixation. In any event the photophores of these two species differ profoundly from those of *S. regalis*. Whereas in the two former species (*S. lucens* and *S. challengerii*) large cells with prominent nuclei, which are without doubt photogenic, occur beneath a well-defined two-layered lens, in the latter species the structures which I have referred to as "photogenic centres" are very different and are not readily interpreted as cells. Furthermore, a lens is absent from these photophores.

Without entering into any discussion on the possible diagnostic significance of the varying number and positions of superficial photophores in the genus *Sergestes*, the suggestion may be entertained that a detailed examination and comparison of all the structures suspected to be luminous, including the organs of Pesta, which are found in the genus, might lead to a clearer elucidation of the relationships existing between the various species. Burkenroad (1937, p. 317) has already suggested that the absence of the organs of Pesta from *S. challengerii* and its close allies is compensated for by the presence of complex lensed photophores, and in *S. robustus* and its relatives by simple subcuticular bodies. The assumption, however, that all the simple bodies are identical in structure would be most unwarranted. In any such survey the occurrence in *S. corniculum*, *S. sargassi*, *S. diapontius*, and *S. edwardsi*, and probably also other species possessing organs of Pesta, of the glandular and probably photogenic streak in the roof of the branchial chamber (p. 320) must be taken carefully into account, as Burkenroad (1937, p. 317) has stated that superficial photophores are lacking in all of the species possessing organs of Pesta.

The photophores described by Ramadan (1938) in *Hymenopenaeus debilis* are also very different from those which I have described in *Sergestes regalis*. While the differences between these organs of *Hymenopenaeus* and those of *Sergestes challengerii* and *S. lucens* mentioned by the author are noteworthy, it would nevertheless appear from the descriptions available that in these three species the luminous organs follow the same basic plan. Extensive proliferation inwards of the photogenic cells of an organ such as that of *S. lucens*, for example, might well lead to a condition very similar to that seen in *Hymenopenaeus debilis*.

The lack of innervation of the simple structures of *Sergestes regalis* is paralleled by the condition in some of the photophores of the Hoplophoridae, and will be again mentioned in discussing the possible means of control of Decapod photophores. The appearance of the organs in *S. regalis* suggests that the fibrous mass may possibly consist of modified muscle strands, and thus the organs may be of mesodermal origin. (In the Lampyrid insects the luminous organs are also of mesodermal origin, being apparently derived from the fat-body.) In other phyla muscle cells are said to be luminous, as for instance in a species of *Ophiura* (Dahlgren and Kepner, 1908, p. 123) and it may perhaps be that these simple photophores of *Sergestes regalis* have resulted from the increasing specialization of portions of luminous muscle. In this connexion, however, the lack of a continuous chitogenous epithelium between the integument and the photogenic mass may perhaps be taken to indicate that the structures are of ectodermal origin. Only observations on the development of the organs can determine the truth concerning their origin, and the difficulties in the way of carrying out such work are only too clear.

The occurrence of dense clusters of modified liver tubules in a number of species of *Sergestes* was first recorded by Pesta (1918, p. 56), who suggested that they might perhaps be luminous organs. (Organs of a similar gross appearance are also found in certain Pandalids (Kemp, 1925, p. 277 and this paper, p. 322).) Their pigmentation supports this view (Burkenroad, 1937 p. 316 and this paper, p. 319), and if the organs

are truly luminous they, with the organs of the Pandalids, stand alone among Crustacean photophores in having an endodermal origin.

As already mentioned (p. 318) the appearance of these organs of Pesta indicates great secretory activity, and the morphological evidence suggests that in different zones of the tubules two different substances may be elaborated. That these substances may be luciferin and luciferase, together responsible for the production of light, is possible, but it must not be overlooked that the function of the organs may be merely one of excretion alone, or of excretion accompanied by incidental luminescence. If the difficulties of keeping these animals alive after capture can be overcome (and the success of Welsh and Chace with *Systellaspis debilis* (1937) is encouraging), then the physiological investigations so clearly necessary may be possible. But whatever the function of the organs of Pesta their presence in some species of *Sergestes* and absence from others is a very curious and at present inexplicable feature. The proximity of the anterior pair at least of the organs of Pesta in *Sergestes*, and of the anterior pair of liver organs in some of the Pandalids, to the roof of the branchial chamber may be a purely inevitable result of the situation of the liver, but if the organs should prove to be definitely luminous their position may perhaps have the same significance as that of other organs illuminating the branchial chamber.

It must be admitted, however, that the meaning of photophores, whether complex and lensed organs like those of *S. challengerii*, or a simple glandular streak like that of *S. corniculum*, so placed as to throw their light downwards on to the gills, is entirely obscure. It is difficult to imagine any way in which their presence might influence the respiratory efficiency of the branchiae, and as far as I am aware there are no structural peculiarities in the gills of those species possessing photophores in this situation. That a supply of oxygen is necessary for luminescence is shown both by physiological investigations and by such morphological findings as the occurrence of tracheoles penetrating deep into the photogenic tissue of luminous beetles, and the existence of a special photophore blood vessel in *Hoplophorus*. The possibility exists that the situation of photophores in the branchial chamber roof is influenced by the passage of an oxygen-laden stream of water through the branchial chamber. The thin integument lining the branchial chamber no doubt allows of ready gaseous interchange, so that the photophores are bathed by body fluid rich in oxygen. If the complex photophores of the Decapoda are luminous by virtue of the oxidation of luciferin induced by the enzyme luciferase, as occurs in the luminous secretion of the ostracod *Cypridina hilgendorffi* (Harvey, 1919) and of a species of *Systellaspis* (Harvey, 1931), and there seems no reason to doubt it, then the situation of photophores in the branchial chamber roof might be regarded merely as a response to a rich oxygen supply.

There are several serious objections, however, to such a view. In the first place, the luminescence of *Cypridina* secretion still continues even in the presence of only very small amounts of oxygen, and great increases in oxygen tension, while increasing the light emitted, do not do so proportionately (Harvey, 1919). It appears then that variations in oxygen tension of the order that might be expected to occur within

the body of the animal can have no influence on the efficiency of the photophores, and that organs in regions of relatively high oxygen concentration are actually in a no more favoured position than those elsewhere, and all photophores, wherever placed, will glow with much the same intensity.

Secondly, although in *Sergestes challengerii* the photophores on the carapace (Hansen, 1903, pl. xii, fig. 2a), shown by Kemp (1910b, pl. liv, fig. 4) to be internal and near the roof of the branchial chamber, appear to be situated above the middle of the series of branchiae, in *S. corniculum*, *S. sargassi*, *S. diapontius*, and *S. edwardsi* the suspected luminous streak is placed a little in advance of the foremost gills, that is, in the least favourable position in the branchial chamber from the point of view of oxygen supply, since the respiratory current flows anteriorly. Furthermore, the occurrence of photophores in this situation is, as far as is known, by no means universal even in the luminous species of *Sergestes*, and it would be difficult to account for this discrepancy even if it could be shown that the situation under consideration is a peculiarly favourable one for photogenesis.

It may be fairly stated that the degree of structural complexity attained by some of the photophores of the Hoplophoridae is equalled nowhere else in the Crustacea, although the complex Euphausiid organs closely rival them. The pleopod photophores of the species of *Hoplophorus* and *Systellaspis* examined, movable in virtue of a surrounding arthrodial membrane and well-developed musculature, and showing complexities of innervation such as those seen in *Hoplophorus novae-zealandiae*, might be expected to be remarkably efficient. However, the single available observation of active light production, in *H. grimaldii*, does not confirm this. Dr Kemp records in his notes made at the time that, on placing the specimen in fresh water all the photophores emitted light, which was "much feebler than that of *Euphausia longirostris*, caught in abundance in the same haul". It is possible, of course, that the animal was more enfeebled than the Euphausiids, and clearly additional observations are desirable, but it should not be assumed that structural complexity of photophores necessarily indicates a high degree of physiological efficiency. The organs of the Lampyrid beetles are relatively simple in structure and yet are remarkably efficient light producers.

Whether the distribution of photophores in the members of the Hoplophoridae will prove to have any profound taxonomic significance cannot be answered from the information at present available. But from the observations so far made it would perhaps appear unlikely. The apparently sporadic occurrence of photophores of different structure in corresponding positions in different species and in different positions in the same species, and of photophores of corresponding structure in differing positions in different species (see table, p. 369) is at present merely confusing. But if a form were to be discovered bearing photophores of only one type these difficulties might be resolved, at least in part. The close similarity of the pleopod organs, and their early appearance in development (Kemp, 1910b, p. 646) suggests that they are of phylogenetic significance, while those organs containing photogenic cells of entirely different form, producing the granular "rosettes", are supernumerary and secondary.

Careful consideration of freshly caught material is necessary in order to determine whether the characteristic clear areas of the photogenic cells of the pleopod and other photophores of the Hoplophoridae are merely products of the methods of fixation and preservation employed, or whether they exist in the living animal, having only fluid contents. Terao (1917) has suggested, as a result of his experience with the photophores of *Sergestes lucens*, where the photogenic cells readily disintegrated, that the clear areas arise as fixation effects, or even from the natural processes in the photophore by the consumption of the secreted products of the photogenic cells. He says: "Thus, it seems to me not unlikely that what Kemp has given as photogenous cells in his representation of the photophores of *Acanthephyra debilis* are not cells at all, but empty spaces left behind by photogenous cells which had disappeared. The lines taken by him for the walls of photogenous cells were probably nothing else than connective strands, while the mass of minute and highly refractive granules at the end of the nerve bundle reaching the photogenic layer may simply be the remnants of the disintegration products of photogenic cells." I do not agree with the view expressed by Terao, for the segmentation of the granular mass in accordance with the number of photogenic cells in *Hoplophorus novae-zealandiae*, and the similarity of the granular mass to the basal caps of the carapace photophores (p. 342), which are again in close relation with the photophore nerve fibres, seems to indicate that it is an intrinsic and essential part of the organ.

It is possible that in life the photogenic cells contain a substance secreted by the distal contents of the cells and which is not apparent in the preserved material. That this substance may be expected to be a luciferase is suggested by the work of Harvey (1919), who finds that in *Cypridina hilgendorfi* the luciferase is only present in the photogenic cells, while luciferin is abundant and is found in various tissues of the body. In view of the small individual size of the photophores, the production in them of a luciferase only required in small quantity and only very slowly consumed during the process of light production would be an economical arrangement.

If this suggestion is correct then two questions remain to be answered. The first concerns the mode of transport of luciferin to the photogenic cells, and it can only be suggested that, carried by the body fluid, it reaches the cells either by osmosis or by simple diffusion. The second question concerns the details of the innervation of the photogenic cells. It will be recalled that the nerve fibres in these organs impinge on a granular cone, which may or may not be segmented, and which is in contact with the basal ends of the photogenic cells (p. 331). The nucleus and small amount of cytoplasm of the cells is distal and remote from the granular cone, and it is not clear what part nerve impulses might play in their activity. In any event, if they produce luciferase, which is apparently of the nature of a catalyst and is only very slowly consumed during photogenic reactions, then variations in nervous stimuli affecting the secretory activity of this zone could hardly be expected to control the luminescence of the organ. Harvey (1919) points out that 1 g. of a luciferase will accelerate the oxidation of 10,000 g. of luciferin.

It will be remembered, however, that not all the fibres impinge on the granular cone, but some, whether nervous or not, pass distally around the periphery of the organ, and terminate in the neighbourhood of certain elongate nuclei in the plane of the photogenic nuclei. The possibility exists that these fibres and nuclei are not concerned with the reflector and screening pigments, but may be involved in the secretion of luciferin. Both a detailed examination of the innervation of the organs, employing suitable special methods, and an investigation into their physiological qualities are urgently necessary. It will be apparent that the foregoing remarks apply equally to other photophores, such as the carapace organs of *Hoplophorus* and those behind the bases of the last thoracic limbs of *Systellaspis affinis* and *S. debilis*, which are composed of similar photogenic cells with basal granular caps and related nerve fibres.

The uropod photophores of *S. affinis* are clearly related structurally to the pleopod organs just discussed, but the absence of any object in their photogenic cells which can be interpreted as a nucleus renders speculation concerning their mode of functioning still more difficult. Further examination of the photophores of members of the Hoplophoridae may possibly reveal a photophore intermediate between these and the pleopod organs. The white opaque granular mass, situated basally in the organ, will be mentioned later after discussing the "rosette" type of photophore of *S. affinis*.

This peculiar type of photophore, as instanced by that on the fifth thoracic limb described on p. 356, is of considerable interest. The white opaque substance, laid down in a very definite manner in the form of radially segmented spheres, was suspected early in the course of this work to be either guanin, or a similar allied substance, since the former is known to occur as a reflecting pigment in the eyes of *Palaemonetes* and *Macrobrachium* (Welsh, 1932) and of *Sergestes*, *Systellaspis*, *Hymenodora*, and *Hoplophorus* (Welsh and Chace, 1937, figs. 13-18 and 1938, figs. 10-15). It is also present in the carapace and limbs of *Hoplophorus* (Coutière, 1905, p. 3). In the photophores of *Systellaspis affinis* the substance is finely granular and apparently amorphous. No positive reaction was obtained to a test for xanthin, but owing to lack of material (only one specimen being available for examination) no further tests were proceeded with. The morphological evidence available from a study of the organs suggests that the granules arise, in part at least, as a breakdown product of the large photogenic nuclei, since only the last remnants of these nuclei are ever apparent when the granular segments of the rosettes begin to appear, and usually the nucleus has completely degenerated even before the first traces of granules are to be seen. On this evidence alone it would seem to be highly probable that the granules might be expected to consist of an accumulated product of nucleo-protein katabolism, and a precise identification of their nature undertaken by a biochemist will be of interest.

These organs of *S. affinis* therefore show a striking resemblance in their fundamental features to those of Lampyrid beetles examined and described by Lund (1911) and many other workers. In these beetles the luminous organs consist of a mass of photogenic cells, containing photogenic granules, situated ventrally in the abdomen and penetrated by tracheae and nerves. Dorsal to and in contact with the photogenic cells

occurs a layer of cells containing (ammonium?) urate granules which is said to constitute a reflector. Briefly, as a result of morphological and physiological investigations, Lund found that "photogenesis is incident upon the utilization of a nitrogenous compound—the photogenic granules—giving staining reactions like those of lecithin and different from those of the true fats, and that this nitrogenous compound appears at least in part at the end of the process in the form of a nitrogenous waste product. This crystalline substance appears from its reactions to be allied to or identical with some of the split products of nucleic acid." Lund also discovered that the minutely crystalline waste product accumulates in the cells of the dorsal layer, and that no direct transformation of photogenic cells into dorsal "urate" cells, by their becoming loaded with the waste product, takes place. He gives dark-ground photographs of the organs (1911, pl. 2, figs. 5, 6) which may be compared with Plate XXV, figs. 4 and 5 of this paper.

It will be readily apparent from the foregoing that a similar phenomenon almost certainly takes place in the photophores of *S. affinis* under discussion. Here, however, the waste product appears, from the morphological evidence at least, to be derived from the katabolism of the nucleus itself, and not from the breakdown of photogenic granules around it. But the increase in size of the radially arranged segments *after* the total disappearance of the nuclei concerned is very peculiar and not in accordance with the general conception of nuclear control of tissue activity, and suggests the possibility that waste material resulting from metabolism in other parts of the body may accumulate in these organs.

Such a consideration raises the doubt that the organs may not actually be luminous, but serve only as part of an accessory excretory system, or at any rate that luminescence may only be a purely incidental accompaniment of such a system. (It is of interest that in the larva of the Tipulid *Bolitophila luminosa* of New Zealand caves the distal ends of the Malpighian tubules are modified as luminous organs, and are associated with a layer of tissue containing reflecting granules (Wheeler and Williams, 1915).) This view, it is true, may receive some support from the observation (p. 360) that the granular deposits occur on the outer and superficial side of the organs, where they would, instead of acting as a reflector, only serve to mask any emission of light by the organs. On the other hand, organs of a very similar structure in *Hoplophorus* (p. 337) have been observed by Dr Kemp actually to luminesce, and, furthermore, the uropod organs of *Systellaspis affinis*, which from a comparison with the pleopod photophores of *Hoplophorus* can be nothing else than photophores, also possess a basal granular deposit of precisely similar opaque white substance.

I suggest, then, if only tentatively, that in these organs of *Systellaspis affinis* reactions resulting in the emission of light take place in the neighbourhood of the nucleus and involve its degeneration, and that the prominent granular masses are, as in the Lampyrids, stored waste products resulting from these reactions. What part is played in these processes by luciferin and luciferase must be left to future workers having the opportunity of studying freshly caught material.

The photophores of *Hoplophorus* such as those behind the bases of the fifth thoracic

limbs (p. 337) and on the limbs themselves (p. 334) are clearly of the same type as those of *Systellaspis affinis*, although their granular substance is of a different nature and exhibits staining reactions not shared by the material in the latter organs. The telson photophores of *S. debilis* (p. 367) also are clearly similar.

With regard to the curious inversion seen in the photophores of the base of the last thoracic limb and the limb itself both in *Hoplophorus* and in *Systellaspis debilis*, I am entirely unable to offer any explanation. Its precise significance is obscure, but is probably that the structures seen in the photogenic cells of the type with a distal nucleus, characteristic clear area, and basal granular mass or cap, while being of importance in actual light production, are not concerned with the way in which this light is emitted to the exterior, a conclusion at variance with the constant and regular manner in which the photogenic cells of the pleopod organs are found to be arranged.

The method of control of the photophores of the bathypelagic Decapoda is completely obscure. In the first place, very few observations on the intensity, colour and periodicity of the flashes emitted are available. Even where such observations have been made it must not be forgotten that the photophores are functioning under completely abnormal conditions. Terao (1917) has recorded some observations on the light emitted by the photophores of *S. lucens* (as *S. prehensilis*) and states that they give an intermittent dim greenish yellow light. Sometimes a serial anterior-posterior succession of flashes takes place, often only one photophore glowing at a time. The photophores in the neighbourhood of the eyes often give a steady light.

It might be expected that photophores with a well-defined nervous supply would function in a similar manner to the above rather than produce a steady glow, but the precise nature of the nervous control cannot be stated. The absence of any morphological evidence of control of non-innervated photophores, such as those of *S. regalis* and those on the limbs of *Systellaspis affinis*, suggests that they produce a luminescence of constant intensity. No structures capable of varying the rate of oxygen supply, or the rate of secretion of any of the cells appear to be present, and it is difficult to see any way in which the amount of light given by such organs might be controlled. It is striking, however, that whereas in the thoracic limb organs, for instance, of *S. affinis*, no indications of innervation have been discovered, organs of a similar nature in *Hoplophorus* possess a well-developed nerve supply.

Many suggestions have been made with regard to the function of the photophores of bathypelagic animals, and reference may be made to such papers as those by Nutting (1899), Doflein (1907), and Kemp (1910*b*). During the course of this purely morphological enquiry no concrete information has been gained on this point. Recently, Welsh and Chace (1937, 1938) have attempted to correlate the size of the eyes of a number of species of Sergestids and Acantheephyrids with the presence or absence of the photophores and the depth of occurrence of the animal, and have come to the conclusion that those species possessing photophores have larger eyes than those lacking these organs. This may indicate that photophores play some part in the life and habits of the animals affecting them directly through the eye, such as facilitating food capture or recognition

for the purposes of swarming or breeding. This, however, cannot account for the existence of photophores in such curious situations as the branchial chamber and interior of the cephalothorax. Furthermore, Dr M. D. Burkenroad has pointed out to me that in most of the small-eyed species of the genus *Sergestes* organs of Pesta which are probably luminous are present, and that in certain undescribed species of *Sergestes* allied to *S. challengerii*, with photophores of the general type which, alone in the genus, have been observed actually to luminesce (see Terao, 1917), the eyes may be relatively quite as small as in such a small-eyed species as *S. atlanticus*. Burkenroad himself suggested (1936, p. 118) that a large eye might perhaps be correlated with the presence of photophores in the species of section 2 of group IV of the genus *Hymenopenaeus*, although I am informed by the author that further investigation has not confirmed this possibility. The presence in some members of the Hoplophoridae of movably articulated photophores whose musculature is under the control of the nervous system and whose whole organization is fitted for concentrating emitted light and directing it in a particular manner strongly suggests, however, that in some cases at least photophores may have a definite function involving vision on the part of the animal itself.

The luminous secretion which is poured out by a number of members of the Crustacea Decapoda has not been touched upon in the course of the present work, although it is hoped to make it the subject of further investigation in the future. It appears to be a not uncommon phenomenon. Alcock (1902, p. 134) remarks that specimens of *Heterocarpus alphonsi* emitted a luminous secretion, glowing with a blue light, from the antennal glands, and this was also observed, though it was less abundant, in *Plesio-penaeus* (as *Aristaeus*) *coruscans*. Harvey (1931) has given the results of his observations on the luminous secretion of the "deep sea shrimp or prawn, *Systemaspis*", and Schmitt (1931) gives a luminous frontispiece depicting the clouds of luminous secretion emitted by *S. debilis*. In his 'Discovery' notes Dr Kemp records that several specimens of *Hoplophorus novae-zealandiae* emitted a luminous secretion from the neighbourhood of the mouth. Dahlgren (1916, pp. 829-32) states that the origin of the luminous secretion is to be found in some of the tegumental glands. That such clouds of luminous secretion, poured out into the exhalant respiratory current, may serve for protection during the backward "escape reaction" of the animal seems highly probable.

Structures, usually marked by well-defined pigment spots and which may be luminous, have been mentioned in many pelagic decapods, and detailed examination of these structures is clearly necessary in order to determine what likelihood there is of these organs proving to be luminous. In addition, from the experience gained in the course of the present work it seems desirable, although tedious, to examine many more of the photophores found in any one species of *Hoplophorus* or *Systemaspis*, as it is possible that there may be an even greater variety of photophores in some of these species than has so far been recorded. The detailed innervation of known photophores, using suitable methods on fresh material will also prove to be necessary. In the physiological and biochemical fields investigations into the functioning of the various types of organs are urgently necessary when opportunity for such work occurs. I hope in the future

to be able to undertake some of these investigations on material available at Bermuda and Woods Hole with the aid of a Fellowship which has been awarded for the purpose by the Leverhulme Trustees.

VII. SUMMARY

1. The superficial photophores of *Sergestes regalis* are of an entirely new type. They consist of horizontal sheets of interwoven fibres, in which the perpendicular photogenic units, of doubtful origin, are scattered. There is no lens, and no associated nerve supply has been discovered (pp. 310-314, Fig. 1, and Plate XXIV, fig. 1).

2. Organs of Pesta (luminous liver tubules) are described in detail in *Sergestes corniculum*, *S. sargassi*, *S. diapontius*, and *S. edwardsi*. They consist of compact groups of modified liver tubules numbering as many as ten in *S. corniculum*, visible from the exterior through the integument, and showing well-marked zones of cytological differentiation. Some of the cells composing the tubules show evidences of disruption and shedding of their contents into the lumen of the tubule, while others are highly vacuolated. Possible lens and reflector cells are also present. The pigmentation of these organs in life is discussed, and their taxonomic significance mentioned (pp. 314-320, Figs. 2-4, and Plate XXIV, figs. 2, 4).

3. All the above-mentioned species of *Sergestes* also possess a linear photophore in the roof of the branchial chamber. This organ is simple, without a lens or any well-marked accessory structures, and is totally different from the organs in the same position in *S. challengerii* (pp. 320-322 and Fig. 5).

4. Photophores of endodermal origin in *Parapandalus richardi* are described. They, like the organs of Pesta in *Sergestes*, are groups of modified liver tubules, but they are of totally different structure from the organs of Pesta. It appears that similar organs are not uncommon in the Pandalidae (pp. 322-327, Figs. 6-8, and Plate XXIV, figs. 3, 5).

5. A simple structure on the pleopods of *Parapandalus richardi*, marked by a deep red pigment spot in the living animal, has been examined, but whether or not it is a photophore remains undecided. It consists merely of a diffuse mass of connective tissue beneath the chitogenous epithelium, which is thicker here than elsewhere, but does not appear to enter into the composition of the organ (p. 327 and Fig. 9).

6. The species of *Hoplophorus* which have been examined show photophores differing profoundly from those of *Sergestes*. The organs on the pleopods (pp. 329-334, Figs. 10-12 and Plate XXV, fig. 1) are closely similar to those of *Systellaspis debilis* (Kemp, 1910b) and of *S. affinis* (p. 346 and Fig. 21). They possess a well-developed musculature capable of orientating the whole organ with respect to the limb (Fig. 12).

The photogenic cells of the carapace organs (pp. 339-344, Figs. 17, 18 and Plate XXV, fig. 2) resemble those of the pleopod organs.

The photogenic streak behind the base of the last thoracic limb, and the photophores on the limb itself, are of an entirely novel type, and consist of clusters of radially segmented granular masses, which are probably derived from cells which lose their nuclei

and progressively acquire the granular substance. Successive phases in this change appear to be visible around the periphery of the organ. While the photophores on the thoracic limb are supplied by a well-defined nerve, no trace of a nerve supply has been found associated with the photogenic streak. On comparison with each other these two organs show a curious inversion of parts (Figs. 14-16 and Plate XXV, fig. 3) (pp. 334-339).

7. The photophores of *S. affinis* are described and compared with those of *S. debilis*. Many of the photophores of *S. affinis* contain a prominent dense white substance, possibly a xanthate or urate, which makes the organs conspicuous even in a long-preserved specimen (Fig. 19 and Plate XXV, figs. 4, 5).

While the pleopod photophores of *S. affinis* (Fig. 21) are very similar to those of *S. debilis*, the uropod organs (Figs. 20, 22-4 and Plate XXVI, fig. 1) contain highly modified photogenic cells with no structure which can be readily interpreted as a nucleus. The lenses of these organs are multiple and intracellular.

Unlike the condition in *Hoplophorus*, the photogenic streak behind the last thoracic limb (Fig. 25) contains photogenic cells resembling those of the pleopod organs, while the organs on the limb itself (Figs. 26, 27; Plate XXV, figs. 4, 5; Plate XXVI, figs. 3-6) bear a general resemblance to those in the same position in *Hoplophorus*, differing however in their possession of the white substance already mentioned, which is deposited here in the form of radially segmented spheres of a similar pattern to those seen in *Hoplophorus*. The development of these spheres or "rosettes" appears to involve, as in *Hoplophorus*, the degeneration of the nuclei of the cells concerned.

The carapace organs (p. 360) resemble those on the thoracic limbs.

Structures (Fig. 28) associated in life with red pigment spots on the telson and last abdominal somite are described, and although not confirmed by their appearance in section may prove to be luminous organs of yet another type (pp. 361-362).

8. Information additional to that already existing is given on the photophores of *Systellaspis debilis*. While in general the photophores are found in very similar positions on the body and limbs to those in *S. affinis*, and while photophores of the two types seen in *S. affinis* are present, there is no general concordance between these two species with regard to the structure of the photophore in any particular position. For example, the photogenic cells of the carapace organs of *S. debilis* (Fig. 30) resemble those of the pleopod organs, while in *S. affinis* they are of the "rosette" type. Also the photogenic cells of the organs on the fifth thoracic limb of *S. debilis* (Fig. 29) are of the pleopod type, but in *S. affinis* (Fig. 26) these organs are closely packed groups of "rosettes" (pp. 363-368).

The photophores on the telson in the two species correspond neither in position nor in structure (Figs. 20, 28 and 31).

9. In general the photophores of the Hoplophoridae can be distinguished as belonging to one of two main types, that with elongated photogenic cells having a distal nucleus and an area devoid of cytoplasm, and that formed of masses of radially segmented non-nucleate structures. The distribution of these organs in those members of the Hoplophoridae examined is shown in a table (p. 369).

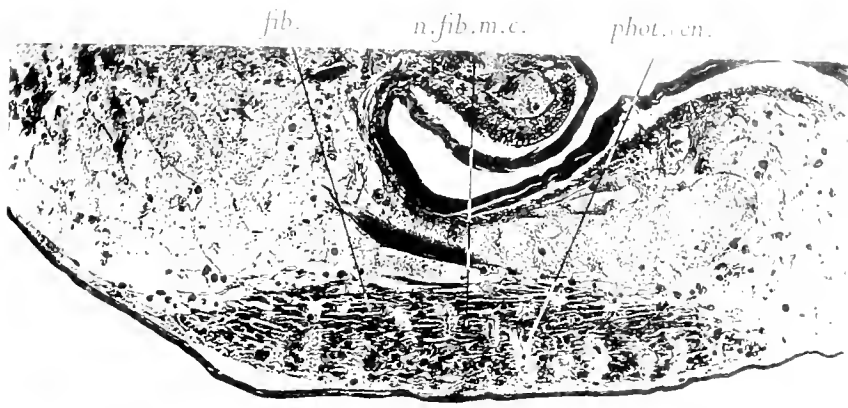
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PLATE XXIV

- Fig. 1. Longitudinal section through one of the maxillary exopod photophores of *Sergestes regalis*. Ventral surface downwards. Compare with Fig. 1. Fixed Duboscq, Mallory's triple stain. $\times 140$. *fib.* interwoven fibrils; *n.fib.m.c.* nucleus of fibril mother cell; *phot.cen.* photogenic centre.
- Fig. 2. Part of a transverse section through the cephalo-thorax of *Sergestes corniculum*, showing the right antero-lateral group of luminous liver tubules (organ of Pesta) very heavily stained with acid-fuchsin. Compare with Fig. 2. Fixed Duboscq, Mallory's triple stain. $\times 110$. *br.ch.* branchial chamber; *lt.* luminous tubule; *n.l.* normal liver.
- Fig. 3. The "mandibular organ" (luminous liver tubules) and part of the mandible of *Parapandalus richardi* in transverse section. Compare with Fig. 7. Fixed Duboscq. Delafield's haematoxylin and eosin. $\times 110$. *lt.* luminous tubule; *md.* mandible.
- Fig. 4. Some of the luminous tubules of the organ of Pesta enlarged from the section seen in Plate XXIV, fig. 2. Compare with Fig. 3. $\times 240$. *er.c.* erupting cell of tubule; *er.cyt.* erupted cytoplasm lying within the lumen of the tubule; *l.c.* lens cell; *vac.c.* vacuolated cell.
- Fig. 5. The luminous portion of the mandibular organ of *Parapandalus richardi*, enlarged from the section seen in Plate XXIV, fig. 3 and Figs. 7 and 8. $\times 240$. *l.c.n.v.* non-vacuolated liver cell; *lt.* luminous tubule; *phot.c.* photogenic cell.



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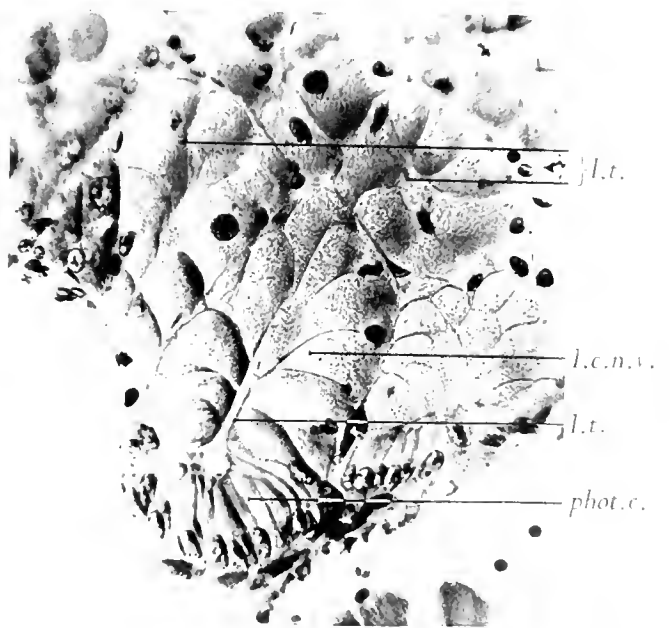


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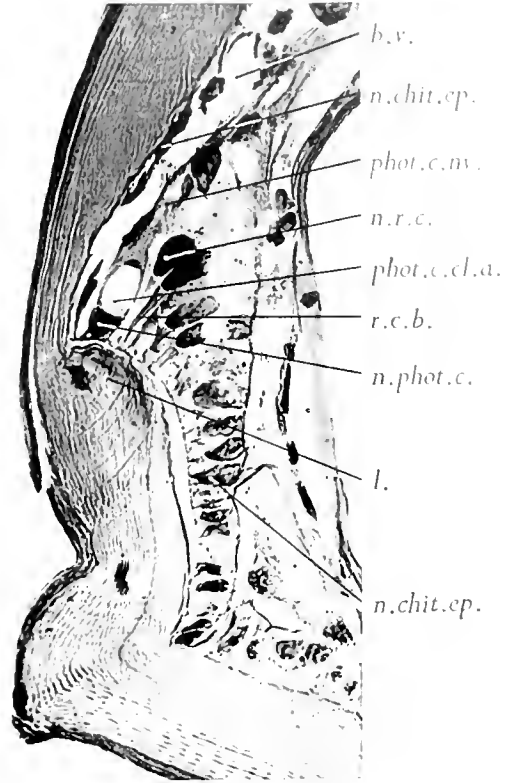
PLATE XXV

- Fig. 1. One of the pleopod photophores of *Hoplophorus novae-zealandiae*. Compare with Fig. 10. Fixed Duboscq, Delafield's haematoxylin and eosin. $\times 240$. *f.r.* fibrous reflector; *gr.z.* granular zone at bases of photogenic cells; *phot.c.c.l.a.* clear area of photogenic cell; *phot.l.m.a.* attachment of longitudinal photophore muscle; *phot.m.l.* photophore muscle loop; *phot.nv.* photophore nerve.
- Fig. 2. Lateral carapace photophore of *Hoplophorus novae-zealandiae* in transverse section. Compare with Fig. 17. Fixed Duboscq, Delafield's haematoxylin and eosin. $\times 240$. *b.v.* blood vessel; *l.* lens; *n.chit.ep.* nucleus of chitogenous epithelium; *n.r.c.* nucleus of reflector cell; *phot.c.c.l.a.* clear area of photogenic cell; *n.phot.c.* nucleus of photogenic cell; *phot.c.nv.* nerve fibres to photogenic cell. *r.c.b.* reflector cell body.
- Fig. 3. Longitudinal section through the right fifth thoracic limb of *Hoplophorus novae-zealandiae*, showing the photophore at the proximal end of the carpus. Compare with Fig. 14. Fixed Duboscq, Delafield's haematoxylin and eosin. $\times 240$. *c.b.* central body; *l.nv.* main trunk of nerve to limb; *n.r.c.* nucleus of reflector cell; *phot.c. 1*, *phot.c. 2*, phases in the appearance of the photogenic cells; *phot.nv.* nerve branch to photophore.
- Fig. 4. The photophore on the carpus of the fifth thoracic limb of *Systellaspis affinis*, seen in longitudinal section by dark-ground illumination, to show the nature of the white granular deposit. Compare with Figs. 26 and 27 and Plate XXVI, figs. 3-6. $\times 80$. *phot.u.* one of the photogenic units ("rosettes").
- Fig. 5. The distal photophore (streak) on the propodus of the fifth thoracic limb of *Systellaspis affinis*, seen in longitudinal section by dark-ground illumination. $\times 80$. *phot.u.* one of the photogenic units ("rosettes").



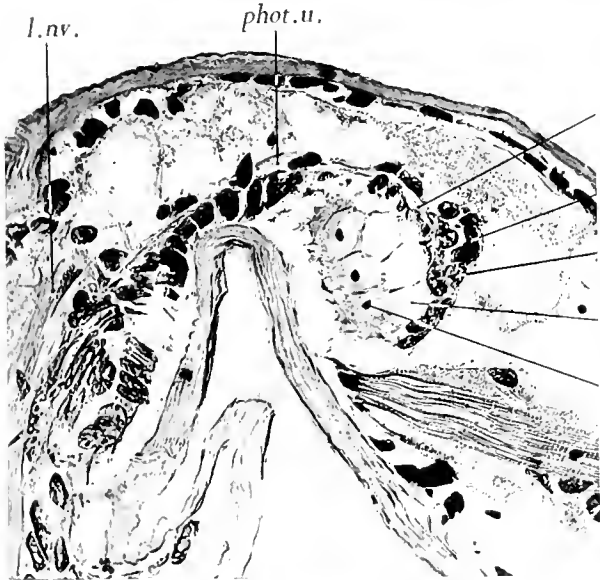
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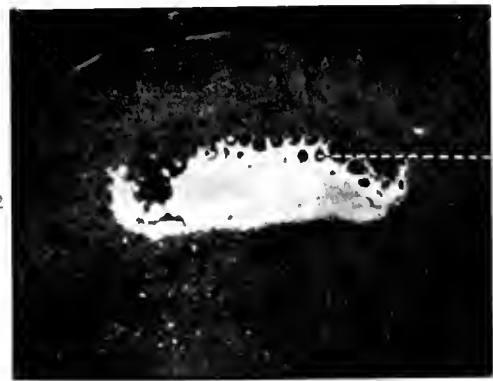
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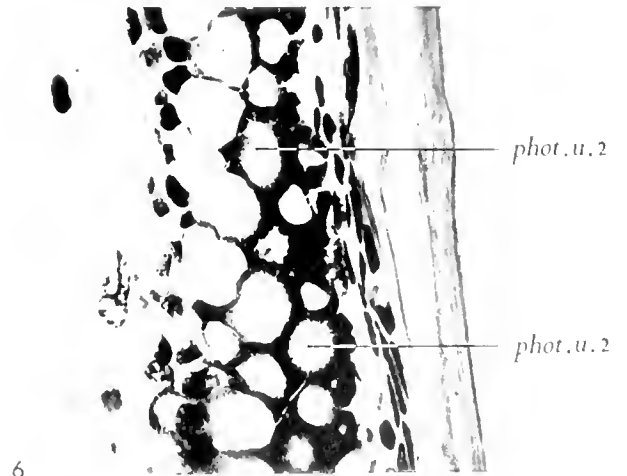
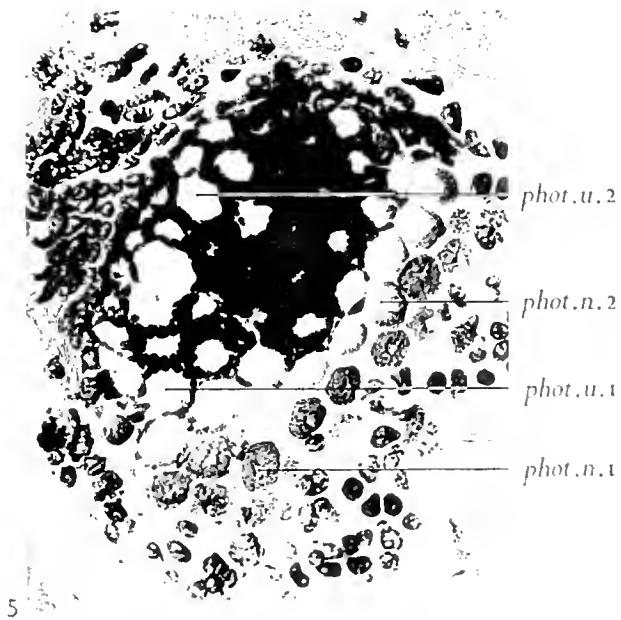
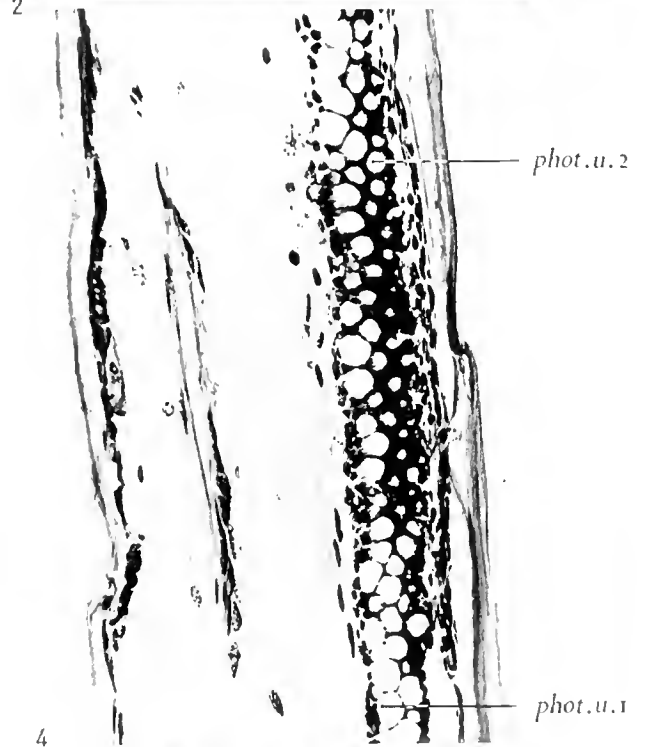
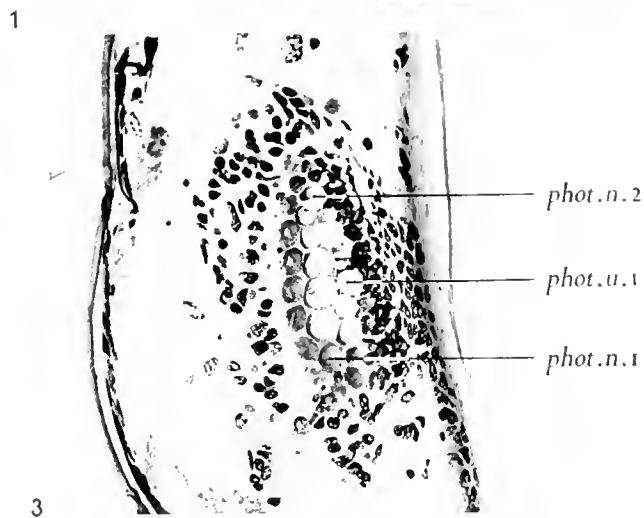
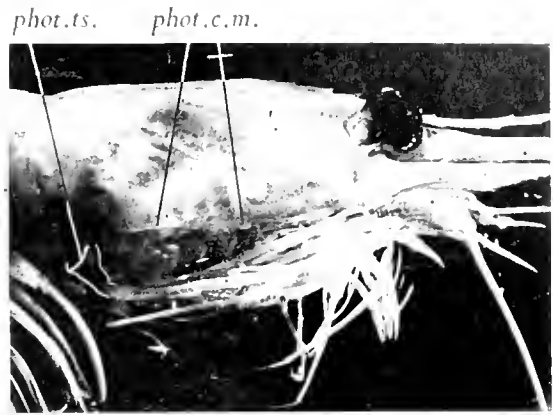


phot.u.

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PLATE XXVI

- Fig. 1. The left uropod photophore of *Systellaspis affinis* seen in thick (100μ) transverse section. Compare with Fig. 24. Mallory's triple stain. $\times 110$. *l.s.* lens-like septum across the photogenic unit; *phot.nv.* nerve to photophore; *phot.u.c.l.a.* clear area of photogenic unit; *phot.u.p.* proximal granular mass of photogenic unit.
- Fig. 2. Right lateral view of the cephalothorax of *Systellaspis affinis*, showing the photophores near the inferior margin of the branchiostegite, and the position, indicated in white, of the transverse streak behind the base of the last thoracic limb. $\times 2$ approx. *phot.c.m.* photophores on the carapace margin; *phot.t.s.* photogenic transverse streak.
- Fig. 3. Section passing through the periphery of the proximal photophore on the propodus of the fifth thoracic limb of *Systellaspis affinis* showing the photogenic nuclei before their degeneration. Compare with Fig. 26. Mallory's triple stain. $\times 110$. *phot.n. 1*, photogenic nucleus before degeneration; *phot.n. 2*, advanced stage in the degeneration of a photogenic nucleus; *phot.u. 1*, photogenic units with first segmentally disposed deposits of the granular substance seen in Plate XXV, figs. 4, 5.
- Fig. 4. The photogenic streak (seen in Plate XXV, fig. 5) on the propodus of the fifth thoracic limb of *Systellaspis affinis*. Mallory's triple stain. $\times 110$. *phot.u. 1*, *phot.u. 2*, stages in the differentiation of the photogenic units (granular "rosettes").
- Fig. 5. Section passing through the photophore at the proximal end of the carpus of the fifth thoracic limb of *Systellaspis affinis*. Successive stages in the differentiation of the granular "rosettes" are clearly seen. Mallory's triple stain. $\times 240$. *phot.n. 1*, *phot.n. 2*, stages in the degeneration of the photogenic nuclei; *phot.u. 1*, *phot.u. 2*, stages in the differentiation of the "rosettes".
- Fig. 6. Part of the longitudinal photogenic streak on the fifth thoracic limb of *Systellaspis affinis*, enlarged from the section seen in Plate XXVI, fig. 4. The radial segmentation of the granular spheres visible in those indicated *phot.u. 2*. $\times 240$.



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DISCOVERY REPORTS

Vol. XX, pp. 1-68

*Issued by the Discovery Committee, Colonial Office, London
on behalf of the Government of the Dependencies of the Falkland Islands*

LARVAE OF DECAPOD CRUSTACEA PART VI. THE GENUS SERGESTES

by

R. Gurney and M. V. Lebour

CAMBRIDGE
AT THE UNIVERSITY PRESS

1940

Price ten shillings net

LONDON

Cambridge University Press

BENTLEY HOUSE, N. W. 1

NEW YORK · TORONTO

BOMBAY · CALCUTTA · MADRAS

Macmillan

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THE CAMBRIDGE
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DISCOVERY REPORTS

Vol. XX, pp. 69-306, plates I-XXIII

*Issued by the Discovery Committee, Colonial Office, London
on behalf of the Government of the Dependencies of the Falkland Islands*

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AT THE UNIVERSITY PRESS

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Price forty-two shillings net

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Cambridge University Press
BENTLEY HOUSE, N. W. 1

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DISCOVERY REPORTS

Vol. XX, pp. 307-382, plates XXIV-XXVI

*Issued by the Discovery Committee, Colonial Office, London
on behalf of the Government of the Dependencies of the Falkland Islands*

ON THE STRUCTURE OF THE PHOTOPHORES OF SOME DECAPOD CRUSTACEA

by

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CAMBRIDGE
AT THE UNIVERSITY PRESS

1940

Price twelve shillings net

LONDON
Cambridge University Press
BENTLEY HOUSE, N. W. I
NEW YORK · TORONTO
BOMBAY · CALCUTTA · MADRAS
Macmillan

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DISCOVERY REPORTS

*Issued by the Discovery Committee, Colonial Office, London
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Vol. XX, pp. i-vi

TITLE-PAGE AND LIST OF CONTENTS



CAMBRIDGE
AT THE UNIVERSITY PRESS

1941

Price ninepence net

CAMBRIDGE
UNIVERSITY PRESS
LONDON: BENTLEY HOUSE
NEW YORK, TORONTO, BOMBAY
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