

ON A *STYGIOMYSIS* FROM THE WEST INDIES,
WITH A NOTE ON *SPELAEOGRIPHUS*
(CRUSTACEA, PERACARIDA)

BY

ISABELLA GORDON, D.Sc., Ph.D.

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With 1 Table, Plates 3-4 and 34 Text-figures.



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ON A *STYGIOMYSIS* FROM THE WEST INDIES, WITH A NOTE ON *SPELAEOGRIPHUS* (CRUSTACEA, PERACARIDA)

By ISABELLA GORDON, D.Sc., Ph.D.

SYNOPSIS

Stygiomysis holthuisi (Gordon), the second known species of the aberrant Mysidacean genus *Stygiomysis*, is described and figured in detail. The systematic position of the family Stygiomysidae is discussed. It is most closely allied to the family Lepidopidae and both families possess certain characters of the suborder Mysida, others of the suborder Lophogastrida. The paragnatha of some other Mysidacea are figured for comparison with those of *Stygiomysis*. The terminology of the thoracic limbs, and of the segments of the thoracic endopodite, is briefly discussed. A note on *Spelaeogriphus lepidops* Gordon is added, together with a few comments on the systematic position of the order Spelaeogriphacea.

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I. ON *STYGIOMYSIS HOLTHUISI* (GORDON) FROM THE WEST INDIES.

INTRODUCTION.

DR. L. B. HOLTHUIS of the Rijksmuseum van Natuurlijke Historie, Leiden, kindly sent me for study three specimens of an interesting cavernicolous "shrimp" which he collected in February, 1957 on the island of St. Martin, Lesser Antilles. When I first examined these specimens I thought that, in spite of the long vermiform body and very short carapace, they looked remarkably like Mysidacea. Then, when I discovered some of their most striking peculiarities, I decided that they did not belong to the Order Mysidacea as at present defined. I fully intended to look up all the literature relating to cavernicolous Mysidacea and, had I done so, I certainly would not have referred these specimens to a new genus. But, when I wrote the preliminary note to *Nature* (Gordon, 1958), I did not realise that I had inadvertently

omitted to refer to Caroli's 1937 paper on the genus *Stygiomysis*. I have to thank Dr. H. Nouvel of Toulouse for calling my attention to this lapse and I fully agree with him that my genus *Rhopalonurus* is a synonym of *Stygiomysis* Caroli.

The discovery of a second species of *Stygiomysis* so far from the locality of the type species of the genus, which is in Italy, is very interesting. Perhaps this rare genus is, or was at some remote period, widely distributed. Caroli had only four specimens of *Stygiomysis hydruntina* when he published his "nota preliminaire" in 1937. As far as I know, he has never published a fuller description of the species, nor has it been collected again although the two Italian grottos must in all probability have been visited since 1937. I made a fairly complete study of the three type specimens of *Stygiomysis holthuisi* and had finished the description and figures before I read Caroli's *Stygiomysis* paper. By that time I also had come to the conclusion that the species was in fact an aberrant member of the Mysidacea, thus confirming Caroli's opinion. So far no ovigerous female of either species has been found, although in each case a somewhat immature female with only four pairs of developing oostegites is known. Caroli thought it most probable that in *Stygiomysis* the full complement of oostegites will be seven pairs; within the order Mysidacea there are as a rule either seven pairs of oostegites, or else two or three pairs—*Thalassomysis* established in 1939 has four pairs, the first two of which are small, the last two pairs forming most of the brood pouch. But, as Caroli rightly points out, in no Mysid are oostegites absent from the *last* pair of thoracic limbs. If *Stygiomysis* should prove to have only four pairs, then they would be absent from the last pair of thoracic appendages and quite exceptional.

Recently Dr. Holthuis sent me another specimen from the type locality; this proved to be a male and the second pair of pleopods differs appreciably from that of the female. Caroli says that in *Stygiomysis hydruntina* none of the pleopods "mostra particolari modificazione sessuali". This admittedly rather slight sexual dimorphism of the second pair of pleopods is similar to that found in all three monotypic genera of the cavernicolous family Lepidopidae (previously Lepidophthalmidae), to which the family Stygiomysidae appears to be most nearly related.

After the manuscript was finished, I received from the Amsterdam Museum a fifth specimen which Dr. J. H. Stock obtained in the same place on St. Martin on 4th February, 1959.

Order MYSIDACEA

Genus *STYGIOMYSIS* Caroli 1937

Stygiomysis Caroli, 1937, p. 220.

Rhopalonurus Gordon, 1958, p. 1552.

DIAGNOSIS. Aberrant cavernicolous Mysidacea with body rather vermiform, somewhat depressed. Carapace short, smooth, fused with tergites of first four thoracic somites, not produced antero-laterally beyond the minute rostral apex and lacking the usual postero-lateral "wings" so that thoracic somites 5 to 8 are *entirely exposed*. Division of the long thorax into subtagmata further emphasized

by the modification of the first *four* pairs of thoracic limbs to assist in feeding (maxilliped and gnathopods—see p. 315), the last four pairs being slender peraeopods. Abdomen widest across third somite, sixth somite *shorter* than fifth. Telson almost as wide as long; spines on truncate posterior margin only. Ocular scales broader than long, without trace of pigment or visual elements. Antennula more robust and rather longer than antenna, the inner flagellum slightly longer than carapace. Antennal scale minute; both segments of antennal protopodite distinct (peduncle therefore four-segmented). Labrum broadly triangular. Labium with long, pendant, widely separated paragnatha which conceal part of mandibles. Mandibles with well developed incisor, poorly developed molar, process and a distinct spine-row; a number of long simple spines on minute third segment of the palp. Maxillula without reflexed palp, distal endite unusually large and robust, the anterior apical spine very large. Maxilla beset with strong spines rather than setae; the two segments of endopodite very short. Maxilliped (first thoracic limb) pediform, without endites or lobes; exopodite a small unsegmented lamella; epipodite rather short and broad. Thoracic appendages 2 to 8 each with well developed multiarticulate exopodite; endopodites 2 to 4 modified as gnathopods, forwardly directed and stronger than those of the peraeopods (5 to 8). Penultimate segment of thoracic endopodites not subdivided. Pleopods all reduced, biramous, with one-segmented endopodite and three-segmented exopodite (exopodite two-segmented in male pleopod 2); alike in both sexes, apart from the sexual dimorphism exhibited by pleopods 2 in *Stygiomysis holthuisi*. A transverse chitinous lamella, or pair of lamellae, with which the protopodites of the pleopods are incorporated, projects from the posterior sternal margin of abdominal somites 3 to 5. Uropods unusual in having a long, stout, backward prolongation of the protopodite, armed with strong curved spines; statocyst absent. Oostegites at least four pairs, but the full complement is unknown (Caroli thinks it may be seven pairs).

Type species: *Stygiomysis hydruntina* Caroli 1937, from Italy. A second species from the West Indies is described below.

Stygiomysis holthuisi (Gordon)

Rhopalonurus holthuisi Gordon, 1958, p. 1552.

MATERIAL. The holotype, a female with developing oostegites measuring 9 mm. in length; the larger paratype is a slightly immature female without oostegites, the smaller paratype is probably immature.¹ In addition to the three original specimens, I received from the same locality at a later date, a male measuring 10 mm. in body length (also in the Leiden Museum).

LOCALITY. Devil's Hole, near Simson's Bay (or Simpson's Bay), in the Dutch part of St. Martin, Lesser Antilles, 10th February, 1957, (the three types) and, 25th May, 1958 (one male).

¹ The holotype and smaller paratype are in the Leiden Museum Collection, and are registered as Crust. G. 434 and Crust. G. 435 respectively. The larger paratype is in the British Museum (reg. no. 1959.vii.3.1).

HABITAT. "Devil's Hole lies to the south east of Simson's Bay bridge near the southern shore of St. Martin, just east of Simson's Bay. It is a sink-hole about 5 m. deep in a limestone slope. The hole itself is wide and rather easily accessible. From the hole a few short dead-ending passages run inwards. In one of these passages, which is about 10 m. long, there is a small puddle, about 30 cm. in diameter and 10 to 20 cm. deep. A film of limestone particles covered the larger part of the surface, and a limestone sediment on the bottom made the water turbid when stirred. The water tasted saltish, its salinity being 8100 mg. Cl/litre. It was not in total darkness as the entrance of the passage could still be seen. The distance of the sink-hole from the sea is about 300 m."

Dr. Holthuis returned to the same pool two days later, but did not obtain any specimens of *Stygiomysis holthuisi*, although he got a few Amphipods which he had not seen during his first visit to the cave. Dr. P. Wagenaar Hummelinck, who collected in the same locality on 26th July, 1955, obtained only Amphipods and Nematodes. (Information supplied by Dr. L. B. Holthuis.)

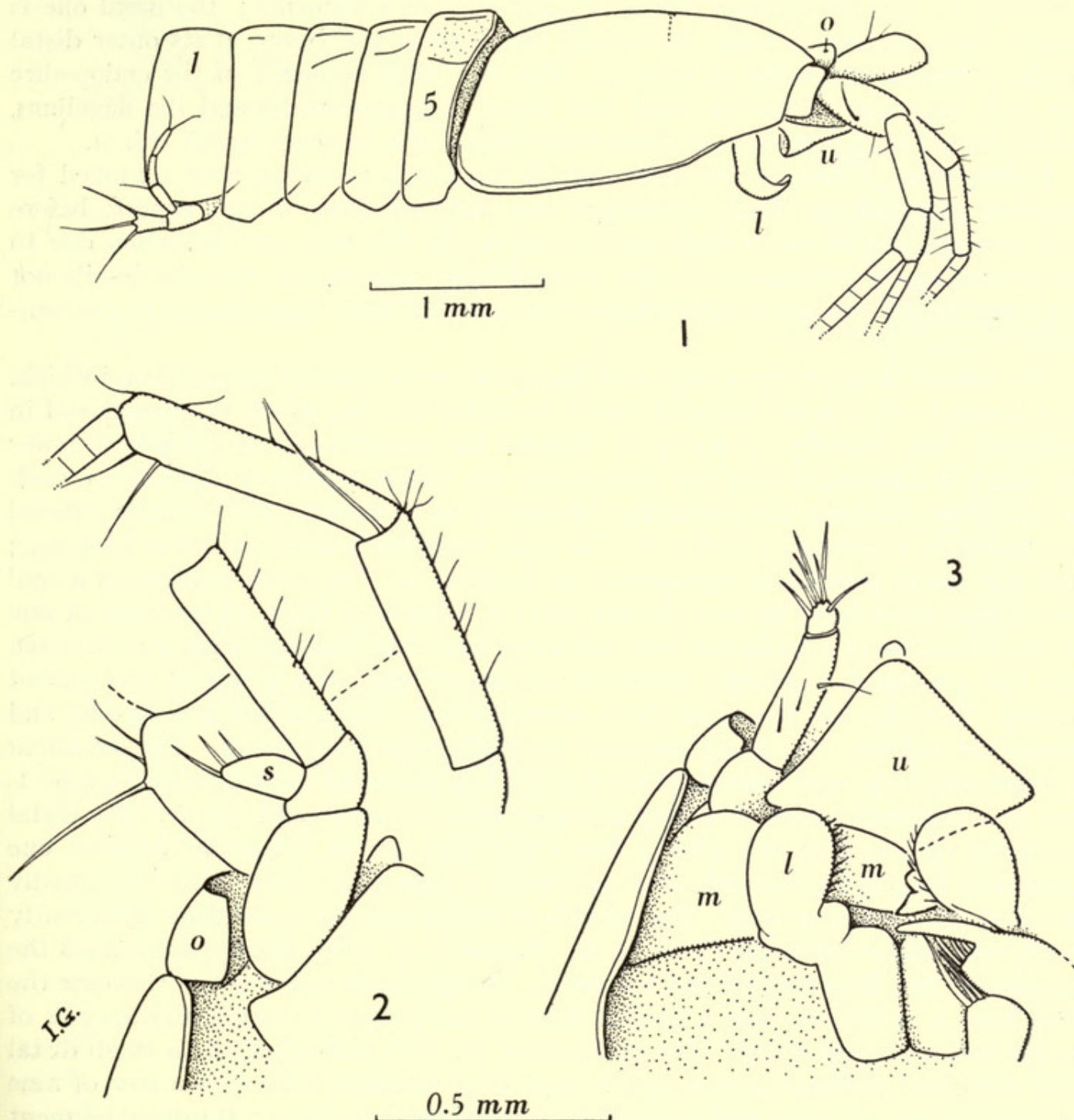
ADDITIONAL MATERIAL. A fifth specimen was received after the manuscript was finished. It was found in a small hole or pitch a few inches square, in the type locality, Devil's Hole, St. Martin, by Dr. J. H. Stock on 4th February, 1959. It is a slightly immature specimen, probably female, without oostegites, and is in the Amsterdam Museum.

DESCRIPTION OF FEMALE.

The largest specimen, measuring 9 mm. in length, and selected as the holotype, is represented in Plate 3. The long, narrow, rather vermiform body is flattened dorsoventrally and is fully segmented behind the carapace, which is just over one-fourth of the total length. The ratio of length to maximum width of *carapace* is 1.6:1 and the surface is smooth (with perhaps the merest hint of the cervical furrow). The carapace is completely fused dorsally with the tergites of thoracic somites 1 to 4, being free only at the sides to enclose long narrow branchial chambers. The anterior margin, on either side of the median triangular apex, which scarcely merits the name of rostrum is rather oblique and slightly concave. In front of each concavity is a short broad scale, presumably an ocular scale without any trace of pigment or visual elements, ((Pl. 3 and Text-figs. 1-3, 0). This scale curves downwards and inwards as shown in Text-figs. 2 and 3. The posterior margin of the carapace does not overlap any part of the fifth (first free) thoracic somite; indeed it is slightly overlapped by the latter in the mid-dorsal line (Text-fig. 1 and Pl. 3, 5).

The four free thoracic somites pass imperceptibly into the *abdomen*, although the two tagmata can easily be recognized by their respective appendages. Together they form a very elongated barrel (in dorsal aspect), widest across abdominal somites 2 and 3; abdominal somites 4 and 5 are longest and equal. The *telson* is as long as the fifth and sixth abdominal somites together, and is nearly as broad as long. The lateral margins are only slightly convergent and the wide posterior margin is armed with strong spines namely, three at each side and a median one flanked by a pair of shorter spines; four or five spinules fill the gaps between lateral and median spine groups (Pl. 3; only the median group is visible in Text-fig. 8).

The *antennula* is longer, and much stouter, than the antenna and is biramous (Text-fig. 1 and Pl. 3). Of the three segments in the protopodite the second is the longest, the first or basal one the widest. The flagella are only slightly unequal in length, the inner one is the more slender, with about 28 segments whereas the outer



FIGS. 1-3. *Stygiomysis holthuisi* (Gordon). Fig. 1. Larger paratype, anterior half of body in lateral aspect, after removal of the mouthparts and some thoracic appendages. Fig. 2. Antero-lateral angle of carapace, basal segment of antennula and antennal peduncle, part of labrum. Fig. 3. Right anterior portion of body, in ventral aspect.

l. Paragnath of lower lip. *m.* Mandible. *o.* Ocular scale. *s.* Antennal scale. *u.* Upper lip or labrum. *5.* Fifth (first free) thoracic somite. *1.* First abdominal somite,

one has only 16 to 18 longer segments most of them with long sensory hairs or aesthetascs on the inner margin. The antennulae arise beneath the ocular scales and are not widely separated.

The *antenna* is shorter and much more slender than the antennula. The peduncle of the right antenna of the larger paratype is represented, highly magnified, in Text-fig. 2. The protopodite seems to have only two segments; the basal one is nearly twice as long as wide, the second one is short and bears, at its outer distal angle, a minute exopodite or scale (s). The two basal segments of the endopodite are each long and slender (at least four times as long as wide) and the flagellum, which has 16 to 18 segments, is about four-fifths of the carapace length (Pl. 3).

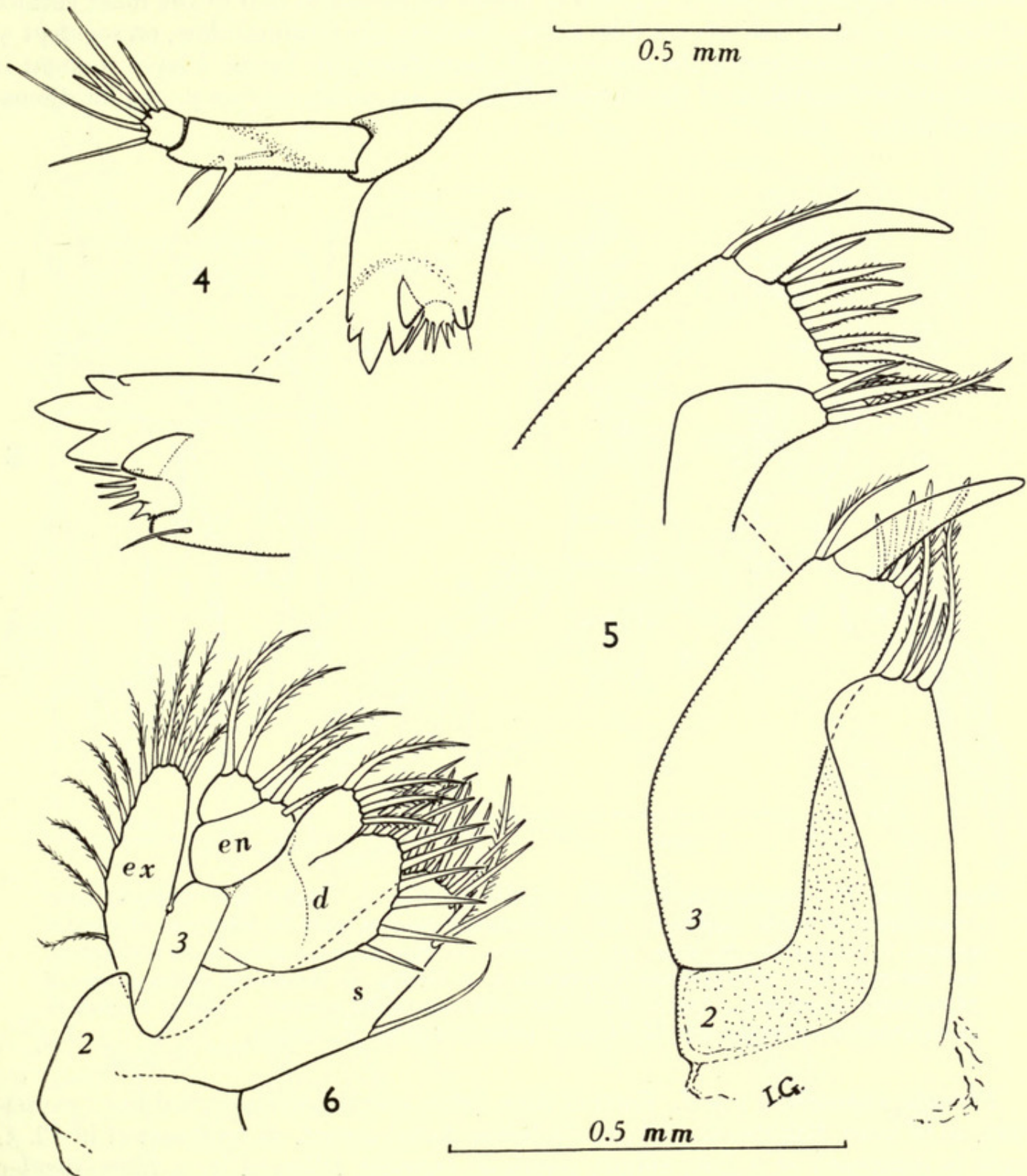
Mouthparts. Those on the right side of the larger paratype were removed for detailed examination. Each appendage was sketched from various aspects before any attempt was made to stain and mount it. In this way any distortion due to movement of, or pressure from, the coverslip was eliminated. Certain details not apparent in the unstained appendages were inserted later from the micro-preparations.

The *labrum* or upper lip is large and triangular, with rounded apex, beyond which, at a lower level, a small rounded lobule is visible (i.e. the lobule is more dorsal in position)—see Text-figs. 1 and 3, *u*. Behind the mandible is the *labium* or lower lip which is unusual in that the paragnatha are widely separated; moreover, each is enormous, pendant and forwardly directed so as to overlap and partially conceal the mandible (Text-figs. 1 and 3, *l*). The right mandible is shown *in situ* in Text-fig. 3 and the distal portion is represented in Text-fig. 4. The crown consists of a well developed, three-lobed incisor process (with a subsidiary tooth at the base of one of the lateral ones) a small but well chitinized knob-like molar process and, between the two processes, a strongly chitinized triangular lobe† and a row of five graded spines. The palp has the usual three segments; the median one is very long and somewhat twisted, the short terminal one has seven long spines. The *maxillula* is unusually large and massive (Text-fig. 5). The proximal endite, Hansen's lobe 1, has four terminal spines, two long and plumose, two short and simple. The distal or major endite, Hansen's lobe 3, has a terminal row of spines the anterior one unusually long and stout and, near its base, is a long seta. There is no backwardly directed endopodite or palp. The *maxilla* is a thin leaf-like appendage abundantly beset with spines and setae (Text-fig. 6). Hansen's pl. 3 was not apparent until the appendage had been stained and mounted. The proximal endite (s), in this case the lobe from 2, is simple, with a median seta on the posterior margin and a series of apical and subapical spines. The endite from pl. 3 (*d*) is divided into a small distal lobe with four terminal spines, and a large oval proximal lobe with a row of nine marginal spines. A short, two-segmented endopodite (*en*) follows; the distal segment bears three long spines, the proximal one has two spines on the inner margin. A long narrow exopodite (*ex*) arises from the outer margin of pl. 3; its margins, the free inner one excepted, bear plumose setae.

The *first thoracic appendage* or maxilliped is represented in Text-fig. 7 at a lower magnification than the other mouth parts. Though much smaller than, it is essenti-

† The fixed lacinia, against which the *lacinia mobilis* works.

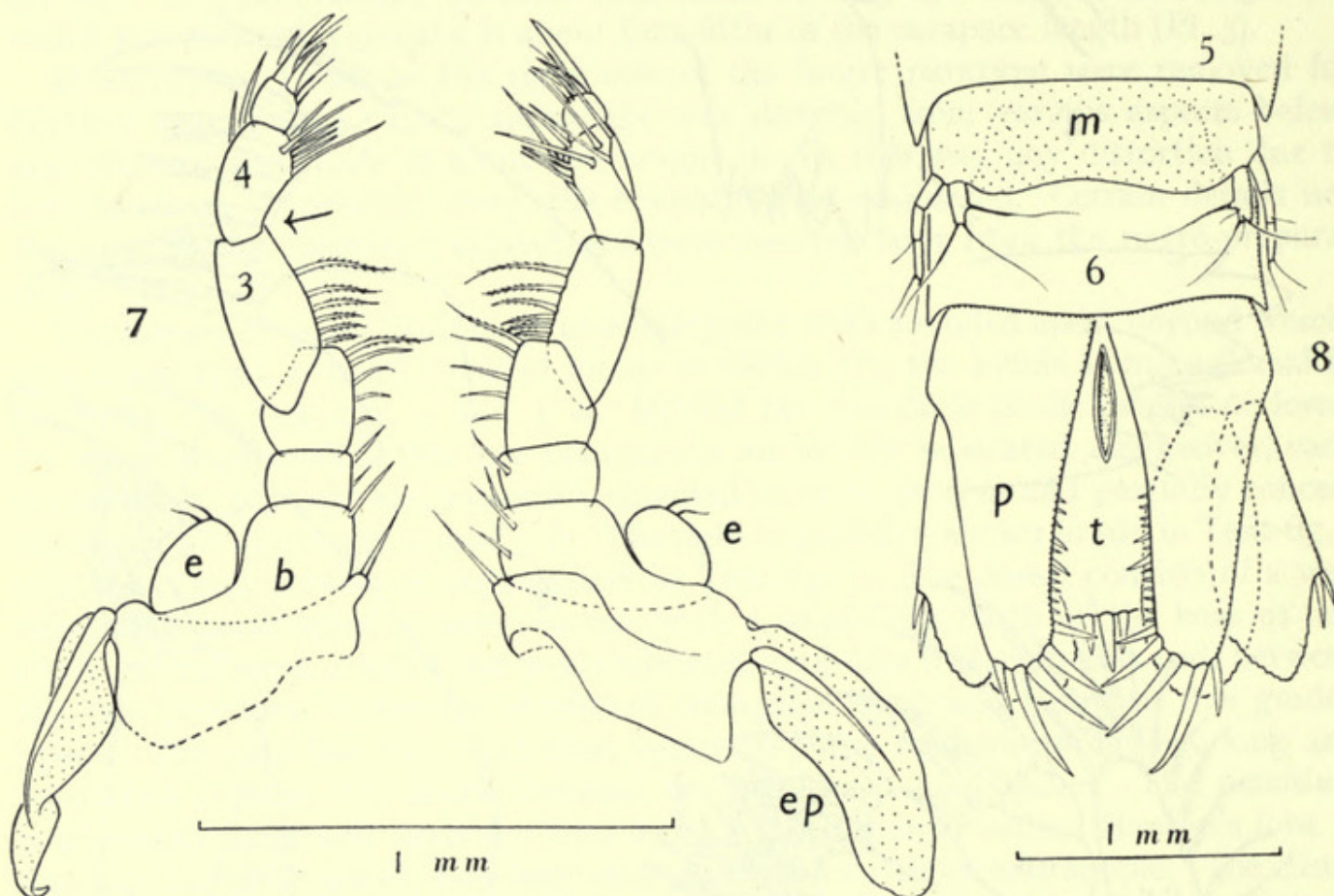
ally similar to, the three following pairs of thoracic limbs. However, it alone bears a fairly large epipodite reflexed into the brancial chamber and, moreover, the exopodite is reduced to a small oval unsegmented lamella (which may also be respiratory).



FIGS. 4-6. *Stygiomysis holthuisi* (Gordon). Mouthparts of larger paratype. Fig. 4. Distal portion of right mandible, with palp. Fig. 5. Right maxillula. Fig. 6. Right maxilla. All at higher scale except upper Fig. 4.

d. Divided endite. *en.* Endopodite. *ex.* Exopodite. *s.* Simple or undivided endite. 2 and 3 Hansen's plates 2 and 3 of protopodite (coxa and basis).

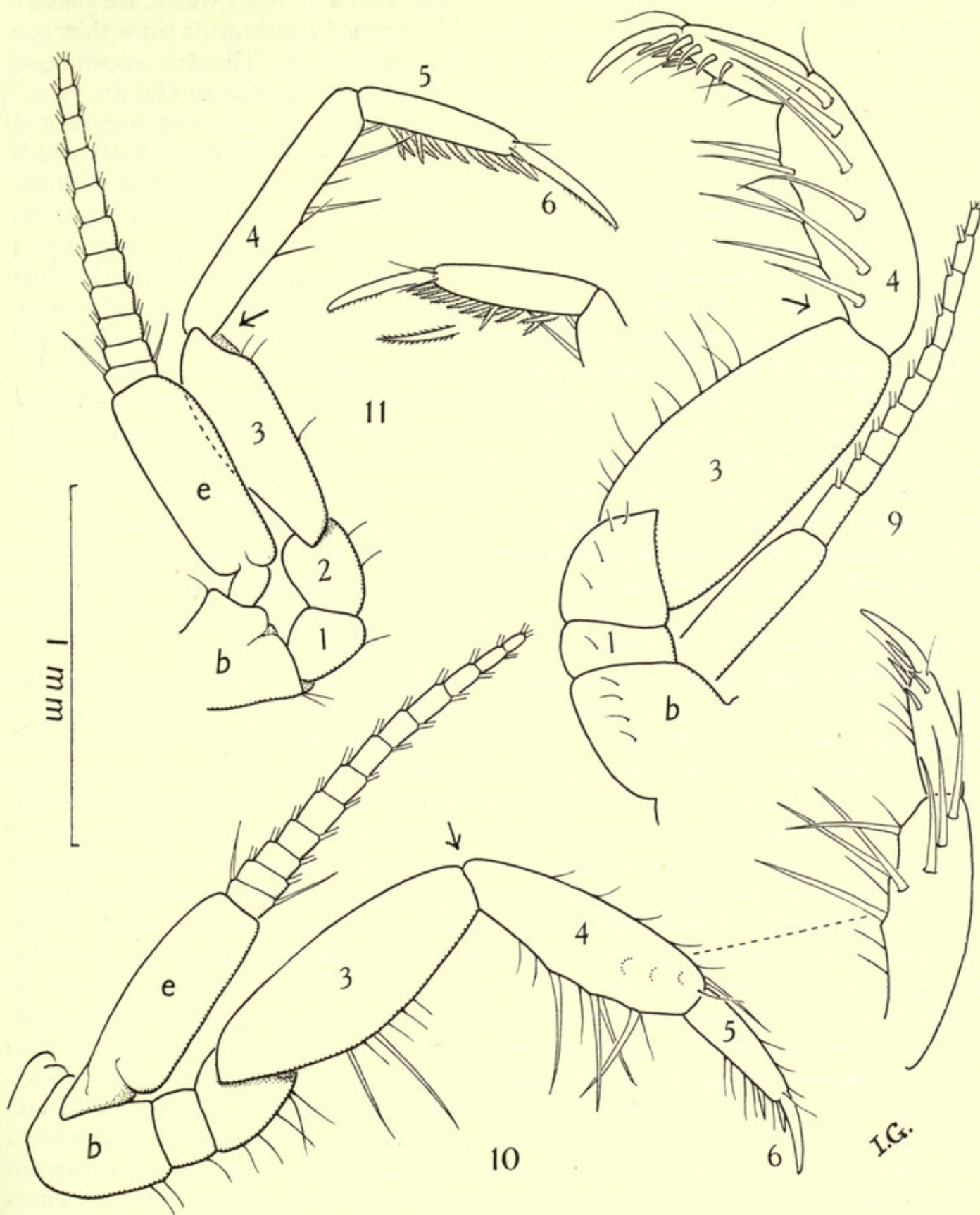
The endopodite—a continuation of the axis of the protopodite—comprises five segments and a strong terminal claw; the “knee” joint between the third and fourth segments is indicated by an arrow. There is a row of strong spines on the inner margin of segments 2 and 3, a group of spines on the distal half of the inner surface of segment 4 and a pair of claw-like spines, flanking the terminal claw, on segment 5. (Since the terminology of the segments of the endopodite varies, I have thought it better in the description of the thoracic limbs to use numbers—see p. 319 for discussion of this).



FIGS. 7 and 8. *Stygiomysis holthuisi* (Gordon). Fig. 7. Right first thoracic limb (maxilliped) of larger paratype. Fig. 8. Posterior part of body of holotype, in ventral aspect. *e*. Exopodite. *b*. Basis. *ep*. Epipodite. *m*. Membranous free lamina connecting and incorporating protopodites of pleopods 5. *t*. Telson. *p*. Backward prolongation of protopodite of uropod. 5 and 6. Fifth and sixth abdominal somites. 3 and 4. Segments of endopodite on either side of “knee” joint (indicated by arrow).

Thoracic appendages 2 to 8. Each of these bears a well developed, natatory exopodite, as in most Mysidacea. All are visible in dorsal aspect, as represented in Pl. 3, each is composed of a long robust proximal segment followed by a more slender tapering flagellum of 10 to 12 segments (Text-figs. 9, 10, 11, *e*). Each segment of the flagellum carries a pair of plumose setae, but only the base of each is inserted in Text-figs. 9–11.

These seven pairs of appendages are arranged in two distinct groups. The three anterior pairs have their endopodites directed forwards, more robust than, and obvi-



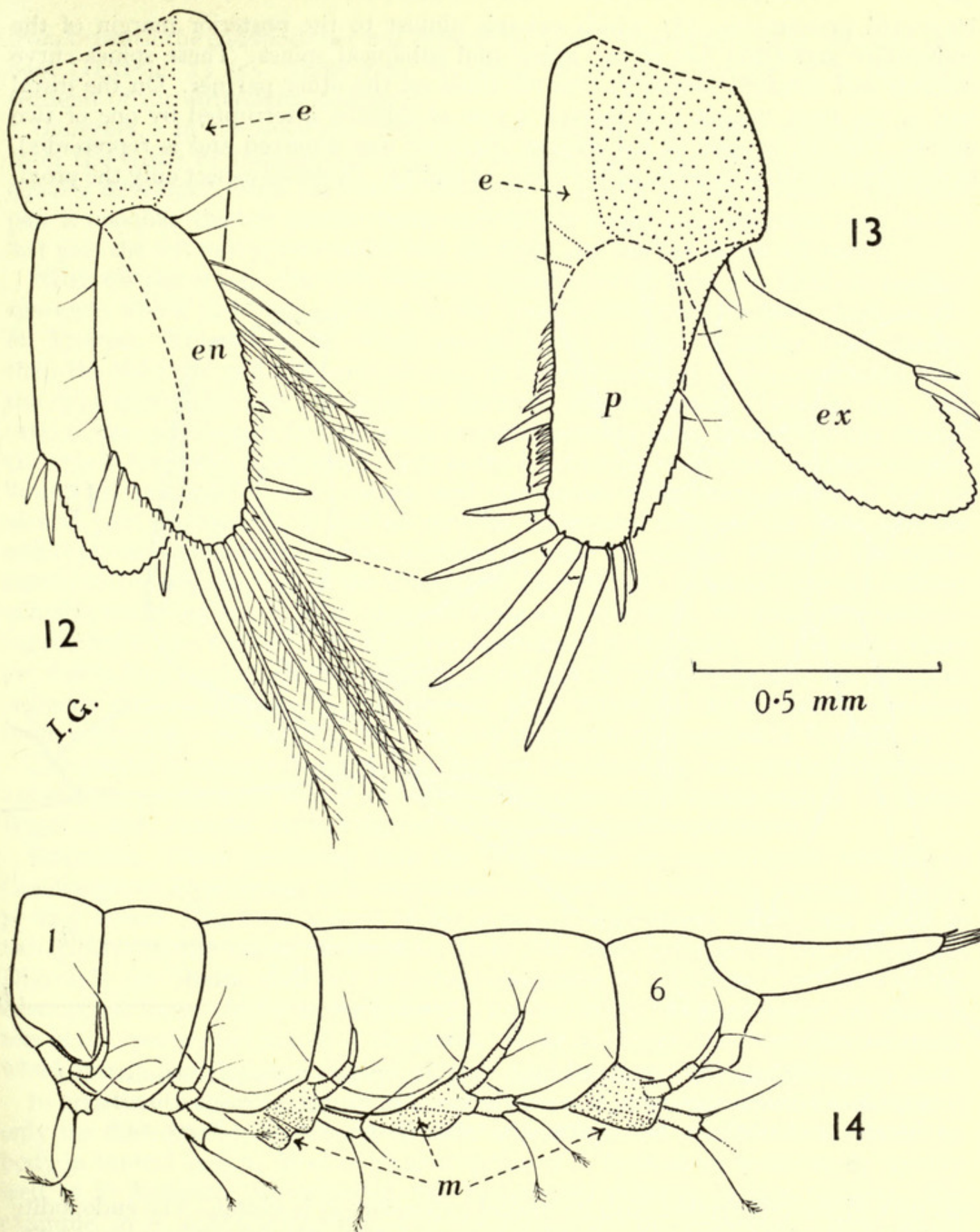
FIGS. 9-11. *Stygiomysis holthuisi* (Gordon). Larger paratype. Fig. 9. Right second thoracic limb (first gnathopod). Fig. 10. Fourth thoracic limb. Fig. 11. Eighth thoracic limb.

b. Basis. e. Exopodite. 1 to 6. Segments of endopodite. "Knee" joint indicated by arrow.

ously differing in function from, those of the four posterior pairs which are slender ambulatories. The three anterior pairs should be termed gnathopods since they are probably used to seize prey and pass it to the mouthparts. Thoracic appendages 2, 4 and 8 were removed from the right side of the larger paratype and are represented in Text-figs. 9, 10, and 11 respectively. Appendage 2 is, however, represented in inner, the other two in outer, aspect. The endopodite, beyond the basis which also bears the exopodite (*e*), comprises, as already mentioned in connection with the maxilliped, five segments, or six if the terminal claw is included (Text-fig. 11, 1-6). The endopodite of gnathopod 1 (thoracic appendage 2) is very robust; segments 1 and 2 are short, 3 is the longest and by far the broadest, 4 is long and armed with a longitudinal series of six setae on the inner surface and 3 on the ventral margin (with another near the margin), segment 5 is not quite half as long as 4 and is armed with a number of short spines in addition to the terminal claw. Gnathopod 2 (appendage 3) is very similar to, but a trifle less robust than, gnathopod 1 and there are only 4 long setae on the distal half of the inner surface of segment 4. As illustrated in Text-fig. 10, the third gnathopod is much more slender than gnathopod 1, with only three setae on the distal third of the inner surface of segment 4. Thoracic appendages 4 to 8 are all very similar; they are in fact peraeopods or walking legs, with the endopodite slender as represented in Text-fig. 11. Segment 4 is the longest but segment 5 and the terminal claw are also elongated so that the portion distal to the "knee" is longer than the proximal part. On the ventral margin of segment 5 is a row of curved serrated spines.

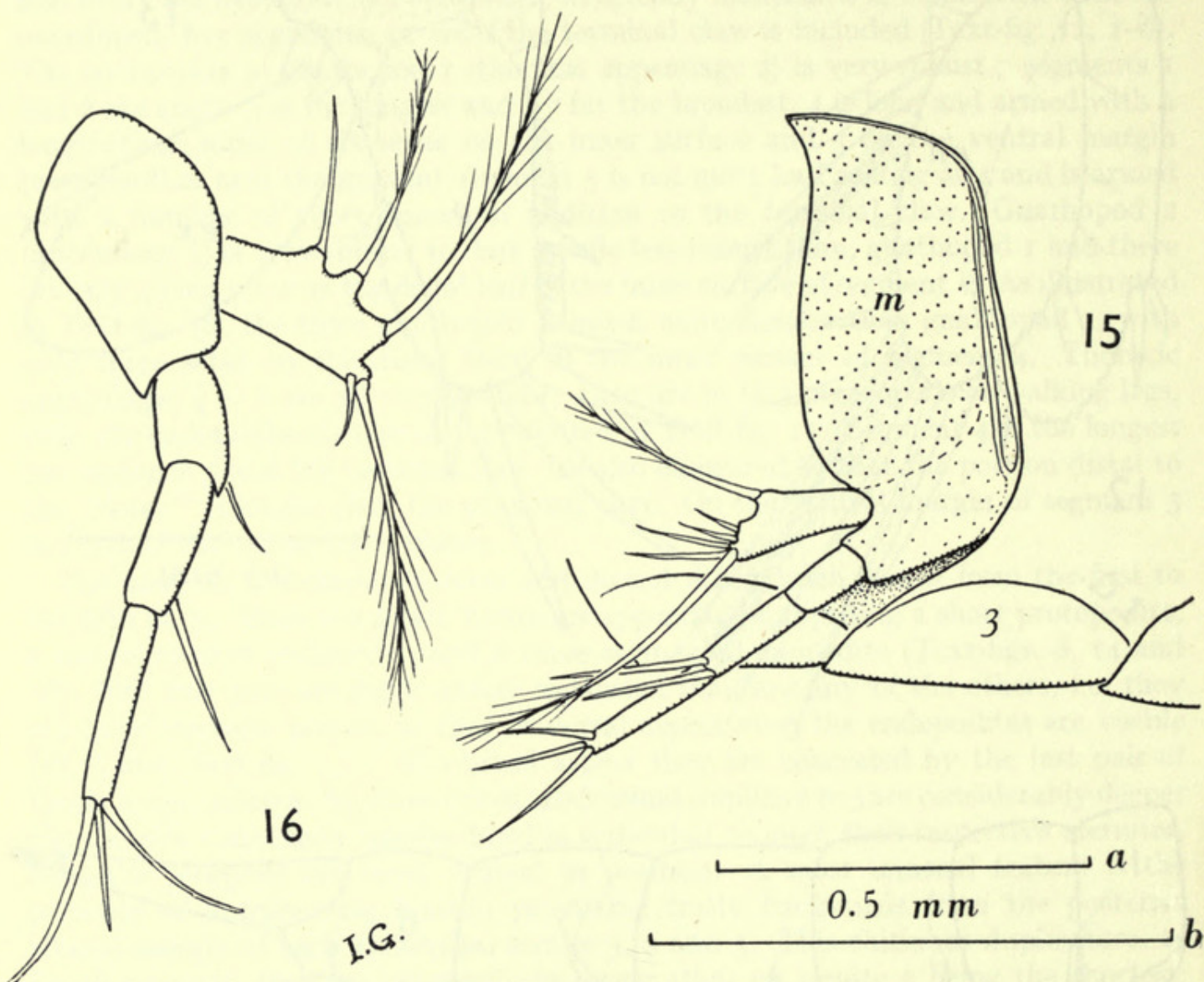
The *pleopods* are similar in form and do not differ much in size from the first to the fifth pairs. Each is a small, biramous appendage comprising a short protopodite, a one-segmented endopodite and a three-segmented exopodite (Text-figs. 8, 14 and 16). The first pair are more widely separated than are any of the others, i.e. they are more laterally placed, so that in dorsal aspect even the endopodites are visible (Pl. 3 and Text-fig. 14); in ventral aspect they are concealed by the last pair of thoracic appendages. In other words, abdominal somites 2 to 5 are considerably deeper than somite 1 and their tergites bend in somewhat to meet their respective sternites, thus the pleopods are more ventral in position. A most unusual feature is the presence of a transverse lamella projecting freely backwards from the posterior sternal margin of each abdominal somite 3, 4 and 5. This chitinous duplicature, as Caroli terms it, becomes progressively longer (that on somite 3 being the shortest, that on 5 the longest). The protopodites of each pair of pleopods are incorporated with the respective lamella, but the muscle bands which work the two rami of each pleopod are visible through the chitin (Text-figs. 8, 14 and 15 *m*). Under certain lighting conditions, at a certain angle, there appears to be a median notch (an inverted V) dividing the lamella on somite 3 of the smaller paratype; when a fine needle point is run along under the free margin of the lamella, however, the posterior margin is found to be continuous.

One of the most distinctive features of this animal is the *uropod* (Text-figs. 8, 12 and 13). The protopodite is expanded medially (*e*), beyond the base of the endopodite (*en*), so that it occupies very nearly half of the posterior margin of the sixth abdominal somite (Text-fig. 8). Moreover, in ventral aspect, it has a long, massive,



FIGS. 12-14. *Stygiomysis holthuisi* (Gordon). Smaller paratype. Fig. 12. Left uropod, in dorsal aspect. Fig. 13. Same, in ventral aspect. The muscle bands within the protopodite are restricted to the stippled area. Fig. 14. Abdomen and telson, in lateral aspect. *e*. Median expansion of protopodite. *en*. Endopodite. *ex*. Exopodite. *m*. Membranous lamellae connecting protopodites of pleopods 3, 4 and 5. *p*. Backward prolongation of protopodite. 1 and 6. First and sixth abdominal somites.

backward prolongation (*p*), which extends almost to the posterior margin of the endopodite and bears five strong apical and subapical spines. These spines curve inwards and upwards (dorsally) towards those on the other partner. On the distal half of the inner margin of *p* there is a row of spinules interrupted by one or two spines. The left uropod of the smaller paratype was removed and is represented, in dorsal and ventral aspects, in Text-figs. 12 and 13. In dorsal aspect only the proxi-



FIGS. 15-16. *Stygiomysis holthuisi* (Gordon). Fig. 15. Third left pleopod of female, and left half of membranous lamella, in ventral aspect. Fig. 16. Second pleopod of holotype (female). *m*. Lamella. 3. Side of third abdominal somite. Fig. 16 at larger scale.

mal part of the protopodite with its medial expansion (*e*) is visible. The endopodite conceals part of the exopodite, and the long marginal plumose setae on exopodite and endopodite (mostly omitted in Text-fig. 12) conceal the apical spines on the prolongation *p*. There is no suture line or diaeresis on the exopodite, at the level of the spines on the outer margin, marking off the distal portion. The uropods are unusually stiff (at any rate in fixed specimens); when I tried to spread out the exopodite

from beneath the endopodite it was difficult to do so without damage to the exopodite base (Text-fig. 13 *ex*). There is no statocyst either in the uropod or in the basal segment of the antennular peduncle.

Oostegites. In the holotype there are four pairs of developing oostegites arising from the coxae of thoracic limbs 4 to 7 respectively. The two anterior pairs are equally developed, each partner in the form of a long narrow lamella. The third pair is unequal, the left partner being appreciably larger than the right one; of the last pair the left one is very small and the right one has not as yet appeared.

NOTE ON THE MALE. On 27th October, 1958 I received from Dr. Holthuis another specimen which had been collected in the type locality on 25th May, 1958 by Mr. M. Vroman. This specimen, which proved to be a male, is rather more slender than the holotype and measures 10 mm. in body length. It is less contracted than the type specimens and not quite so flattened dorsoventrally (Text-fig. 24). The ratio of carapace length to total body length is perhaps more as in the living animal (1 : 4.74 in the male, as against 1 : 3.93 in the holotype). Apart from the more slender build, the presence of short penes, and the sexual dimorphism exhibited by the second pair of pleopods, I find no obvious differences between the male and the holotype—the antennula is often modified in male Mysidacea. Pleopod 2 is represented in Text-fig. 18, that of the holotype in Text-fig. 16. As far as I can see without actually removing one of these pleopods from each specimen, the exopodite is three-segmented in the holotype and only two-segmented in the male. In the latter there are 8 or 9 long, strong, thorny setae (or spines) on the inner margin of the proximal segment and, in addition, 5 to 7 shorter setae which are more oblique (directed more ventrally)—see Text-fig. 18. The first pleopod is represented in Text-fig. 17.

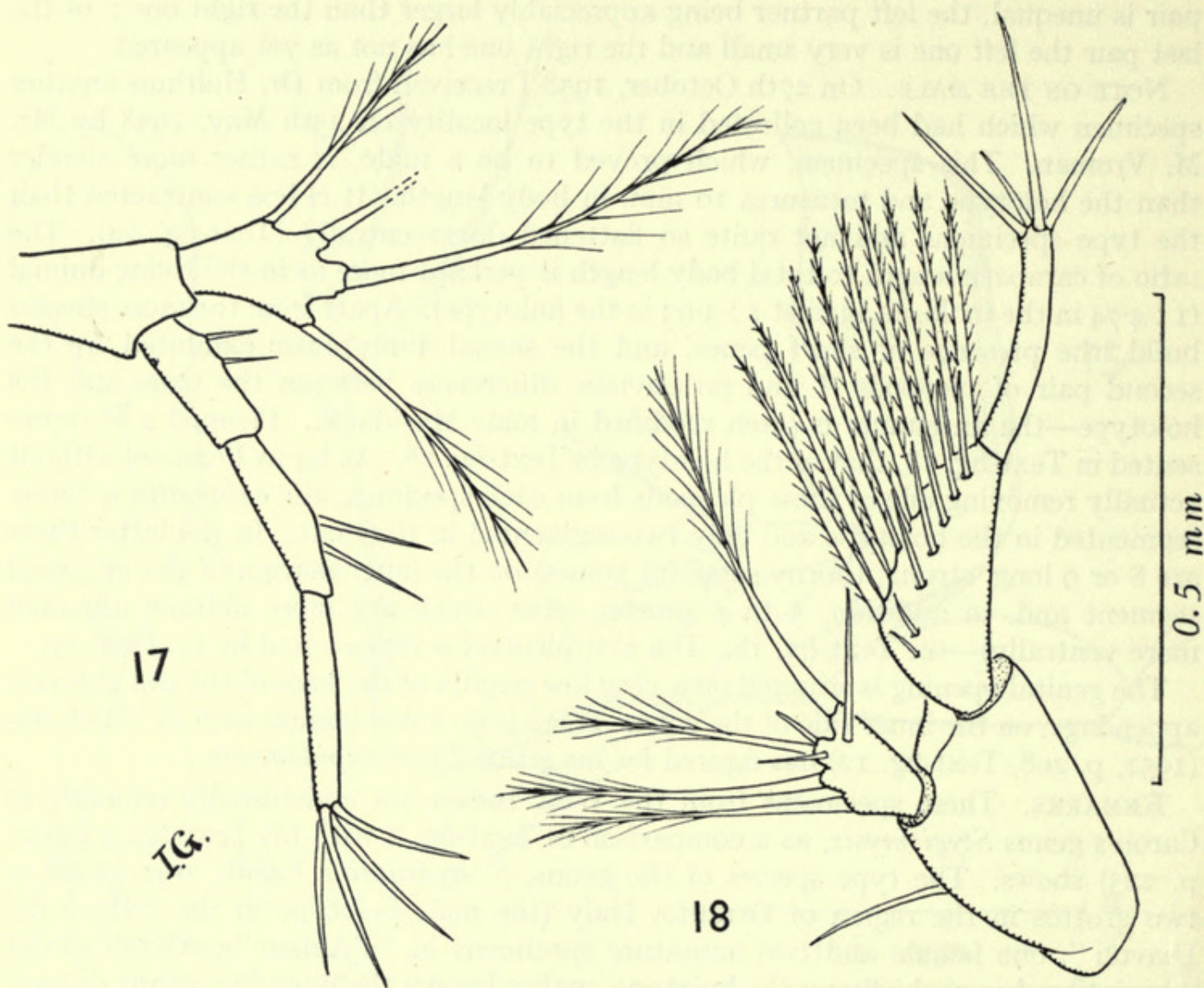
The genital opening is situated on a very low papilla at the base of the last thoracic appendage, on the inner side of the coxa. There is no coxal lamina such as Villalobos (1951, p. 208, Text-fig. 12) has figured for his genus *Typhlolepidomysis*.

REMARKS. These specimens from the West Indies are undoubtedly referable to Caroli's genus *Stygiomysis*, as a comparison of Text-fig. 8 with his Text-fig. 3 (1937, p. 223) shows. The type species of the genus, *S. hydruntina* Caroli, was found in two grottos in the region of Ótranto, Italy (the male holotype in the "Buco dei Diavoli", one female and two immature specimens in "l'Abisso"). Caroli's brief description, based chiefly on the holotype, makes known the most important characters of the species, and indeed of the genus. As far as I know, the more detailed study which was to have followed (Caroli, 1937, p. 220) has never been published.

In addition to the photograph of the whole animal in lateral aspect, Caroli figured only the first gnathopod (second thoracic appendage) and the posterior end of the body in ventral aspect. Most of his description of *S. hydruntina* would apply equally well to *S. holthuisi*. Nevertheless, the two species differ in certain respects. For example, in *S. holthuisi* segment 5 of the endopodite of gnathopod 1 (that which bears the terminal claw) is much longer than in *S. hydruntina* and the terminal claw and the pair of spines flanking it are very much shorter (in *hydruntina* they are much longer than the segment that bears them—cf. Text-fig. 9 with Caroli, 1937, fig. 2, p. 222). In *S. holthuisi* the terminal claw of pereopod 4 (last thoracic limb) is rather shorter than segment 5, whereas in *S. hydruntina* the claw is longer than the dactylopodite.

The shape of the uropod differs appreciably in the two species; in *S. hydruntina* the outer margin of the prolongation *p* of the protopodite is distinctly concave, the exopodite is much broader, with a more semicircular apex (cf. Text-figs. 8, 12 and 13 with Caroli, 1937, p. 223, fig. 3).

According to Caroli, the pleopods of the male increase very slightly in length from



FIGS. 17-18. *Stygiomysis holthuisi* (Gordon). Male. Fig. 17. First pleopod. Fig. 18. Second (modified) pleopod.

the first to the fifth pair, but “nessuno di essi mostra particolari modificazioni sessuali”. In *S. holthuisi*, however, the second pair of pleopods in the male are modified; as far as I can ascertain without removing one of these pleopods, the exopodite has only two, instead of the usual three, segments, and the proximal segment has a row of 9 long spines as represented in Text-fig. 18 (compare with the first male pleopod, Text-fig. 17 and with the second female pleopod, Text-fig. 16). Also, the membranous flaps between the third, fourth and fifth pairs of pleopods differ in

the two species. Caroli says that, in each of these three pairs, "the peduncle (protopodite) is completely fused with a wide duplicature of the integument, in the form of an almost semicircular lamina, movably articulated with the posterior margin of the sternite, [extending] from the external margin to the middle line, where it meets that of the other side" (my translation). He adds that the peduncle proper is indicated by the presence of the muscle bands which work the two rami, but that there is no suture between it and the duplicature (Caroli, 1937, pp. 223-224 and fig. 3). In *S. holthuisi* these duplicatures unite to form a single membranous flap, or lamina in which the muscle bands are visible at either side (Text-figs. 8 and 15). I thought at first that there was a median slit separating the two halves of the membrane of the third pair of pleopods of the smaller paratype of *S. holthuisi*. But, on re-examination, I find that there also the membrane is continuous although it is slightly creased in the middle (Text-fig. 14).

The female specimen of *S. hydruntina* measured only 7 mm. in length, but it also had 4 pairs of developing oostegites arising from thoracic limbs 4-7. These oostegites were probably not quite so well developed as those in the holotype of *S. holthuisi* (c.l. = 9 mm.). Caroli is almost certain that the full complement of 7 pairs will be found in *Stygiomysis*. If not, then *Stygiomysis* will be quite exceptional. Seven pairs of oostegites are found in the Lophogastrida (Lophogastridae and Euco-piidae), in the Lepidopidae (all three genera), Petalophthalmidae and Boreomysinae. All the rest of the Mysida (*Thalassomysis* excepted) have only two or three pairs of oostegites arising from the last two or three pairs of thoracic appendages. It is to be hoped that an ovigerous female of either species of *Stygiomysis* will soon be found, so that the exact number of oostegites can be ascertained.

II. ON THE SYSTEMATIC POSITION OF THE STYGIOMYSIDAE

Up to the present time the following cavernicolous Mysidacea have been described or mentioned in the literature :—

STATOCYST ABSENT

- Lepidopidae : *Lepidops servatus* (Fage) 1924, 1925. Zanzibar.
Spelaeomysis bottazzii Caroli 1924. Italy. (Found a second time by Stammer—see Caroli 1937, p. 226).
Typhlolepidomysis quinterensis Villalobos 1951. Mexico.
- Stygiomysidae : *Stygiomysis hydruntina* Caroli, 1937. Italy.
Stygiomysis holthuisi (Gordon) 1958. West Indies.

STATOCYST PRESENT

- Mysidae : *Heteromysis cotti* Calman 1932. Lanzarote.
Troglomysis vjetrenicensis Stammer 1933, 1936. Herzegovina.
Antromysis cenotensis Creaser 1936. Yucatan.
Antromysis sp. Bolivar y Pieltain 1943-44, and 1950. Cuba.

Most of these species occur in fresh or brackish water; *Heteromysis cotti* is a marine species since the cave in which it lives communicates with the sea. (*Antromysis anophelinae* W. M. Tattersall, 1951, p. 230, was discovered in the holes made by a land crab, *Cardisoma crassum* Smith, along with mosquito larvae, far up the mangrove inlets behind Puntarenas, Costa Rica—in water which must have been nearly, if not quite fresh). The cavernicolous species with a statocyst in the endopodite of the uropod are referred to the large family Mysidae, in the suborder Mysida. Those that have no statocyst are peculiar or aberrant in certain respects and their systematic position is less easy to determine. Fage referred the family Lepidopidae to the suborder Mysida while admitting that it had a number of Lophogastrida characters; Caroli thought the family might be regarded as modified or aberrant Lophogastrida and Villalobos thought that it should be placed in a new suborder (see p. 306). Caroli had no hesitation in referring the Stygiomysidae to the suborder Mysida.

GENERAL APPEARANCE. In all three genera referred to the family Lepidopidae (formerly Lepidophthalmidae) the carapace agrees with the accepted definitions of the order Mysidacea. Calman (1909, p. 171), in his definition of the order writes “the carapace extends over the greater part of the thoracic region, but does not coalesce with more than three thoracic somites”. Under morphology lower down on the same page he adds “from five to seven of the thoracic somites are distinct, and the last two or three may be left uncovered by the carapace on the dorsal side”. Calman’s definition is adopted by Tattersall, (1951, p. 11) and that given by Zimmer (1927, p. 609) is in agreement with it. It has been altered by Dr. Olive Tattersall to read “carapace shield-like, covering the greater part of the thoracic region, fused dorsally with the head region and not more than four anterior somites including the first, which is incorporated in the head” (Tattersall and Tattersall, 1951, p. 11). Dr. Tattersall, in a letter dated 12th November, 1958, informs me that, as far as she can make out, “in some Mysidae there does appear to be fusion of at any rate part of the fourth somite with the carapace (in e.g. *Mysidopsis*, some *Siriella* and in *Neomysis*). I do not know quite how much one can rely on the “saddle” on the carapace in so many mysids, but I always considered it to represent the area of fusion of the two surfaces, i.e. the inner surface of the carapace with the dorsal surface of the thoracic somites involved.”

I have examined specimens of *Lepidops servatus* (Fage) but they are delicate and none too well preserved, and it is not easy to discover exactly how many thoracic tergites are free. As in most Mysidacea, the anterior thoracic somites are short and rather crowded together, especially dorsally, and the suture lines are visible laterally. As far as I can see four are certainly free and perhaps five. The last two tergites, which are uncovered by the emarginated carapace, are each as long as the first abdominal somite. The large lateral “wings” of the carapace extend to the first abdominal somite, and can easily be moved away from the body. All three genera retain the “caridoid facies” as do most Mysidacea.

Stygiomysis, on the other hand, does not agree with Calman’s definition, even as emended by Dr. Tattersall. The carapace is unmistakably fused with the first four thoracic tergites but has no “wings” to speak of, so that the last four thoracic

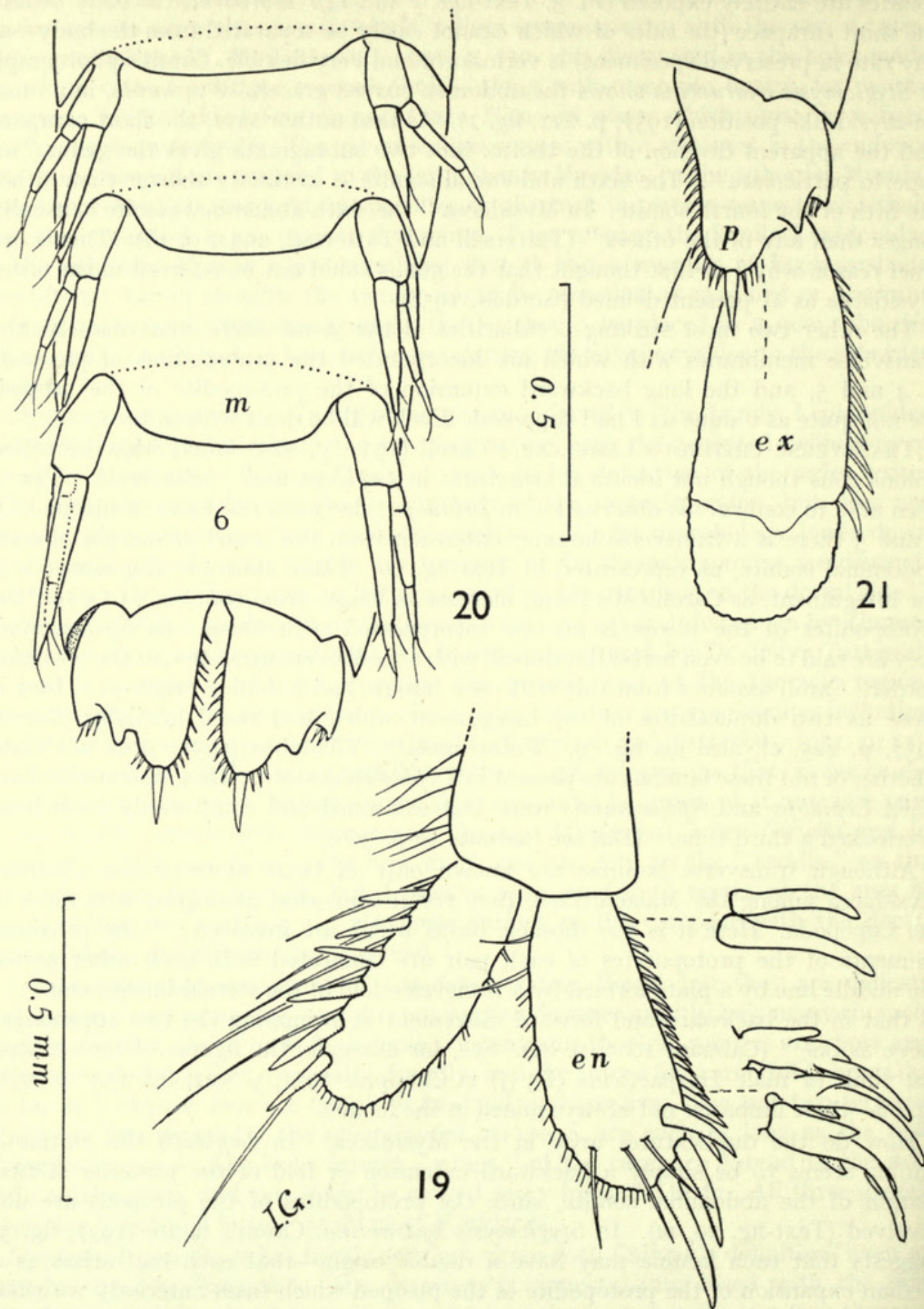
somites are entirely exposed (Pl. 3, Text-figs. 1 and 24). Moreover, the body behind the short carapace (the sides of which cannot easily be separated from the body—at any rate in preserved specimens) is vermiform and very flexible. Caroli's photograph of *Stygiomysis hydruntina* shows the abdomen curved gracefully upwards, in a most un-mysid-like position (1937, p. 221, fig. 1). As that author says, the short carapace and the apparent division of the thorax into two subtagmata gives the genus "un aspetto particolare". The sixth abdominal somite is distinctly shorter than either the fifth or the fourth somite. In Mysidacea "the sixth abdominal somite is usually longer than any of the others" (Tattersall and Tattersall, 1951, p. 16). This is the chief reason why I at first thought that the genus could not be referred to the order Mysidacea as at present defined (Gordon, 1958).

The other two most striking peculiarities of the genus *Stygiomysis* namely, the transverse membranes with which are incorporated the protopodites of pleopods 3, 4 and 5, and the long backward extension of the protopodite of the uropod, are not quite as unique as I had supposed. Each will be dealt with in turn.

TRANSVERSE CHITINOUS LAMELLAE. Caroli (1937, p. 225) found what he called homologous though not identical structures in *Lepidops* and *Spelaeomysis*. I have been able to confirm his observation in *Lepidops*; between the bases of pleopods 3, 4 and 5 there is a transverse laminar extension from the posterior margin of each abdominal somite, as represented in Text-fig. 20. These chitinous duplicatures of the integument, as Caroli calls them, increase in length from somites 3 to 5 but the protopodites of the pleopods are *not* incorporated with them. In *Spelaeomysis* they are said to be even better developed, with a median emargination in the posterior border. Caroli assumes from this that each lamina had a double origin—i.e. that it arose as two duplicatures of the integument which had fused medially (Caroli, 1937, p. 225, cf. also his fig. 3). Unfortunately, Villalobos (1951) does not state whether or not these laminae are present in *Typhlolepidomysis*; they were overlooked when *Lepidops* and *Spelaeomysis* were first examined and could easily have been overlooked a third time. (But see footnote to p. 308).

Although transverse laminae are known only in these more or less aberrant Mysidacea among the Malacostraca, they recall somewhat analogous structures in the Copepoda. Here it is the thoracic limbs which are involved; "the proximal segments of the protopodites of each pair are connected with each other across the middle line by a plate formed by a transverse fold of the sternal integument . . . so that in the backward and forward movement in swimming the two appendages move as one" (Calman, 1909, p. 81). See, for example, the figures of the reduced last limb of male Harpacticids (P5 ♂) in Chappuis 1931, p. 521, fig. 13; p. 538, fig. 60—these limbs are not always joined in the female.

How do the duplicatures arise in the Mysidacea? In *Lepidops* the chitinous lamina seems to be simply a backward extension or fold of the posterior sternal margin of the abdominal somite, since the protopodites of the pleopods are not involved (Text-fig. 20, *m*). In *Stygiomysis hydruntina*, Caroli's figure (1937, fig. 3) suggests that each lamina may have a double origin—that each half arises as a median expansion of the protopodite of the pleopod which fuses anteriorly with the sternal margin of the abdominal somite, since the two halves merely meet in the



middle line. In *Stygiomysis holthuisi* the lamina might arise in either of these ways, since the protopodites of the pleopods are incorporated and there is no trace of a median suture line (see also p. 294). It would be interesting to know how these chitinous laminae develop and what their function can be, since the pleopods are almost certainly not natatory. The very thin sternal wall above each lamella may be respiratory.

UROPOD. In *Lepidops servatus* the protopodite is broad, occupying half of the posterior margin of the last abdominal somite. Moreover, on the ventral side, there is a short but distinct backward prolongation armed with a terminal spine and with numerous spinules on the inner border (Text-fig. 21, *p*). This might represent an initial stage in the development of a massive backward prolongation such as is found in *Stygiomysis*, although Caroli prefers to regard it as a last vestige retained in the family Lepidopidae (1937, p. 225). At any rate, this incipient or vestigial structure in *Lepidops* (and presumably also present in *Spelaeomysis*), together with the transverse laminae mentioned above, suggest a fairly close relationship between the Lepidopidae and the Stygiomysidae (see also p. 308). A somewhat analogous structure is characteristic of the uropod of the Stomatopoda, which might indicate that the prolongation of the protopodite is archaic and, as Caroli thinks, may at one time have been much more widely distributed among Malacostraca. I am inclined to think that it is a highly specialized structure which has arisen independently in the Stygiomysidae, and to a lesser extent in the Lepidopidae, in response to some special habit.

It may be mentioned in passing that, in the genus *Micraspides* (Syncarida, Anaspidae), the uropod is also armed with strong spines, not on the protopodite (which is not prolonged) but on the endopodite. On the dorsal surface, near the postero-median angle, are three strong spines directed obliquely upwards; in addition there is a row of special spines on the inner margin (Text-fig. 19, *en*). Nicholls' figure (1931, pl. 32, fig. 15) of the uropod of the type species *Micraspides calmani* is rather small and does not show the row of spines near the external margin of the exopodite. In *Thermosbaena mirabilis* Monod the exopodite of the uropod is remarkably spiny (Monod, 1940, fig. 19).

PLEOPODS. The pleopods of *Stygiomysis*, though smaller and not increasing much in length from the first to the fifth pair, are of the same general form as those of Lepidopidae (Pl. 3, and Text-fig. 14, cf. Text-fig. 20). In both families they are reduced, non-natatory, and biramous in both sexes. In *Stygiomysis holthuisi* the second pair is modified in the male although it is not longer than the others (Text-figs. 17 and 18); Caroli's statement that there is no sexual dimorphism of the pleopods in

FIGS. 19-21. *Micraspides calmani* Nicholls. Fig. 19. Left uropod of syntype, in dorsal aspect, omitting long marginal setae. *Lepidops servatus* (Fage). Syntype from Paris Museum. Fig. 20. Abdominal somites 3 to 6, and protopodites of uropods, in ventral aspect, showing membranous free laminae (*m*) on posterior margin of somite 3, 4 and 5, between bases of the pleopods. Fig. 21. Left uropod, in ventral aspect (endopodite damaged). *en.* endopodite. *ex.* Exopodite. *p.* Short backward prolongation of protopodite. Scale = 0.5 mm.

S. hydruntina requires corroboration. The second pleopod of the male is similarly modified in all three genera of the Lepidopidae—see Fage, 1925, fig. VI, 2 and 2 ♂; Caroli 1924, p. 513; Villalobos 1951, fig. 13, A and B. (A glance at fig. 1 of Villalobos' paper shows that pleopod 2 is shorter than pleopod 5 in the male holotype; it seems, therefore, that in his fig. 13, C and D are drawn at a smaller scale than A and B). Pseudobranchiae are absent in both Stygiomysidae and Lepidopidae.

In Lophogastrida the pleopods of both sexes are well developed, biramous, multi-segmented and natatory; they may be considerably larger in the male than in the female, but are unmodified or very slightly so. In Mysida they are seldom alike in both sexes and generally exhibit marked sexual dimorphism. In the female they are, as a rule, rudimentary, uniramous (rarely the first may be biramous) and non-natatory; occasionally those of the male are all rudimentary as in the female (*Mysidella*, *Mysidetes*, *Heteromysis*). In the male they are sometimes biramous, natatory and unmodified (Petalophthalmidae), or the third, or second and third, pairs are slightly modified (Boreomysinae); more often one or more pairs are reduced as in the female and one or more pairs are modified as accessory copulatory organs; pseudobranchiae are present. The pleopods which are most commonly modified are the third and/or fourth pairs. In the genus *Rhopalophthalmus* it is the second pair (Tattersall, O.S. 1957, fig. 7H, compare with G, J, K and L); but here the pleopods are biramous, multiarticulate, with conspicuous pseudobranchial lobes at the bases of the endopodites. The modified pair, or pairs, of male pleopods are usually long and conspicuous in the family Mysidae, to which *Rhopalophthalmus* belongs. It is just a coincidence that the same pair of male pleopods is modified in this genus as in the cavernicolous families under discussion.

MOUTHPARTS. There are numerous differences in detail between the individual mouthparts of the two families and these are doubtless correlated with differences in feeding habits. For example, in the Lepidopidae the molar process of the mandible is better developed, the palp is larger and the second and third segments are each armed with a close row of thorny spines (cf. Text-fig. 27, where many of the spines and setae are omitted, Fage, 1925, fig. IV, *M* and Villalobos, 1951, fig. 6 with figs. 4 and 5).

According to Tattersall and Tattersall, (1951, pp. 20–21), in Mysidacea the maxillula is smaller than the maxilla and always lacks a backwardly directed palp or endopodite except in the genus *Gnathophausia*. This statement requires amplification however, because there is a palp in all three genera of the Lepidopidae (Fage, 1925, fig. IV, *m*¹; Caroli, 1924, p. 513 and Villalobos, 1951, fig. 7). In each of three specimens of *Lepidops servatus* which I have examined, this palp has a median constriction and appears, therefore, to be two-segmented as in *Typhlolepidomysis* (see Text-figs. 27 and 28). Moreover, in *Stygiomysis holthuisi* the maxillula is larger than the maxilla; the outer endite is stout and one of its apical spines is greatly enlarged; there is no palp (Text-figs. 2 and 5; cf. the small maxillula of *Lepidops* represented in Text-figs. 28 and 27).

The maxilla of *Stygiomysis* has strong spines rather than setae on the whole inner margin but they do not continue along the lower border of the simple endite (Text-fig. 6, on *en*, *d* and *s*); in the Lepidopidae the inner and lower margins of the maxilla

bear numerous finer setae and spines, and the segments of the endopodite are much longer (Fage, 1925, fig. IV, m^2 and Villalobos, 1951, fig. 8). The first thoracic appendage or maxilliped of *Stygiomysis* is more pediform, lacks the large endites, but has strong spines on the inner margin of the distal segments of the endopodite (Text-fig. 7; cf. Fage, 1925, fig. VI, mp and Villalobos, 1951, fig. 9). According to Siewing (1958, pp. 250–251) this appendage should be called a gnathopod in the Stygiomysidae and a maxilliped in the family Lepidopidae (see later, under terminology, p. 316). Differences such as these may be found between closely related families of Mysidacea. The exopodite of the first thoracic limb is reduced to a simple unsegmented lamina, which is relatively smaller in *Stygiomysis holthuisi* than in either *Lepidops* or *Typhrolepidomysis* (cf. Text-fig. 7 with Fage, 1925, fig. VI, mp and Villalobos, 1951, fig. 9). In this respect both families are nearer to the suborder Lophogastrida and to the Petalophthalmidae (in which the exopodite is lacking, as in some species of *Gnathophausia*) than to the Mysidae.

LABIUM. The paragnatha in *Stygiomysis* are unusual and very conspicuous, although Caroli did not mention them. To discuss the labium at this point would necessitate rather a lengthy digression; it will be dealt with in a separate section later on (p. 309). Of the paragnatha that I have examined, those of *Lepidops* seem to be nearest to those of *Stygiomysis*.

THORACIC APPENDAGES 2–4. Many of the peculiarities of the mouthparts mentioned above are doubtless correlated with the fact that in Stygiomysidae three pairs of thoracic appendages (2–4) are modified as gnathopods, whereas in Lepidopidae only one pair, the second, is thus modified (cf. Pl. 3, Text-figs. 9 and 10 with Fage 1925, fig. V, p^2 and Villalobos, 1951, fig. 10). Incidentally, Villalobos refers to the second thoracic limb as “primer par de pereiópodos” in the text and as “maxillipedo del secundo par” in the legend to fig. 10 and Caroli (1937, p. 226) says “toracopodi 2–4 (gnathopodi) massillipediformi”! Only in the family Eucopiidae of the suborder Lophogastrida are the same three pairs of thoracic limbs modified as gnathopods; but in this family the following three pairs of appendages are elongated and specially modified (Tattersall and Tattersall, 1951, p. 111, figs. 13C, D and E and 12A). When Sars (1885, p. 59) suggested that the long prehensile thoracic limbs 5 to 7 might be used for seizing hold of Hydroids or Crinoids fixed at the sea bottom, he was unaware of the fact that the Eucopias are bathypelagic (Fage, 1941, p. 3 and 1942 pp. 3 and 60). There is nothing in mid-water for a bathypelagic animal to cling to; these prehensile endopodites, reaching well beyond the body, seem admirably suited for keeping the animal suspended and for seizing prey which could be passed to the short robust endopodites of the gnathopods (see p. 319). *Stygiomysis* is probably raptorial in its feeding habits whereas the Lepidopidae are probably predominantly filter feeders.

OOSTEGITES. In Lophogastrida, Lepidopidae, Petalophthalmidae and Boreomysinae (Mysidae) a pair of oostegites or brood lamellae arises from each pair of thoracic appendages 2–8. Throughout the rest of the large family Mysidae there are either three or two pairs, arising from the last three or two pairs of thoracic appendages. The only exception to this rule is the genus *Thalassomysis* Tattersall 1939, p. 238 (established two years after Caroli's genus *Stygiomysis*). Here reduction has not

gone quite as far and four pairs of oostegites are present. Of these the first pair is vestigial, the second pair small and the last two pairs form the major part of the brood chamber. Oostegites disappear from the more anterior limbs first so that, no matter what their number, a pair is always present on the seventh and the eighth thoracic appendages. In *Stygiomysis* the full complement is unknown but, unless the genus is quite exceptional, there ought to be a pair on the eighth thoracic limbs; this means that there ought to be at least five pairs and Caroli may be right in thinking that there may be seven pairs.

DISCUSSION. The family Stygiomysidae seems to be distinct from, but most closely related to, the family Lepidopidae. But, as already mentioned, opinion differs as to the systematic position of the family Lepidopidae. Since gills are absent and the pleopods are reduced, non-natatory, Fage (1924, 1925) referred his new family "Lepidophthalmidae" to the sub-order Mysida (Mysidea of some authors), at the same time stressing its affinities with the sub-order Lophogastrida. Both Caroli and Villalobos have raised objections to this. Caroli's announcement of *Spelaeomysis* appeared before Fage's main paper (in December, 1924). He says that the discovery of a second genus in Italy, so far from the habitat of the first genus (Zanzibar), shows that these forms must have had at one time a very wide distribution. "Però è forse prematuro ritenerle come forme di passaggio dai *Lophogastrida* ai *Mysida*. A mio avviso, potrebbero anche essere considerate *Lophogastrida* modificati (perdite delle branchie, riduzione dei pleopodi) dalla vita cavernicola assunta in epocha remota" (Caroli, 1924, p. 513). That Fage adheres to his original opinion is evident from a remark he makes in a later work on Lophogastrida (1941, p. 3); discussing some primitive characters he mentions "le palpe retroversé, hérité des Cumacés et des Tanaidacés, que portent au premières maxillae les *Gnathophausia*. Seuls parmi les Mysidés [*Mysida*] les genres *Lepidops* (*Lepidophthalmus* Fage 1924) et *Spelaeomysis* Caroli 1924 en sont pourvus, qui révèlent ainsi leur part du même héritage". Villalobos (1951, p. 216), after a brief discussion of the systematic position of the Lepidopidae concludes: "Según nuestro punto de vista, la posición adoptada por Fage es un poco forzada, porque si los caracteres distintivos de la familia se encuentran representados ya sea en *Lophogastridea* o en *Mysidea*, lo conveniente sería crear un soborden intermedio". He did not, however, propose a new sub-order because of the paucity of material and the small number of genera and species known (three monotypic genera).

When Caroli (1937, p. 225) discovered the transverse lamellae and a short but distinct backward prolongation of the protopodite of the uropod in *Lepidops* and *Spelaeomysis* (see Text-fig. 20, *m* and Text-fig. 21, *p* of this paper) he said that he could not judge whether the presence of these two characters indicated a closer affinity between the Lepidopidae and *Stygiomysis*. "Si può anche supporre che si tratta di caratteri arcaici, comuni probabilmente in passato ad altre e più numerose forme, e conservatisti, benché in via di graduale riduzione, nei nostri Misidacei, in grazia dello speciale *habitat*". He does not explicitly say that he has altered his earlier opinion (1924) namely, that the Lepidopidae are perhaps modified Lophogastrida, and he has no hesitation in referring the Stygiomysidae to the sub-order Mysida.

The family Lepidopidae shares its diagnostic characters with the rest of the Mysidacea as follows :—

- (i) Gills absent : Stygiomysidae and the whole of the Mysida.
- (ii) Oostegites seven pairs : Lophogastrida, Petalophthalmidae, Boreomysinae and ? Stygiomysidae.
- (iii) Statocyst absent : Lophogastrida, Stygiomysidae and Petalophthalmidae.
- (iv) Palp present on maxillula : *Gnathophausia* only (Lophogastrida).
- (v) Exopodite of maxilliped (first thoracic limb) a small unsegmented lamella or absent : Lophogastrida, Stygiomysidae and Petalophthalmidae.
- (vi) Second thoracic appendage modified as a gnathopod : most Lophogastrida and Mysida—in the Stygiomysidae and Eucopiidae the next two pairs are similarly modified.
- (vii) Endopodites of thoracic appendages 3–8 (or 5–8) without subdivision of the penultimate segments : Lophogastrida, Stygiomysidae, Petalophthalmidae and a few Mysidae.
- (viii) Pleopods reduced, non-natatory, but biramous in *both* sexes ; second pair slightly modified in ♂ ; Stygiomysidae (see p. 303).
- (ix) Transverse lamellae arising from the posterior sternal margins of abdominal somites 3, 4 and 5 ; Stygiomysidae, though here the protopodites of the pleopods are also incorporated in the lamellae. (Text-figs. 20 and 8 and Caroli, 1937, fig. 3).
- (x) A short but distinct backward prolongation of the protopodite of the uropod : Stygiomysidae, here it is very much longer (Text-figs. 21 and 13, *p*).
- (xi) Exopodite of second thoracic limb normal, multiarticulate : most Mysidacea (except *Petalophthalmus*, where it is absent). It is long and natatory as in forms with reduced pleopods. The basal segment of this and the following exopodites are long and narrow as in *Stygiomysis* and Lophogastrida, not blade-like as in most Mysida.

Certain characters mentioned by Fage in his diagnosis of the family Lepidopidae are of less importance in trying to elucidate affinities since they may vary within one and the same family : (a) Endites or lobes on the first thoracic endopodite may be large, poorly developed or absent, depending on the feeding habits. They are well developed in all three genera of Lepidopidae, absent in Stygiomysidae ; in the family Mysidae they are large in *Mysis*, one only is present in *Mysidetes* and they are absent in *Mysidopsis*. In the Petalophthalmidae they are absent in *Hansenomysis*, present in *Petalophthalmus*. In the Lophogastridae they are present in *Gnathophausia* (Text-figs. 33–34), absent in *Lophogaster*. (b) Presence or absence of a suture line (diaerisis) on the exopodite of the uropod. In the Lepidopidae there is one in *Lepidops* (which only shows up well in reflected light) ; it is said to be present in *Typhlolepidomysis*, absent in *Spelaeomysis*. It is present in the majority of the Lophogastrida and in Petalophthalmidae, is faint and incomplete in Siriellinae, absent in other subfamilies of Mysidae and in Stygiomysidae. *Rholapophthalmus* is exceptional in having a suture in both exopodite and endopodite.

From the above general survey of the characters used to subdivide the order Mysidacea, it is obvious that, as far as external morphology is concerned, the only constant character separating the Lophogastrida from the Mysida, Lepidopidae and Stygiomysidae, is the presence of podobranchiae or gills on some or all of the thoracic limbs. A negative character like the absence of gills does not necessarily imply that the Lepidopidae and the Stygiomysidae belong to the Mysida—as Caroli 1924, p. 513 implies, loss of gills may have occurred more than once in the course of evolution. Several of the Lophogastrid characters are shared by the Lepidopidae, Stygiomysidae and Petalophthalmidae and the large number of oostegites is shared by the Boreomysinae also (as are natatory pleopods in the male). But I do not see that anything is to be gained by erecting a third suborder for the Lepidopidae and Stygiomysidae. In that case something would have to be done about the Petalophthalmidae and perhaps the Boreomysinae, as well. In the meantime, I prefer to leave both families (Lepidopidae and Stygiomysidae) in the Mysida since podobranchiae are absent and the pleopods are reduced. These two families are very closely related to each other and differ in several important characters from the rest of the Mysida—the similar pleopods, the transverse lamellae on abdominal somites 3, 4 and 5 and the greater or lesser prolongation of the protopodite of the uropod. Their relationship to each is much the same as that of the Lophogastridae and Eucopiidae. Whatever future specialists may decide to do with the Lepidopidae, I am convinced that the Stygiomysidae should be ranked along with it—even if there should be fewer than seven pairs of oostegites in *Stygiomysis*.

The family Lepidopidae requires redefinition, because certain characters were overlooked at first; also for comparison with that of the Stygiomysidae, which is the same as for the genus *Stygiomysis* (see p. 286).

DIAGNOSIS OF THE FAMILY LEPIDOPIDAE: Cavernicolous Mysidacea exhibiting the “caridoid facies”. Carapace relatively long, smooth or with a sinuous furrow; produced antero-laterally beyond the rounded rostral margin, postero-lateral “wings” well developed, reaching the first abdominal somite laterally, but leaving the last two thoracic tergites exposed dorsally. (A scale-like process on penultimate thoracic tergite in *Typhlolepidomysis*)¹. Abdomen, including telson, half as long again as the cephalothorax, not broader in middle, sixth somite as long as, or longer than, fifth. Telson truncate or tapering; spinules or spines on distal half of each lateral margin as well as on the rounded apex (spinulation not mentioned in *Spelaeomysis*). Ocular scales quadrangular, distal margin oblique, without or with traces of visual elements (a few ommatidia in *Lepidops*). Antennular and antennal flagella as long as (*Lepidops*), or far exceeding, the length of the body (*Typhlolepidomysis*)¹; antennal scale well developed, with setae on inner and outer margins. Labrum oval, longer than wide (*Lepidops*). Labium with paragnatha well separated proximally, but not as long as in Stygiomysidae. Mandible with well developed incisor and molar processes; a row of strong thorny spines on second and third segments of the palp. Maxillula small, with a 2-segmented reflexed palp ending in a long curved

¹ Since this paper went to press I have collected specimens of *Spelaeomysis bottazzii* from the type locality. It has enormously long antennae and a scale behind the dorsal posterior emargination of the carapace. *Typhlolepidomysis* is therefore a synonym of *Spelaeomysis*. 24.xi.59.

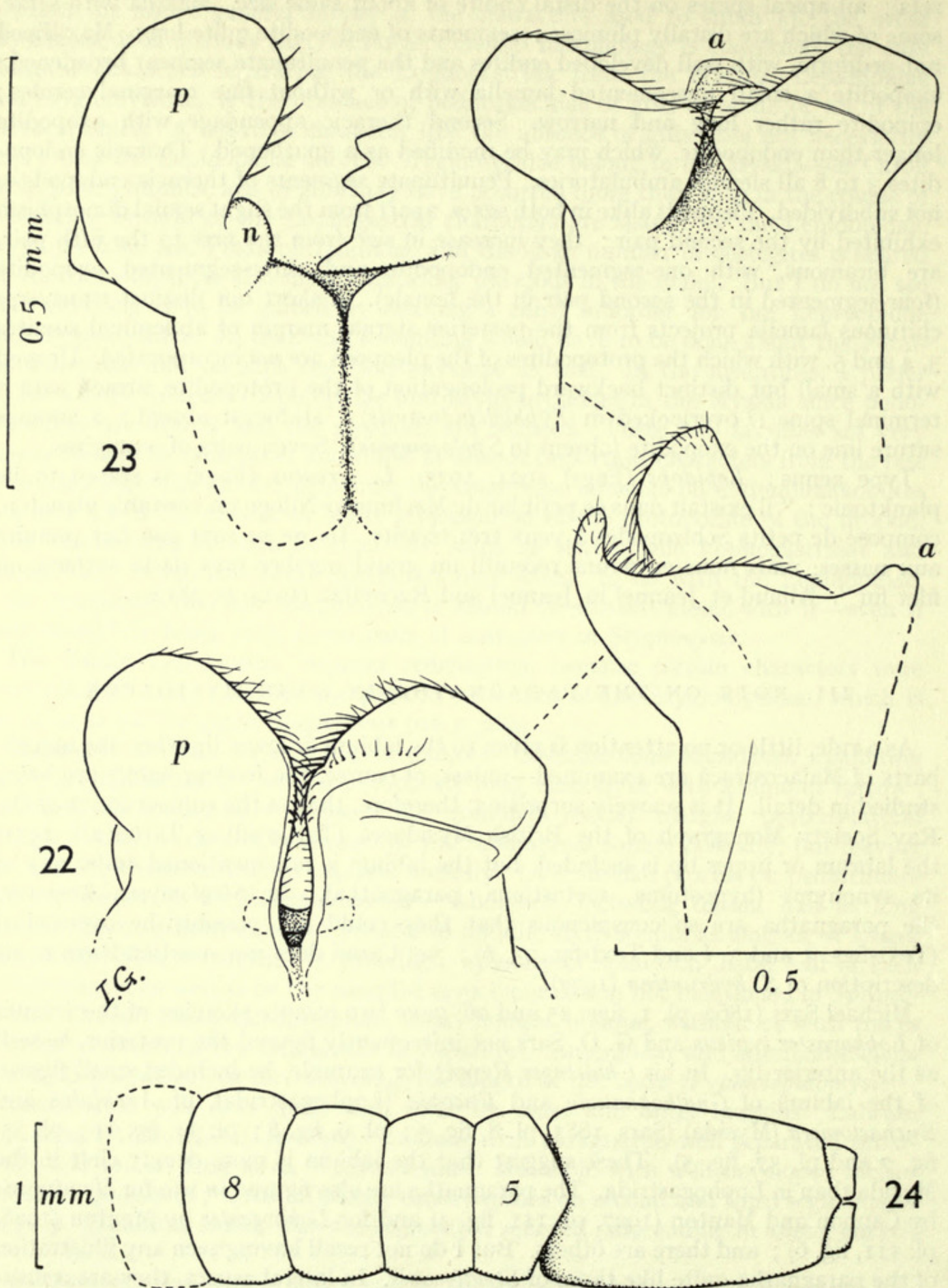
seta ; all apical spines on the distal endite of about same size. Maxilla with setae, some of which are distally plumose ; segments of endopodite quite long. Maxilliped not pediform, with well developed endites and the penultimate segment broadened ; exopodite a small unsegmented lamella with or without fine marginal setules ; epipodite rather long and narrow. Second thoracic appendage with exopodite longer than endopodite, which may be modified as a gnathopod. Thoracic endopodites 3 to 8 all slender ambulatories. Penultimate segments of thoracic endopodites not subdivided. Pleopods alike in both sexes, apart from the slight sexual dimorphism exhibited by the second pair ; they increase in size from the first to the fifth pair, are biramous, with one-segmented endopodite and three-segmented exopodite (four-segmented in the second pair in the female). A short but distinct transverse chitinous lamella projects from the posterior sternal margin of abdominal somites 3, 4 and 5, with which the protopodites of the pleopods are *not* incorporated. Uropod with a small but distinct backward prolongation of the protopodite, armed with a terminal spine (? overlooked in *Typhlolepidomysis*) ; statocyst absent ; a sinuous suture line on the exopodite (absent in *Spelaeomysis*). Seven pairs of oostegites.

Type genus : *Lepidops* (Fage) 1924, 1925. *L. servatus* (Fage) is stated to be planktonic : " il existait dans ce petit lac de Machumwi-Ndongo un véritable plancton, composé de petits Schizopodes à yeux très réduits. Ils ne se sont pas fait prendre aux nasses, mais nous en avons recueilli un grand nombre près de la surface, au filet fin ". Allaud et Jeannel in Jeannel and Racovitza (1914, p. 381).

III. NOTE ON THE PARAGNATHA IN SOME MYSIDACEA

As a rule, little or no attention is given to the labium or lower lip when the mouth-parts of Malacostraca are examined—unless, of course, the feeding habits are being studied in detail. It is scarcely surprising, therefore, that in the subject index of the Ray Society Monograph of the British Mysidacea (Tattersall & Tattersall, 1951) the labrum or upper lip is included, but the labium is not mentioned under any of its synonyms (hypostoma, metastoma, paragnatha). In *Stygiomysis*, however, the paragnatha are so conspicuous that they could not possibly be overlooked (Text-figs. 1 and 3, *l* and Text-fig. 23, *p*) ; yet Caroli does not mention them in his description of *S. hydruntina* (1937).

Michael Sars (1862, pl. 1, figs. 25 and 26) gave two minute sketches of the labium of *Lophogaster typicus* and G. O. Sars not infrequently figured the posterior, as well as the anterior lip. In his *Challenger* Report for example, he included small figures of the labium of *Gnathophausia* and *Eucopia* (Lophogastrida), of *Anchialus* and *Euchaetomera* (Mysida) (Sars, 1885, pl. 8, fig. 5 ; pl. 9, fig. 8 ; pl. 34, fig. 11 ; pl. 35, fig. 7 and pl. 37, fig. 5). These suggest that the labium is more deeply cleft in the Mysida than in Lophogastrida. The paragnatha are also figured *in situ* for *Hemimysis* by Cannon and Manton (1927, pl. III, fig. 4) and for *Lophogaster* by Manton (1928, pl. III, fig. 6) ; and there are others. But I do not recall having seen any illustration of the paragnatha quite like those of *Stygiomysis*. In lateral aspect, they are unusually pendant, falling well below the level of the labrum, and the distal part of each



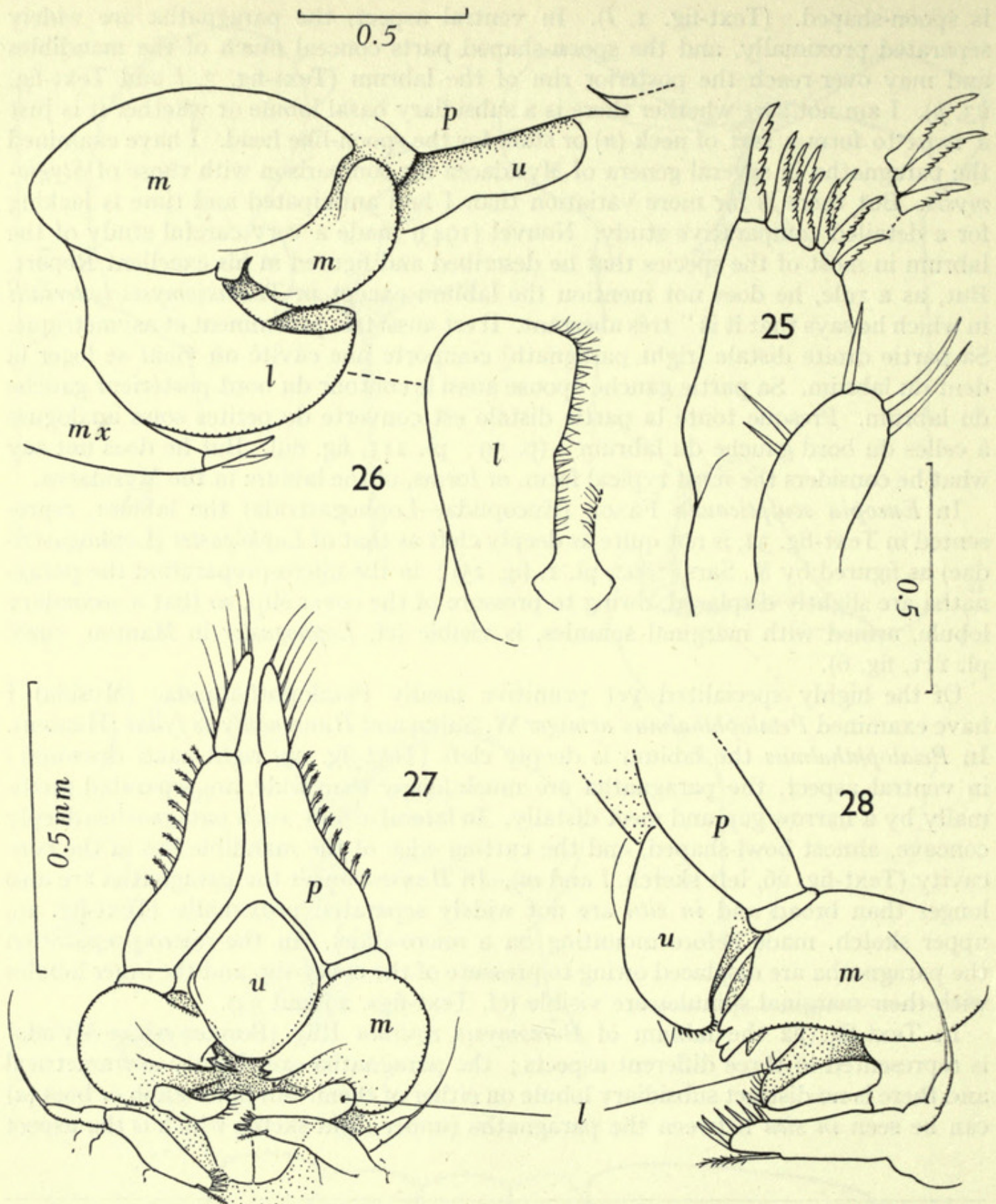
is spoon-shaped. (Text-fig. 1, *l*). In ventral aspect, the paragnatha are widely separated proximally, and the spoon-shaped parts conceal much of the mandibles and may over-reach the posterior rim of the labrum (Text-fig. 3, *l* and Text-fig. 23, *p*). I am not sure whether there is a subsidiary basal lobule or whether it is just a twist to form a sort of neck (*n*) or stalk for the spoon-like head. I have examined the paragnatha in several genera of Mysidacea for comparison with those of *Stygiomysis*. But there is far more variation than I had anticipated and time is lacking for a detailed comparative study. Nouvel (1943) made a very careful study of the labrum in most of the species that he described and figured in his excellent Report. But, as a rule, he does not mention the labium except in *Thalassomysis tattersalli* in which he says that it is "très aberrant. Il est aussi très proéminent et asymétrique. Sa partie droite distale [right paragnath] comporte une cavité où vient se loger la dent du labrum. Sa partie gauche épouse aussi le contour du bord postérieur gauche du labrum. Presque toute la partie distale est couverte de petites soies analogues à celles du bord gauche du labrum" (p. 59; pl. III, fig. 89). But he does not say what he considers the most typical form, or forms, of the labium in the Mysidacea.

In *Eucopia sculpticauda* Faxon (Eucopiidae-Lophogastrida) the labium, represented in Text-fig. 32, is not quite as deeply cleft as that of *Lophogaster* (Lophogastridae) as figured by M. Sars (1862, pl. 1, fig. 25); in the micro-preparation the paragnatha are slightly displaced, owing to pressure of the cover slip, so that a secondary lobule, armed with marginal spinules, is visible (cf. *Lophogaster* in Manton, 1928, pl. III, fig. 6).

Of the highly specialized yet primitive family Petalophthalmidae (Mysida) I have examined *Petalophthalmus armiger* W. Suhm and *Hansenomysis fyllae* (Hansen). In *Petalophthalmus* the labium is deeply cleft (Text-fig. 26, right-hand drawing); in ventral aspect, the paragnatha are much longer than wide, are separated proximally by a narrow gap and meet distally. In lateral aspect, each paragnath is deeply concave, almost bowl-shaped, and the cutting edge of the mandible lies in the concavity (Text-fig. 26, left sketch, *l* and *m*). In *Hansenomysis* the paragnatha are also longer than broad and *in situ* are not widely separated proximally (Text-fig. 29, upper sketch, made before mounting on a micro-slide). In the micro-preparation the paragnatha are displaced owing to pressure of the cover-slip and the inner lobules with their marginal spinules are visible (cf. Text-figs. 29 and 32).

In Text-fig. 22 the labium of *Boreomysis rostrata* Illig (Boreomysinae-Mysida) is represented in three different aspects; the paragnatha are slightly asymmetrical and there is no distinct subsidiary lobule on either of them. An inner knob or boss (*a*) can be seen *in situ* between the paragnatha (upper right sketch which is the aspect

FIGS. 22-24. *Boreomysis rostrata* Illig. Fig. 22. Labium or lower lip, in three different aspects. *Stygiomysis holthuisi* (Gordon). Fig. 23. Right half of labium, in ventral aspect (incisor edge of left mandible also shown). Fig. 24. Anterior half of male, in dorsal aspect. (first abdominal somite represented by broken line). *a*. Boss on labium. *n*. Neck. *p*. Paragnath. 5 and 8. Fifth and eighth thoracic somites.

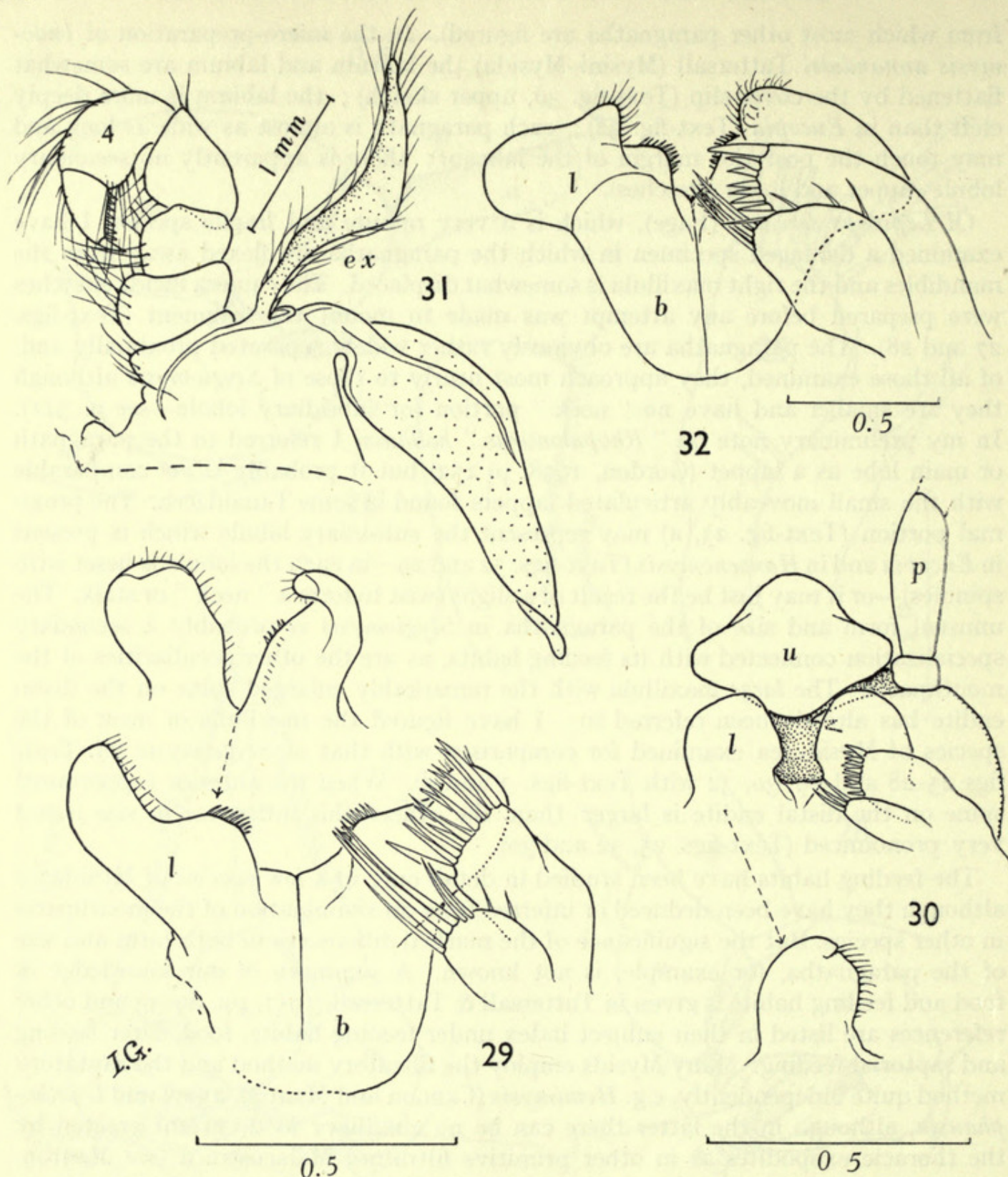


FIGS. 25-28. *Petalophthalmus armiger* W. Suhm. (Reg. no. 1940,viii.5. 568-569). Fig. 25. Right maxillula. Fig. 26. Labrum, right mandible, paragnath and maxillula, in lateral aspect; also right paragnath in ventral aspect. *Lepidops servatus* (Fage). Syntype from Paris Museum. Fig. 27. Labrum, labium, mandibles and maxillulae, in ventral aspect. Fig. 28. Same, in lateral aspect, at higher magnification. *l*. Paragnath of labium. *m*. Mandible. *mx*. Maxillula. *p*. Mandibular palp. *u*. Labrum or upper lip.

from which most other paragnatha are figured). In the micro-preparation of *Indomysis annandalei* Tattersall (Mysini-Mysida) the labrum and labium are somewhat flattened by the cover-slip (Text-fig. 30, upper sketch); the labium is more deeply cleft than in *Eucopeia* (Text-fig. 32); each paragnath is almost as wide as long and may touch the posterior margin of the labrum; there is apparently no secondary lobule (upper and lower sketches).

Of *Lepidops servatus* (Fage), which is a very minute and fragile species, I have examined a damaged specimen in which the paragnatha are flexed away from the mandibles and the right maxillula is somewhat displaced. The camera lucida sketches were prepared before any attempt was made to mount the fragment (Text-figs. 27 and 28). The paragnatha are obviously rather widely separated proximally and, of all those examined, they approach most nearly to those of *Stygiomysis* although they are smaller and have no "neck" portion (or subsidiary lobule—see p. 311). In my preliminary note on "*Rhopalonurus*" *holthuisi* I referred to the paragnath or main lobe as a lappet (Gordon, 1958, p. 152) but it probably is *not* comparable with the small moveably articulated lappets found in some Tanaidacea. The proximal portion (Text-fig. 23, *n*) may represent the subsidiary lobule which is present in *Eucopeia* and in *Hansenomysis* (Text-figs. 32 and 29—in each the lobule is beset with spinules)—or it may just be the result of a slight twist to form a "neck" or stalk. The unusual form and size of the paragnatha in *Stygiomysis* is probably a secondary specialization connected with its feeding habits, as are the other peculiarities of the mouthparts. The *large* maxillula with the remarkably enlarged spine on the distal endite has already been referred to; I have figured the maxillula of most of the species of Mysidacea examined for comparison with that of *Stygiomysis* (cf. Text-figs 25–28 and 29, 30, 32 with Text-figs. 3 and 5). When the anterior (uppermost) spine on the distal endite is larger than the others this difference in size is not very pronounced (Text-figs. 25, 32 and 30).

The feeding habits have been studied in detail only in a few species of Mysidacea although they have been deduced or inferred from an examination of the mouthparts in other species. But the significance of the marked differences in both form and size of the paragnatha, for example, is not known. A summary of our knowledge of food and feeding habits is given in Tattersall & Tattersall, 1951, pp. 29–33 and other references are listed in their subject index under feeding habits, food, filter feeding and raptorial feeding. Many Mysids employ the filtratory method and the raptatory method quite independently, e.g. *Hemimysis* (Cannon and Manton, 1927) and *Gnathophausia*, although in the latter there can be no auxilliary food current created by the thoracic exopodites as in other primitive filtratory Malacostraca (see Manton, 1928, p. 117). Others are incapable of filter feeding and depend entirely on large food masses, like *Lophogaster* (Manton, 1928, p. 110) and *Petalophthalmus* (Tattersall & Tattersall, 1951, p. 113). The number of thoracic limbs adapted to aid in feeding varies considerably. In the Lepidopidae, as in many Mysids, the first and second pairs are modified as maxilliped and gnathopod respectively. But others may also assist, though not specially modified—e.g. in many Mysidae all the thoracic endopodites may assist in dealing with large food masses, although this is not their main function (Tattersall & Tattersall, 1951, p. 30). In *Stygiomysis* the first four



FIGS. 29-32. *Hansenomysis fyllae* (Hansen). (Reg. no. 1909.xii.24. 100-103) Fig. 29. Labium and maxillula, in ventral aspect (paragnatha displaced by pressure of cover slip); above, paragnatha figured before mounting the preparation.

Indomysis annandalei Tattersall. (Reg. no. 1946.xi.26. 45-64). Fig. 30. Labrum, labium, left mandible and maxillula; below, right paragnath. (Preparation slightly flattened by cover slip). *Eucopia sculpticauda* Faxon. (Reg. no. 1949.vii.13. 65-75). Fig. 31. Right maxilliped, inner (or dorsal) surface. Fig. 32. Labium and left maxillula, in ventral aspect. (Scales for Figs. 29-32 all = 0.5 mm.). *b*. Sternal surface. *ex*. Exopodite. *l*. Paragnath. *p*. Mandibular palp. *u*. Upper lip or labrum. 4. Segment of endopodite distal to "knee".

pairs are modified as maxilliped and gnathopods ; the same is true of the Eucopiidae, but here the following three pairs (5-7) are long and prehensile (see pp. 305 and 319). This brings up the question of the terminology of the thoracic appendages, which is discussed in the next section.

IV. TERMINOLOGY OF THE THORACIC APPENDAGES.

(a) TERMINOLOGY OF THE APPENDAGES. Various names have been given to the thoracic appendages of Malacostraca according to the special functions for which they may be adapted. Dr. O. S. Tattersall writes of the Mysidacea : " since different appendages may be adapted for this or that function in different genera, I consider such terms most confusing, and in this work I propose to use one term, thoracic limbs, for these eight appendages, and to refer to each under its appropriate number, irrespective of the particular function for which it has become adapted." (Tattersall & Tattersall, 1951, pp. 18-19.) That there is some confusion is apparent if one examines certain statements in the joint work just cited. For example, under the definition of the order Mysidacea (pp. 11-12) " first, and sometimes the second, pairs modified as gnathopods or maxillipeds " might be interpreted in different ways—that both pairs are either gnathopods or maxillipeds, or that one pair is to be regarded as maxillipeds the other as gnathopods. On p. 24 " *second thoracic limb* (= gnathopod or 2nd maxilliped) " is also ambiguous—are the terms used synonymously or not ? On p. 97 " endopods of the second to the fourth pairs of thoracic limbs . . . developed as gnathopods " implies that the first pair are maxillipeds. Most of the confusion centres round these two terms. Sometimes they are used synonymously ; sometimes each is used in a narrower sense, the anterior pair (or pairs) which are more markedly modified for " Nahrungszerkleinerung " being called maxillipeds in contrast to the less markedly modified succeeding pair (or pairs) of gnathopods (see Zimmer, 1927, pp. 302-303).

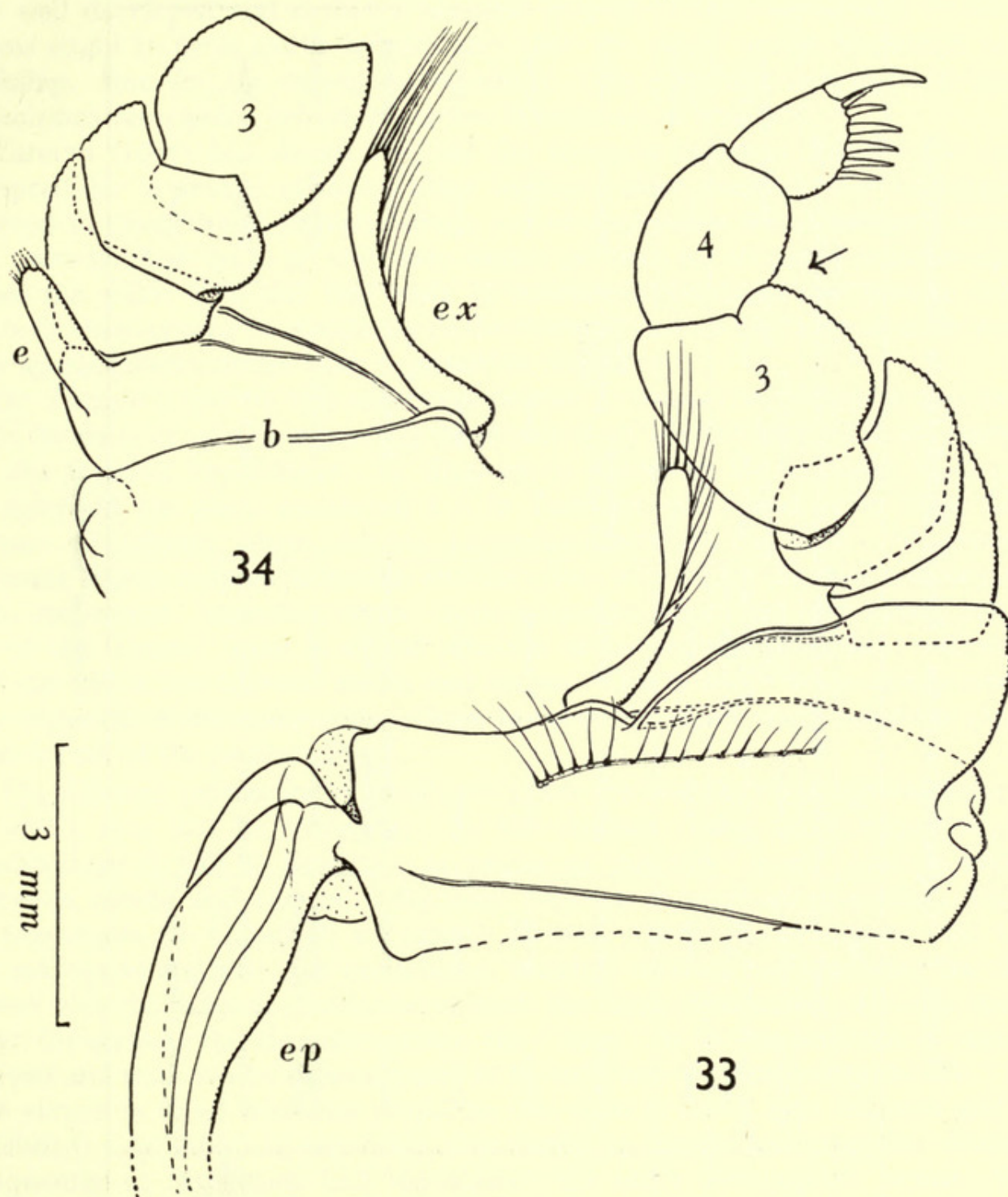
Nor is there agreement as to the number of pairs of thoracic appendages which are modified as maxillipeds in the various orders of Malacostraca (the term gnathopod is commonly used in literature dealing with the superorder Peracardia, rarely if at all in that dealing with Eucarida, Hoplocarida or Syncarida). In primitive types none of the thoracic limbs are differentiated as maxillipeds (Calman, 1909, p. 145) ; this is the case in Nebaliacea and Euphausiacea according to most authors. In other orders one, two, or three pairs are generally regarded as maxillipeds. With regard to the Stomatopoda Calman (1909, p. 322) wrote : " The first five pairs of thoracic appendages are similar in structure and are commonly called maxillipeds, though, as they possess no endites or other adaptations for mastication, the name is hardly appropriate ". Yet it is still often said that the Stomatopods have five pairs of maxillipeds—here the term gnathopod might be more appropriate. Hansen (1925, pp. 94, 128 and 154) thought that throughout the whole of the Malacostraca there is one pair of *real* maxillipeds. In his summing up (p. 154) he says : " *Maxillipeds and thoracic legs*.— . . . They are similar in Leptostraca, while in the other orders the first pair, the real maxillipeds, differ somewhat or considerably or very much from the following pairs, the legs." Yet even he inadvertently introduces

further confusion because: (i) the reader has to bear in mind that his thoracic legs 1-7 are in reality thoracic appendages 2-8 and (ii) under the Decapoda he has reverted to the usual terminology of maxillipeds 1-3 and peraeopods or walking legs 1-5 (= thoracic limbs 4-8). Also under the Mysidacea he speaks of "intermediate" legs.

The terminology of the thoracic limbs has recently been discussed by Siewing (1958, pp. 250-251). The maxillipeds, he says, are chiefly adapted for chewing or filtering food and are characterized above all by the presence of endites. "Sind die Endite deutlich grösser als die den nach hinten folgenden Extremitäten, so wird man sie betreffenden Extremitäten als Maxillipeden von den folgenden differenzieren. In diesem Sinne ist das 1 Thorakalbeinpaar, zum Teil auch das zweite, der Mysidacea als Maxilliped zu bezeichnen, denn es besitzt an der Basis einen abgegliederten Endite; Kaufortsätze werden ausserdem an Praeischium und Ischium beobachtet." Gnathopods, on the other hand, have he says their *distal* segments modified, often to form chelae or subchelae; but according to Tattersall & Tattersall (1951, p. 24) the first thoracic limbs of Mysidacea may sometimes be subchelate.

Siewing's statement concerning the Mysidacea agrees in part with that of Calman (1909, p. 174): "The first pair of thoracic limbs are always specialized as maxillipeds. In the Lophogastridae and Eucopiidae *they are without distinct endites* (italics mine). In the Mysidae an endite is generally borne on the basipodite, and sometimes also by each of the two following segments." Tattersall & Tattersall (1951, p. 97) also say that in *Eucopia* there are "no gnathobasic lobes on second, third or fourth segments". If Siewing's definitions are strictly applied, the first thoracic limb of *Eucopia*, though smaller than, and appreciably different from, each of the three succeeding pairs of appendages, would also have to be called a gnathopod (see Text-fig. 31 of this paper). The same applies to the first thoracic limb of, e.g. *Mysidopsis* which also has no endites (gnathobasic lobes) on second, third or fourth segments (Tattersall & Tattersall 1951, p. 316) and to that of *Stygiomysis* although it is much smaller, and more intimately associated with the mouth parts, than are the three following pairs (Text-figs. 7, 9 and 10). Caroli (1937, pp. 22 and 226), who refers to the first pair as maxillipeds, gives the neatest possible definition of the next three pairs with his "Toracopodi 2-4 (gnatopodi) massillipediforme"! *Typhlolepidomysis*, on the other hand, exemplifies the two categories exceptionally well, having large endites on the first pair which are not pediform, none on the pediform second pair which have strong spines on the more distal segments. Unfortunately, Villalobos (1951, p. 205) refers to the latter as "primer par de pereiópodos" in the text and as "maxilipedo del secundo par" in the legend to Text-fig. 10. In *Lepidops* the second pair differs but slightly from the following pairs of thoracic limbs. In the family Petalophthalmidae the second thoracic limb has a large lamellar expansion on the ischium (merus of some writers) which, with its partner, forms a floor to the whole mouth region. (I have seen a specimen which had been preserved while enjoying a meal, and these lobes apparently help to retain the food mass while it is being chewed). Should this appendage be termed a maxilliped? It is much larger than the first thoracic limb (which in *Hansenomysis* has no endites) and its distal segments are modified to assist in manipulating the food mass. It seems illogical

to term the first thoracic appendage a maxilliped in *Mysis* but not in *Mysidopsis*, in *Petalophthalmus* but not in *Hansenomysis*, in *Gnathophausia* (Text-figs. 33 and 34) but not in *Lophogaster*—see p. 316. Form depends on function and the feeding, locomotor and other habits of the animals determine how many appendages will be modified, and to what extent. The requirements of a raptorial animal differ



FIGS. 33-34. *Gnathophausia ingens* (Dohrn). (Unregistered specimen from Madeira).
 Fig. 33. Right maxilliped, in ventral aspect. Fig. 34. Part of same, in dorsal aspect.
e. Endite. *ep*. Epipodite. *ex*. Exopodite. 3 and 4. Segments of endopodite on either side of "knee" joint.

TABLE I.—Segmentation of the Thoracic Endopodite in Eumalacostraca

TERMINOLOGY of the endopodite— i.e. beyond basis. The claw is not a true segment.	A	B ₁	B ₂	B ₃	B ₄	C ₁	C ₂	D ₁	D ₂	E ₁	E ₂
	Calman 1909 and many authors	Mysidacea Pl. vi, Figs. 2a and 2b.	Mysidacea Pl. vi, Figs. 3a, 4a and 6a	Mysidacea Pl. vi, Figs. 1c, 5a.	Mysidacea and other PERACARIDA Pl. vi, Figs. 10c, f.	EUCARIDA Pl. viii, Figs. 7a, Pl. viii, Fig. 8b, 4a, 8a, 9a, 10a.		Anaspides tasmaniae Pl. v, Figs. 3c to 3l.		Siewing (1958) in Thermosbaena mirabilis 2nd thoracic limb.	
basis	basis	basis	basis	basis	basis	basis	basis	basis	basis + preischium	basis + ischium	basis
Segment 1	ischium	preischium	preischium	preischium	preischium	{ preischium + ischium	basis + preischium + ischium	preischium	ischium	merus	ischio- merus
"	merus	ischium	ischium	ischium	ischium	merus	merus	ischium	merus	>	>
"	carpus	merus	merus	merus	merus	>	>	merus	>	carpus	carpus
"	propodus	carpus	carpus	carpo-propodus (subdivided)	carpo-propodus (simple)	propodus	propodus	carpus	propodus	propodus	propodus
"	dactylus	propodus (simple)	propodus (subdivided)	dactylus	dactylus	dactylus	dactylus	propodus	dactylus	dactylus	dactylus
"	[claw + or —] (often fused with dactylus)	dactylus	dactylus	[claw + or —]	[claw + or —]	[claw + or —]	[claw + or —]	dactylus	[claw]	[strong claw]	[strong claw]
[7]		[claw + or —]	[claw + or —]					[claw]			

> = Position of "knee" joint.

from those of a filter feeder, even if the latter can also manipulate large food masses. The habitat to which an animal is adapted, even the niche within the habitat, may lead to modifications in both filtratory and raptatory feeders. *Eucopia*, with its long, slender "prehensile" endopodites 5-7, may remain suspended in mid water and seize any food that happens to come within range of these long legs, passing it on to the short gnathopods (2-4); it may even pursue its prey since the pleopods are well developed and natatory (see also p. 305). I fully agree with Siewing that terms ought to be properly defined, and that the terms under discussion need re-defining. But, for the reasons given above, I do not think that one can apply his definitions too rigidly, within the order Mysidacea at any rate.

Cannon (1927) has shown that *all* the thoracic limbs in *Nebalia* are specially adapted for a unique mode of filter feeding. More recently Barkley (1940) has figured in great detail thoracic limbs 1-6 of *Euphausia* and has found that these six pairs together form an elaborate basket or filter for straining minute organisms from the water (the last two pairs of thoracic appendages are greatly reduced). In both these genera the similarity of the thoracic limbs would appear to be a secondary specialization rather than a primitive character.

(b) TERMINOLOGY OF THE SEGMENTS OF THE ENDOPODITE: There is also considerable diversity of opinion regarding the terminology of the segments in the endopodite of the thoracic appendages. In *Stygiomysis holthuisi*, for example, it is possible to interpret the parts numbered 1-6 in Text-figs. 9, 10 and 11 in three different ways: (i) ischium, merus, carpus, propodus, dactylus, and claw; (ii) preischium, ischium, merus, carpus, propodus, and dactylus (with which the claw is incorporated); (iii) preischium, ischium, merus, carpo-propodus, dactylus, and claw. According to (i) the "knee" joint is at the junction of carpus and propodus; according to (ii) and (iii) it lies between merus and carpus. This is why I have simply numbered the segments of the endopodite—those distal to the basis which bears the exopodite and is part of the protopodite.

The different terminologies which are in use are best shown in tabular form (Table I, which may not be complete). To the student reared on Calman's text book terminology **A** will be familiar; according to this the "knee" joint is sometimes between merus and carpus, sometimes between carpus and propodus. The other terminologies (**B**, **C** and **D**) we owe to Hansen (1925). He maintains that there is an additional segment, the preischium, which is distinct in Peracarida but is often fused with the ischium (Eucarida) or with the basis (Syncarida). He also maintains that throughout the Eumalacostraca the "knee" is at the junction of merus and carpus and that, where there appears to be only two segments distal to the "knee", the carpus is fused with the propodus (the claw is not a true segment and is not included). As shown in the table, this fusion of carpus and propodus occurs very frequently in Mysidacea and throughout the other Peracaridan orders. Siewing (1958) has recently studied *Thermosbaena* and his interpretation of the segmentation is shown as **E1** and **E2**. In minute animals like *Thermosbaena* and the Bathynellacea there is a reduction in the number of segments and it is by no means easy to decide where the "knee" is. Siewing thinks that here there is no preischium, and that the ischium is either fused with the basis or more or less completely fused with the merus.

In *Stygiomysis holthuisi* the number of segments in the endopodite is identical in each of the eight pairs of thoracic limbs (Text-figs. 7, 9–11). In each there are three segments proximal to the “knee” and three distal to it (including the claw or claw-like dactylus, according to the terminology used). Hansen would doubtless have regarded segment 4 as a fused carpo-propodus (B₄) rather than as the carpus followed by the propodus and claw-like dactylus (B₁). In Tattersall & Tattersall (1951, p. 24) it is stated that, in both first and second pairs of thoracic limbs of Mysidacea, carpus and propodus are always fused to form a single segment. Yet in fig. 42, C on p. 199 the first thoracic endopodite of *Erythrops elegans* (G. O. Sars) is represented as having *four* segments proximal to the “knee” joint and two plus claw distal to it. This can only be interpreted (if correct and not a slight lapse on the part of the artist) as: preischium, ischium, merus, carpus, [“knee”], propodus, dactylus and claw. According to Hansen the “knee” joint in Peracarida does not come at the junction of carpus and propodus. Since fig. 42, D shows the second endopodite of *Erythrops elegans* with only three segments proximal to the “knee”, fig. 42, C may not be correct. Hansen (1925) based his interpretation of the segmentation, in part at least, on a study of the muscles (see his figures of the distal segments of the thoracic endopodite in Mysidacea on pl. vi). In *Stygiomysis* there appear to be no muscle bands in segment 5, which might support Hansen’s interpretation of 5 and 6 being dactylus and claw respectively. Perhaps the time has come for a thorough reappraisal of Hansen’s work along the lines of the detailed functional analysis of limb structure undertaken in recent years by Dr. Manton in terrestrial Arthropoda (Manton, 1950–58—a series of papers on the Evolution of Arthropodan Locomotory Mechanisms; the work is still in progress).

V. ADDITIONAL NOTE ON *SPELAEGRIPHUS LEPIDOPS* GORDON

Order SPELAEGRIPHACEA Gordon, 1957

Spelaeogriphacea Gordon, 1957, p. 45.

Spelaeogriphacea, Siewing, 1958, p. 267; Kaestner, 1959, p. 918.

“Reihe” Spelaeogriphacea Siewing, 1959, p. 110, Fig. 65.

SYSTEMATIC POSITION. Siewing (1958, p. 247) placed the order Spelaeogriphacea among those Eumalacostraca with the telson and last abdominal somite fused. But, as stated in my original description and as shown in Pl. 4 of this paper, the sixth pleonite is free from, and much larger than, the telson. In a later work, which has just appeared, Siewing (1959, p. 110, fig. 65—cited in his 1958 paper as if it had already been published) has raised the Spelaeogriphacea to the rank of a “Reihe” or superorder, without apparently stating his reasons for doing so.

Since *Spelaeogriphus*, the only known genus, undoubtedly possesses a Peracaridan brood pouch composed of oostegites, I still regard the Spelaeogriphacea as an order belonging to the superorder (“Division” of Calman) Peracarida. Its precise relationship to the other Peracaridan orders cannot be determined until the internal anatomy and the embryology of *Spelaeogriphus* are known. However, from its external

morphology, it appears to have affinities with the Tanaidacea, since it has a small but distinct carapace and a pair of cup-shaped respiratory organs beneath the carapace, near the bases of the first thoracic limbs (the maxillipeds). Siewing (1956, p. 87) has pointed out that in the Tanaidacea "der hinter dem Maxillipeden an der Körperwand liegende löffelfartige Fortsatz ist kein Epipodit, wie Dohrn bei seinen embryologischen Untersuchungen zeigen konnte." (Dohrn, 1870, pl. xi). The respiratory organ in *Spelaeogriphus* may also be of this kind and not a true epipodite, but I called it an epipodite since that is the term commonly used in systematic descriptions of Tanaidacea.

However, I could not include *Spelaeogriphus* in the order Tanaidacea, since it differs in many respects from that group, having certain affinities with the Syncarida and with *Monodella* and some which are unique. In his earlier paper Siewing (1957, p. 267, phylogenetic diagram) placed it within the Peracarida, provisionally near the Isopoda-Tanaidacea line. Unless Dr. Siewing has studied material of *Spelaeogriphus lepidops* and has found that it differs markedly, anatomically and/or embryologically, from the other Peracaridan orders, his decision to separate Spelaeogriphacea from the "Reihe" Peracarida is premature, and in my opinion this step is unnecessary. It is a pity that this alteration was made in a text book because in all probability his phylogenetic scheme will be reproduced in future text books. The one thing that all Peracaridan orders have in common is that the young are incubated until a late stage of development in a *ventral* thoracic brood pouch or marsupium; Siewing's (1958) separation of the order Thermosbaenacea from the true Peracarida is much more reasonable, since in both the known genera there is a *dorsal* carapacial marsupium. Stella (1959, p. 122) has accepted the "Reihe" Pancarida although she unfortunately refers to it as a "*phylum*". Raising the Spelaeogriphacea to superordinal rank does not solve the problem of its relationships. The greatest caution should be exercised in establishing higher categories like superorders and subclasses until the animals have been thoroughly studied.

Genus *SPELAEOGRIPHUS* Gordon, 1957

Spelaeogriphus Gordon, 1957, p. 32.

Spelaeogriphus, Kaestner, 1959, p. 918.

Spelaeogriphus lepidops Gordon, 1957

Spelaeogriphus lepidops Gordon, 1957, p. 33, Text-figs. 1-26.

Spelaeogriphus lepidops, Kaestner, 1959, p. 918, Text-fig. 816.

ADDITIONAL MATERIAL. Bats Cave, Table Mountain, 30.ix.56, six specimens fixed in Bouin's solution (4 ♂, 1 ovigerous and 1 smaller ♀). From a stream at bottom of Bats Cave (temp. of water 50.5° F.), 1.ix.57, seven specimens (5 ♂, 1 ovigerous ♀ and 2 immature specimens).

REMARKS. The specimens were collected by the South African Spelaeological

Association ; the 1957 material was fixed in 96 per cent ethyl alcohol (97 parts) and glacial acetic acid (3 parts). This fixative seems to be too drastic, causing the specimens to curl up to such an extent that in one instance the uropods got entangled among the thoracic appendages bunched up beneath the carapace region.

I have had several requests for a good figure of the entire animal, suitable for reproduction in a text book. My original Text-fig. 1 was incomplete, since I did not include the appendages, and Kaestner (1959, fig. 816) has based his figure on Dr. Barnard's sketch which I reproduced as Text-fig. 26 of my 1957 paper. The antennulae and antennae are not represented and these alter the look of an animal appreciably ; in Kaestner's reproduction the first three thoracic exopodites look not unlike the gills of Lophogastrid Mysids. I take this opportunity, therefore, of publishing an original drawing of the whole animal, an ovigerous female, in dorso-lateral aspect as Pl. 4. This figure will also illustrate my article on Spelaeogriphacea which will appear in due course in the McGraw-Hill Encyclopedia of Science and Technology.

The female represented in Pl. 4 measures 6 mm. in length, from rostral apex to tip of telson, and the antenna is almost or quite as long as the body. The two antennular flagella are slightly unequal (they are more so in the male) ; the inner flagellum has about 30, the outer one about 24, segments. The faint line down the right side of the body, from carapace to first abdominal somite, is an artefact, a slight fold or crease in the integument. The marsupium contains ten to twelve rather large ova. I have not attempted to straighten out the thoracic limbs, which in preserved material tend to bend inwards beneath the body, because they easily break off if touched.

There is not much to add to my original description, since the animals do not seem to grow much larger ; the largest male measures 8.6 mm. in length. Its antenna is at least 8 mm. long ; the inner flagellum of the antennula is appreciably longer than the outer one and the number of segments in each is about 45 and 26 respectively.

In my original description I used Calman's terminology for the various segments of the thoracic limbs (see Table I, A). But, according to Hansen (1925), there is always a distinct preischium in the Peracarida (Table I, B₁ to B₄). The segments of the endopodite would thus be termed : preischium, ischium, merus, ["knee" joint], carpo-propodus and dactylus (Table I, B₄). I have re-examined these appendages and in some there seems to be a faint indication of separation of the claw from the dactylus. In one specimen the distal sharp point is broken off neatly, beyond the longest spine on the ventral margin ; this part doubtless represents the claw or nail (Gordon, 1957, Text-figs. 19 and 21-25).

The entire length of the gut is filled with a dark brown or blackish mass, suggesting that the animal feeds largely on detritus.

The registration numbers of the type specimens in the British Museum Collection are : holotype (♂), 1957.xi.12.1 and allotype (♀), 1957.xi.12.2.

I have a correction to make : in my 1957 paper (p. 43) I said that the Tanaidacea are entirely marine. But I overlooked a paper by Stephensen (1936) in which he described *Tanais stanfordi* from a freshwater lake in the Kurile Islands and mentions at least one other freshwater species from South America.

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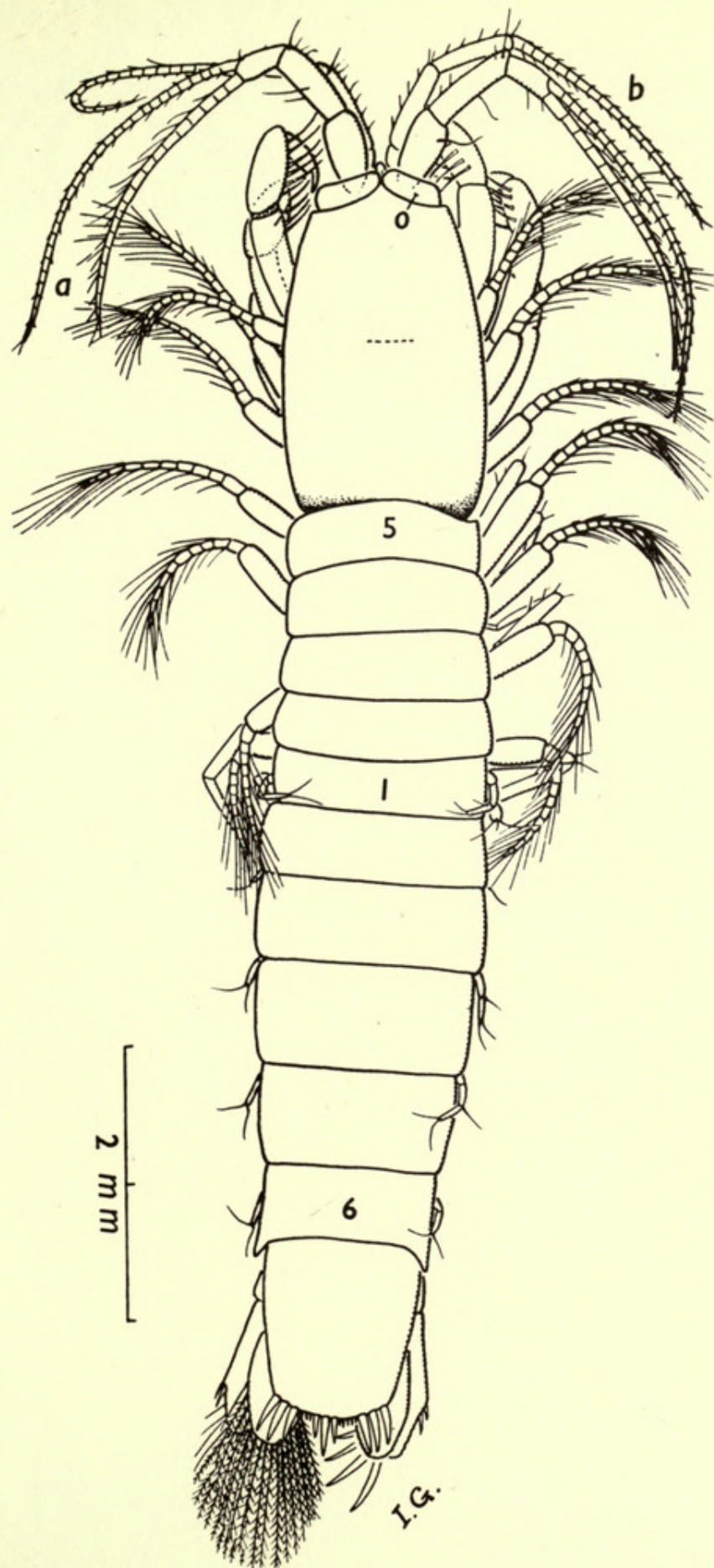
PLATE 3

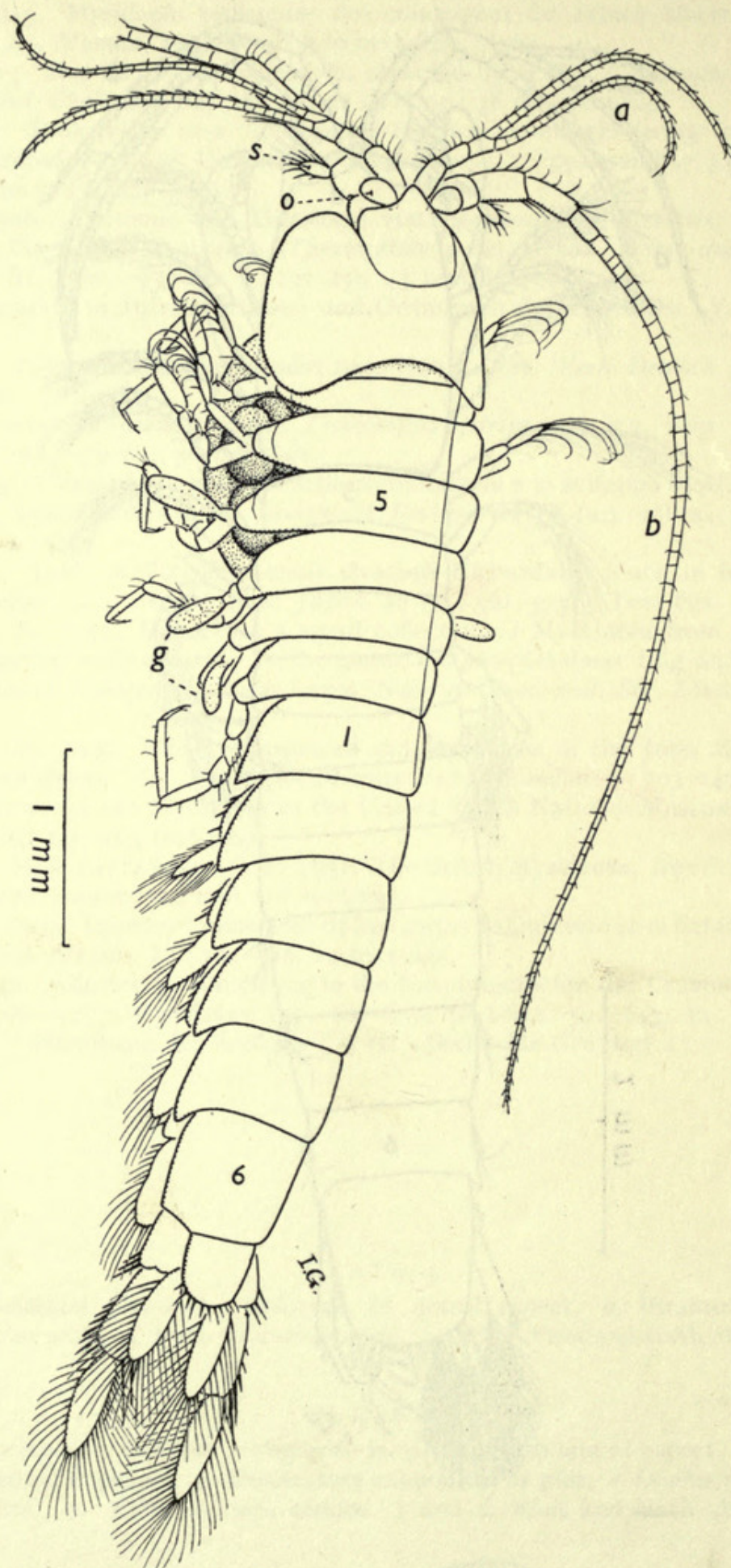
Stygiomysis holthuisi (Gordon). Holotype, in dorsal aspect. *a.* Biramous antennula. *b.* Antenna. *o.* Ocular scale. 5. Fifth thoracic somite. 1 and 6. First and sixth abdominal somites.

PLATE 4

Spelaeogriphus lepidops Gordon. Ovigerous female in dorso-lateral aspect. *a.* Biramous antennula. *b.* Antennal flagellum. *g.* Respiratory exopodites or gills. *o.* Ocular scale. *s.* Antennal scale or exopodite. 5. Fifth thoracic somite. 1 and 6. First and sixth abdominal somites.









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