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SPLANCHNOTROPHID SYSTEMATICS: A CASE OF POLYPHYLY AND TAXONOMIC MYOPIA

Rony Huys

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD,
United Kingdom (e-mail: r.huys@nhm.ac.uk)

ABSTRACT

The Splanchnotrophidae is a small family of bizarre poecilostomatoid copepods which utilize marine opisthobranch gastropods, including nudibranchs and pteropods, as hosts. Species have traditionally been placed in this family primarily on the basis of host affiliation, largely neglecting the fundamental differences in morphology and paying virtually no attention to the concept of homology. Morphological analysis based on detailed re-examination of types and newly obtained material from existing museum collections revealed that the Splanchnotrophidae comprises genera drawn from three different families in addition to one non-copepodan taxon. The family Splanchnotrophidae is redefined to include only *Splanchnotrophus* Hancock and Norman, 1863, *Ismaila* Bergh, 1867, *Lomanoticola* Scott and Scott, 1895, and two new monotypic genera. All splanchnotrophids are endoparasites of nudibranch and sacoglossan opisthobranchs and show a vast size disparity between the sexes caused by hypermorphosis in the female. The genus *Splanchnotrophus* is restricted here to the European species and assumes a boreo-mediterranean distribution. It is redefined on the basis of redescriptions given for *S. gracilis* Norman and Hancock, 1863, and *S. angulatus* Hecht, 1893. The Western Australian species *S. elysiae* Jensen, 1990, and *S. sacculatus* O'Donoghue, 1924, are re-examined and placed in two new genera, *Arthurius* and *Ceratosomicola*, respectively. Re-examination of the mouthparts provided unambiguous evidence justifying formal placement of *Briarella* Bergh, 1876, in the Philoblennidae, a family thus far known only as ectoparasites from prosobranch gastropods in the Far East. The inadequately described genus *Chondrocarpus* Bassett-Smith, 1903, is provisionally placed as *genus incertae sedis* in this family. A new family Micrallectidae is proposed to accommodate *Micrallecto* Stock, 1971. The genus *Nannallecto* Stock, 1973, is regarded as a junior subjective synonym of the latter because the generic distinction was largely based on two glaring observational errors: the absence of maxillae in *M. uncinata* Stock, 1971, caused by imperfect removal of the parasite from the host, and the presence of a chelate leg 2 in *N. fusii* Stock, 1973, which in reality is a feature of the developing nauplii visible through the body wall of the brooding female. Previous interpretations of the mouthparts in *Micrallecto* were essentially unsound. Micrallectids are ectoparasites of gymnosome pteropods and display a unique, extremely abbreviated life cycle, involving lecithotrophic nauplii and highly paedomorphic ovoviviparous adults that attain sexual maturity at the metanaupliar stage. Inspection of pteropod collections in the Natural History Museum led to the discovery of the first male specimen providing conclusive evidence for the proposal of a new family. The Micrallectidae is placed in the Poecilostomatoida on the basis of antennary armature, mandibular palp morphology and mating posture. The genus *Megallecto* Gotto, 1986, is based on a head fragment of a hyperiid amphipod that was erroneously interpreted upside down and back to front. Its type species *M. thirioti* Gotto, 1986, is identified as a junior subjective synonym of *Phrosina semilunata* Risso, 1822, a widely distributed and very abundant hyperiid in the Atlantic.

Splanchnotrophidae are highly modified copepods which exclusively utilize a variety of marine opisthobranch gastropods as hosts. This strong host affiliation has inspired past workers on parasitic copepods to associate a number of bizarre genera with this poecilostomatoid family (Bassett-Smith, 1903; Stock, 1971, 1973; Gotto, 1986). Although host utilization can be employed in *a posteriori* testing of newly proposed classifications, it should never be regarded as the sole arbiter to place highly transformed taxa in existing families. A recent example of such testing is shown by Humes and Boxshall's (1996) revision of the lichomolgoid complex which demonstrated that the majority of the families, established on the basis of morphological similarity, utilized exclusively or predominantly a single host category. Such strong congruence between common ancestry and host utilization, which is diametrically opposed to Ho's (1991) suggestion that ". . . symbiosis in Poecilostomatoida developed in a random manner", is indeed striking for some families but should by no means be taken as universal. The apparently narrow host distributions of many ecto- and endoparasitic families in the Poecilostomatoida can be explained by phylogenetic relatedness only if such scenario of common descent is backed up by morphology based cladistic analysis. The many complex interactions in host-parasite co-evolution, such as host switching, however, do not permit adopting the reverse approach of linking taxa in monophyletic clades solely on the basis of their shared host affiliation.

The current systematic concept of the Splanchnotrophidae is a demonstrable example of bad taxonomic practice, resulting from accumulated observational errors, uncritical acceptance of previously published questionable data, and lack of attention to the concept of homology. For example, the claim that the mandible of *Megallecto* Gotto is quite similar to its counterpart in the splanchnotrophid genus *Ismaila* Bergh is, to say the least, remarkable for a creature that appears to display not a single copepodan character but instead is proven to be based on a head fragment of a pelagic peracarid. Similarly, it may ". . . be easy to homologize the 2nd leg of *Micrallecto* to that of *Splanchnotrophus insolens*" (Stock, 1971) on the basis of published descriptions, but it throws a different light on relationships if one knows that the former is in reality a naupliar attribute visible within the hind-body of the brooding female.

Examination of representatives of virtually all genera, based on museum collections, strongly indicates that currently accepted splanchnotrophid unity bears no relation to reality, showing on the contrary the fundamental differences in morphology and, by inference, developmental and reproductive biology, between the genuine splanchnotrophids and the genera associated with pteropod hosts.

MATERIALS AND METHODS

Habitus drawings of Splanchnotrophidae were prepared using the hanging drop method (Humes and Gooding, 1964), those of Micrallectidae using the "sandwich mounting method" (Huys and Boxshall, 1991). Specimens were dissected in lactic acid, and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a *camera lucida* on a Leitz DMR differential interference contrast microscope.

The male of *Micrallecto fusii* was examined with a Philips XL30 scanning electron microscope. The specimen was prepared by dehydration through graded acetone, critical point dried, mounted on a stub and sputter-coated with palladium.

The descriptive terminology is adopted from Huys and Boxshall (1991). Scale bars in figures are indicated in µm. Material examined is deposited in the Natural History Museum, London (NHM), the Muséum National d'Histoire Naturelle, Paris (MNHN), and the Zoölogisch Museum, Amsterdam (ZMA).

SYSTEMATICS

Revision of the Splanchnotrophidae

Hancock and Norman (1863) placed the genus *Splanchnotrophus* in the Chondracanthidae on the basis of the structure of the antennules and antennae, the general arrangement of the mouthparts, the unsegmented thorax of the female, the reduced posterior legs, and the vast disproportion in size between the sexes. Bergh (1867, 1876) described the genera *Ismaila* and *Briarella* and made a cursory comment on their superficial similarity to *Splanchnotrophus* but refrained from formally placing them in a particular family. Bergh (1867) questioned the chondracanthid affinity of *Splanchnotrophus* because he regarded its mouthpart design and that of *Ismaila* as gnathostome rather than poecilostome. The dorsal body processes of the latter led him to suggest an affinity with the genus *Pachypygus* in the Notodelphyidae. He also believed that *Splanchnotrophus* should be allocated to a different gnathostome family and that *Briarella* showed affinities with the Philichthyidae. Gerstäcker (1866–1879) placed both *Splanchnotrophus* and *Ismaila* in the Chondracanthidae.

Scott and Scott (1895) did not discuss family relationships when they proposed the genus *Lomanoticola*, neither were they aware of Hancock and Norman's (1863) paper on *Splanchnotrophus*. Hecht (1895) formally relegated *Lomanoticola* to a junior synonym of the latter. For some unknown reason Canu (1898) listed *Splanchnotrophus* under the Lichomolgidae, a convenient repository for invertebrate parasites at that time. Bassett-Smith (1903) added *Chondrocarpus* to the Chondracanthidae and regarded it as most closely related to *Splanchnotrophus*.

In 1906 Norman and Scott introduced the

family name Splanchnotrophidae without an accompanying diagnosis. This family name was adopted by Norman and Brady (1909) but remained unnoticed by other workers such as O'Donoghue (1924), who fixed the type species of *Splanchnotrophus* and continued to refer the genus to the Chondracanthidae.

Monod (1928) discussed the relationships of *Briarella* and removed it from its floating status by placing it in the Chondracanthidae. Oakley (1930) clearly demonstrated his indecisiveness on the position of *Splanchnotrophus* by simultaneously listing it in his revision of the Chondracanthidae under the rejected genera and suggesting a new subfamily Splanchnotrophinae on the basis of shared egg-sac arrangement with other chondracanthid subfamilies.

Monod and Dollfus (1932) reinstated the Splanchnotrophidae and included in it the genera *Ismaila, Briarella, Chondrocarpus,* and *Splanchnotrophus,* treating *Lomanoticola* as a subgenus of the latter. Delamare Deboutteville (1951b) revised the higher level classification of the Chondracanthidae and recognized three subfamilies, Chondracanthinae, Pharodinae, and Lernentominae. Pharodid males are relatively large, feeding and attaching to the host independently of the adjoining females. Delamare Deboutteville (1951b) regarded this as evidence for the transitionary position of the Pharodinae between the Splanchnotrophidae and other Chondracanthidae. Delamare Deboutteville and Nuñes-Ruivo (1955a, b) proposed the chondracanthoid complex in which they included the Chondracanthidae and Philichthyidae, parasitic on fishes, and the Staurosomidae (= Antheacheridae), Echiurophilidae, and Splanchnotrophidae, which utilize exclusively invertebrate hosts.

Laubier (1964) reinterpreted the mouthparts of *Splanchnotrophus* and concluded that the absence of maxillules and maxillipeds in conjunction with the shape of the mandible and maxilla unambiguously diagnosed the Splanchnotrophidae as a distinct family. He excluded *Briarella* and removed it provisionally to the Chondracanthidae, failed to place *Ismaila* on the basis of available published information and did not consider *Chondrocarpus*. Laubier (1966) studied developmental aspects of *S. dellachiajei*, including the hypertrophy of the adult female, and claimed that the lateral body processes found in *Echiurophilus, Briarella,* and *Splanchnotrophus* are the result of convergence.

In his description of *Micrallecto,* Stock (1971) relied heavily on Laubier's (1964) study which unfortunately led him to erroneously homologize the mouthparts and presumptive swimming legs of *M. uncinata*. Only by adopting this practice could Stock justify placing this pteropod associated genus in the Splanchnotrophidae. Another genus, *Nannallecto,* also associated with pteropods, was placed by Stock (1973) in this family despite the presence of a pair of large maxillipeds, a character that was explicitly promulgated by Laubier (1964) as non-splanchnotrophid.

Belcik (1981) demonstrated the close similarity in mouthpart morphology between *Ismaila* and *Splanchnotrophus* and the discrepancies with *Briarella* and Stock's genera ectoparasitic on gymnosome pteropods. This issue was further elaborated by Ho (1981a) who studied *Ismaila* in detail and pointed out the various problems involved in uniting the splanchnotrophid genera in a single family. He treated *Ismaila* as a valid genus in the Splanchnotrophidae but disputed the widely accepted relationship between this family and the Chondracanthidae (e.g., Gotto, 1979). In a later study based on ontogenetic data Ho (1987b) considered a relationship between the Philichthyidae and the Splanchnotrophidae more likely. However, his subsequent phylogenetic analysis of the Poecilostomatoida (Ho, 1991) identified the latter as the sister-group of the Shiinoidae.

Gotto (1986) speculated that adaptation to parasitism on gastropod hosts may have greatly affected the morphology of the cephalic appendages, leaving little or no trace of common ancestry and explaining the diversity in mouthpart structure exhibited by the various splanchnotrophid genera. Such a liberal approach was obviously required to accommodate his bizarre genus *Megallecto* in the Splanchnotrophidae.

Jensen (1987) concluded that current knowledge on mouthpart morphology did not permit inferences to be drawn on relationships and suggested maintaining in the Splanchnotrophidae all genera that are endoparasitic in opisthobranch molluscs. Based on host utilization and gross body shape, she regarded the inclusion of *Micrallecto* and *Nannallecto* in this family as questionable but did not propose an alternative placement.

Although various authors have repeatedly expressed the need for further investigation of the various genera before relationships can be firmly established, this has not led to any significant course of action other than the continued use of the Splanchnotrophidae as a catch-all taxon for curious opisthobranch-associated copepods. The family currently comprises seven genera: *Splanchnotrophus, Ismaila, Briarella, Chondrocarpus, Micrallecto, Nannallecto,* and *Megallecto*. Most descriptions are fragmentary, contain internal inconsistencies or display a distinct lack of attention to the concept of homology. In order to test the monophyly of the Splanchnotrophidae and to define its morphological boundaries, representatives of all genera, except *Chondrocarpus,* were examined in detail. It is suggested below that the family should contain only the classically known genera *Splanchnotrophus* and *Ismaila,* in addition to *Lomanoticola* (upgraded to genus level) and two new genera. These five genera form a monophyletic group characterized by the following diagnosis.

Family Diagnosis.—Poecilostomatoida. Sexes strongly dimorphic in body shape, tagmosis, and size.

Adult ♀ body highly transformed, with large prosome lacking external segmentation, and small urosome with 1–3 somites. Prosome comprising cephalosome, often demarcated by constriction, and trunk consisting of 4 fused pedigerous somites. Trunk usually divisible into anterior broader part, corresponding to 1st and 2nd pedigerous somites, and narrow, retractile posterior part representing fused 3rd and 4th prosomites. Anterior part of trunk with 2 or 3 pairs of laterally directed processes of variable size; posterolateral angles and protopods of legs 1 and 2 sometimes produced into additional pairs of processes, dorsal surface with median process in *Ismaila*. Urosome protruding out through host integument; with distinct integumental pores; comprising genital (double-)somite and either P5-bearing somite or 0–2 postgenital somites. Genital apertures paired, located dorso- or ventrolaterally on genital (double-)somite or genito-abdomen; without armature. Caudal rami present, setal number variable. Anus a terminal dorsoventral slit between caudal rami. Egg-sacs paired, multiseriate.

Adult ♂ much smaller than ♀; body cyclopiform or moderately modified. Major articulation located behind P2-bearing somite, dividing body into swollen anterior part and cylindrical posterior part. Cephalosome free or fused to first (and sometimes second) pedigerous somite(s), forming large cephalothorax. No lateral or dorsal processes present. Posterior part 5-segmented, comprising somites bearing P3–P5, genital somite and anal somite; no conspicuous integumental pores present. Genital apertures paired, located ventrally on genital somite, with 0–3 elements. Caudal rami with well-developed terminal seta/spines and up to 6 smaller elements. Spermatophores elongate-ovoid, paired.

Rostrum vestigial or absent. Antennule short, 1- to 4-segmented; often with strong spines on proximal segments. Antenna strongly developed, with short coxo-basis and 1- or 2-segmented endopod; distal compound endopod segment hook-like, with 5 or 6 accessory elements. Mandible without palp; gnathobase forming single blade of variable form; mandible absent in *Arthurius*. Maxillule represented by small lobe or sclerite tipped with 1 or 2 setae; sometimes absent. Maxilla 2-segmented; comprising unarmed syncoxa and spinous or lanceolate allobasis with 0–2 elements. Maxillipeds absent in adults; at most represented by Anlagen in copepodids I and II.

Legs 1 and 2 ♀ biramous, unsegmented; usually with long exopodal and minute endopodal lobe, sometimes strongly reduced to small outgrowths; either slightly (*Splanchnotrophus, Ismaila, Lomanoticola*) or strongly (*Arthurius*) sexually dimorphic. Leg 3 rudimentary, with 1 or 2 setae or completely absent. Leg 4 never expressed. Leg 5 represented by 1 or 2 setae or absent.

Endoparasites in kidney, pericardium, and digestive diverticula of marine opisthobranch gastropods. Nauplii planktotrophic; infective stage presumably copepodid I.

Type Genus.—*Splanchnotrophus* Hancock and Norman, 1863.

Other Genera.—*Ismaila* Bergh, 1867; *Lomanoticola* Scott and Scott, 1895; *Arthurius,* new genus; *Ceratosomicola,* new genus.

Splanchnotrophus Hancock and Norman, 1863

Members of the genus *Splanchnotrophus* were first illustrated but not named by 19th century molluscan workers such as Chiaje (1830, 1841) and Alder and Hancock (1845–1855). Chiaje's illustrations of a splanchnotrophid in the Mediterranean aeolidian *Spurilla neapolitana* remained unnoticed for almost a century until Monod and Dollfus' (1932) review of copepods associated with molluscs. Alder and Hancock (1845–1855) recorded the first boreal splanchnotrophid from *Acanthodoris pillosa* in Devonshire and gave brief illustrated descriptions of both sexes. This animal, which was identified by William Baird as an imperfectly developed *Bomolochus*, became the subject of a thorough account by Hancock and Norman (1863) in which they proposed the genus *Splanchnotrophus* for two new species, *S. gracilis* and *S. brevipes*. Two geographically close species were described from nudibranch hosts in NW France (Canu, 1891; Hecht, 1893) before O'Donoghue (1924) reported the discovery of the genus in the Indo-Pacific and fixed *S. gracilis* as the type species. Delamare Deboutteville (1950, 1951a) formally named Chiaje's (1830, 1841) species as *S. dellachiajei* and identified earlier Mediterranean splanchnotrophid records from the host *Spurilla neapolitana* with this species (e.g., Monod and Dollfus, 1932). A second Indo-Pacific species was recently recorded by Jensen (1990) from a sacoglossan gastropod.

Delamare Deboutteville (1950) was first to note that female body shape is potentially misleading as a species discriminant because it transforms progressively subsequent to fixation inside the host. He therefore suspected that several species were ill-defined and that the (sub)generic distinction between *Splanchnotrophus* and *Lomanoticola* was untenable. His alternative suggestion to base species identification solely on ovigerous females is not workable because considerable variability was observed between specimens of *S. angulatus* inhabiting the same host individual (see below; Fig. 1A, B).

The genus *Splanchnotrophus* is redefined here to include only the species formerly assigned to the nominotypical subgenus, with the exception of the W Australian species *S. sacculatus* O'Donoghue, 1924. Species belonging to the *Lomanoticola*-group (*sensu* Jensen (1990)) are not considered here. The diagnosis below is based on the re-examination of both sexes of *S. angulatus* and the type-species *S. gracilis*.

Diagnosis.—Splanchnotrophidae. Body ♀ compact, comprising large unsegmented prosome and very short 2-segmented urosome. Prosome consisting of short and narrow, weakly demarcated cephalosome and large lobate trunk (homologous to fused pedigerous somites 1–4). Trunk with 3 pairs of very long lateral processes (arising from pleural areas of first 2 pedigerous somites) and pair of large lobate outgrowths derived from posterolateral angles of P2-bearing somite; posterior part narrow and cylindrical, corresponding to fused 3rd and 4th pedigerous somites. Urosome comprising P5-bearing somite and 1-segmented genito-abdomen. Caudal rami with spatulate apical seta and 5 or 6 smaller accessory setae. Genital apertures ventrolateral, without armature.

Body ♂ cyclopiform, comprising cephalothorax, two free cylindrical prosomites and 3-segmented urosome; without any lateral or dorsal processes. Cephalothorax swollen, incorporating somites bearing P1 and P2. Urosome comprising P5-bearing somite, genital somite and anal somite. Caudal rami drawn out into styliform, apically pinnate spine; with 6 small accessory setae. Genital opercula with 2 or 3 vestigial elements.

Cephalic appendages without marked sexual dimorphism. Antennule short, indistinctly or distinctly 4-segmented; segment 1 with 2 strong spines. Antenna 3-segmented, comprising coxo-basis and 2-segmented endopod; distal endopod segment drawn out into strong hook, with 5 accessory elements. Mandible with short gnathobase tapering into apically dentate blade. Paragnaths densely pinnate lobes. Maxillule a small sclerite fused to mandible and tipped with 1 seta. Maxilla 2-segmented; syncoxa unarmed, allobasis a small segment with 1 spine and 1 seta.

Legs 1 and 2 ♀ biramous, unsegmented; protopod with outer basal seta; endopod a small lobe; exopod elongate with constriction between middle and distal third, tipped with claw and bearing several vestigial elements. Legs 1 and 2 ♂ similar but with narrow protopod and exopod not constricted. Leg 3 ♀ a minute unisetose segment; in ♂ represented by single seta on surface. Legs 4 and 5 absent.

Egg-sacs very large, multiseriate, containing hundreds of small eggs; attached at about midlength to genito-abdomen, with anteriorly and posteriorly directed lobes.

Type Species.—*Splanchnotrophus gracilis* Hancock and Norman, 1863 [by subsequent designation: O'Donoghue (1924)].

Other Species.—*S. willemi* Canu, 1891; *S. angulatus* Hecht, 1893; *S. dellachiajei* Delamare Deboutteville, 1950.

Splanchnotrophus angulatus Hecht, 1893

Type Locality.—Roscoff, France. Endoparasitic in *Aeolidia papillosa* (Linné, 1761) and *Aeolidiella glauca* (Alder and Hancock, 1845) (Opisthobranchia, Nudibranchia, Aeolidiidae).

Material Examined.—In coelomic cavity around gut of 15 mm long *Aeolidiella alderi* (Cocks, 1852), collected at La Rocque, Jersey (Channel Islands), August 1977, E. A. Platts: 3 ♀♀ (2 in alcohol; 1 dissected on 8 slides), 7 ♂♂ and 1 copepodid ♂ (NHM reg. no. 1987.403–414).

Redescription of Female.—Body length measured from rostral margin to distal end of posterior pair of lateral processes: 2.89–3.15 mm ($n = 3$). Body (Fig. 1A, B) compact, about as wide as long; comprising large, lobate prosome and small 2-segmented urosome. Cephalosome not demarcated from rest of prosome. Prosome unsegmented; pleural areas produced into 3 pairs of long processes, middle pair dorsal to anterior and posterior pairs. Prosome shape variable (compare Fig. 1A, B); variability noted in differential expansion of posterolateral angles, length and slenderness of lateral processes, and degree of development of collar at posterior end of prosome; in one specimen with pair of additional lobate outgrowths at level of anterior pair of lateral processes (Fig. 1A). Urosome not variable in shape or size (Fig. 2C); clearly separated from prosome by functional articulation; comprising short P5-bearing somite and bilaterally constricted, bulbous genito-abdomen; genital apertures located ventrolaterally in anterior half of genito-abdomen, opercula unarmed. Both urosomites with numerous integumental pores (Fig. 2C). Caudal rami (Fig. 2E, F) minute, scarcely discernible in ventral aspect (Fig. 2C); about twice as long as wide; drawn out into apically spatulate seta V; posterior margin with spinous process near inner corner; setae II–IV, VI and VII small, seta I possible represented by minute spinous outgrowth.

Antennule (Fig. 2A) 2-segmented; distal portion with 2 constrictions marking original segmentation; segment 1 with 2 large, blunt spines; segment 2 with 2 blunt spines and 1 seta in proximal part, 3 setae and 1 aesthetasc in middle part, and 9 setae and 2 aesthetascs in distal part; aesthetascs all minute (arrows in Fig. 2A). Antenna (Fig. 4F, G) 3-segmented; coxo-basis and proximal endopod segment transversally enlarged, each with spine; distal endopod segment drawn out into strong apical claw, with 1 long and 4 short accessory elements. Labrum well-developed bilobate outgrowth, without spinular ornamentation but with paired angular swellings medially (compare ♂: Fig. 3B). Mandible and maxillule fused at base (Fig. 3E, F). Mandible tapering distally into single recurved blade bearing series of dentiform processes around apex. Maxillule a small lobate sclerite tipped with 1 basally fused seta (Fig. 3E, F). Paragnaths (Fig. 2B) well developed, represented by widely separated pinnate lobes; area between maxillae forming median swelling with paired setular patches (Fig. 2B). Maxilla (Fig. 2B) 2-segmented, comprising unarmed syncoxa and short allobasis drawn out into unipinnate spine and with short seta.

Legs 1 and 2 (Fig. 1C, D) unsegmented, weakly chitinized; protopod drawn out into small endopodal lobe and long exopodal lobe; outer margin with minute basal seta. Exopodal lobes with multiple constrictions, gradually tapering to apex tipped with basally fused acutely recurved claw; additional elements discernible as minute setiform outgrowths. Endopodal lobe very small in leg 1, tipped with minute recurved element; longer in leg 2, constricted at about midlength, with 1 pore and 2 setal rudiments. Leg 3 (Fig. 2D) a minute sclerite with 1 recurved spine apically and 1 hyaline element along inner margin; located near posterior margin of prosome (Fig. 2C). Legs 4 and 5 absent.

Egg-sacs with posterior and anterior lobes, containing several rows of small eggs (70 µm); attached at about midlength to genito-abdomen.

Redescription of Male.—Body length measured in lateral aspect from rostral margin to posterior margin of caudal rami: 1.58–1.65 mm ($n = 7$). Body (Figs. 3A, 4A, B) cyclopiform, relatively unmodified; comprising pear-shaped cephalothorax and 5 cylindrical somites; without any lateral or dorsal processes. Cephalothorax incorporating first two pedigerous somites; ventral surface also fused to tergites of leg 3- and (to a minor extent) leg 4-bearing somites (Figs. 3A, 4B); separation of cephalosome marked only by minor surface folding. Homologues of P3-

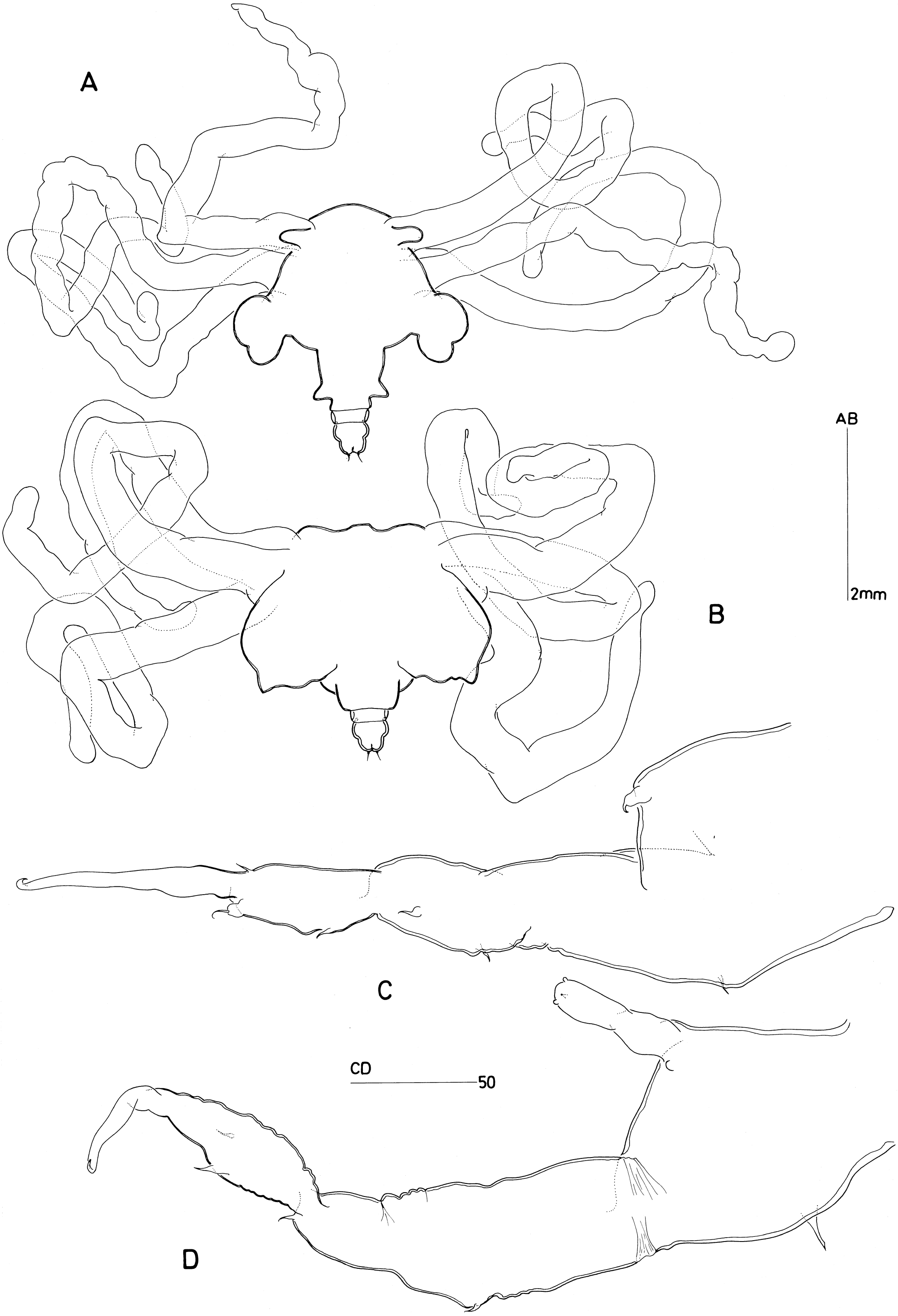

Fig. 1. *Splanchnotrophus angulatus* Hecht, 1893 [♀]: A, B, habitus of different specimens, dorsal; C, leg 1, anterior; D, leg 2, anterior.

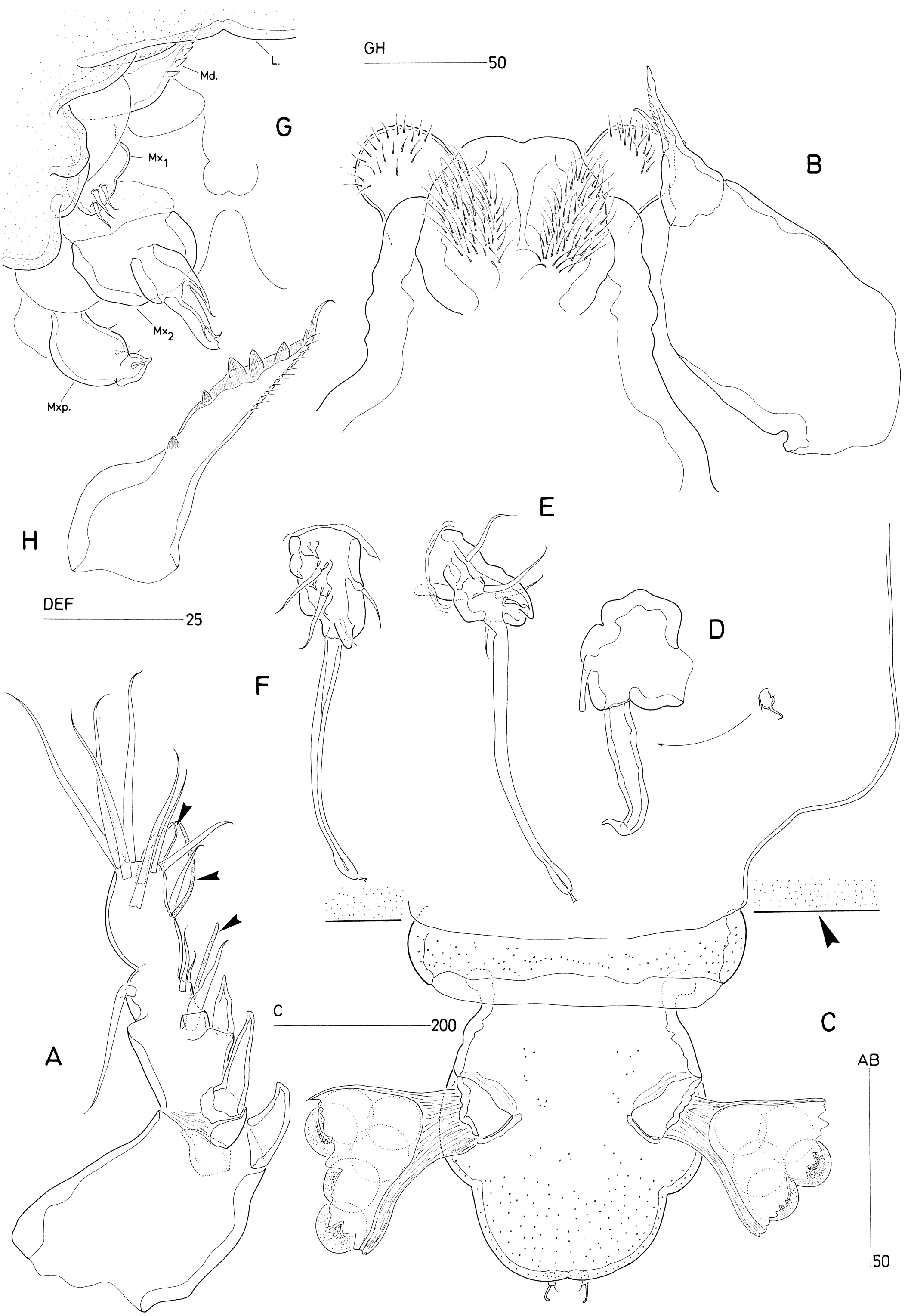

Fig. 2. *Splanchnotrophus angulatus* Hecht, 1893 [♀]: A, antennule [aesthetascs, arrow]; B, labium and right maxilla, posterior; C, urosome, ventral [arrow indicating host integument]; D, leg 3, anterior; E, left caudal ramus, lateral; F, left caudal ramus, dorsal. *Briarella disphaerocephala* Monod and Dollfus, 1932 [♀]: G, oral area, showing labrum (L.), mandible (Md.), maxillule (Mx_1), maxilla (Mx_2) and maxilliped (Mxp.). *Briarella risbeci* Monod, 1928 [♀]: H, mandible.

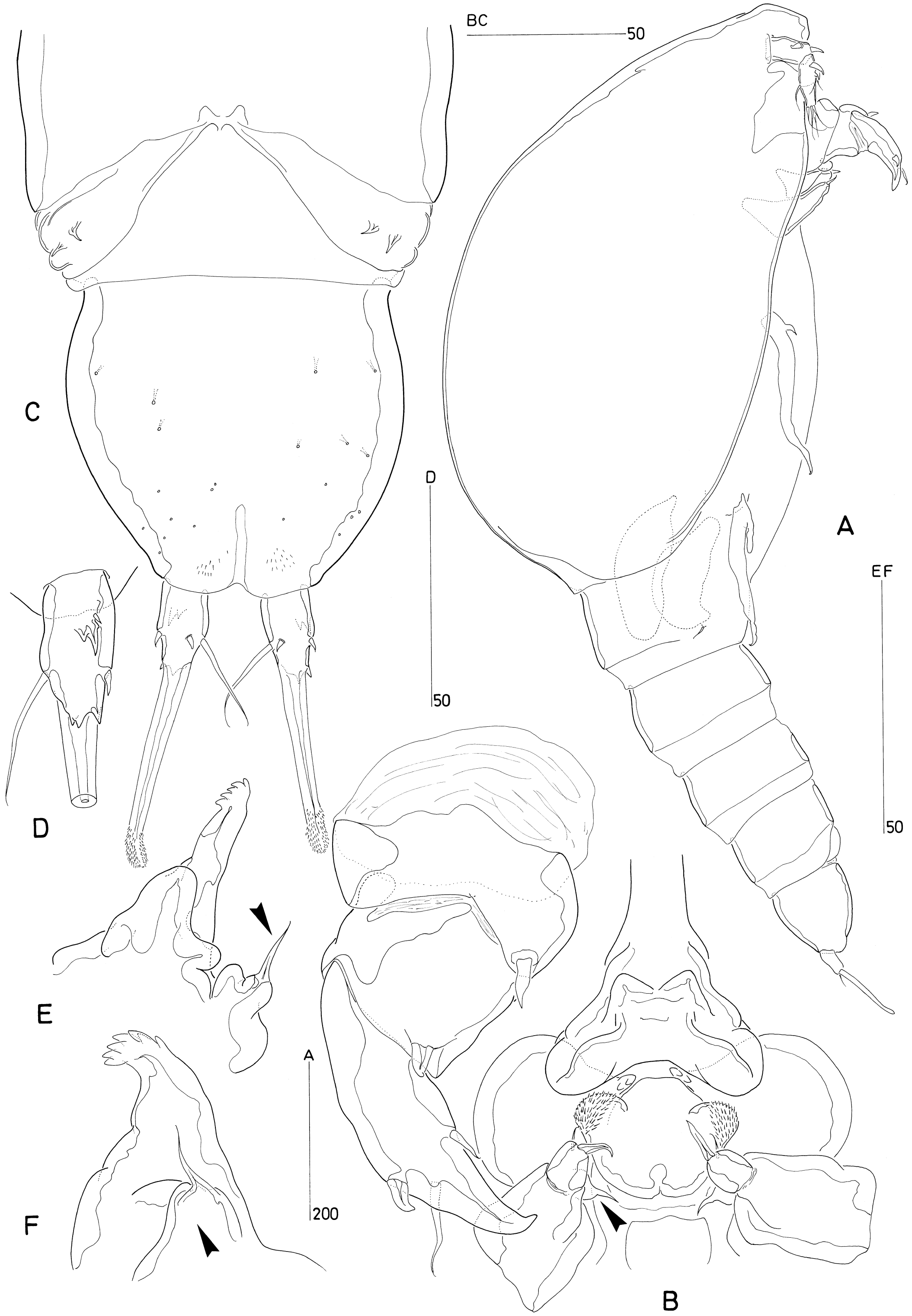

Fig. 3. *Splanchnotrophus angulatus* Hecht, 1893 [♂]: A, habitus, lateral; B, oral area, showing right antenna, labrum, and mouthparts, ventral [maxillule, arrow]; C, genital and anal somites, ventral; D, right caudal ramus, dorsal; E, mandible and maxillule [arrow], medial; F, same, posterior.

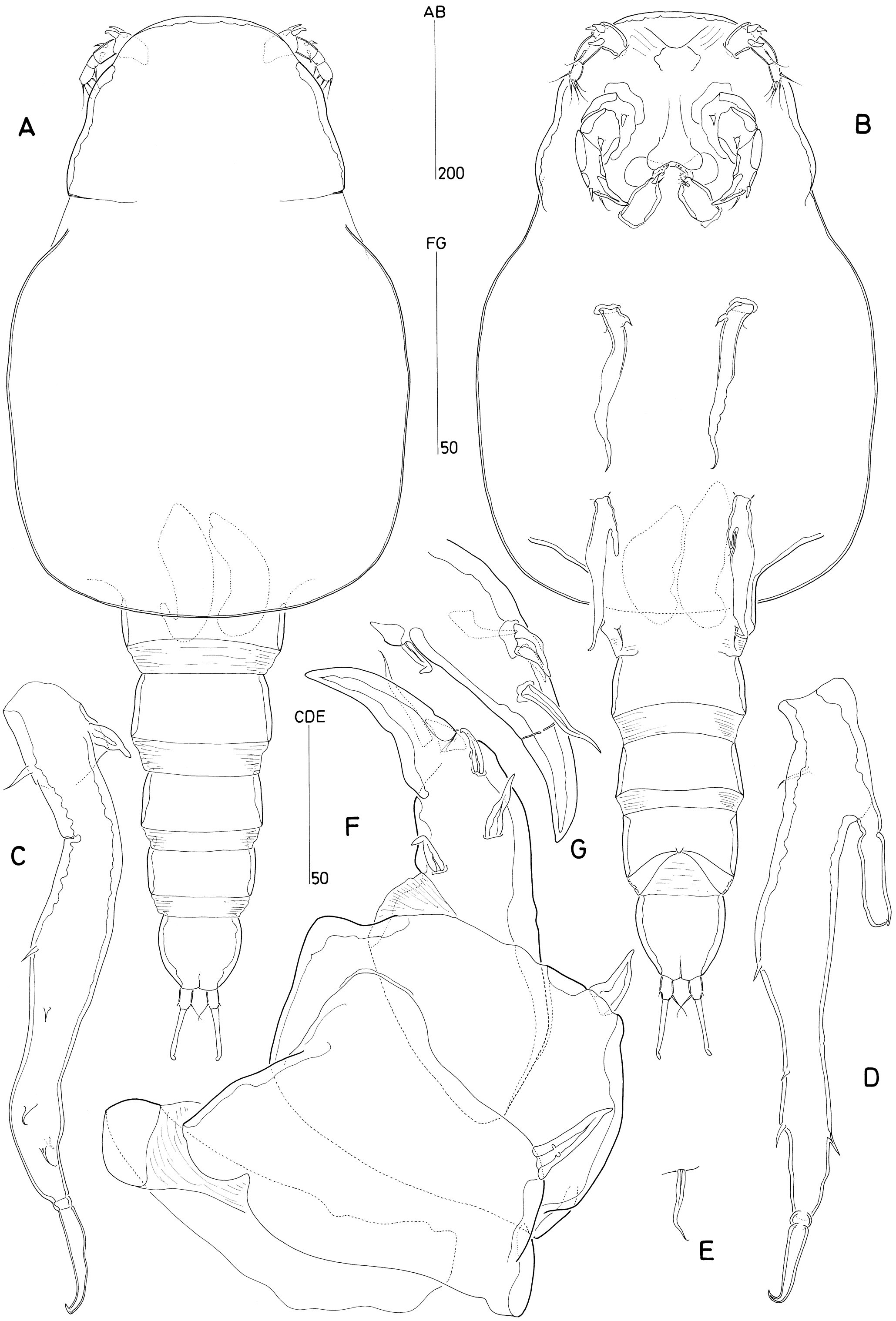

Fig. 4. *Splanchnotrophus angulatus* Hecht, 1893: A, habitus ♂, dorsal; B, same, ventral; C, leg 1 ♂, anterior; D, leg 2 ♂, anterior; E, leg 3 ♂; F, antenna ♀, anterior; G, antenna ♀, distal posterior.

and P4-bearing somites cylindrical. Urosome 3-segmented, comprising P5-bearing somite, genital somite and anal somite (Fig. 4A, B). Genital somite with paired apertures (Fig. 3C); opercula with 2 minor processes representing setal vestiges. Anal somite with convex lateral margins; with integumental pores and paired patches of minute spinules on ventral surface (Fig. 3C). Caudal rami (Fig. 3C, D) cylindrical, about twice as long as wide; drawn out into styliform seta V bearing densely pinnate apex; setae VII well developed, displaced to inner margin; other setae rudimentary, represented by articulating spinule-like elements or small spinous processes (Fig. 3D).

No marked sexual dimorphism in antennules, antennae and mouthparts.

Legs 1 and 2 (Fig. 4C, D) biramous, widely separated; with basic structure as in ♀ but protopodal part much narrower and exopodal lobe more slender and more chitinized. Leg 3 (Fig. 4E) represented by single lateroventral seta. Legs 4 and 5 absent.

Spermatophores oval-elongate, paired (Fig. 4A, B).

Splanchnotrophus gracilis Hancock and Norman, 1863

Type Locality.—Hancock and Norman recorded the species first from the Devonshire coast (in *Acanthodoris pilosa* (Müller, 1789); Onchidorididae) and subsequently also from an unspecified locality off the West coast of Ireland (in *Okenia aspersa* (Alder and Hancock, 1845); Goniodorididae), but did not explicitly state the type locality. The syntype material deposited in the NHM refers to the Devonshire locality only.

Material Examined.—Norman Collection: (a) syntypes (NHM reg. nos 1911.11.8.47708–717): 1 damaged ♀ and 6 ♂♂ in alcohol, 1 ♂ dissected on 6 slides; from *Acanthodoris pilosa* (Müller, 1789); Devonshire coast; (b) NHM reg. no. 1911.11.8.47718; 1 damaged ♀ from *A. pilosa*; near Eddystone, coll. Mr. Edinsworth.

Partial Redescription of Male.—Antenna (Fig. 6E) similar to that of *S. angulatus* but spine on coxo-basis fused at base, position of setae/spines on distal endopod segment different and segment itself more slender. Mandible (Fig. 5B) with few dentiform processes on apical portion of blade. Maxillule (arrows in Figs. 5B, 6D) represented by small sclerite fused to mandibular gnathobase, with 1 short seta. Maxilla (Fig. 6D) with allobasis drawn out into apically serrate spine and with stout seta. Anal somite (Fig. 5A) with concave lateral margins; ventral surface with integumental pores but no spinules discernible. Genital opercula (Fig. 5A, G) largely fused to somite; original articulation revealed by incomplete surface sutures; armature consisting of 1 fused and 2 articulating elements, decreasing in size medially. Caudal rami (Fig. 5E, F) with setae generally better developed than in *S. angulatus*; all 7 setae present; seta V subterminal, articulating, displaced to ventral surface. Legs 1 and 2 (Fig. 5C, D) more robust than in *S. angulatus*; endopodal lobes being larger and with distinct apical spine; terminal claws on exopodal lobes being bigger and lateral setal elements better developed. Leg 3 (Fig. 5A) represented by single seta on small lateroventral lobe.

Remarks.—Interpretation of Hecht's (1893) original description of *S. angulatus* poses some difficulties. Firstly, Hecht's text was based on specimens from Roscoff, and his only illustration is a habitus view of an ovigerous female in ventral aspect. As part of the description of *S. dellachiajei* from Banyuls, Delamare Deboutteville (1950) reproduced the same drawing which he claimed to have discovered in the archives of the French zoologist Henri de Lacaze-Duthiers in the Laboratoire Arago. Delamare Deboutteville regarded this as possible evidence for an earlier record of *S. dellachiajei* in the Banyuls area. Obviously, he had not consulted Hecht's (1893) paper on *S. angulatus* because he referred only to the later description published in 1895. The latter provides a more complete account of the species but shows a non-ovigerous female that looks more robust and differs from the original in the slenderness of the head region, the length of the lateral processes, and the segmentation of the hindbody. At that time de Lacaze-Duthiers was director of the marine laboratories in Roscoff and Banyuls and also editor of the *Archives de Zoologie expérimentale et générale* in which Hecht published his 1893 description. It is therefore likely that de Lacaze-Duthiers was not the illustrator as Delamare Deboutteville had assumed but only received a copy of the drawing from Hecht. Identification of the NHM material from Jersey is based on

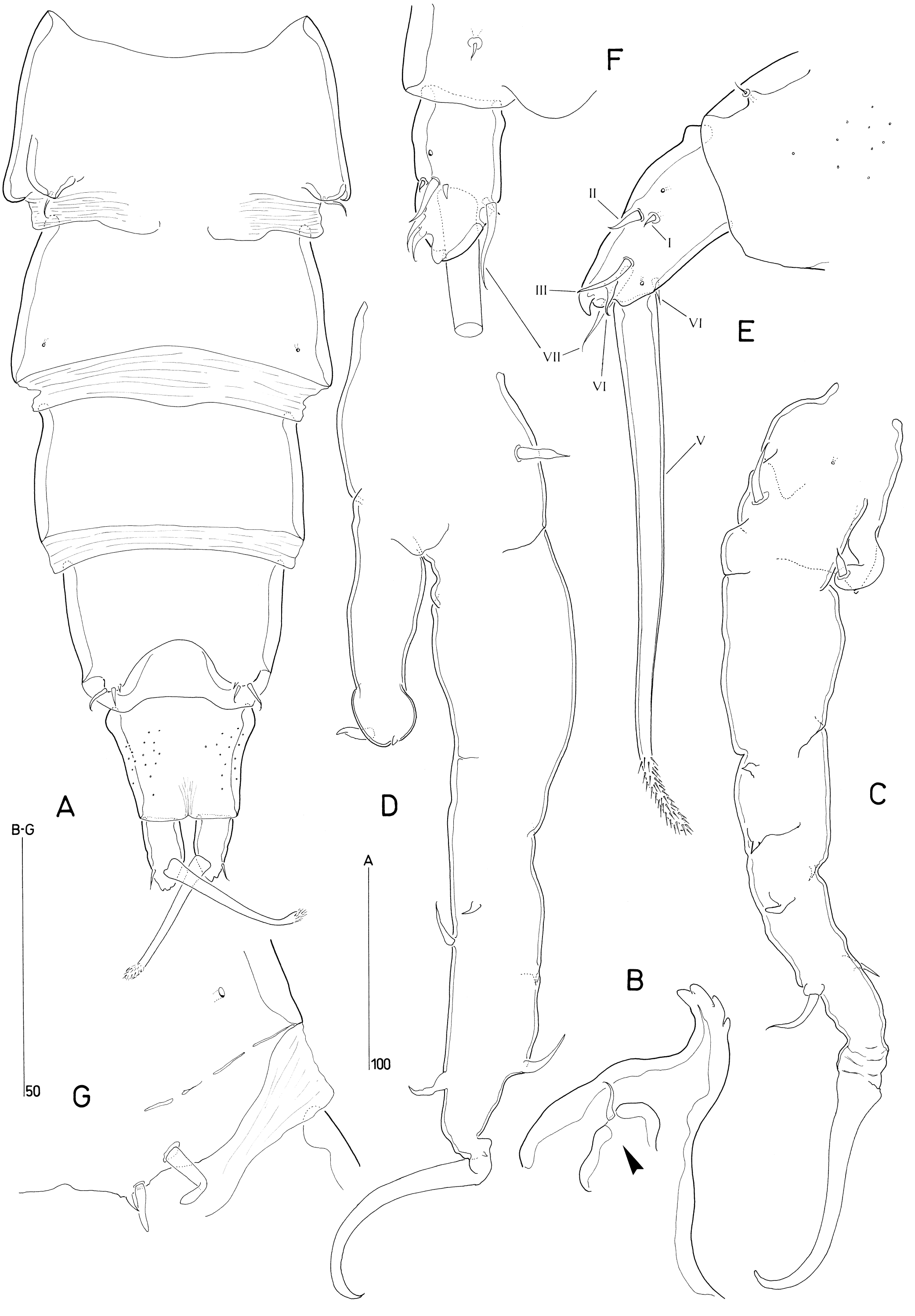

Fig. 5. *Splanchnotrophus gracilis* Hancock and Norman, 1863 [♂]: A, free thoracic somites and abdomen, ventral; B, mandible and maxillule [arrow], posterior; C, leg 1, anterior; D, leg 2, anterior; E, right caudal ramus, lateral; F, left caudal ramus, dorsal; G, armature of leg 6.

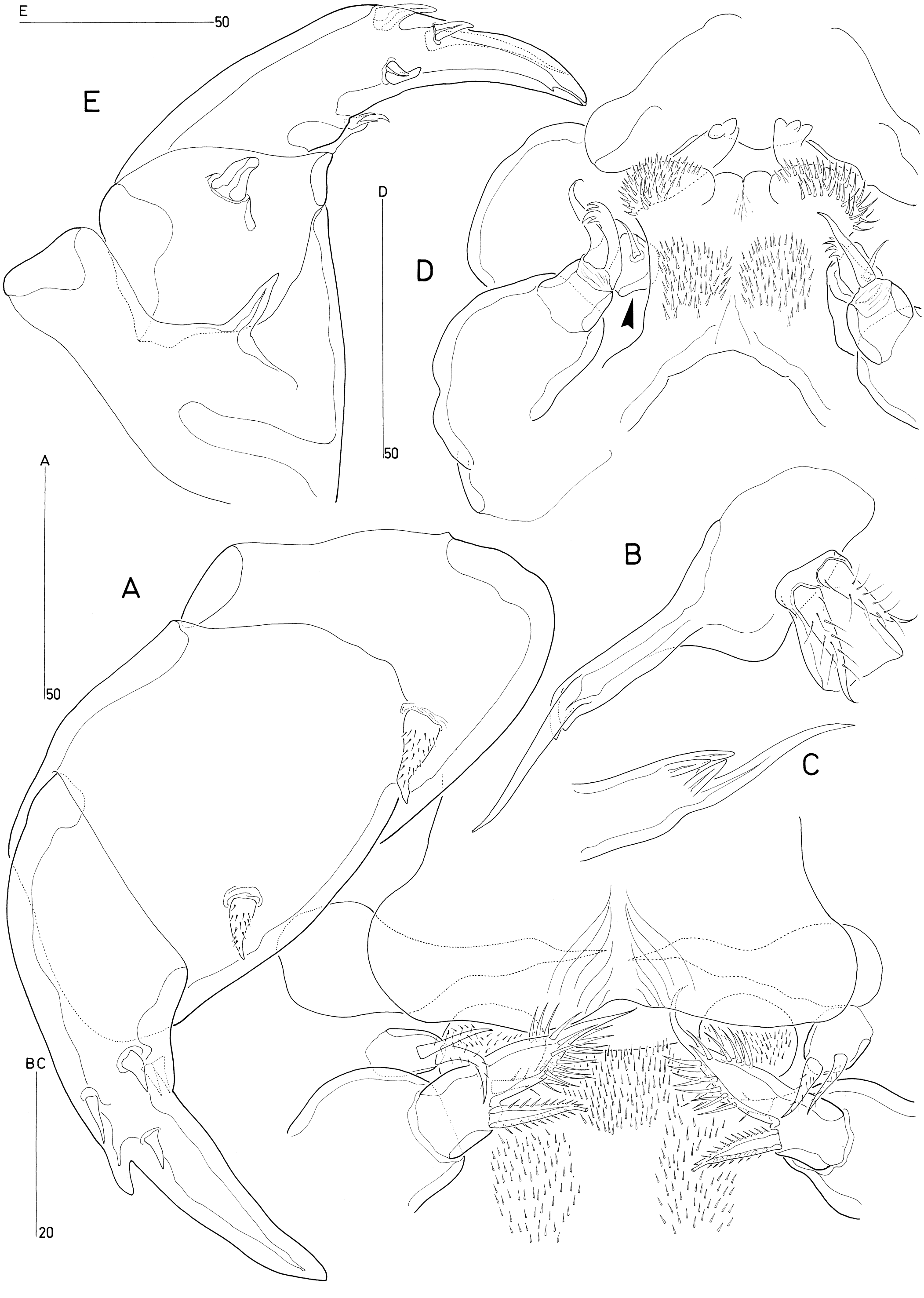

Fig. 6. *Ismaila belciki* Ho, 1987a [♀]: A, oral area, showing right antenna, labrum, and mouthparts; B, mandible and maxillule; C, distal part of mandibular gnathobase. *Splanchnotrophus gracilis* Hancock and Norman, 1863 [♂]: D, oral area, showing labrum and mouthparts [maxillule, arrow]; E, antenna.

Hecht's (1895) illustrations which show the characteristic shape of the genito-abdomen. In *S. angulatus* there is a distinct bilateral constriction posterior to the genital apertures (Fig. 2C), and the shape of the genito-abdomen is constant, irrespective of prosome variability (Fig. 1A, B). In *S. dellachiajei* the postgenital portion of the genito-abdomen is significantly shorter, and no constriction is discernible (Delamare Deboutteville, 1950).

Secondly, Hecht (1893) compared *S. angulatus* only with *S. gracilis* but not with the second NW French species, *S. willemi*. Canu's (1891) description of the latter is completely lacking in illustrations and provides only the bare minimum to distinguish adult females from those of *S. gracilis:* host specificity, shape of lateral processes, egg colour, egg-sac form, and presence of angular posterolateral processes. Hecht (1895) claimed that *S. angulatus* and *S. willemi* co-occurred in Roscoff but admitted that identification of the latter was primarily based on host specificity and size. It is possible that both species are conspecific because parasite size is frequently only a function of host size as reported by Jensen (1987) for *Ismaila monstrosa*. The specimens from Jersey seem to approach *S. willemi* in size.

The morphology of the mouthparts in the genus has been a matter of debate ever since the first species description by Hancock and Norman (1863). In addition to the mandibles, these authors observed one pair of maxillae and two pairs of "foot-jaws" in *S. gracilis*, which according to modern terminology refer to the maxillules, maxillae, and maxillipeds, respectively. Hecht (1895) identified mandibles and two pairs of foot-jaws ("mâchoires") in *S. angulatus*, the posterior pair of which was fused medially forming an unpaired plate. In his attempt to relate the Splanchnotrophidae to the Chondracanthidae, Monod (1928) re-interpreted the maxillule of *S. gracilis* as the mandibular palp since presence of the latter was mistakenly believed to be a chondracanthid feature. Laubier (1964) re-examined *S. gracilis* and *S. dellachiajei* and concluded that both species had only two pairs of mouthparts, i.e., mandibles and maxillae. The maxillipeds referred to in earlier descriptions were in reality based on the midventral sclerites found posterior to the paragnaths. Ho (1987b) demonstrated that the absence of maxillipeds in adult *Ismaila* is the result of developmental arrest early in ontogeny, which he assumed to be the typical splanchnotrophid pattern. New observations not only confirm the absence of maxillipeds in *Splanchnotrophus* but also reveal that Hancock and Norman's (1863) observation of the maxillules is correct and Laubier's (1964) erroneous.

Ovigerous females of *Splanchnotrophus* can be readily identified by the shape of their egg-sacs, having anteriorly and posteriorly directed lobes and attaching at about midlength to the genital apertures. This apomorphy serves to distinguish the genus from other splanchnotrophids which have kidney-shaped (*Lomanoticola*), sausage-shaped (*Arthurius*), or cylindrical (*Ismaila*, *Ceratosomicola*) egg-sacs that attach terminally or subterminally to the genito-abdomen. In addition to egg-sac shape, *Splanchnotrophus* differs from *Lomanoticola* also in the excessive development of the lateral processes, the presence of a lobate endopod on leg 2, the reduction of the caudal rami, and the spatulate nature of seta V. The discovery of the male of *Lomanoticola* and the description of the mouthparts of the female may reveal additional differences. Both genera are regarded as sistergroups on the basis of the morphology of the antennules and legs 1 and 2, and the presence of a two-segmented urosome, comprising the leg 5-bearing somite and the unsegmented genito-abdomen.

The genus *Splanchnotrophus* assumes a typical European boreo-mediterranean distribution (Table 1). The Western Australian outliers (*S. sacculatus, S. elysiae*) represent independent evolutionary lineages and are placed in separate genera (see below). The unnamed *Splanchnotrophus* species recorded from a Red Sea notaspidean by Gohar and Abul Ela (1957) is possibly a philoblennid.

Ismaila Bergh, 1867

Bergh (1867) proposed the genus for a new species *I. monstrosa,* based on a single female found in the cerata of the aeolid nudibranch *Phidiana lynceus* Bergh, 1867, collected in Saint Thomas, U.S. Virgin Islands. An abridged version of the original Danish description was published in English the following year (Bergh, 1868). Jensen (1987) redescribed *I. monstrosa* from the type locality and significantly extended its known host range by reporting it from *Ercolania funerea*

Table 1. Splanchnotrophidae associated with opisthobranch gastropods. Systematic position of hosts indicated by following abbreviations: CE = order Cephalaspidea; SA = order Sacoglossa; NU = order Nudibranchia (1 = suborder Doridina; 2 = suborder Aeolidina; 3 = suborder Dendronotina; 4 = suborder Arminina). Opisthobranch classification largely follows Rudman and Willan (1998).

Species	Host	Family	Order	Locality	References
Splanchnotrophus gracilis	*Acanthodoris pilosa* (Müller, 1789)	Onchidorididae	NU 1	England (not specified)	Alder and Hancock (1845-1855: as *Bomolochus* sp.)
				Devonshire, England	Hancock and Norman (1863)
				near Eddystone, England	Marine Biological Association (1931), present account
	Okenia aspersa (Alder and Hancock, 1845)	Goniodorididae	NU 1	W coast Ireland	Hancock and Norman (1863)
willemi	*Ancula gibbosa* (Risso, 1818)	Goniodorididae	NU 1	NW France (not specified)	Canu (1899), Pelseneer (1906)
	Facelina coronata (Forbes and Goodsir, 1839)	Glaucidae	NU 2	Boulonnais, France	Canu (1891), Pelseneer (1894: as *S.* sp.), Bonnier (1900)
				Normandy, France	Canu (1898)
				Roscoff, France	Hecht (1895)
				Arcachon, France	Cuénot (1927)
angulatus	*Aeolidia papillosa* (Linné, 1761)	Aeolidiidae	NU 2	Roscoff, France	Hecht (1893, 1895)
	Aeolidiella alderi (Cocks, 1852)	Aeolidiidae	NU 2	Jersey, Channel Islands	present account
	Aeolidiella glauca (Alder and Hancock, 1845)	Aeolidiidae	NU 2	Roscoff, France	Hecht (1893, 1895)
dellachiajei	*Hervia costai* Haefelfinger, 1961	Aeolidiidae	NU 2	Banyuls, France	Laubier (1964, 1966)
	Spurilla neapolitana (Chiaje, 1841)	Aeolidiidae	NU 2	Naples, Italy	Chiaje (1830, 1841: figure only)
				Banyuls, France	Monod and Dollfus (1932: as *S.* sp. (? *gracilis*)), Delamare Deboutteville (1950), Laubier (1964, 1966)
				Toulon, France	Delamare Deboutteville (1950)
				Algeciras Bay and El Portil, Spain	López-González (personal communication)
	Flabellina affinis (Gmelin, 1791)	Flabellinidae	NU 2	Banyuls, France	Laubier (1964, 1966)
				Tarifa, Spain	López-González (personal communication)
	Facelina bostoniensis (Couthouy, 1838)	Glaucidae	NU 2	Banyuls, France	Delamare Deboutteville (1951a)
sp.	*Doris verrucosa* (Linné, 1758)	Dorididae	NU 1	Arcachon, France	Cuénot (1903, 1927)
	Favorinus branchialis (Rathke, 1806)	Glaucidae	NU 2	Bergen, Norway	Bergh (1879)
Ismaila monstrosa	*Phidiana lynceus* Bergh, 1867	Glaucidae	NU 2	U.S. Virgin Islands	Bergh (1867, 1868)
	Archidoris incerta Bergh, 1898	Archidorididae	NU 1	Tumbes, Chile	Bergh (1898)
	Aeolidia papillosa var. *serotina* Bergh, 1873	Aeolidiidae	NU 2	Tumbes, Chile	Bergh (1898)
	Ercolania funerea (Costa, 1867)	Limapontiidae	SA	U.S. Virgin Islands	Jensen (1987)

Table 1. Continued.

Species	Host	Family	Order	Locality	References
occulta	*Dendronotus iris* Cooper, 1863	Dendronotidae	NU 3	Long Beach, California	Ho (1981a, 1987b)
belciki	*Antiopella fusca* (O'Donoghue, 1924)	Zephyrinidae	NU 4	Oregon	Belcik (1981), Ho (1987a)
sp.	*Okenia luna* Millen *et al.*, 1994	Goniodorididae	NU 1	Peru, N Chile	Millen *et al.* (1994), Schrödl (1996)
	Flabellina sp. 1	Flabellinidae	NU 2	Chile	Schrödl (1997)
	Thecacera darwini Pruvot-Fol, 1950	Polyceridae	NU 1	Chile	Schrödl (1996)
	Archidoris sp.	Archidorididae	NU 1	California	Monod and Dollfus (1934)
Lomanoticola					
brevipes	*Doto coronata* (Gmelin, 1791)	Dotidae	NU 3	Northumberland, U.K.	Hancock and Norman (1863), O'Reilly and Geddes (2000)
	Doto pinnatifida (Montagu, 1804)	Dotidae	NU 3	Roscoff, France	Hecht (1895)
	Coryphella rufibranchialis (M. Sars, 1829)	Flabellinidae	NU 2	Whitley, U.K.	Alder and Hancock (1845–1855: as gen. et sp. indet.)
				Northumberland, U.K.	Hancock and Norman (1863)
	Coryphella verrucosa (M. Sars, 1829)	Flabellinidae	NU 2	Gullmar Fjord, Sweden	Bresciani and Lützen (1962)
	Cuthona genovae (O'Donoghue, 1926)	Tergipedidae	NU 2	Lough Hyne, Ireland	Holmes and Nunn (1996)
	Eubranchus tricolor Forbes, 1838	Eubranchidae	NU 2	Hellebæk, Denmark	Bergh (1867, 1868, 1873)
	Facelina bostoniensis (Couthouy, 1838)	Glaucidae	NU 2	Isefjord, Denmark	Rasmussen (1973)
insolens	*Lomanotus genei* (Vérany, 1846)	Lomanotidae	NU 3	Valentia Harbour, Ireland	Scott and Scott (1895)
				Plymouth, England	Garstang (1890b: as *S.* sp.)
				Banyuls, France	Delamare Deboutteville (1950)
				Marseille, France	Vayssière (1901: as *Ismaila* sp.; 1903: as *S.* sp.?)
				Naples, Italy	Bergh (1879: as *Ismaila* sp.)
Ceratosomicola gen. nov.					
sacculatus	*Ceratosoma brevicaudatum* Abraham, 1876	Chromodorididae	NU 1	Houtman Abrolhos Islands	O'Donoghue (1924)
sp. ?	*Hypselodoris festiva* (Adams, 1861)	Chromodorididae	NU 1	Japan	Fujita (1895)
Arthurius gen. nov.					
elysiae	*Elysia australis* (Quoy and Gaimard, 1832)	Plakobranchidae	SA	Eagle Bay, W Australia	Jensen (1990)
				Rottnest Island, W Australia	present account
sp.	*Elysia ornata* (Pease, 1860)	Plakobranchidae	SA	New Caledonia	Risbec (1930), Monod and Dollfus (1932, 1934)
Splanchnotrophidae indet.					
	Rostanga pulchra MacFarland, 1905	Rostangidae	NU 1	Chiloé Island, Chile	Marcus (1959)
	Acanthodoris falklandica Eliot, 1907	Onchidorididae	NU 1	Chiloé Island, Chile	Marcus (1959)
	Eubranchus agrius Marcus, 1959	Eubranchidae	NU 2	Chiloé Island, Chile	Marcus (1959)
	Aglaja diomedia	Aglajidae	CE	Friday Harbor, Washington	Illg in Belcik (1981)
	Dirona sp.	Dironidae	NU 4	Friday Harbor, Washington	Illg in Belcik (1981)
	Triopha sp.	Polyceridae	NU 1	Friday Harbor, Washington	Illg in Belcik (1981)
	Dendronotus sp.	Dendronotidae	NU 3	California	Illg in Belcik (1981)
	Eubranchus sp.	Eubranchidae	NU 2	California	Illg in Belcik (1981)

(Costa, 1867), the first ascoglossan nudibranch recorded as host for a named endoparasitic copepod. She also gave the first description of the male and re-examined Bergh's (1867) type material of *I. monstrosa*. Contrary to Bergh, Jensen (1987) pointed out that the middorsal process is unbranched in the type species as in all its congeners.

Ho (1987a) challenged the reported disjunct distribution of *I. monstrosa* along the west coast of North America. His re-examination of Belcik's (1981) Oregonian material from the aeolid *Antiopella fusca* (O'Donoghue, 1924) resulted in the recognition of a distinct species, *I. belciki*, based on consistent differences in the dorsal process and legs 1 and 2 of both sexes (note that Ho had inadvertently mislabelled the legs in Fig. 1D–F, which should read F, D, and E, respectively).

The generic diagnosis below is based on Ho's (1981a) excellent description of *I. occulta* from the giant dendronotid nudibranch *Dendronotus iris* Cooper, 1863. Monod and Dollfus' (1934) brief description of an unidentified *Ismaila* from a Californian *Archidoris* species is possibly attributable to *I. occulta*. This identification requires confirmation since recent studies on Chilean opisthobranchs revealed several new species of *Ismaila* (Schrödl and Haumayr, unpublished data). This also feeds the conjecture (Monod and Dollfus, 1934; Jensen, 1987) that Bergh's (1898) record of *I. monstrosa* from Chile is not conspecific with the type from Saint Thomas in the Caribbean. From the data available for *Ismaila* (Table 1), it would appear that host specificity is not particularly high and geographical distribution is rather limited.

Diagnosis.—Splanchnotrophidae. Body ♀ elongate, comprising large unsegmented prosome and short 3-segmented urosome. Prosome consisting of well-demarcated globular cephalosome and elongated lobate trunk (homologous to fused pedigerous somites 1–4). Trunk with 3 pairs of lateral processes (arising from pleural areas of first 2 pedigerous somites) and 1 middorsal process on P2-bearing somite; posterior part elongate and highly contractile. Urosome comprising P5-bearing somite, genital (double-)somite and anal somite.

Body ♂ modified, comprising cephalothorax, indistinctly 3-segmented prosome, and 3-segmented urosome; without any lateral or dorsal processes. Cephalothorax incorporating P1-bearing somite; transversally dilated, typically bent at almost right angle with rest of body. P2-bearing somite broad, remaining prosomites cylindrical. Urosome comprising P5-bearing somite, genital somite, and anal somite exhibiting faint subdivision.

Antennule short, 2-segmented (distal segments expressed in other genera fused). Antenna 3-segmented, comprising coxo-basis and 2-segmented endopod; distal endopod segment drawn out into large spinous apex, with 6 accessory elements. Mandible with slender gnathobase bearing one stylet-like and several short teeth. Paragnaths densely pinnate lobes. Maxillule a distinct lobe with 2 setae. Maxilla 2-segmented; syncoxa unarmed, allobasis drawn out into multipinnate endite with 2 accessory elements.

Leg 1 uniramous, endopod absent; exopod lobate, tipped with claw and bearing several smaller elements; protopod with outer basal seta, in ♀ with large lobate outgrowth. Leg 2 with similar structure and sexual dimorphism but biramous, endopod a lobate outgrowth. Leg 3 a small unisetose lobe. Leg 4 absent. Leg 5 a bisetose lobe. Male genital opercula with 3 setae. Female genital apertures dorsolateral.

Caudal rami squarish, drawn out into stylet-like seta, with 5 additional setae.

Egg-sacs cylindrical, multiseriate, containing numerous small eggs; attached at proximal end to genital somite.

Type Species.—*Ismaila monstrosa* Bergh, 1867 [by monotypy].

Other Species.—*I. occulta* Ho, 1981; *I. belciki* Ho, 1987.

Remarks.—Ho (1981a) treated *Ismaila* as a valid genus of the Splanchnotrophidae. However, he noted that the marked difference in mandibular morphology with that of *Splanchnotrophus* could also be indicative of familial distinctiveness. Re-examination of the mandible of *I. belciki* (Fig. 6B, C) proved that placing excessive weight on this difference is unwarranted. The *Ismaila* type can be readily derived from the *Splanchnotrophus* type by secondary elongation of one of the proximal teeth, producing a medially directed stylet (compare Fig. 3F). The presence of a radically divergent mandible type in *Ceratosomicola* (Fig. 11E) and the complete absence of this appendage in *Arthurius* (Fig. 10B, C) further undermine the usefulness of mandibular morphology as a unifying splanchnotrophid character.

In addition to mandibular morphology, other autapomorphies of *Ismaila* include the fusion of the distal antennulary segments, the presence of a middorsal process on the leg 2-bearing somite, and the sexual dimorphism of legs 1 and 2 (protopod with lobate outgrowth in ♀). The genus displays the most primitive character states known in the family for the maxillule (distinct bisetose lobe), maxilla (allobasis with two accessory elements), and leg 5 (free segment with two setae).

The genus *Ismaila* is distributed along almost the entire Pacific seaboard of the Americas from at least Washington in the north (Illg in Belcik (1981)) to the Magellan Strait in the south (Schrödl, personal communication). The genus may have arisen in the eastern Pacific and subsequently reached the Caribbean (Bergh, 1867; Jensen, 1987) by eastward dispersal through the open Panama Strait. Monod and Dollfus (1932) pointed out that the unnamed Mediterranean *Ismaila* species recorded by Bergh (1879) and Vayssière (1901) are conspecific with *Lomanoticola insolens*.

Lomanoticola Scott and Scott, 1895

Scott and Scott (1895) proposed this genus for a new species *Lomanoticola insolens* found in the dendronotid nudibranch *Lomanotus genei* (Vérany, 1846) off Valentia harbour, Ireland. Because the single female was damaged during dissection, their habitus drawing showing four pairs of lateral processes is a reconstruction. They also failed to observe the antennules, antennae, mouthparts, and swimming legs. Scott and Scott remarked that Garstang (1890b) had possibly found the same species on *L. genei* in the Plymouth area, which he had misinterpreted as "pieces of spawn" in an earlier study (Garstang, 1890a). The authors were clearly unaware of Hancock and Norman's (1863) descriptions of *Splanchnotrophus* and Bergh's studies. Hecht (1895) considered the presence of a fourth pair of lateral processes as insufficient ground to maintain *Lomanoticola* and synonymized it with *Splanchnotrophus*, considering the type species *L. insolens* a close relative of *S. brevipes*. Norman and Brady (1909) pointed out the close resemblance and possible identity of *S. gracilis* and *L. insolens*.

Monod and Dollfus (1932) retained *Lomanoticola* as a subgenus of *Splanchnotrophus* and based the division solely on the form of the lateral processes. *Lomanoticola insolens* and *S. brevipes*, which have short, stocky processes, were referred to the subgenus *Lomanoticola*. Although Delamare Deboutteville (1950) remarked on the artificiality of this classification, he nevertheless maintained it, suggesting that the caudal rami could provide potentially informative characters for subgeneric distinction. Laubier (1964, 1966) expressed grave doubts about the validity of *Lomanoticola* and restricted the subgenus to *S. insolens*. Belcik (1981) accepted both subgenera, and Jensen (1990) added a third species, *S. elysiae,* to *Lomanoticola*. The latter taxon is here raised to genus level and is redefined to include only *L. insolens* and *L. brevipes,* new combination. The diagnosis below is based on Hancock and Norman's (1863) original description of *S. brevipes* and Delamare Deboutteville's (1950) redescription of *L. insolens*. Although Monod and Dollfus (1932) recorded both sexes of *L. insolens* from Banyuls, no males of this genus have ever been illustrated.

Diagnosis (based on ♀ only).—Splanchnotrophidae. Body compact, comprising large unsegmented prosome and very short 2-segmented urosome. Prosome consisting of short and narrow, weakly demarcated cephalosome and large lobate trunk (homologous to fused pedigerous somites 1–4). Trunk with deep transverse furrows; with 3 pairs of short, robust lateral processes (arising from pleural areas of first 2 pedigerous somites) and pair of large lobate outgrowths derived from posterolateral angles of P2-bearing somite; posterior part narrow and cylindrical, corresponding to fused 3rd and 4th pedigerous somites. Urosome comprising P5-bearing somite and 1-segmented genito-abdomen. Caudal rami with stylet-like apical seta and at least 2 well-developed accessory setae along outer margin. Genital apertures ventrolateral, without armature.

Antennule short, indistinctly 4-segmented; segment 1 with 2 strong spines. Antenna 3-segmented, comprising coxo-basis and 2-segmented endopod; distal endopod segment drawn out into strong hook. Mandible with short gnathobase tapering into apically dentate blade. Maxillule unconfirmed. Maxilla 2-segmented; syncoxa unarmed, allobasis a small segment with 1 spine and 1 seta.

Legs 1 and 2 minute, biramous, unsegmented; protopod with outer basal seta; endopod represented by small spinous outgrowth; exopod short, drawn out into apical claw and bearing several vestigial elements. Legs 3–5 absent.

Egg-sacs relatively small, kidney-shaped, multiseriate, containing large eggs; attached subterminally to genital somite.

Type Species.—*Lomanoticola insolens* Scott and Scott, 1895 [by monotypy].

Other Species.—*Splanchnotrophus brevipes* Hancock and Norman, 1863 = ***L. brevipes*** (Hancock and Norman, 1863), new combination.

Remarks.—Delamare Deboutteville (1950) reviewed the synonymy of *L. insolens* and the remarkably strong affiliation to its only host, *Lomanotus genei,* permitted him to attribute earlier misidentified splanchnotrophid records to this species (Bergh, 1879; Vayssière, 1901, 1903). He also pointed out that Scott and Scott's (1895) claim of four pairs of lateral processes in *L. insolens* was based on an observational error, the supernumerary pair of processes being in reality the produced posterolateral angles of the P2-bearing somite. The species shows a boreo-mediterranean distribution, whereas *L. brevipes* is restricted to NW Europe but utilizes a wider range of nudibranch hosts (Table 1).

Arthurius, new genus

Jensen (1990) described *Splanchnotrophus elysiae* from the sacoglossan *Elysia australis* (Quoy and Gaimard, 1832) and placed it in the subgenus *Lomanoticola*. Re-examination revealed radical differences in the morphology of both sexes, justifying its placement in a new genus.

Diagnosis.—Splanchnotrophidae. Body ♀ compact, comprising large, bulbous prosome and very small, incompletely 2-segmented urosome. Prosome unsegmented, consisting of small cephalosome demarcated by lateral constriction, and lobate trunk (homologous to fused pedigerous somites 1–5). Trunk with 3 pairs of large lateral processes and 1 pair of small anteroventral processes; all processes ending in terminal bulb; anteroventral and posterior pair of lateral processes possibly derived from protopodal outgrowths of legs 1 and 2. Urosome dorsally displaced, comprising wide genital (double-)somite and minute anal somite. Caudal rami oval, longer than wide, unarmed. Legs 1 and 2 vestigial, associated with anteroventral and posterolateral processes; represented by small exopodal and endopodal lobes bearing rudimentary elements. Legs 3–5 absent. Genital apertures large laterodorsal slits.

Body ♂ relatively unmodified, cyclopiform; comprising cephalosome, indistinctly 4-segmented prosome and 3-segmented urosome; without any lateral or dorsal processes. Somites bearing P1 and P2 fused laterally; remaining prosomites limbless and cylindrical. Cephalosome and pedigerous somites expanded laterally and dorsally. Urosome comprising P5-bearing somite, genital somite and small anal somite. Caudal rami elongate, with 2 ventral spinular patches and 2 terminal spines. Legs 1 and 2 biramous, comprising coxa, basis, 1-segmented endopod and incompletely 2-segmented exopod; rami armed with well-developed spines. Legs 3–5 absent. Genital opercula unarmed.

Antennule very short and dorsoventrally flattened, 1-segmented; with several vestigial setae; further reduced in ♂. Antenna sexually dimorphic; 2-segmented, comprising coxo-allobasis and 1-segmented endopod; coxo-allobasis slender in ♀, robust in ♂; endopod drawn out into strong hook in ♂ and less chitinized, blunt claw with 6 rudimentary elements in ♀. Mandibles and maxillules absent. Oral opening a narrow transverse slit. Labrum and paragnaths completely absent in ♀; labrum a small chitinized outgrowth in ♂, and paragnaths possibly represented by medially incised crest. Maxilla sexually dimorphic; 2-segmented in ♀, comprising unarmed syncoxa and short, sigmoid allobasis; represented by unsegmented pointed appendage in ♂.

Egg-sacs sausage-shaped, multiseriate, eggs large; attached at proximal end to genital somite.

Type Species.—*Splanchnotrophus elysiae* Jensen, 1990 = ***Arthurius elysiae*** (Jensen, 1990), new combination.

Etymology.—The genus is named after Arthur G. Humes in recognition of his tremendous contribution to parasitic copepod taxonomy. Gender: masculine.

Arthurius elysiae (Jensen, 1990), new combination

Type Locality.—Eagle Bay, Cape Naturaliste, Western Australia. Endoparasitic in *Elysia australis* (Quoy and Gaimard, 1832) (Opisthobranchia, Sacoglossa, Elysiidae).

Material Examined.—From Dr. K. R. Jensen: 2 ♀♀ (1 ovigerous) in alcohol (NHM 2000.893–894), 1 ♀ dissected on 5 slides and remaining parts in alcohol (NHM 2000.892), and 1 ♂ dissected on 6 slides (NHM 2000.891). All specimens dissected out of 2 specimens of *Elysia australis*. Radar Reef, Rottnest Island, Western Australia; 16 January 1996; coll. K. R. Jensen.

Redescription of Female.—Body length measured from rostral margin to distal end of posterior pair of lateral processes: 1.42–1.45 mm (*n* = 3). Body (Figs. 7A, 8A) compact, about as wide as long; comprising large, swollen prosome and very small urosome. Cephalosome globular, demarcated from rest of prosome by lateral constriction (Fig. 8A). Prosome unsegmented, showing considerable allometric growth ventrally causing dorsad displacement of urosome (Fig. 7A); pleural areas produced into 3 pairs of robust processes, anterior and middle pairs laterally directed, posterior pair backwardly directed; additional pair of smaller ventral processes arising from raised area between first and second pair of lateral processes; all processes typically constricted subdistally forming terminal bulb.

Urosome pointing upwards, discernible only in lateral (Fig. 7A) or dorsal aspect; clearly separated from prosome by functional articulation; comprising laterally expanded genital (double-)somite and minute anal somite (Fig. 7B); somites separated ventrally but completely fused dorsally. Genital (double-)somite (Fig. 7B) with numerous integumental pores; genital apertures large laterodorsal slits without armature. Caudal rami (Fig. 7C) oval, slightly divergent; about 2.2 times as long as wide; with 2 pores along outer margin and 2 minute spinous projections around distal margin.

Antennule (Fig. 8B) very short, represented by dorsoventrally flattened, paddle-shaped segment; ventral surface with 8 rudimentary elements and distal margin with 9 vestigial setae. Antenna (Fig. 8C) 2-segmented; coxo-basis and proximal endopod segment fused, forming cylindrical coxo-allobasis, with 2 spiniform elements; free endopod 1-segmented, modified into a claw-shaped segment with blunt apical portion and 6 rudimentary elements. Labrum not developed but area between antennae with slight median swelling bearing irregular pattern of pores (Fig. 10C). Mandibles, maxillules, and paragnaths absent. Oral opening (arrow in Fig. 10C) a narrow transverse slit (Fig. 8D). Maxilla (Fig. 8D) 2-segmented, comprising unarmed syncoxa with bulbous medial margin and short allobasis drawn out into sigmoid claw and bearing accessory spinous process at base.

Legs 1 and 2 widely separated, vestigial (Figs. 7A, 8A). Leg 1 (Fig. 7D, E) arising from ventral swelling and associated with anteroventral processes; biramous, rami represented by small lobate outgrowths; endopod smaller than exopod, with 2 rudimentary elements; exopod with 1 apical and 3 lateral rudimentary elements. Leg 2 (Figs. 7F, 8A) arising from proximal portion of posterolateral processes; smaller than leg 1, biramous; exopodal lobe largest, with 1 rudimentary element; endopodal lobe bifid at tip. Legs 3–5 absent.

Egg-sacs (Figs. 7A, 8A) sausage-shaped, containing several rows of large eggs (130 µm); attached proximally to genital somite.

Redescription of Male.—Body length measured from rostral margin to posterior margin of caudal rami: 440 µm. Body (Fig. 9A) relatively unmodified; comprising indistinctly 5-segmented prosome and 3-segmented urosome; without any lateral or dorsal processes. Cephalosome not fused to first pedigerous somite; with several integumental pores (Fig. 9A). First and second pedigerous somites fused laterally but with distinct tergites dorsally; expanded laterally (being wider than cephalosome) and dorsally, concealing remaining prosomites. Homologues of P3- and P4-bearing somites cylindrical and limbless; with pair of ventrolateral pores (Fig. 10A). Urosome comprising P5-bearing somite, genital somite and small anal somite (Fig. 10A). Genital somite with paired apertures forming common median genital slit without armature (arrowed in Fig. 10A). Caudal rami (Fig. 10A) flaccid and elongate, about 3.5 times as long as wide; with 2 spinular patches on ventral surface and 2 terminal spines.

Antennule (Fig. 9B) very short, more reduced than in ♀, 1-segmented; with large

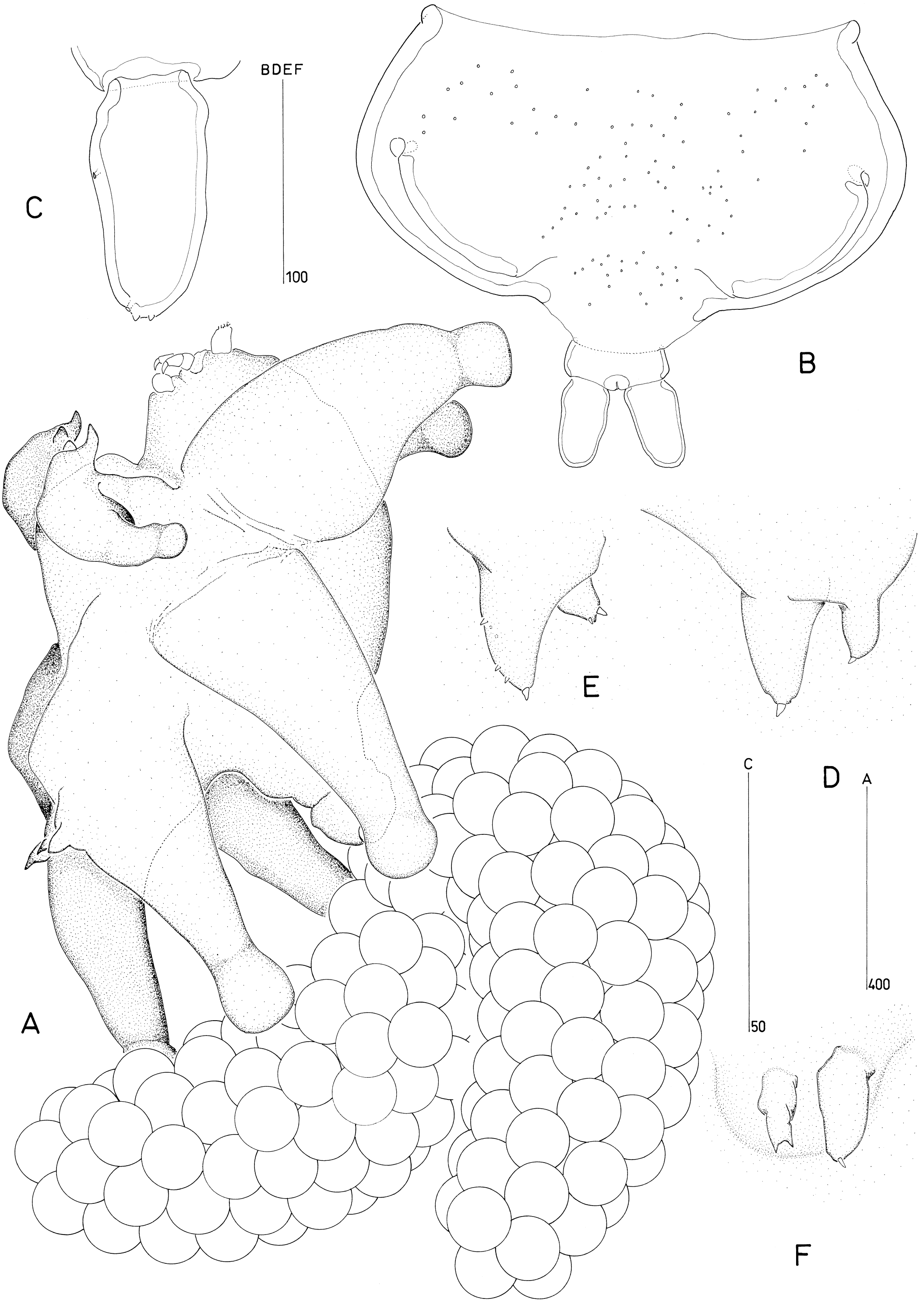

Fig. 7. *Arthurius elysiae* (Jensen, 1990), new combination [♀]: A, habitus, lateral; B, urosome, dorsal; C, caudal ramus, ventral; D, leg 1, anterior; E, same, lateral; F, leg 2, anterior.

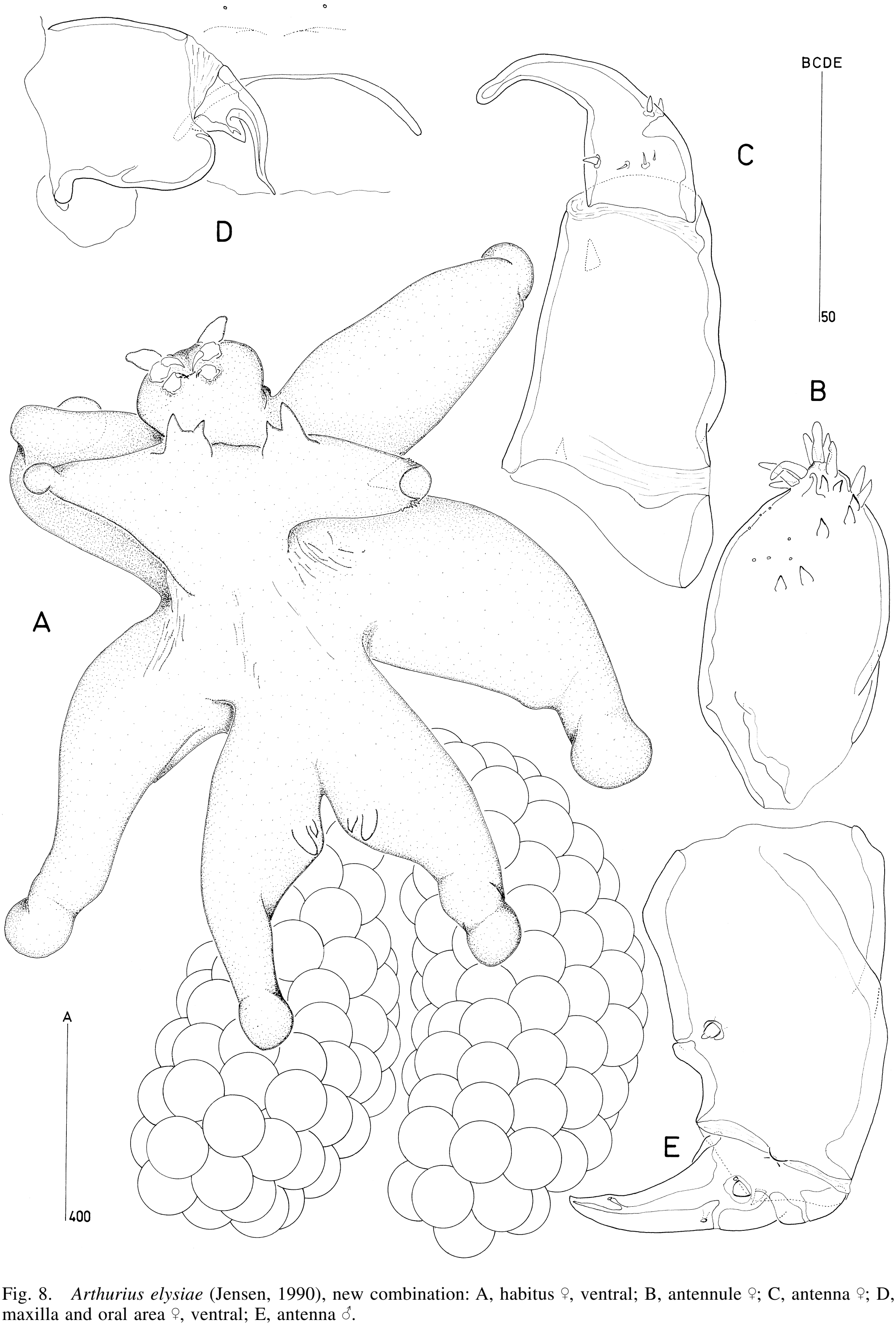

Fig. 8. *Arthurius elysiae* (Jensen, 1990), new combination: A, habitus ♀, ventral; B, antennule ♀; C, antenna ♀; D, maxilla and oral area ♀, ventral; E, antenna ♂.

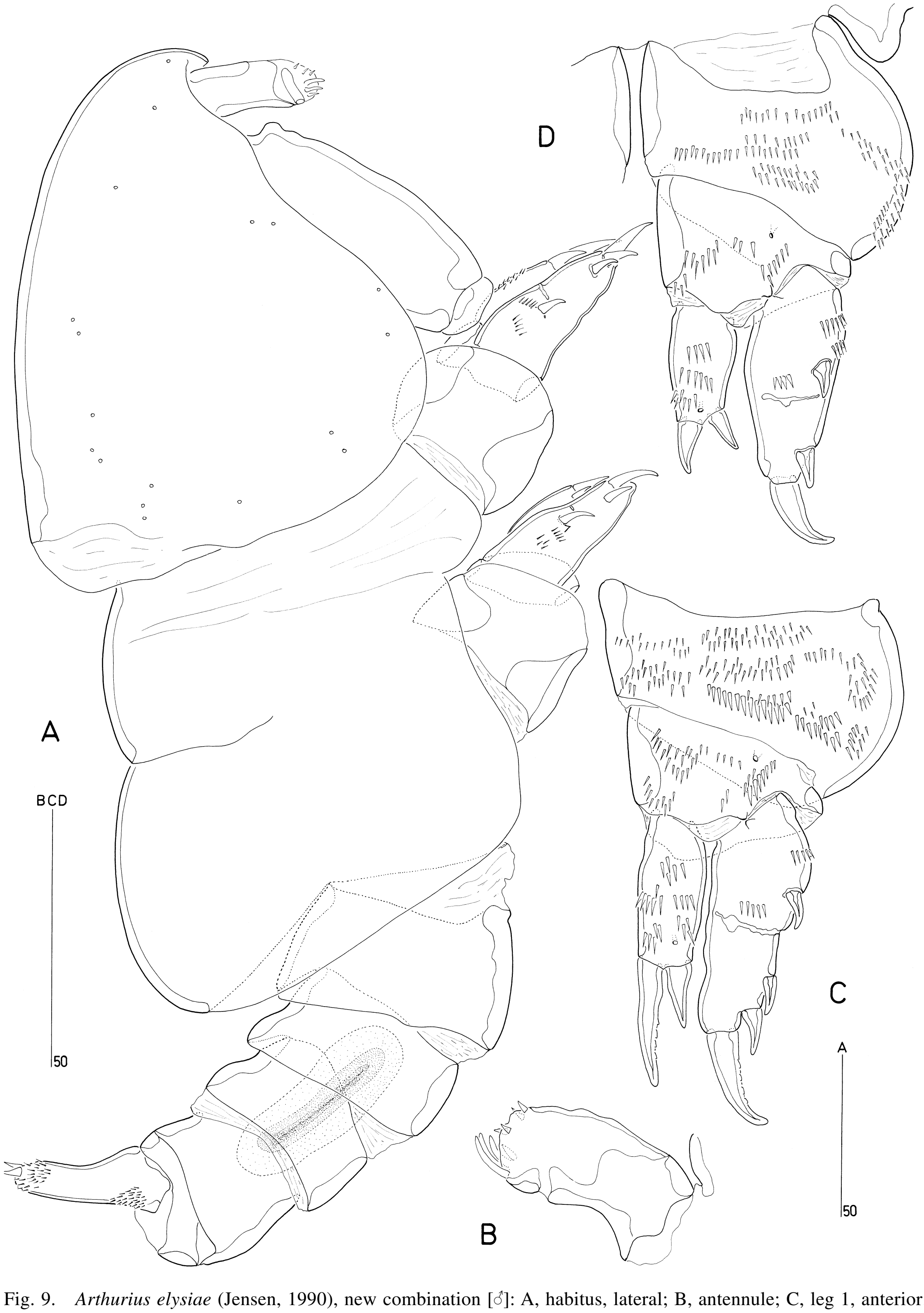

Fig. 9. *Arthurius elysiae* (Jensen, 1990), new combination [♂]: A, habitus, lateral; B, antennule; C, leg 1, anterior; D, leg 2, anterior.

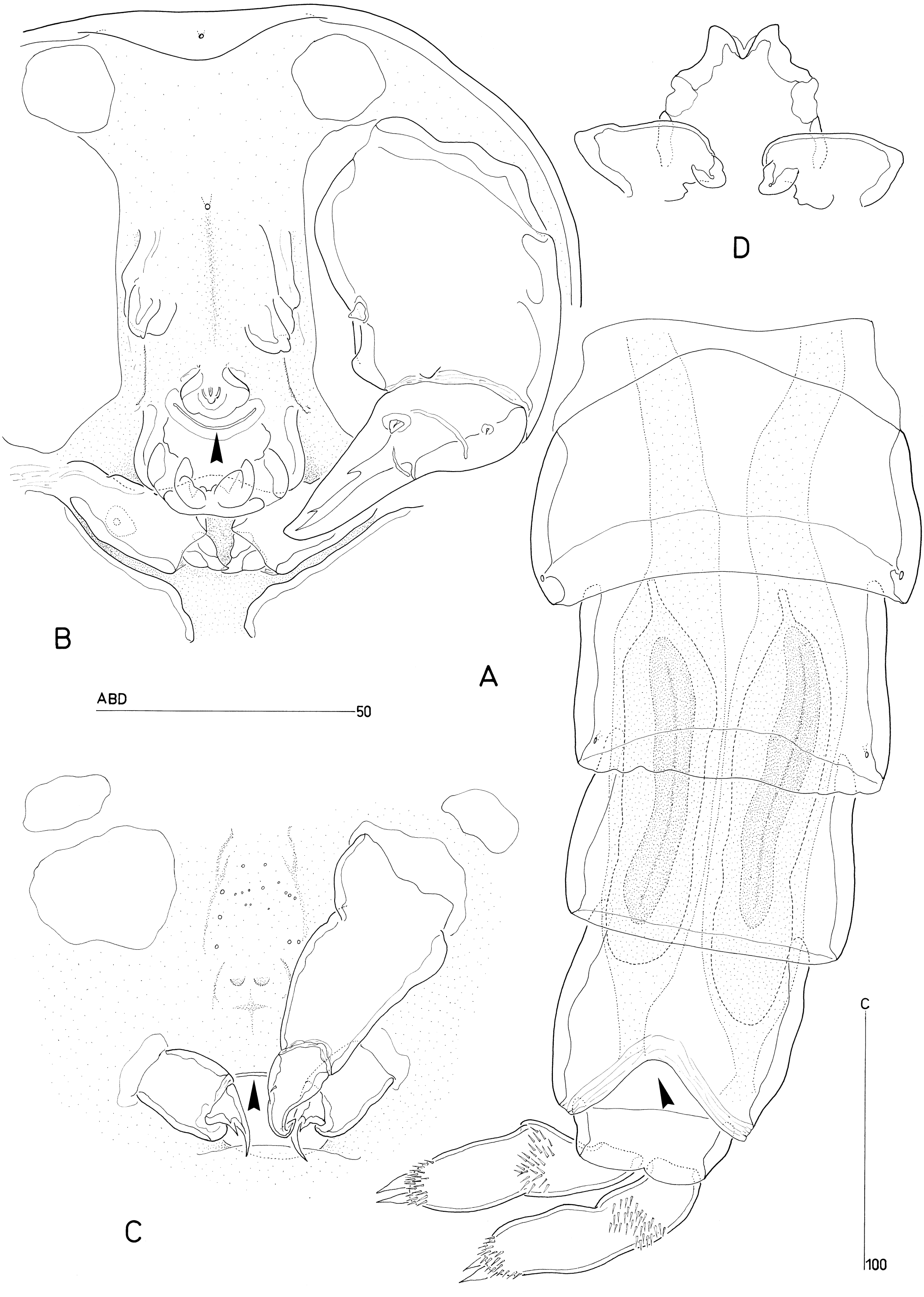

Fig. 10. *Arthurius elysiae* (Jensen, 1990), new combination: A, hind-body ♂, ventral [genital aperture, arrow]; B, oral area ♂, ventral [oral slit, arrow]; C, oral area ♀, ventral [oral slit, arrow]; D, labium and maxillae ♂, posterior.

membranous area; with at least 8 rudimentary elements around apex. Antenna (Figs. 8E, 9D, 10B) strongly chitinized, robust and much larger than in ♀; 2-segmented, comprising coxo-allobasis and 1-segmented endopod; coxo-allobasis with 2 spinous elements, medial margin with blunt process; endopod drawn out into powerful hook bearing 2 minute accessory elements and several pores. Area between antennae slightly raised medially and with paired spinous projections. Labrum a small chitinized, posteriorly directed plate, partly overlying slit-like oral opening (arrow in Fig. 10B). Mandibles and maxillules absent (Fig. 10B). Paragnaths possibly represented by conspicuous, medially incised crest (Fig. 10B, D). Maxillae (Fig. 10D) represented by unsegmented pointed appendages; opening of maxillary gland clearly discernible (stippled in Fig. 10B).

Legs 1 and 2 (Fig. 9C, D) biramous, comprising coxa, basis, 1-segmented endopod, and incompletely 2-segmented exopod; intercoxal sclerites absent; original segmentation of exopods marked by transverse surface suture; all segments with spinular pattern on anterior surface; bases and endopods with integumental pore on anterior surface. Coxae strongly developed, with lobate outer portion; bases without outer seta. Leg 1 (Fig. 9C) exopod with 3 small outer spines and 1 large curved spine distally; endopod with 2 apical spines, inner one twice the size of outer one. Leg 2 (Fig. 9D) with shorter rami; exopod with only 2 lateral spines and apical spines on endopod subequal in length. Legs 3–5 absent.

Spermatophores oval-elongate, paired (Fig. 10D).

Remarks.—The genus *Arthurius* is radically divergent from other splanchnotrophids in the gross reduction of the antennules in both sexes; the absence of both mandibles and maxillules; and the presence of distinct sexual dimorphism in the antennae, maxillae, and the oral area. In no other genus for which both sexes are known is the morphological divergence between males and females so pronounced as in *Arthurius*.

The male of *A. elysiae* is unique in having the cephalosome fully separated from the first pedigerous somite and in possessing two pairs of fully functional swimming legs. The legs have a two-segmented protopod and articulating rami armed with strong spines. Their counterparts in the female are represented by vestigial lobate appendages bearing rudimentary armature elements; at least for leg 1 the number of rudiments in the female corresponds to the number of spines in the male (Figs. 7E, 9C). Despite these unique plesiomorphies, the male is highly derived in other regions of the body. The antennules and the oral area are highly reduced, being concordant with the female pattern, and legs 3 to 5 and the armature of leg 6 are completely lost.

The female of *A. elysiae* differs from other splanchnotrophids in the pattern of the body processes. Comparison with *Splanchnotrophus* suggests that the three pairs of lateral processes in the latter are homologous to the anterior and middle pairs of robust lateral processes and the smaller anteroventral pair associated with the first legs in *Arthurius*. The posterior pair associated with the second legs in the latter is probably homologous with the produced posterolateral angles in *Splanchnotrophus*. Alternatively, comparison with *Ismaila* indicates that the anteroventral and posterior pair of lateral processes could well be derived from protopodal outgrowths of legs 1 and 2 as shown by Ho (1981a, 1987b).

The mosaic of derived and plesiomorphic character states observed in *A. elysiae* demonstrates that the tempo of morphological evolution in different tagmata is not only highly variable but that evolutionary character transformation also proceeds at different rates in each sex, possibly as a result of different functional constraints. In families such as the Splanchnotrophidae and Chondracanthidae, where female- and male-based character sets generate conflicting phylogenetic signal in parsimony analysis, these datasets require to be analysed both separately and combined in a total-evidence approach. A robust phylogeny of the Splanchnotrophidae is at present difficult to obtain since recent surveys (Schrödl and Haumayr, unpublished) have indicated that only a fraction of the taxa is known.

Risbec (1930) illustrated a remarkable copepod from another sacoglossan, *Elysia ornata* (Pease), collected in New Caledonia. The animal, which bears a certain resemblance with lamippids of the genus *Linaresia* Zulueta, 1908, possesses six pairs of slender claviform processes. Monod and Dollfus (1932) identified it as a member of the

Splanchnotrophidae. The attached dwarf male figured by Risbec (1930) is in reality the urosome of the female. Monod and Dollfus (1934) re-examined the single damaged female and concluded that the species probably belongs to a new genus. Their illustrations of the urosome, showing its two-segmented nature, the dorsal displacement and unarmed elliptical caudal rami, in conjunction with the one-segmented antennules, reduced antennae and oral area, and the claviform shape of the body processes reveal an undeniable relationship with *A. elysiae*. Risbec's unnamed species is provisionally placed as *species inquirenda* in *Arthurius*.

Ceratosomicola, new genus

Re-examination of the single extant syntype of *S. sacculatus* O'Donoghue, 1924, the only other species of *Splanchnotrophus* reported from the Indo-Pacific, revealed a suite of unique character states justifying its removal from the latter genus.

Diagnosis (based on ♀ only).—Splanchnotrophidae. Body relatively elongate, comprising large unsegmented prosome and small 3-segmented urosome. Prosome tripartite, comprising small trilobate cephalosome, large middle region and flask-shaped posterior region; middle region widest, produced into 3 transverse bulges dorsally and bearing 3 pairs of very long ventrolateral appendages. Urosome comprising genital (double-)somite, first (or second) abdominal somite and anal somite.

Antennule short, 4-segmented; segment 1 inflated, with 4 spines. Antenna 3-segmented, comprising coxo-basis and 2-segmented endopod; distal endopod segment claw-like, with 6 vestigial elements. Oral area very compact. Labrum well developed, bilobate. Mandibular gnathobase a recurved spinulose blade. Labium produced into paired anterior spinulose lobes and backwardly directed spinulose lobes posteriorly. Maxillule absent. Maxilla weakly chitinized, produced into unarmed, lanceolate endite (allobasis?).

Legs 1 and 2 rudimentary, largely absorbed in ventral wall of prosome; with isolated outer basal seta, exopod represented by small lobe (leg 1) or free elongate segment (leg 2), and exopod represented by spinous ridge (leg 1) or small lobe (leg 2). Leg 3 without basal seta but with vestigial exopod and endopod. Leg 5 (or leg 4?) a single seta. Genital apertures laterodorsal.

Caudal rami globular, with 3 spiniform elements apically.

Egg-sacs cylindrical, multiseriate, containing numerous small eggs; attached at proximal end to genital somite.

Type and Only Species.—*Splanchnotrophus sacculatus* O'Donoghue, 1924 = ***Ceratosomicola sacculata*** (O'Donoghue, 1924), new combination.

Etymology.—The genus is named after the nudibranch host genus *Ceratosoma*. Gender: feminine.

Ceratosomicola sacculata (O'Donoghue, 1924), new combination

Type Locality.—Houtman Abrolhos Islands, Western Australia. Endoparasitic in *Ceratosoma brevicaudatum* Abraham, 1876 (Opisthobranchia, Nudibranchia, Chromodorididae).

Material Examined.—Syntype ♀ of *Splanchnotrophus sacculatus* (NHM reg. no. 1923.1.29.1) dissected on 5 slides (antennules, antennae, mandibles, maxillae, and urosome), remaining parts preserved in alcohol.

Redescription of Female.—Total body length from rostral area to posterior margin of caudal rami: 6.68 mm. Body (Fig. 11A) comprising large prosome, bearing 3 pairs of ventrolateral appendages, and small 3-segmented urosome (Fig. 12B). Prosome (Fig. 11A) tripartite; anterior region small, trilobate, corresponding to cephalosome (Fig. 12A); middle region large, with 3 transverse dorsal bulges, i.e., anterior to first pair, in between first and second pairs, and at level of third pair of ventrolateral appendages; posterior region separated from middle region by strong bilateral constriction posterior to third pair of appendages, posterior 1/5 tapering abruptly. Ventrolateral appendages very long and slender; each distinctly longer than body. Urosome (Fig. 12B) inverted pear-shaped, swollen anteriorly; comprising genital (double-)somite and 2 free urosomites separated by membranous zone; all somites with pattern of distinct integumental pores. Genital somite with paired laterodorsal genital apertures; no armature. Caudal rami (Fig. 11G) globular, with 3 spiniform elements terminally and few spinules on dorsal surface.

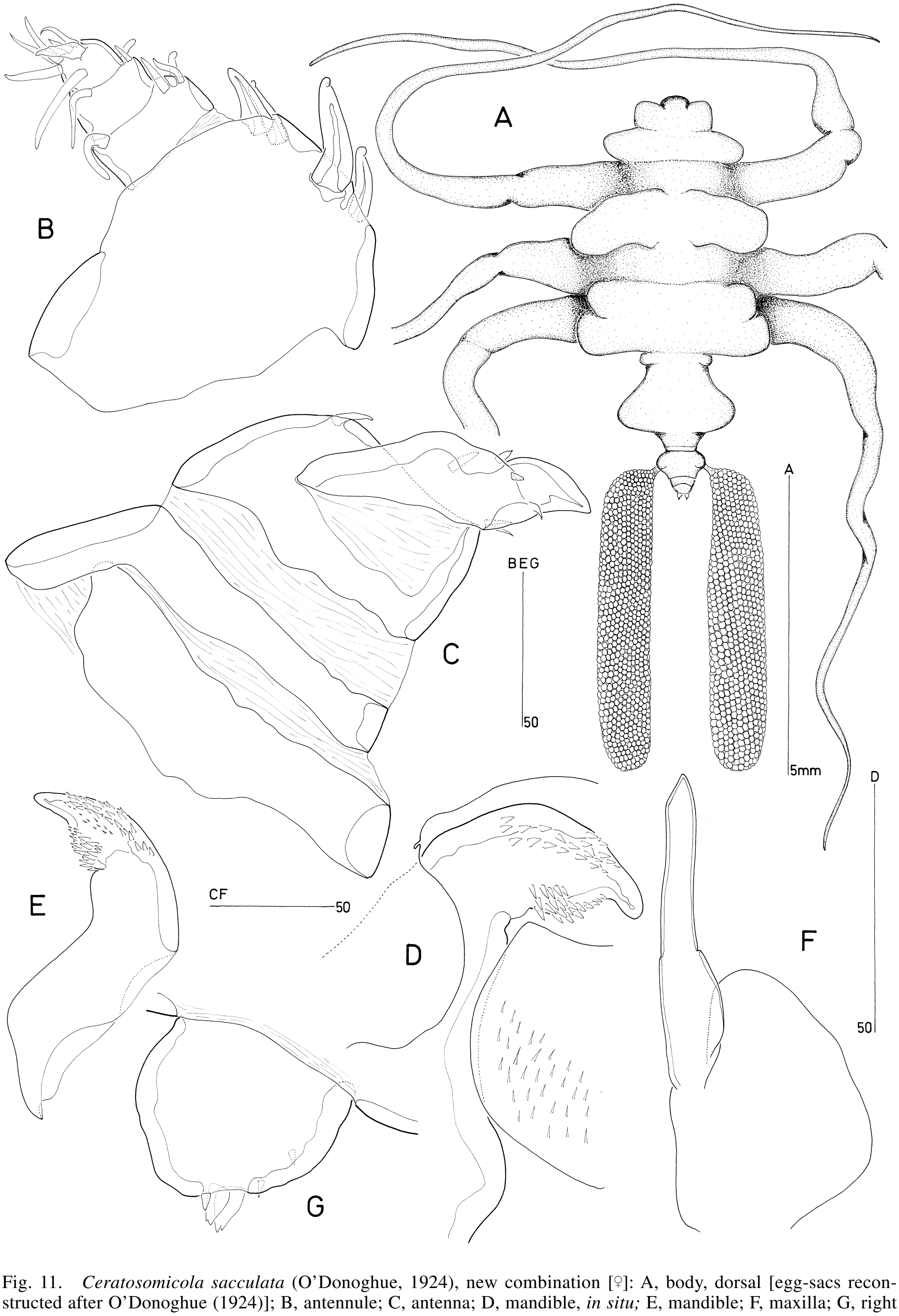

Fig. 11. *Ceratosomicola sacculata* (O'Donoghue, 1924), new combination [♀]: A, body, dorsal [egg-sacs reconstructed after O'Donoghue (1924)]; B, antennule; C, antenna; D, mandible, *in situ;* E, mandible; F, maxilla; G, right caudal ramus, dorsal.

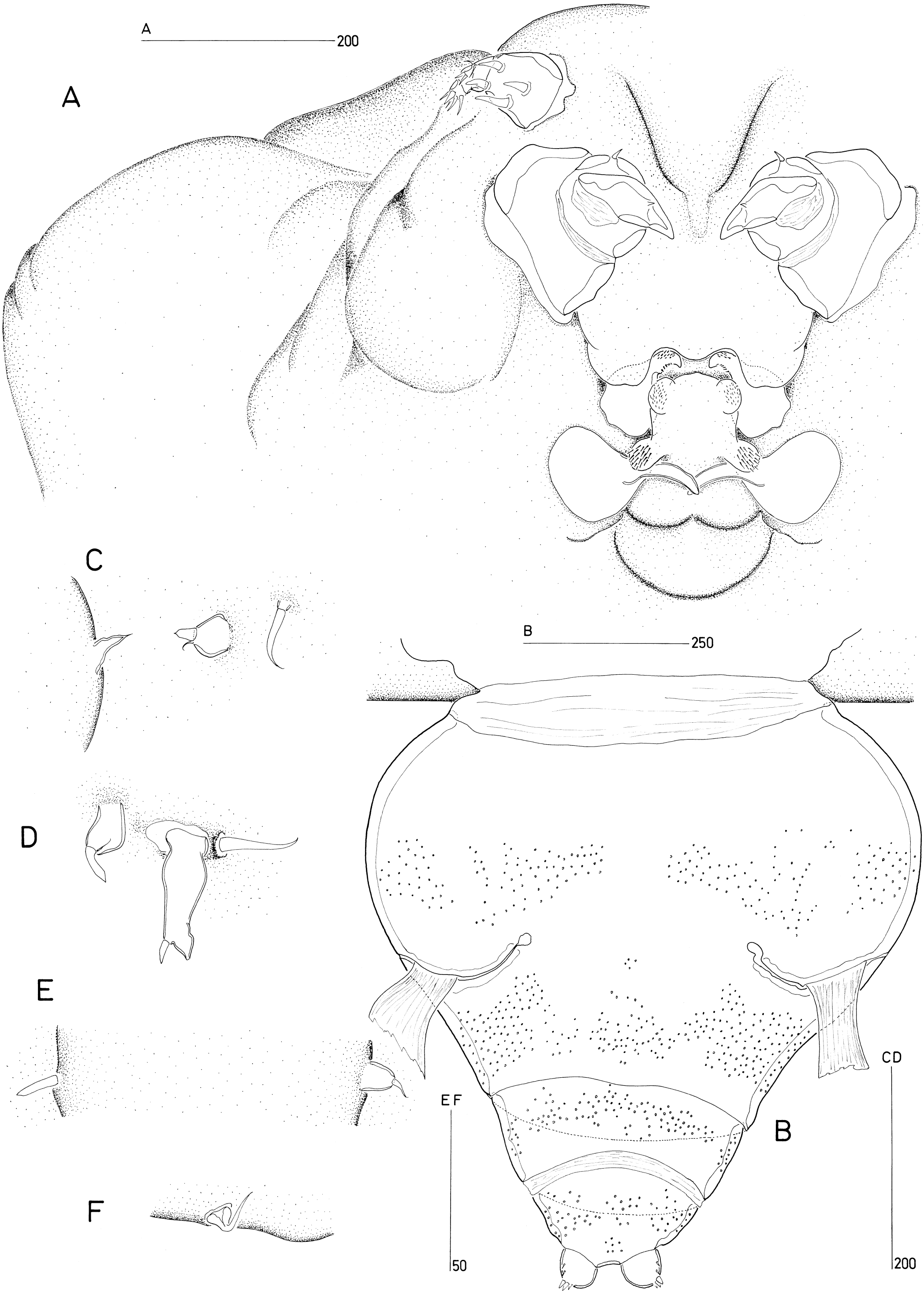

Fig. 12. *Ceratosomicola sacculata* (O'Donoghue, 1924), new combination [♀]: A, cephalosome, ventral view of anterior portion showing antennules, antennae and mouthparts; B, urosome, dorsal; C, left leg 1; D, left leg 2; E, left leg 3; F, left leg 4.

Antennules (Fig. 11B) small, widely separated by midventral rostral swelling (Fig. 12A); 4-segmented; segment 1 inflated and much larger than others, with 4 spines along anterior margin; segment 2 with 1 posterior and 3 anterior elements; segment 3 with 1 posterior and 2 anterior elements; segment 4 with 1 spiniform and 6 setiform elements. Antenna (Fig. 11C) with large sclerite at base; 3-segmented, comprising coxo-basis and 2-segmented endopod. Coxo-basis very short, unarmed; proximal endopod segment with 1 short seta; distal endopod segment claw-like, with total of 6 vestigial elements. Oral area very compact. Labrum (Fig. 12A) bilobate, without ornamentation; lateral lobes enclosing mandibular gnathobases (Fig. 11D). Mandibular gnathobase (Fig. 11D, E) produced into single recurved blade bearing numerous spinules along both anterior and posterior margins. Labium (Fig. 12A) produced into paired anterior spinulose lobes adpressed to mandibular gnathobases (Fig. 11D) and backwardly directed spinulose lobes posteriorly. Maxillules and maxillipeds absent. Maxillae (Figs. 11F, 12A) represented by weakly chitinized appendages, tapering abruptly to unarmed, lanceolate, medially directed endites (probably homologous to allobasis).

Swimming legs rudimentary, largely absorbed in ventral wall of prosome. Leg 1 (Fig. 12C) represented by outer basal seta on small tubercle, small exopodal lobe with 2 apical elements (1 minute), and spinous endopodal element arising from lobate ridge. Leg 2 (Fig. 12D) with basal seta, free elongate exopodal segment bearing 1 subapical element and produced into conical pore, and endopodal lobe bearing curved apical element. Leg 3 (Fig. 12E) with widely separated exopod and endopod, represented by small unisetose lobe and single seta on faint ridge, respectively; no basal seta present. Leg 5 (or leg 4?) (Fig. 12F) represented by single basally swollen seta.

Egg-sacs large (about 75% of body length), cylindrical, containing numerous rows of small eggs (diameter 75 μm).

Male.—Unknown.

Remarks.—O'Donoghue (1924) recorded two specimens of *S. sacculatus* from a single host individual of *C. brevicaudatum*. The present redescription is based on the larger ovigerous specimen which was found lying within the renal duct of the nudibranch with the abdomen and egg-sacs exposed to the exterior. According to O'Donoghue this specimen measured 8.5 mm (our measurement 6.68 mm) and was bigger than the second specimen which was found to be partially embedded in the body wall near the renal pore. The latter specimen is no longer extant.

O'Donoghue described the antennule as three-segmented, possibly as a result of overlooking one of the smaller distal segments. His claim that there are two spines on the basal joint of the antenna is difficult to accept because the segment boundaries shown do not coincide with those illustrated in Fig. 11C. O'Donoghue observed no less than three pairs of postmandibular appendages: maxillae, first and second maxillipeds. His Fig. 66 bears little resemblance to the present observations. The maxillae indicated as minute slender sclerites are difficult to interpret but probably reflect some kind of internal skeletal structures supporting the labium. The first pair of maxillipeds corresponds to the dilated basal portions of the maxillae. The right and left members of the second pair of maxillipeds in reality are the lanceolate endite of the left and right maxillae, respectively. O'Donoghue observed two pairs of papilliform processes in the same relative position as the reduced swimming legs figured by Hancock and Norman (1863) for *S. gracilis*; the less conspicuous third and fourth pairs were overlooked. He also misinterpreted the abdomen as four-segmented, considering the genital (double-?)somite to be subdivided at the level of the genital apertures.

Splanchnotrophus sacculatus resembles typical *Splanchnotrophus* in the presence of three pairs of lateral processes; however, significant differences in virtually every appendage preclude its position in that genus. O'Donoghue differentiated *S. sacculatus* from *S. gracilis* by the presence of dorsal bulges on the prosome, the further reduced swimming legs, the greater length of the ventrolateral appendages, and additional discrepancies noted in the mouthparts. The description of additional *Splanchnotrophus* species has shown that these and other differences are of generic rather than specific value, justifying removal of *S. sacculatus* to a new genus *Ceratosomicola*.

The female of *C. sacculata* combines a number of unique plesiomorphies with many highly derived character states. It is the only splanchnotrophid that has a clearly four-segmented antennule, and the position of the four spines on the first segment indicates that the boundary with the second segment is not homologous with that expressed between the first two segments of *Splanchnotrophus* (Fig. 2A). This implies that the ancestral splanchnotrophid antennule is five-segmented even though the maximum number of segments expressed in any splanchnotrophid is four. The presence of two postgenital somites in the female is also a unique plesiomorphic state in the family. The cylindrical shape of the egg-sacs is shared with *Ismaila* and is probably the ancestral condition.

The isolated position of *Ceratosomicola* is particularly illustrated by the many reductions such as in the armature of the antenna and caudal ramus, the complete loss of the maxillules (as in *Arthurius*), and the transformation of the maxillae into unarmed lanceolate appendages. The mandible is radically different from the types found in *Ismaila* and *Splanchnotrophus* and is probably derived from the latter through reduction. All four pairs of swimming legs are present, but each is strongly reduced to mere rudiments possibly as a result of extreme neotenic development.

Fujita's (1895) description of an unnamed species of *Splanchnotrophus* associated with the nudibranch *Hypselodoris festiva* (Adams) was based on a slightly incomplete specimen; however, his illustrations of the body and cephalic region appear to indicate that he was dealing with a species of *Ceratosomicola*.

Affiliation of *Briarella* Bergh, 1876, and *Chondrocarpus* Basset-Smith, 1903

The genus *Briarella* exclusively contains copepods endoparasitic in dorid nudibranchs in the Indo-Pacific. Bergh (1876) briefly compared the genus with *Splanchnotrophus* and *Ismaila* but claimed that it was probably closely related to the phylichthyids. His original descriptions of the type species *B. microcephala* Bergh, 1876, and of a second unnamed species parasitizing *Glossodoris elisabethina* (Bergh, 1876), are both inadequate and contain no information on mouthpart morphology. Monod (1928) illustrated the full complement of cephalic appendages in *B. risbeci* Monod (1928), however, misinterpreted the maxillule as the mandibular palp. He allocated *Briarella* to the Chondracanthidae but subsequently (Monod and Dollfus, 1932) transferred it to the Splanchnotrophidae. In their illustrations of *B. disphaerocephala*, Monod and Dollfus (1932) correctly labelled the maxillules but did not make any reference to these appendages in the text. Monod and Dollfus claimed that they were unable to observe the maxillipeds in the female of *B. disphaerocephala,* yet clearly show these appendages in the illustrations and furthermore state that the male maxillipeds differ in shape from those of in female. This internal inconsistency and the ambiguities surrounding the correct interpretation of the maxillules and mandibles are the main reasons why the position of *Briarella* remained in a state of flux. Laubier (1964) considered the presence of maxillipeds sufficient evidence to justify its exclusion from the Splanchnotrophidae.

Izawa (1976) recognized *Briarella* as a likely candidate for inclusion in the Philoblennidae, a monogeneric family of endoparasitic copepods associated with gastropod molluscs in the Far East. Supporting evidence for this affinity was found in the close similarity of the antenna, labrum, and maxilla between *Philoblenna* and *Briarella*. Izawa pointed out that the major antennary claw in these genera is derived from a transformed apical element, whereas in the Chondracanthidae it originates from the penultimate segment. On the basis of these non-homologous character states he rejected Laubier's (1964) placement of *Briarella* in the Chondracanthidae. Ho (1981b) supported Izawa's (1976) conviction, but Jensen (1987) proposed maintaining *Briarella* as a member of the Splanchnotrophidae pending thorough re-examination of the mouthparts.

Re-examination of the syntypes of both *Briarella ribesci* (♀: reg. no. MNHN Cp1046) and *B. disphaerocephala* (♀: reg. no. MNHN Cp1483) provides strong evidence justifying placement of *Briarella* in the Philoblennidae. Both *Briarella* and *Philoblenna* have two subequal strong claws on the distal margin of the antenna. The prominent labrum (Fig. 2G) typically encloses the mouthparts by forming lateral lobes that extend to the bases of the maxillae as described for *Philoblenna arabici* by Izawa (1976). The mandible (Fig. 2H) has the typical philoblennid morphology, bearing coarse teeth along the ventral margin and fine setules or spinules along the dorsal margin. The maxillule (Fig. 2G) is not an unarmed lobe as figured in previous descriptions but possesses 3 setae. The maxilla (Fig. 2G) displays a subapical element on the allobasis which is a philoblennid attribute (Ho, 1981b; Avdeev *et al.,* 1986; Ho and Kim, 1992), probably overlooked by Izawa (1976). Finally, the female maxilliped (Fig. 2G) resembles that of *Philoblenna* in the reduction of the endopodal claw and the indistinct separation of the endopod and basis.

The genus *Philoblenna* is known only from prosobranch gastropods, including littorinids and cowries, and is more primitive than *Briarella* in swimming-leg segmentation and armature. The latter differs primarily from the type genus by the presence of four pairs of lobate extensions on the prosome.

Eliot (1903) illustrated an unnamed copepod from the dorid *Sclerodoris coriacea* Eliot, 1903, collected from a cave on the east coast of Zanzibar. The general habitus, showing the lobate extensions, leaves little doubt that he was dealing with a species of *Briarella,* possibly *B. microcephala* according to Monod and Dollfus (1934).

Bassett-Smith (1903) proposed the genus *Chondrocarpus* for two endoparasitic copepods from unnamed pleurobranchids collected in Zanzibar. Due to the grossly inadequate description of *C. reticulosus,* the position of the genus has remained enigmatic since its inception. Despite the large size (12 mm!) of the parasite, Bassett-Smith claimed that antennules, antennae, and thoracic appendages were lacking, and only two pairs of uncinate appendages, possibly representing mandibles and maxillae, were discernible. The dwarf male attached to the posterior end of the female urosome is almost certainly one of the caudal rami. On the basis of general body facies the genus *Chondrocarpus* is here provisionally placed as *genus incertae sedis* in the Philoblennidae. The presence of four pairs of lobate processes on the prosome is reminiscent of the condition in *Briarella,* but the excessively short abdomen, the apparent absence of swimming legs, and the total lack of information on the mouthparts prevent synonymizing both genera. Differences in the shape and relative position of the prosomal processes seems to suggest that Bassett-Smith's (1903) unnamed species *Chondrocarpus* sp. is not conspecific with the type species *C. reticulosus* but rather close to *Splanchnotrophus* sp., illustrated by Gohar and Abul Eha (1957) and recorded from the pleurobranchid notaspidean *Berthellina citrina* (Rüppell and Leuckart, 1828) near Al Ghardaqa (Egypt).

Proposal of Micrallectidae, new family

The marginal position of *Micrallecto* and *Nannallecto* in the Splanchnotrophidae has been hinted at by various authors, but none of them was able to make a strong recommendation for placement in another family. Both genera utilize gymnosome pteropods as hosts, are known from females only, and have remained monotypic since their original description. Re-examination of the type material of *M. uncinata* and *N. fusii* revealed glaring observational errors in Stock's (1971, 1973) descriptions. Collections of the pteropod *Pneumodermopsis* (*Pneumodermopsis*) *paucidens* (Boas, 1866) (the type host of *N. fusii*) deposited in the Mollusca Section of the Natural History Museum were examined for parasitic copepods. This resulted in the discovery of the first male micrallectid, which provided the final piece of evidence justifying the proposal of a new family. There is no relationship with the genus *Megallecto* Gotto, 1986, which is based on an artefact as illustrated below.

Micrallectidae, new family

Diagnosis.—Poecilostomatoida. Body unsegmented, bulbous; anterior part retractable under dorsal shield; no differentiation of tagmata; with 4 pairs of conspicuous lateral sensillae. Sexual dimorphism in oral area, maxillule, and genital region. Rostrum lobate. Antennule short, bipartite; with several flaccid setae on distal portion. Antenna comprising coxo-basis and indistinctly 2-segmented endopod; proximal endopod segment with 1 seta; distal segment with 1 lateral element and 2 coronary grasping spines plus 1 vestigial seta apically. Labrum unarmed lobe. Mandible with rudimentary asetose palp and short gnathobase bearing 3 or 4 ventrally directed, curved teeth. Paragnaths forming membranous labium. Maxillule anteriorly displaced to base of antennule, modified into strong grasping appendage in ♀; absent in ♂. Maxilla strongly developed, chelate; comprising syncoxa and allobasis. Maxilliped well developed, 3-segmented, not sexually dimorphic; comprising syncoxa, basis, and enlarged endopod bearing 2 serrate lobes. Swimming legs completely absent. Postmaxillipedal region highly folded in ♀, with large, longitudinal genital slit; produced into ventrally directed cylindrical extension in ♂, bearing apical genital aperture. Caudal rami presumably represented by paired areas of highly folded invaginated cuticle.

Nauplii lecithotrophic, developing inside ♀ (ovovivipary); maxilla appearing before other appendages.

Marine; ectoparasites of gymnosome pteropod gastropods.

Type and Only Genus.—*Micrallecto* Stock, 1971.

Micrallecto Stock, 1971

Synonym.—*Nannallecto* Stock, 1973.

Diagnosis.—As for family.

Type Species.—*Micrallecto uncinata* Stock, 1971 [by monotypy].

Other Species.—*Nannallecto fusii* Stock, 1973 = ***M. fusii*** (Stock, 1973), new combination.

Micrallecto fusii (Stock, 1973), new combination

Type Locality.—Off French Guiana; 07°09.8′–07°11.5′N, 53°37.2′–53°33.2′W, surface tow; on *Pneumodermopsis (Pneumodermopsis) paucidens* (Boas, 1866).

Material Examined.—(a) Paratype ♀ dissected on slide (ZMA Co. 102.398b); (b) The Natural History Museum: 3 ♀♀ and 1 ♂ found on specimens of *P. (P.) paucidens* deposited in Mollusca Section under reg. no. 1921.9.14.222–247; collected by Irish Fishery Board off W and SW Ireland; 16 November 1912; 126 m depth; 1 ♀ dissected on 6 slides (NHM reg. no. 2000.1050), 2 ♀♀ (1 incomplete) in alcohol (NHM reg. no. 2000.1051–1052), 1 ♂ prepared for SEM.

Redescription of Female.—Body length 305–315 μm ($n = 2$). Body (Fig. 13A) bulbiform, comprising anterior region bearing antennules, antennae, mandibles and maxillules, and posterior region bearing maxillae and maxillipeds. No differentiation in tagmata but anterior region apparently retractable under dorsal shield of posterior region. Dorsal surface without ornamentation but lateral areas with 4 pairs of conspicuous annulated sensillae (arrows in Figs. 13A, 16A). Rostrum relatively small, represented by lobate extension.

Antennule (Fig. 13B, C) short, without segment boundaries but clearly bipartite; major flexure point indicated by membranous area (cf. ♂: Fig. 17D); proximal portion unarmed, distal portion outwardly directed, armed with 19 flaccid or rudimentary elements; only 7 elements well developed, others represented by stumpy spines or setal Anlagen.

Antennae (Fig. 13D) located between antennules (Fig. 14A); indistinctly 3-segmented. Coxo-basis well developed, unarmed. Endopod indistinctly 2-segmented; proximal segment with 1 stubby lateral seta; distal segment with similar lateral seta, apical margin with 2 coronary grasping spines and vestigial seta (arrow in Fig. 13E); grasping spines each fused to small basal sclerite and consisting of corona of 14–18 recurved hooks; area around sclerites membranous and capable of invaginating (Fig. 13D) during retraction of grasping spines (Fig. 13D, F).

Labrum (Fig. 14A) posteriorly directed, abruptly tapering lobe; no ornamentation discernible. Lateral margins of oral cavity forming anterior notch encircling rudimentary mandibular palp (arrow in Fig. 14A). Posterior margin of oral cavity formed by steep membranous labium (Fig. 14A); surface highly folded and posterior face with cuticular reinforcements around oesophagus (Fig. 14B); no trace of individual paragnaths discernible.

Mandible (Fig. 14A, F) comprising large robust coxa and rudimentary palp. Coxal gnathobase narrow, with 3 curved teeth; directed ventrally (Fig. 14B). Palp asetose, highly wrinkled vestige.

Maxillule anteriorly displaced to preoral position, near base of antennule (Fig. 14A); modified into powerful grasping appendage. Outer lobe separated from basal part of maxillule by membranous inserts allowing for flexure (Fig. 14C, E); typically reflexed, positioned alongside outer surface of basal portion (Fig. 14C, D); drawn out into 2 recurved hooks, anterior one being twice the size of posterior; with 1 accessory element near base. Basal portion robust, dilated proximally; with 1 stubby element near transition to outer lobe (Fig. 14A, C–E); inserting laterally on bulbous cephalic pedestal housing strong extrinsic maxillulary musculature (p. in Fig. 13A).

Maxilla (Fig. 14G–I) chelate, arising from broad cylindrical outgrowth consisting of chitinized anterior face and thin posterior and lateral flexure zones (Fig. 13A); 2-segmented,

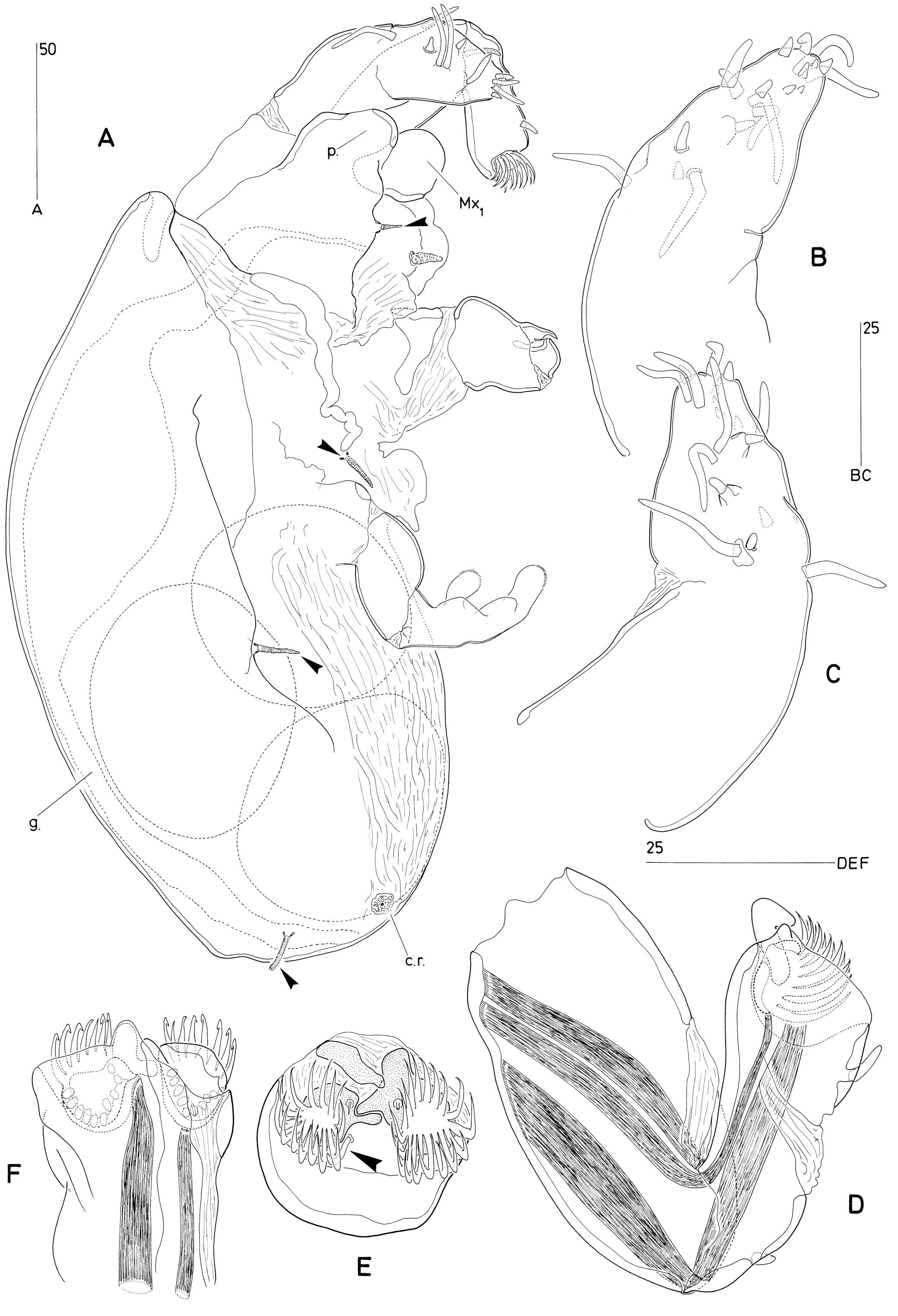

Fig. 13. *Micrallecto fusii* (Stock, 1973), new combination [♀]: A, habitus, lateral [arrows indicate sensillae; c.r., rudimentary caudal rami; g., gut; p., cephalic pedestal supporting maxillule (Mx_1)]; B, antennule, ventral; C, antennule, dorsal; D, antenna; E, distal part of antennary endopod, frontal [vestigial element, arrow]; F, same, ventral.

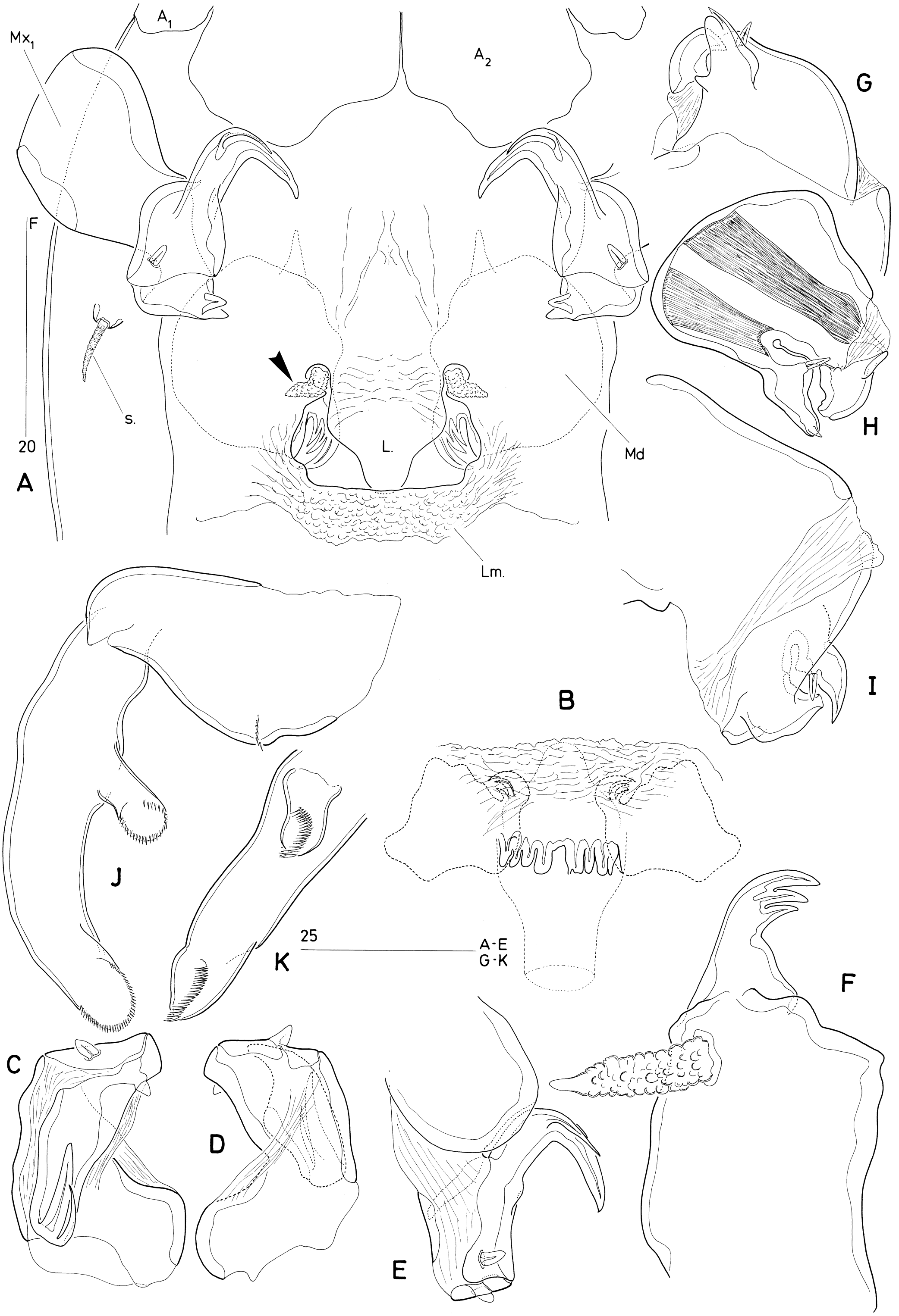

Fig. 14. *Micrallecto fusii* (Stock, 1973), new combination [♀]: A, oral area, ventral [rudimentary mandibular palp, arrow; A$_{1-2}$, insertion sites of antennules and antennae; L., labrum; Lm., labium; Md, mandible; Mx$_1$, maxillule; s., sensilla]; B, posterior view of labium showing cuticular reinforcements around oesophagus; C, maxillule, medial; D, maxillule, outer; E, maxillule, anterior; F, mandible; G, maxilla, medial; H, maxilla, showing musculature in distal segments; I, maxilla, outer; J, maxilliped; K, endopod of maxilliped, medial.

comprising large syncoxa and small allobasis. Syncoxa produced into posteriorly directed spinous process bearing 1 small element laterally. Allobasis short, represented by small hook-shaped segment without accessory armature; tip probably broken off during removal from host (compare ♂).

Maxilliped large, well developed, medially directed; 3-segmented, comprising syncoxa, basis, and endopod. Syncoxa small, unarmed. Basis elongate, with few spinules along palmar margin (Fig. 14J), unarmed. Endopod enlarged, slightly longer than basis; bearing 1 apical and 1 medial unilaterally serrate lobe (Fig. 14J, K); lobes possibly representing modified incorporated elements. Maxillipeds widely separated; small sclerite discernible at outer basal corner.

Swimming legs completely absent. Postmaxillipedal region highly folded ventrally and ventrolaterally (Figs. 13A, 16A); with large, longitudinal genital slit running from bases of maxillipeds to just anterior to rudimentary caudal rami (arrow in Fig. 16A). Posterior part of body containing small number of large eggs (about 80 μm in diameter). No trace of copulatory pore(s) or genital armature.

Caudal rami presumably represented by paired areas of internally folded cuticle (possibly homologous to invaginated caudal seta); located subterminally and ventral to anus (Figs. 13A, 16A).

Description of Male.—Markedly smaller than ♀ (Figs. 15, 17A); body length 220 μm (n = 1). Body shape generally as in ♀ but slightly more compact. Cephalic outgrowth supporting maxillule absent. Postmaxillipedal region shorter than in ♀; produced into large ventrally directed cylindrical extension, bearing single apical genital slit. Single median testes lying dorsal to gut at about level of maxillae and maxillipeds (Fig. 15); with paired lateral lobes extending backwards; various stages of spermatogenesis discernible. Spermatophore containing spindle-shaped spermatozoa stored in seminal vesicle. Ejaculatory duct lined by strongly folded cuticle.

Antennules, antennae, and maxillipeds not sexually dimorphic.

Mandibles (Figs. 16B, 17B) as in ♀ but largely fused to lateral margins of oral cavity. Labrum and labium less well developed. Functional gut and anus present.

Maxillules completely absent.

Maxilla (Fig. 16C) as in ♀ but accessory element on spinous process of syncoxa fused at base; process with small socket functioning as cavity to receive tip of allobasal claw (Fig. 17C).

Micrallecto uncinata Stock, 1971

Type Locality.—West of Bermuda, 32°10′–31°58′N, 62°49′–62°47′W; on *Pneumoderma pygmaeum* (Tesch, 1903); plankton haul 0–860 m.

Material Examined.—Holotype ♀ dissected on slide (ZMA Co. 102.348).

Additional Observations of ♀.—Antennule bipartite with membranous flexure zone along posterior margin, not clearly 2-segmented as illustrated by Stock (1971); setal number similar to that of *M. fusii;* triangular spine-like projection shown by Stock representing an incomplete element.

Antenna (Fig. 18A, B) with indistinctly 2-segmented endopod as in *M. fusii;* proximal segment presumably bearing lateral element, position of which indicated by round scar (large arrow in Fig. 18A); distal segment with well-developed lateral seta, two coronary grasping spines, and one minute element (small arrow in Fig. 18A) around the apex. Each grasping spine with about 25 curved hooks.

Mandible (Fig. 18C) with rudimentary palp; gnathobase with 4 curved teeth.

Maxillule (Fig. 18D) with membranous inserts between hooked outer lobe and basal portion; anterior hook only slightly larger than posterior; no accessory elements discernible.

Maxilla missing in slide preparation.

Maxilliped with segmentation as in *M. fusii;* endopodal subdivision drawn by Stock based on integumental fold accentuated by excessive squashing. Endopodal lobate extensions unilaterally serrate.

Posterior body region containing developing nauplii (Fig. 18E), each with 1 pair of chelate appendages (Fig. 18F).

Caudal rami as in *M. fusii.*

Discussion.—Reinterpretation of Appendages.—Stock (1971) recognized six pairs of limbs in *M. uncinata,* which he identified as the antennules, antennae, mandibles, maxillae, and legs 1 and 2. A seventh pair, the maxillipeds, was recognized in his description of *M. fusii* (cf. Stock, 1971). He explained the alleged absence of maxillules by assuming that *Micrallecto* and *Nannallecto* belonged to the

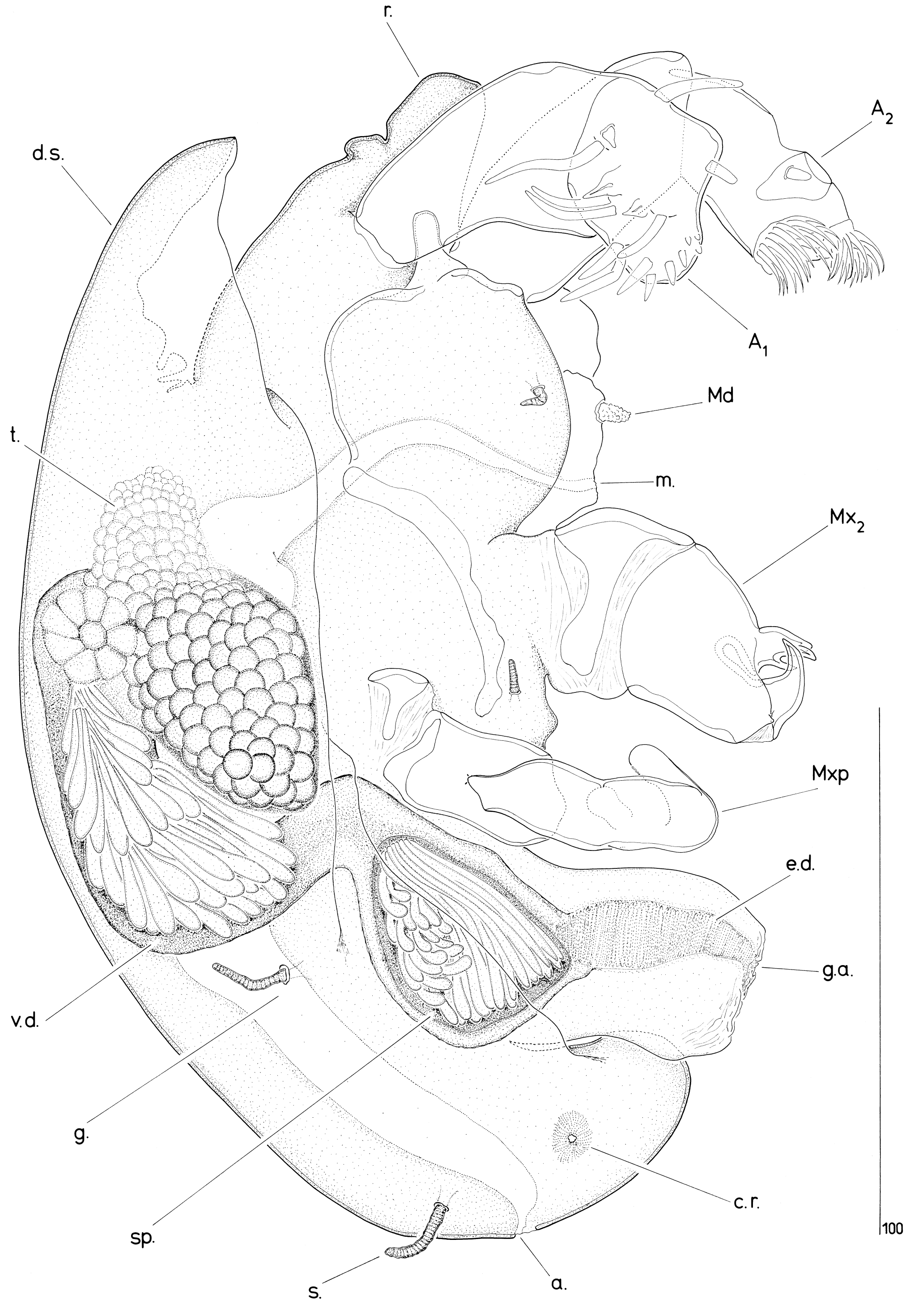

Fig. 15. *Micrallecto fusii* (Stock, 1973), new combination: Adult ♂, lateral [a., anus; A$_1$, antennule; A$_2$, antenna; c.r., caudal ramus; d.s., dorsal shield; e.d., ejaculatory duct; g., gut; g.a., genital aperture; m., mouth; Md, mandible; Mx$_2$, maxilla; Mxp, maxilliped; r., rostrum; s., sensilla; sp., spermatophores; t., testis; v.d., vas deferens].

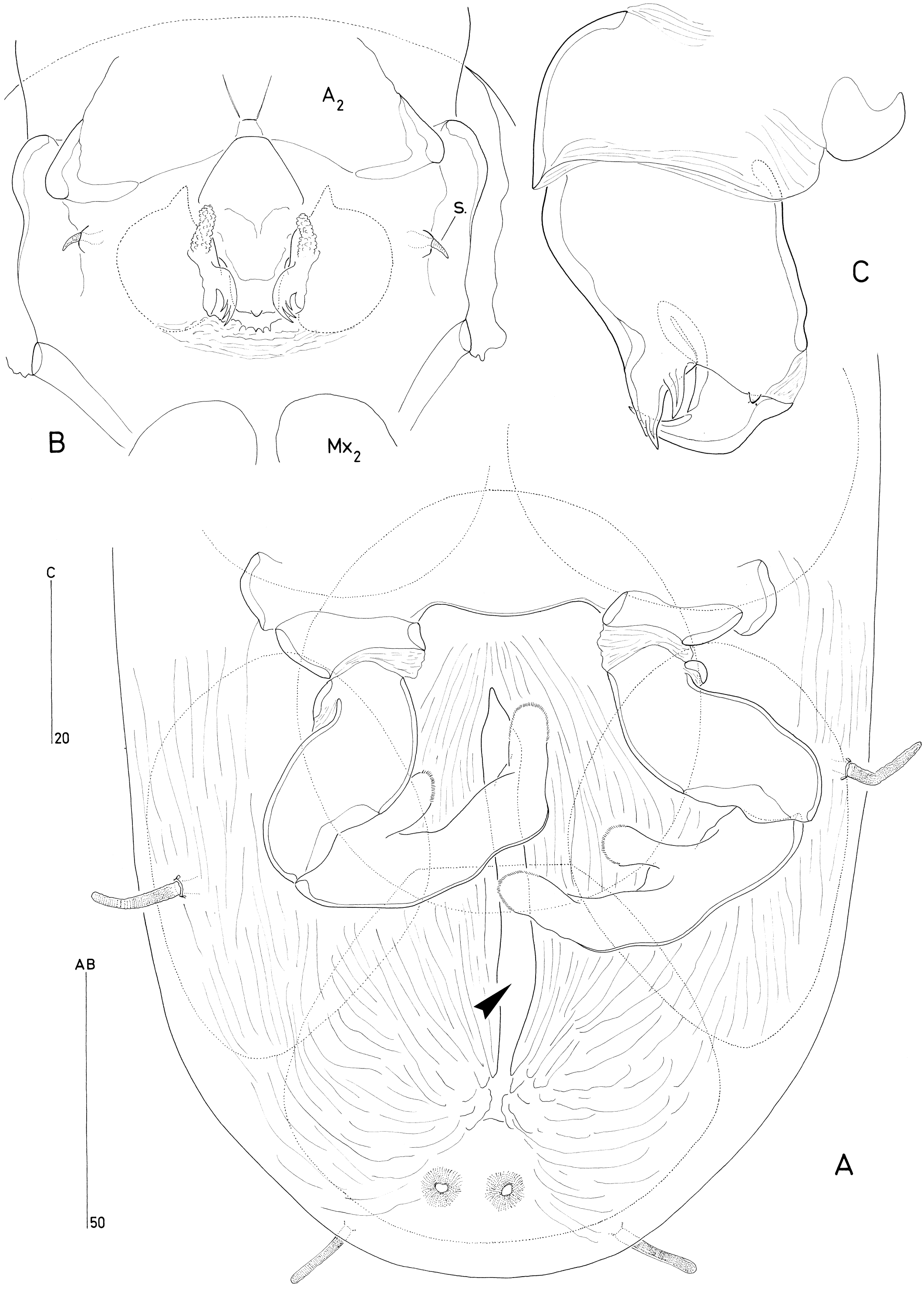

Fig. 16. *Micrallecto fusii* (Stock, 1973), new combination: A, posterior half of ♀ body, ventral [genital aperture, arrow]; B, oral area ♂, ventral [A$_2$ and Mx$_2$, insertion sites of antenna and maxilla; s., sensilla]; C, maxilla ♂.

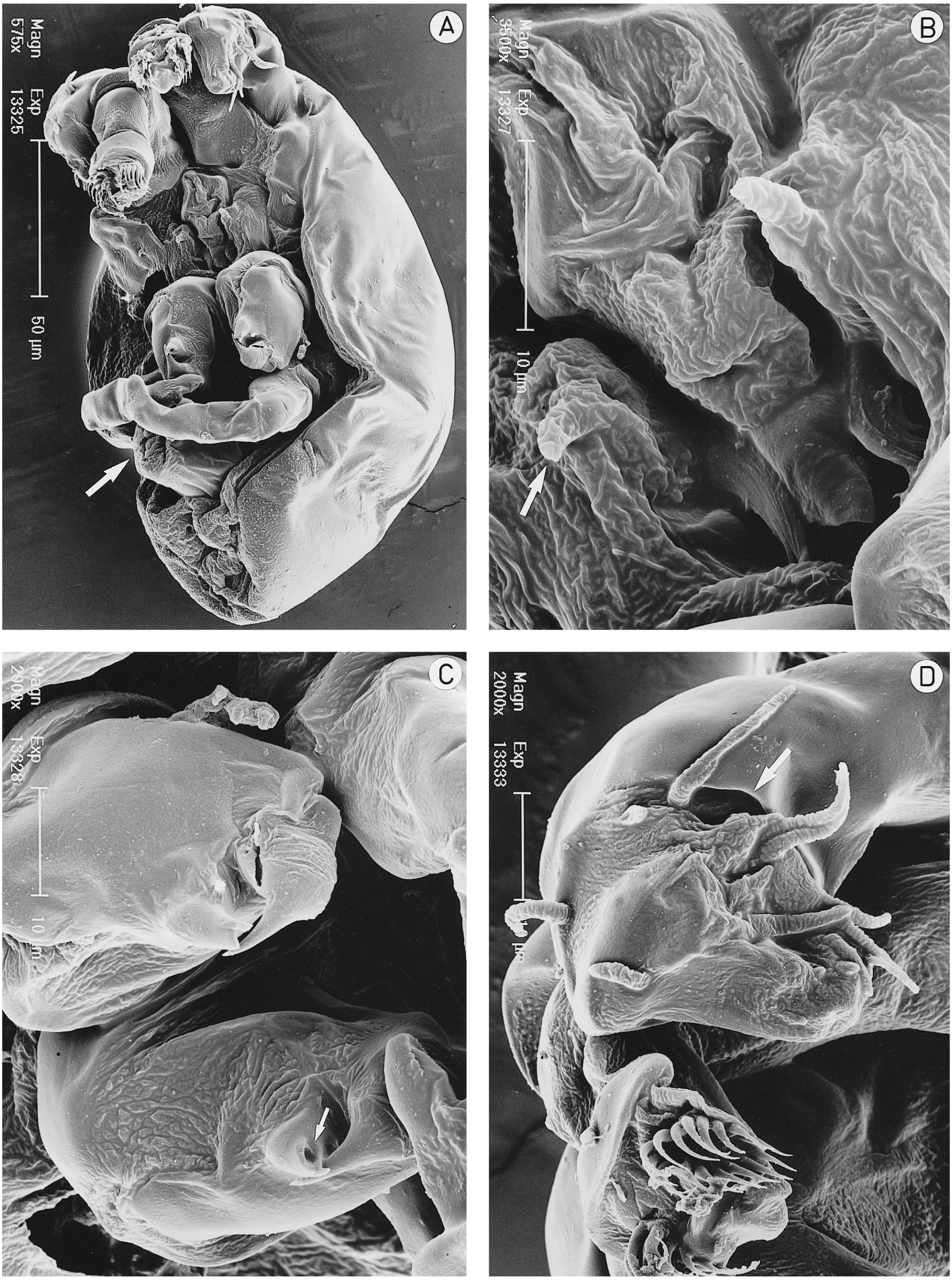

Fig. 17. *Micrallecto fusii* (Stock, 1973), SEM photographs [♂]. A, habitus, lateroventral [genital aperture, arrow]; B, oral area [rudimentary mandibular palp, arrow]; C, maxillae [socket on syncoxa, arrow]; D, left antennule and antenna, frontal [incomplete articulation on antennule, arrow].

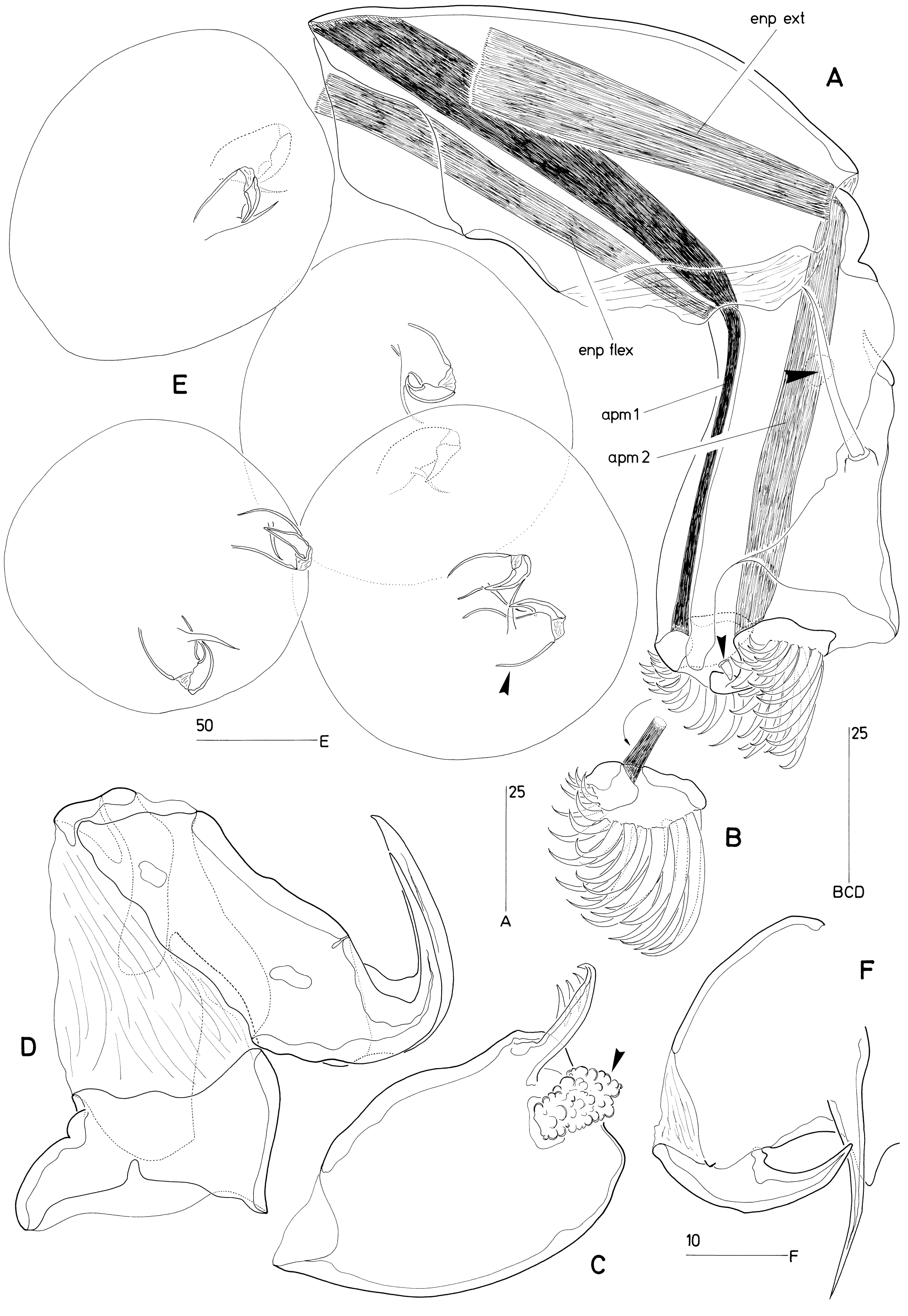

Fig. 18. *Micrallecto uncinata* Stock, 1971 [holotype ♀]: A, antenna [small arrow, vestigial element; large arrow, scar indicating missing element; apm 1–2, apical antennary muscles 1 and 2; enp ext, endopod extensor; enp flex, endopod flexor]; B, outer coronary grasping spine; C, mandible [rudimentary palp arrowed]; D, maxilla; E, developing nauplii inside ♀ [maxilla illustrated by Stock (1971) as leg 2, arrow]; F, naupliar maxilla.

Splanchnotrophidae and by adopting Laubier's (1964) erroneous conclusion that these appendages are lacking in that family. This argument not only suffers from circularity, but it has also been demonstrated since that at least some splanchnotrophid genera (*Ismaila, Splanchnotrophus*) possess maxillules (Ho, 1981a; see above). Stock (1971), seemingly influenced by Laubier's (1964) study of *Splanchnotrophus*, also called ". . . the post-mandibular oral appendage a posterior maxilla", and used it as a reference point to homologize the remaining limbs.

In situ observations of the mouthparts in *M. fusii* have revealed their correct position and orientation. The uncinate appendage referred to by Stock as the maxilla is clearly not postmandibular but prelabral, arising from a distinct ventrolateral pedestal near the base of the antennule. Its position is similar to that of the postantennary process found in the Taeniacanthidae and some caligiform families. In these families the process represents a mere elaboration of a ventral cephalic sclerite. In *Micrallecto,* the presence of both extrinsic and intrinsic musculature suggests a different origin for the uncinate structure. Its anterior position is obviously the result of secondary displacement; however, it is unlikely that the maxilla has migrated over such a great distance. The alternative option that it represents only part of a preoral appendage, such as the accessory antennule in some Chondracanthidae (Ho, 1984), is equally unacceptable. The third pair of appendages is here identified as the modified maxillules which have undergone anterior and lateral displacement. The recurved portion bearing the paired hooks is homologous with the outer lobe ("palp" *sensu* Huys and Boxshall, 1991); the inner lobe is vestigial and represented by a small hump bearing at most one minute element. Extensive membranous inserts (not arthrodial membranes!) around the base of the outer lobe allow considerable flexion of the distal part of the maxillule. The intrinsic muscles are concentrated in the basal part, with both flexors and extensors originating on the basal rim of the limb and inserting distal to the membranous inserts. The powerful extensors swing the distal uncinate part medially, presumably until it engages with the surface of the pteropod host. Very strong extrinsic muscles are housed in the heavily sclerotized cephalic pedestal that supports the maxillule. Lateral displacement of the maxillules onto the outer edge of the cephalic region permits a considerably wider grasp. The maxillules and their pedestals are absent in the male.

The chelate appendages identified by Stock (1973) as the maxillipeds in the female of *N. fusii* are interpreted here as the maxillae. Stock claimed that they were two-segmented and medially fused along two-thirds of the length of their basal segments. Re-examination failed to reveal such fusion. The prominent segment boundary drawn by Stock represents the proximal articulation between the syncoxa and a cylindrical raised area of the ventral body surface, the pedestal. A range of whole limb movements is facilitated by the presence of membranous areas all around the pedestal. The syncoxa is drawn out into a spinous process, which is probably homologous with the distalmost coxal endite. It articulates distally with a curved claw-like segment, the allobasis, which opposes the coxal endite. The syncoxa contains two broad intrinsic muscles that originate proximally near the joint with the pedestal. The first has a tendinous section distally and inserts on the outer proximal rim of the allobasis. The second inserts on a U-shaped thickened area at the base of the coxal endite. Contraction of the latter deforms the syncoxal integument, thereby altering the angle between the endite and the allobasal claw. This mechanism ensures that the claw can be received in the socket on the coxal endite, securing an efficient grip of the host integument (Fig. 17C).

The last pair of appendages, interpreted by Stock (1971, 1973) as the first swimming legs, are the maxillipeds. They articulate with a common transverse pedestal (Fig. 16A). None of the three segments has discrete armature elements, but it is possible that the two serrate lobes on the endopod represent transformed spines. Stock (1973) suggested that these lobes could be the exopod and endopod; however, the segmentation pattern refutes such an interpretation.

Adults of both sexes lack any trace of swimming legs. Stock's (1971) record of a prehensile second pair of legs in the female of *M. uncinata* only is based on an observational error. Re-examination of the holotype revealed that his leg 2 in reality corresponds to a naupliar limb that was visible through the integument of the ventral surface of the hindbody. The larger eggs inside the adult female each possessed a pair of such chelate appendages and should consequently be referred to as developing nauplii (Fig. 18E). The largest eggs contained in the females of *N. fusii* are all at an earlier state of development, providing the underlying evidence for the apparent "absence" of leg 2 in this species.

Attachment.—The mode of attachment employed in micrallectids permits free movement over the body of the pteropod host. At least three appendages are involved in attachment, but none anchors the copepod permanently. The maxillae are the principal attachment devices, maintaining a firm hold on the host during feeding. This hold is probably enhanced by assistance from the antennae and, in females only, from the maxillules.

The antenna is perhaps the most conspicuous appendage. It comprises a coxo-basis and a free endopod. The endopodal segments are largely fused, but a suture with arthrodial membrane marks the position of the original articulation. There are four strong intrinsic muscles (Fig. 18A). The flexor (enp flex) and extensor (enp ext) originating on the wall of the coxo-basis act antagonistically, flexing and extending the whole endopod. The coronary grasping spines are manipulated by two apical muscles. The first (apm 1) originates proximally on the lateral wall of the coxo-basis and passes right down the endopod to insert at the base of the outer spine (Fig. 18B) without attaching at any (expressed or non-expressed) intersegmental joint. Originating proximally on the lateral wall of the endopod is the second apical muscle (apm 2), which passes distally to insert on the base of the inner grasping spine. It is interesting to note that the two apical antennary muscles described by Boxshall (1982) for the misophrioid *Benthomisophria palliata* Sars follow a similar course. Contraction of the apical muscles causes protraction of the coronary spines. These muscles are presumably opposed by the elasticity of the thickened cuticle around the bases of the spines.

The maxillipeds, designed for prehension, are probably of minor importance in attachment. The only male specimen found was holding an adult female in a relatively loose ventral-to-ventral posture, using its maxillipeds. No other appendages assisted in securing the grasp, nor was there any physical contact with the host. This explains why the male maxilla remained intact, this in contrast to those of females manually removed from the host (see below). It is likely that the observed grasping position is similar to that employed during copulation because the male genital aperture was opposing the female's postmaxillipedal region.

Synonymy.—The generic separation of *Micrallecto* and *Nannallecto* was exclusively based on observational errors. Stock (1973) established *Nannallecto* on the basis of (a) the presence of a pair of strongly developed, prehensile maxillipeds (= maxillae) that are fused medially; (b) the presence of only one pair of swimming legs (= maxillipeds); and (c) the caudal rami that are reduced to rugose patches.

It has been shown that the firm maxillary grip is achieved by a highly efficient key-and-lock mechanism. Attempts to remove the parasites from the host almost invariably caused distal fracture of the allobasal claw, leaving a blunt tip (Fig. 14H, I). In one instance, removal resulted in tearing off the entire maxilla at a level proximal to the membranous sections of the pedestal. The fact that the maxillae are the primary means of attachment in *N. fusii* raises grave doubts about their alleged absence in *M. uncinata*. I regard this dissimilarity unreal and suspect that the holotype of *M. uncinata,* which had not been removed by J. H. Stock himself, was incomplete.

As illustrated above, both genera lack swimming legs and possess the same number of appendages. The chelate second leg of *N. fusii* is erroneously based on an internal structure.

Stock (1971) mistakenly homologized the posterior pair of sensillae with the caudal rami in *M. uncinata*. He overlooked the remaining sensillar pairs as well as the invaginated folded areas which presumably represent the actual caudal rami. These sockets were later (Stock, 1973) correctly identified as the caudal rami but erroneously interpreted as rugose patches in *N. fusii*. No mention was made of the four pairs of annulated sensillae.

According to these reinterpretations there is no factual justification to maintain *Nannallecto* as a distinct genus, and it is relegated here to a junior subjective synonym of *Micrallecto*. The remaining differences mentioned by Stock (1973), including body size, the number of teeth on the mandibular gnathobase, and the proportional length of the maxillulary hooks are species discriminants.

Ordinal Position.—The paedomorphic facies and highly specialized cephalic appendages of the Micrallectidae make an assessment of its ordinal position difficult. The morphology of the mandibular gnathobase, often a useful discriminant between the Poecilostomatoida and Siphonostomatoida, does not provide any conclusive evidence in this respect. The gnathobase can either be interpreted as representing a single pectinate blade, superficially resembling the condition found in some poecilostomatoid families such as the Splanchnotrophidae. The alternative interpretation is based on the arrangement of teeth along one side near the apex of the gnathobase, which is typical for the mandibular stylet of many fish-parasitic taxa in the Siphonostomatoida such as the caligiform and dichelesthiiform families. A plausible scenario could be that the micrallectid gnathobase is derived from such rod-shaped stylet by extreme shortening of the shaft. This would imply that the Micrallectidae evolved from (or within) a fish parasitizing ancestral stock by extreme abbreviation of the life cycle. It is interesting to note that some Pennellidae such as *Cardiodectes* C. B. Wilson use pelagic gastropods (and particularly thecosome pteropods) as first hosts in their life cycle (Ho, 1966; Perkins, 1983), although this association is clearly the result of secondary host switching.

The Micrallectidae is placed in the Poecilostomatoida on the basis of two characters that were overlooked in previous descriptions, i.e., antennary armature and mandibular palp morphology. The micrallectid antenna is basically two-segmented, comprising a coxo-basis and an unsegmented endopod. The identity of the only segment boundary is confirmed by reference to the sites of insertion of the endopodal flexor and extensor muscles and the site of origin of the apm 2 muscle (Fig. 18A), ruling out the possibility of the proximal endopod segment being incorporated in the coxo-basis. The membranous insert along the medial margin of the endopod marks the fusion plane between the proximal segment and the compound distal segment (derived by fusion of second and third segments). The armature pattern of the endopod reveals that the proximal segment has retained its lateral seta. Huys and Boxshall (1991) showed that this segment is always unarmed in the Siphonostomatoida, even in primitive Asterocheridae exhibiting the ancestral three-segmented pattern (Boxshall and Huys, 1994). The fact that siphonostomatoid affinity of the Micrallectidae can be unequivocally eliminated on the basis of a single seta demonstrates the potential explanatory power of individual setation elements, even in highly modified parasites.

The rudimentary mandibular palp discovered in the adults of *Micrallecto* is an unusual feature that is reminiscent of the condition found in the first copepodid of various poecilostomatoid families (Izawa, 1986). Although this rudiment disappears at the subsequent moult to copepodid II, it could conceivably persist in later stages as a result of heterochrony. Except for the Erebonasteridae, all adult Poecilostomatoida lack the mandibular palp (Huys and Boxshall, 1991). The highly paedomorphic nature of *Micrallecto* suggests that the rudimentary palp is a larval attribute that persisted in the adult either by slowing down the developmental rate or by early cessation of the development. The mandibular palp is also absent in the adults of many siphonostomatoid families. Few studies document early copepodid development of siphonostomatoids, but at least in the Caligidae, Pennellidae, and Lernaeopodidae it has been confirmed that a rudimentary palp never develops in the first copepodid stage (Kabata, 1976; Lin *et al.,* 1996; Izawa, 1997) and consequently cannot persist in later stages as a result of paedomorphic development.

Unlike other podoplean copepods, male poecilostomatoids typically grasp females around the prosome-urosome junction, using the maxillipeds. Sexual dimorphism in the maxillipeds is virtually universal in this order and clearly related to the mating posture. Micrallectids do not display noticeable sexual dimorphism in these limbs, but the only male discovered was found attached to the female by means of the maxillipeds.

The position of the Micrallectidae in the Poecilostomatoida is enigmatic due to the many unique apomorphies found in the cephalic appendages. The antenna with coronary grasping spines has no equivalent in the order, and the transformation of the maxillae into chelate grasping appendages is not found in any other poecilostomatoid family. Similarly, the uncinate shape, anterior displacement (in the female), and sexual dimorphism displayed by the maxillules have not been recorded before in any other copepod. Male micrallectids are radically different by the presence of a ventral cylindrical outgrowth bearing the genital slit and by the complete absence of maxilliped sexual dimorphism.

BIOLOGY

Prior to this revision, the Splanchnotrophidae accommodated representatives drawn from three different unrelated families, all of which utilize marine opisthobranch gastropods as hosts. Each of them differs not only morphologically but deviates significantly from the others in their biology.

Splanchnotrophidae

All splanchnotrophids are endoparasitic. They are typically associated with the kidney, pericardium, or the digestive gland of the host, which is typically a sacoglossan or a nudibranch opisthobranch (Table 1). Canu (1891) believed that females were really mesoparasitic, occupying pouches excavated in the host's integument, but Delamare Deboutteville (1951a) disproved this by observations on young females metamorphosing inside the host. The gross disparity in size between the sexes has traditionally been regarded as evidence for a splanchnotrophid-chondracanthid relationship because Chondracanthidae typically possess dwarf males. Laubier's (1966) study of *S. dellachiajei* showed that it is not the male that is paedomorphic but the female that is peramorphic. Sexually mature females continue to enlarge their lateral body processes as a result of local hypermorphosis in the prosomal region. This can lead to substantial variability in the gross body morphology and size of adult females and forms an impediment to accurate species identification. The processes perform the dual function of housing the branches of the ovaries and enwrapping the viscera on which the females feed. O'Donoghue (1924) suggested that they were also involved in the absorption of nutritive material from the host, but the presence of functional mouthparts, gut, and anus makes this assumption unlikely. The size of the processes is conceivably linked to the state of gonad development, a correlation already suggested for some Nicothoidae (Bocquet *et al.,* 1958). Hancock and Norman (1863) noted that the lateral processes are not homologous with transformed thoracopods but are structures formed *de novo*. Laubier (1966) demonstrated their derivation from the pleural areas of the first and second pedigerous somites, but not the third as claimed by Ho (1981a) for *Ismaila.*

Female splanchnotrophids are remarkable in penetrating their host twice during their life cycle, first during initial infection probably at copepodid I stage (Ho, 1987b) and a second time upon attaining sexual maturity and following copulation when they protrude the genito-abdomen through the host's integument but remain attached inside with the prosome. The posterior part of the trunk is the only region that is enclosed by the host's integument and is consequently variable in length, contractile and often specialized forming a collar (cf. *Ismaila;* Ho, 1981a). This area is homologous to the third and fourth pedigerous somites, and the loss or gross reduction of legs 3 and 4 has probably evolved in relation to its altered function. In the absence of large orifices connecting the coelomic cavity with the exterior, the secondary penetration of the host has probably evolved as an adaptation to enhance successful eclosion and subsequent dispersal of the numerous nauplii. Ho (1981a) noted that large females of *I. occulta* lying inside the cerata were likely to be spent females that had secondarily withdrawn their urosomes back into the host following naupliar eclosion.

Males are only found in hosts already infested by females and are frequently attached to the genito-abdomen of the females (Hancock and Norman, 1863). There are several reports of the presence of a tripartite nauplius eye in male splanchnotrophids (e.g., Hancock and Norman, 1863; Canu, 1891), which is a highly unusual feature for an endoparasite. It is possible that the retention of a photoreceptor in the males is related to their limited movement inside the host and their need to maintain close contact to the surface of the viscera immediately beneath the transparent integument. The tagmosis of the splanchnotrophid male is remarkable because the major body articulation coincides with the boundary between the second and third pedigerous somites. The presence of only one postgenital somite indicates a progenetic development, marked by the early offset of somite addition at the copepodid III stage.

According to Belcik (1981; and Dudley therein), there are at least two nauplius stages in the life cycle, and at least the first nauplius is clearly planktotrophic. Ho's (1987b) ontogenetic study of *I. occulta* indicates that splanchnotrophid development involves the basic number of six copepodid stages, even though he failed to find the first and fifth instars.

Jensen (1987) remarked that splanchnotrophids are predominantly associated with opisthobranchs that exhibit dorsal digitiform outgrowths (cerata) such as the aeolids and dendronotaceans in the Nudibranchia and the Limapontiidae in the Sacoglossa. Adult females are often found within the hepatic diverticulae inside the cerata, their urosomes and attached egg-sacs protruding through the host's integument. Jensen (1987) regarded this location as particularly suitable for camouflaging the frequently brightly coloured egg-sacs (Jensen, 1990), whereas Hancock and Norman (1863) noted that such external position would allow the eggs to ". . . obtain the advantage of the branchial currents of the infested host."

Philoblennidae

Data on philoblennid biology are scanty. Representatives of *Philoblenna* are ectoparasites of prosobranch gastropods, attaching to the gill filaments in the mantle groove using the prehensile antennae (Izawa, 1976; Ho, 1981b; Avdeev *et al.*, 1986; Ho and Kim, 1992). Both sexes in the genus *Briarella* species are clearly endoparasitic, living in the pericardium, renal cavity, and canals of the hepatopancreas of dorid nudibranchs (Monod, 1928). Izawa (1986) described the first three nauplius stages and the first copepodid of *Philoblenna arabici* and suggested that there are probably six naupliar stages. Although he considered the nauplii to be lecithotrophic, there is nothing in the appendages that is indicative for this.

Micrallectidae

The life cycle of the Micrallectidae is highly abbreviated as a result of extreme paedomorphic development. The gross adult morphology, including the dorsal shield and the distinctive lack of segmentation, tagmosis, and swimming legs, is clearly reminiscent of that of a late nauplius stage. The adult has a complete set of fully functional mouthparts and maxillipeds, and is in all other aspects clearly comparable to a metanauplius. This is interpreted here as strong evidence for the first case of global progenesis recorded in copepods, resulting in the early sexual maturation at the metanauplius stage and the complete cessation of somite and limb development normally progressing during the copepodid phase. This has obvious consequences for the internal reorganization of reproductive tissues, because the somites (and the entire tagma) normally associated with the gonoducts and genital apertures are not expressed. In the absence of clear segmental markers, such reorganization may in part explain the unusual gonopore configuration in Micrallectidae, being a large longitudinal slit running across the postmaxillipedal region in females, and a single apical aperture positioned on a ventral cylindrical extension of the same area in males.

The discovery of developing nauplii inside the female of *M. uncinata* is extraordinary. The nauplii are clearly lecithotrophic and have only one pair of appendages. The chelate nature of these limbs is very similar to that of the maxillae in the adult, which are the primary attachment devices. This would imply that the maxillae appear in the nauplius before the onset of any other appendages, which can be viewed as an extreme case of peramorphosis. Predisplacement of maxillary development is possibly an adaptation to increase the probability of successful attachment to the host, although it would seem difficult to explain the mechanisms involved in host location without having any other appendages. It is interesting to note that Monod and Dollfus (1932) illustrated a similar uncinate appendage in a developing naupliar embryo of *Trochicola entericus* Dollfus, 1914 (Mytilicolidae). The presence of such structure is remarkable because the first and second metanauplii do not have any chelate limbs (Bocquet *et al.,* 1963). Various copepod families possess brood-pouches such as some Gastrodelphyidae in the Poecilostomatoida and the Ascidicolidae and some Notodelphyidae in the Cyclopoida; however, there is as yet no published evidence that nauplii develop inside these chambers. Micrallectidae do not have a brood-pouch, and naupliar development is clearly ovoviviparous, which once again demonstrates that the life cycle and development of the parasite are closely linked to the biology of the pelagic host.

THE TRUE IDENTITY OF *MEGALLECTO* GOTTO, 1986

Gotto (1986) based the description of *Megallecto thirioti* on two specimens collected in horizontal plankton hauls off the

Mauretanian coast. The presence of thecosome pteropods in the same haul and the "general resemblance . . . to *Micrallecto* and *Nannallecto*" led the author to suggest that *M. thirioti* was a parasitic copepod associated with pteropod hosts. By analogy with Stock's (1971, 1973) genera, he identified both type specimens as females and placed the species in the Splanchnotrophidae.

Re-examination of the paratype (ZMA Co. 102.718) showed that *M. thirioti* is not a complete animal but only represents the head end of a larger crustacean that does not belong to the Copepoda and was erroneously orientated back to front and upside down (compare Fig. 19A, B). Consequently, Gotto's efforts to homologize the appendages are all basically erroneous.

Evidence for Gotto's misinterpretation was first found when the paratype was examined in posterior aspect. A large round opening (arrow in Fig. 19D), symmetrical in outline and well defined by a continuous chitinized rim (except for the more membranous ventral side) was observed at the opposite side of the presumptive ventral surface. This scar clearly corresponded with the articulation between the head and the lost trunk, thus enabling correct polarization and identification of the head appendages. The head capsule was virtually empty but some tendons and the anterior portion of the alimentary canal were discernible (Fig. 19B, D). The complete lack of musculature and connective tissue accounts for the considerable cuticular distortion mentioned by Gotto.

The appendages interpreted by Gotto as the antennules are in reality the outer lobes of the maxillipeds, and the outgrowth separating them is not the ventrally projecting rostrum but their medially fused inner lobes. Because this median lobe is positioned anterior to the outer maxillipedal lobes (Fig. 20C) and not visible in posterior (= "frontal" according to Gotto) aspect (Fig. 19E), misinterpretation of the appendages must have occurred after their dissection and not as a result of *in situ* observation.

The second pair of appendages, interpreted as the antennae on the basis of hints of podomere segmentation, are the outer lobes of the maxillae (Fig. 20D). No such rudimentary segment boundaries could be observed in the paratype. The small lobate mandibles identified by Gotto at the bases of these appendages are in reality the inner maxillary lobes (Fig. 20D).

The powerful maxillules (Fig. 20E) were misinterpreted by Gotto as the maxillae, claiming that the maxillules were seemingly absent.

Gotto admitted having difficulties in correctly observing the last pair of oral appendages but on positional grounds homologized them with the maxillipeds. His illustration clearly refers to the mandible (Fig. 20F) and his observation of a medially cleft lower lip ". . . immediately behind the maxilliped" undoubtedly alludes to the bilobate labrum (Fig. 20B).

Finally, Gotto's identification of a pair of biramous legs on ". . . the ventral surface of the posterior body region" results from conflating into a single appendage two different structures, the 2-segmented antennules (Fig. 20A) and the conical rostral points, which were homologized as the endopods and exopods, respectively. The hyaline leg setae are in reality antennulary aesthetascs, and the linear array of minute setae observed around the base of the antennules are simple pores similar to those arranged in patches on the frontal face (Fig. 19C).

The cephalic appendages of *M. thirioti* are clearly not copepodan but peracaridan in nature; more specifically, they are strongly indicative of affiliation to the suborder Hyperiidea in the Amphipoda (Bowman and Gruner, 1973). Hyperiid amphipods are amongst the major groups of crustacean zooplankton, ranking third in overall abundance behind the copepods and the euphausiids. In the absence of characters referring to the pereion and abdomen, familial assignment of hyperiids in general is severely hampered. Following Bowman and Gruner's (1973) widely accepted classification, the absence of an inner lobe on the maxillule and the complete medial fusion of the inner lobes of the maxillipeds into a single median lobe places *Megallecto* in the infra-order Physocephalata, and the insertion of the antennules on the anterior surface of the head conforms with the Phronimoidea, which comprises four families. *Megallecto* can be unequivocally assigned to the family Phrosinidae on the basis of the absence of a mandibular palp, the 1-segmented flagellum of the antennule, and the structure of the maxillipeds comprising slender outer lobes and a well-developed median lobe. The family Phrosinidae currently accommodates

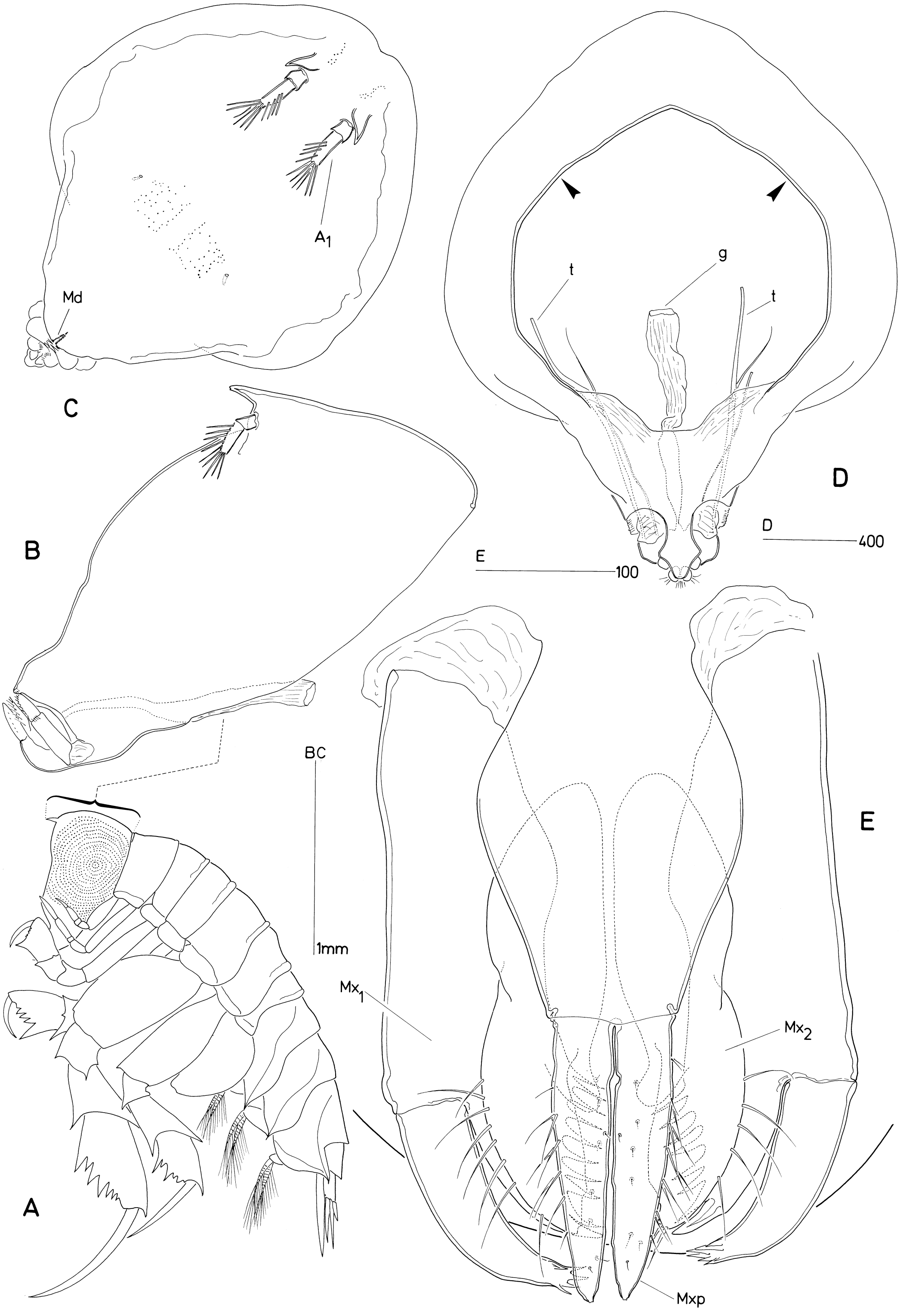

Fig. 19. *Phrosina semilunata* Risso, 1822: A, habitus ♀, lateral [after Bovallius (1889)]. *Megallecto thirioti* Gotto, 1986 [paratype ♀]: B, head, lateral; C, head, frontal [A_1, antennule; Md, mandible]; D, head, posterior [g, gut; t, tendon; chitinized rim marking opening, arrow]; E, posterior view of cephalic appendages showing maxillipeds (Mxp), maxillae (Mx_2) and maxillules (Mx_1).

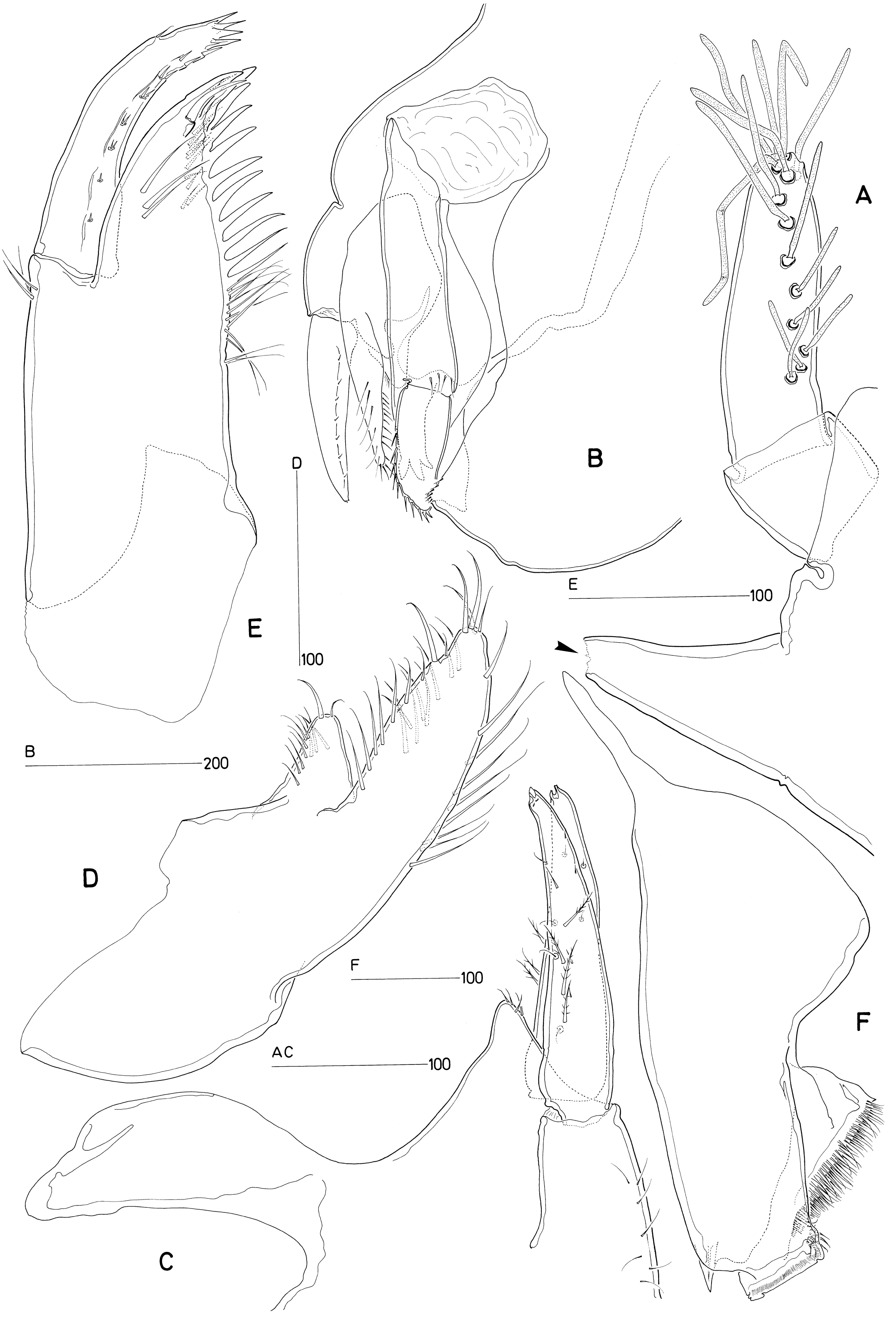

Fig. 20. *Megallecto thirioti* Gotto, 1986 [paratype ♀]: A, antennule and rostral projection [broken apex, arrow]; B, lateral view of oral area showing labrum, maxillules, maxillae and maxillipeds [oesophagus indicated by dashed lines]; C, maxillipeds, lateral; D, maxilla; E, maxillule; F, mandible.

three genera (Bowman and Gruner, 1973). The presence of paired rostral projections on the head, the very short antennule, and the complete absence of the antenna leave no doubt that *Megallecto* should be relegated to a junior subjective synonym of *Phrosina* Risso, 1822. The genus was established for the type species *P. semilunata* Risso, 1822, and has remained monotypic since (Vinogradov *et al.,* 1982). Comparison with Bovallius' (1889) excellent redescription demonstrates that conspecificity of *P. semilunata* and *M. thirioti* is indisputable. Phrosinids are strongly sexually dimorphic in the antennules, antennae, and mandibles. The absence of antennae and mandibular palps (both present in ♂♂) in conjunction with the one-segmented flagellum of the antennule (long and filiform in ♂♂) clearly identify both type specimens of *M. thirioti* as females. The rostral projections are usually slightly longer in typical *P. semilunata,* but examination of the paratype of *M. thirioti* revealed that the apex of the projections was missing (arrow in Fig. 20A), a feature described by Gotto (1986) as a "roughened point." The compound eyes appear to occupy most of the head surface in the genus *Phrosina* (Bovallius, 1889; Bowman and Gruner, 1973). Because no ommatidia were observed in the paratype, it is assumed that the eyes were removed with the associated musculature and other cephalic tissues when the trunk was torn off.

Phrosina semilunata is an epipelagic and shallow mesopelagic species that can be very abundant locally and undergoes a limited upward migration at night during at least part of the life cycle (Thurston, 1976). It is the fifth most abundant species in horizontal hauls around the Canary Islands; this is in relatively close proximity to the type locality of *M. thirioti*. It is now widely assumed that all hyperiids are associated with mostly gelatinous planktonic hosts during all or particular phases of their life cycle (Laval, 1980). Hosts include radiolarians, ctenophores, medusae, siphonophores, heteropods, salps, and pteropods. There are a few unconfirmed records of Phrosinidae being associated with tunicates (in pyrosomes) and siphonophores (Laval, 1980). The only hyperiids recorded as associates of pteropod gastropods (*Gleba, Corolla, Cavolinia*) belong to the family Lycaeidae (Harbison *et al.,* 1977), but the degree of host specificity is unknown.

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