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**On the identity of the Namakosiramiidae Ho & Perkins 1977
(Crustacea, Copepoda), including a review of harpacticoid associates of
Echinodermata.**

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The female of the ectoparasitic copepod *Namakosiramia californiensis* Ho & Perkins 1977, recovered from the holothurian *Stichopus parvimensis*, is redescribed and refigured. It is suggested that the species should be included in the Laophontidae and tentatively placed in the subfamily Laophontinae, implying the synonymization of the family name Namakosiramiidae. Previous records of harpacticoid associates of Echinodermata are summarized. A compilation of associations between Laophontidae and marine invertebrate hosts is given.

KEYWORDS: *Namakosiramia*, Echinodermata, associates, Laophontidae

Introduction

Ho & Perkins (1977), during a study of copepod parasites of southern Californian echinoderms, discovered a new family of minute ectoparasitic copepods, the Namakosiramiidae. *Namakosiramia californiensis* Ho & Perkins 1977 was recovered from the body surface of the holothurian *Stichopus parvimensis* and constitutes thus far the sole member of the family.

The family was originally placed in the Cyclopoida on the basis of the oral appendages which "... are clearly of the cyclopoid type" and because of a certain similarity to the Siphonostoma and Poecilostoma (at the time of the description these taxa were not recognized as separate copepod orders; see Kabata, 1979), including having a reduced antennary exopodite and the complete absence of a labium forming the posterior half of the oral cone. With respect to the latter character it should, however, be stressed that the presence of a labium (formed by the medial fusion of the paired paragnaths) is a diagnostic character for the Siphonostomatoida (Boxshall, 1986). Gotto (1979), synthesizing previous work on the association of copepods with marine invertebrates, also treated *Namakosiramia* as a siphonostome, at the same time indicating a possible relationship with the families Microponiidae, Nanaspidae and Stellicomitidae which all show oral cone reduction and a more or less specific association with echinoderms (Ho & Perkins, 1977). Bowman & Abele (1982) listed the Namakosiramiidae as a family of Cyclopoida.

Ho (1986) demonstrated the true identity of the Namakosiramiidae and concluded that the family should have been placed in the Harpacticoida because of certain non-cyclopoid features: (1) oviducal openings located on the mid-ventral surface of the genital segment, (2) antenna with a rudimentary exopodite, (3) modification of the first and second legs into prehensile structures to aid in grasping the host.

The precise taxonomic position within the order, however, remained unclear. Within the framework of a phylogenetic analysis of the higher harpacticoid taxa, the

type material of *N. californiensis* was re-examined in order to clarify the relationships of the Namakosiramiidae.

Material and methods

The re-examination is based on 3 paratype females of *Namakosiramia californiensis* recovered from *Stichopus parvimensis* (collected north of St. Vincente, off Palos Verdes, California) and retained in the personal collection of Dr J.-s. Ho, California State University, Long Beach. The holotype and 6 additional paratypes are deposited in the Smithsonian Institution (U.S. NMNH), Washington, D.C. under no 168012 and 168013, respectively.

All the details of body ornamentation and of each limb were clearly visible by observation in lactophenol without any dissection. All figures have been prepared using a camera lucida on a Leitz Dialux 20 microscope with interference-contrast. Structures viewed by transparency on the far side of the item bearing them, are shown dotted.

N. californiensis was examined by scanning electron microscopy (SEM) with a JEOL JSM-840 microscope. Females were prepared by dehydration through graded ethanol, critical-point dried, mounted on stubs and sputter-coated with gold.

The terminology and presentation of the setal formulae are adopted from Lang (1948, 1965). The terms pars incisiva, pars molaris and lacinia mobilis are omitted in the description of the mandibular gnathobasis (Mielke, 1984). Boxshall's (1985, pp. 341–345) terminology for the mandible and maxilliped and that of Huys (1988) for the caudal ramus structure are followed.

Abbreviations used in the text and figures are: P1–P6 = first to sixth legs respectively.

Systematics

Genus *Namakosiramia* Ho & Perkins 1977

Diagnosis. Laophontidae. Body dorsoventrally depressed; maximum body width measured at posterior margin of cephalothorax; urosome occupying one third of total body length. Rostrum prominent and fused with cephalothorax. Cephalic shield forming a lobe-shaped protrusion on either side. Second pedigerous somite as broad as cephalothorax. Genital double-somite completely fused; genital complex simple, with remnants of P6. Anal operculum smooth, rounded. Caudal ramus as long as wide; with 7 setae, inner terminal seta (V) strongly developed. Antennula 4-segmented, without process on the 2nd segment; 3rd and 4th segments with aesthetasc. Antenna with unisetose allobasis; exopodite unisegmented with 4 bipinnate spines; endopodite with distal claw. Labrum with spinulose protrusion on either side. Mandibular gnathobasis elongated with long teeth at cutting edge; palp represented by 2 setae. Maxillula unisegmented, reduced. Paragnaths well developed, with long outer spinules. Maxilla minute, bilobate, with claw and 4 setae. Maxilliped robust, prehensile; with asetose syncoxa and basis; endopodite forming a strong claw with 2 minute setae. P1 with 1-segmented exopodite; proximal endopodite segment without inner seta, distal one with a strong claw and a small seta. P2 adapted for grasping, uniramous; coxa and basis strongly developed; exopodite (?) a triangular hook-like segment with 4 slender setae. P3–P4 vestigial, each consisting of a small plate with 1 outer and 2 distal setae. P5 baseoendopodite and exopodite fused; with 1 outer seta and 3 non-articulating setae. Ectoparasitic on holothurians. Male unknown.

Type species: *N. californiensis* Ho & Perkins 1977 (by monotypy)

Namakosiramia californiensis Ho & Perkins 1977*Description.*

Ho & Perkins' figures (1977) are detailed but there are certain oversights which can now be corrected.

Female.

Body length: 490 μm , rostrum and caudal rami included. Antennula (Figs 3-A; 5-E) 4-segmented, short, robust. First segment densely covered with spinules and bearing 1 seta; 2nd segment wider than long, without process, furnished with 7 bare setae; 3rd segment longest and indistinctly subdivided (i.e. segments 3 and 4 fused), bearing 4 setae in the proximal half, 2 setae at about two-thirds distance and 3 setae in addition to an aesthetasc on the anterior margin; distal segment with 11 setae and a short aesthetasc.

Antenna (Figs 3-B,C; 6-A,B). Coxa not observed. Allobasis strong, armed with a pinnate spine and some minute denticles on the surface. Exopodite unisegmented, small, with 4 bipinnate spines. Endopodite covered with numerous spinules along the inner margin of the proximal half; furnished with a spinular row, 1 bare seta and 2 spines (the outermost of which is strongest and bearing a minute process) at about 1/3 distance from the top; anterior margin bearing a short thick spine at the inner edge, one strong denticulated and abruptly curved claw terminally and 4 setae standing on a small process along the outer side.

Labrum (Fig. 3-D) a broad plate with slightly protruding posterolateral corners, each covered with a patch of denticles.

Mandible (Figs 3-D; 6-C,D) reduced. Gnathobasis fairly elongated and provided with several long teeth at the cutting edge. Palp represented by 2 separated setae which are biarticulated at base.

Maxillula (Figs 3-D; 6-C,E) reduced, apparently represented only by the elongated arthrite of the praecoxa, bearing a strong spine and 3 smaller ones; no intersegmental boundaries.

Paragnath (Figs 3-D; 6-C) well developed, and forming a distinct plate which is armed with short spinules on the inner side and long slender spinules along the outer margin.

Posterior margin of oral opening furnished with diminutive denticles (Fig. 3-D).

Maxilla (Figs 3-D; 6-C,F) reduced, bilobate, no segmentary boundaries; endites absent; basis with a strong claw and 2 setae; endopodite represented as 2 setae.

Maxilliped (Figs 3-E,F; 5-A,B) strongly developed, prehensile. Praecoxa and coxa forming unarmed syncoxa. Basis without setae but with 3 patches of small spinules on the surface. Endopodite unisegmented, forming a strong hook-like segment with a small seta at the anterior surface and a minute setule and several denticles at the posterior surface.

Swimming legs, except for leg 1, profoundly reduced in segmentation; the outlines of the intercoxal plates are not clear, but their sites are extremely broad so that the insertions of the swimming legs are far more abaxially situated (relative to the total widths of their respective somites) than in other Laophontidae.

P1 (Figs 1-A; 4-A; 5-A; 7-B,D) biramous. Praecoxa forming a distinct triangular segment. Coxa pitted on anterior surface and bearing an oblique spinular row. Basis with tube-pore (near junction with coxa), pitted, and furnished with spinules at the distal margin, a small inner seta, and a spiniform outer one. Exopodite unisegmented, bearing 2 long setae terminally and 3 shorter setae on the outer edge, in addition to some minute spinules. Endopodite prehensile, 2-segmented; proximal segment as

broad as basis and coxa, unarmed; distal segment trapezoidal, with a subdistal small seta and a strong apical claw, curved outwards.

P2 (Figs 1-A; 4-B,C; 5-A; 7-A) uniramous, prehensile. Praecoxa not observed. Coxa and basis extremely enlarged, forming a semi-circular unit. Outer side of basis forming a rounded process and furnished with a patch of small spinules and a stout curved spine. Exopodite forming a hook-shaped segment; inner side covered with a few denticles and bearing 2 sets of 2 setae. No trace of endopodite could be found.

P3 and P4 (Figs 1-A,B; 2-B,C; 5-A,D) vestigial, uniramous; with 1 outer and 2 distal setae (the innermost being bipinnate); provided with a conical pore near proximal margin. Distal edge of P3 with some spinules; anterior surface of P4 pitted.

P5 (Figs 1-A,B; 2-D; 5-A,D) reduced, baseoendopodite and exopodite fused; with a conical pore, one outer seta and 3 distal non-articulating setae (the middle one being longest and bipinnate).

Genital complex (Figs 1-B; 5-A,C) simple; P6 represented as 2 small setae on either side of the genital furrow.

Caudal ramus (Figs 1-A,B,C; 4-D; 7-C) as long as wide; ventrally, the posterior and inner margins with spinules; bearing 7 setae: anterolateral accessory seta (I) diminutive; anterolateral (II) and posterolateral (III) setae slender and in close contact; outer terminal seta (IV) short and bare; inner terminal accessory seta (VI) small; dorsal seta (VII) slender and tri-articulated at base.

Male. Unknown.

Discussion

It is apparent from the redescription that *Namakosiramia californiensis* cannot be assigned to the Siphonostomatoida. The paired paragnaths are situated on both sides of the oral opening and are not fused into a median labium. The latter structure was found to be a unifying character for the Siphonostomatoida (Boxshall, 1986). In *N. californiensis* not a single trace of an oral cone was observed. The mandibular palp is profoundly reduced as in siphonostomes, yet the gnathobasis is not stylet-like and certainly constitutes no part of a siphon-like construction. Finally, reduced setation of the antennal endopodite is characteristic of the siphonostomes; the distal segment typically bears a long claw and at most two additional setae. *N. californiensis*, on the contrary, displays 6 armature elements on the terminal margin of the endopodite.

Because of the presence of a unisegmented exopodite ('compound seta' in Ho & Perkins, 1977) in the adult, it is clear that *Namakosiramia* should be excluded from the Poecilostomatoida as well. Furthermore, the genital openings are located on the ventral surface of the genital double-somite as in harpacticoids, instead of dorsally or dorsolaterally as commonly found in cyclopoidea and most poecilostomatoids.

Comparison with the various harpacticoid families reveals an undeniable relationship to the Laophontidae in general and to Laophontinae in particular. Affinity with this subfamily is substantiated by the tetrasetose unisegmented exopodite of the antenna and the detailed structure of the P1 endopodite, viz. proximal segment without inner seta, distal segment with a strong claw and one minute accompanying seta. It is interesting to note, however, that the bulk of the laophontinid genera exhibits a spinous process on the second antennular segment. The exceptions to this include *Esola* and the closely related genus *Mourephonte*, and *Asellopsis*. All these genera occupy a more or less peripheral position within the subfamily. Such a process is probably also absent in the ectocommensal *Mictyricola*; however, it is possible that

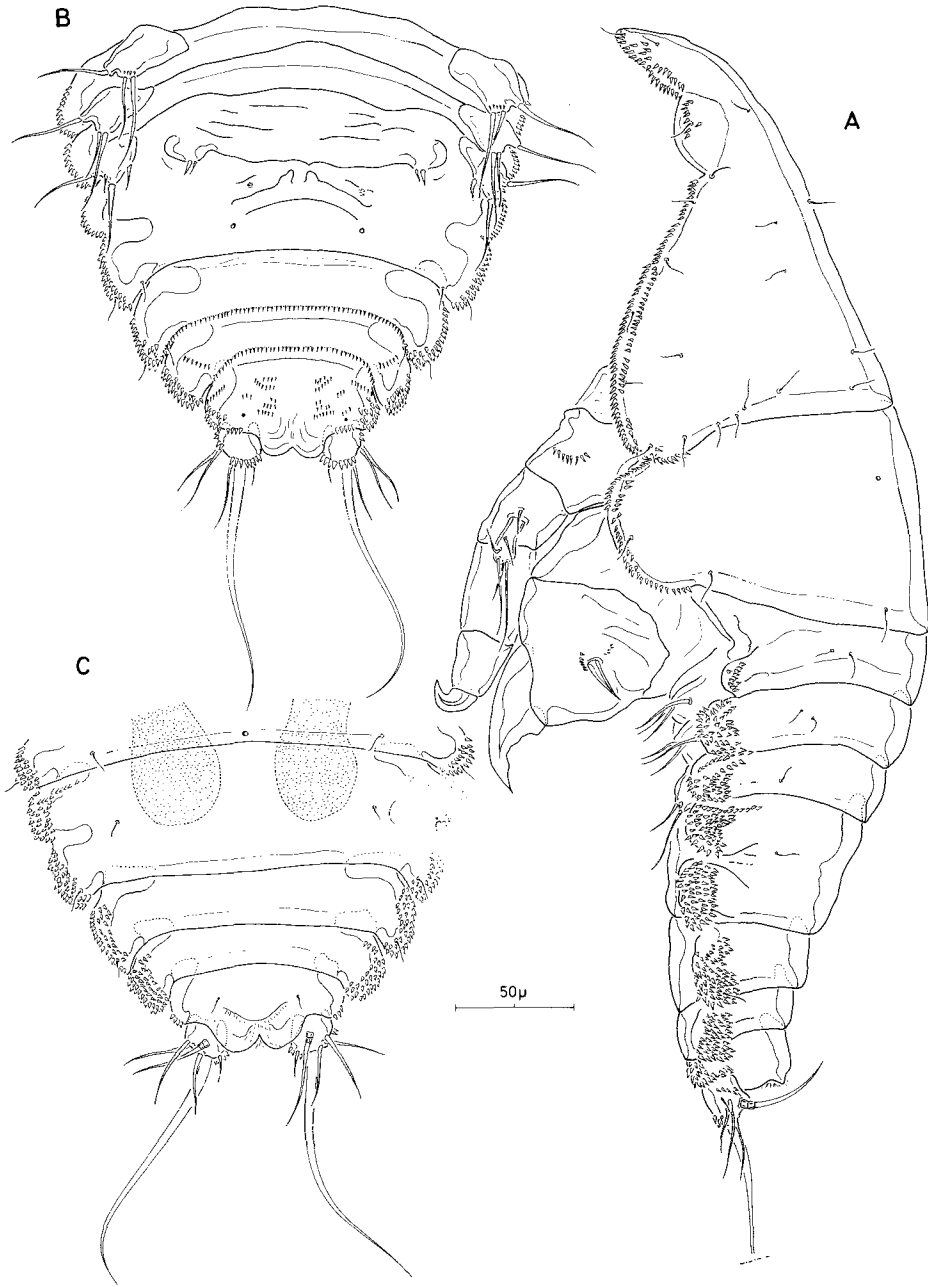


FIG. 1. *Namakosiramia californiensis* Ho & Perkins 1977 (♀). A. Habitus, lateral view. B. Urosome and posterior part of metasome, ventral view. C. Urosome, dorsal view.

this structure has been overlooked in the original description (as is the case in a lot of earlier descriptions of laophontid species) as the genus shows a certain affinity with *Heterolaophonte*.

The absence of this process in *Namakosiramia* raises great difficulties as to the systematic position within the Laophontinae. In fact, only the discovery of the male

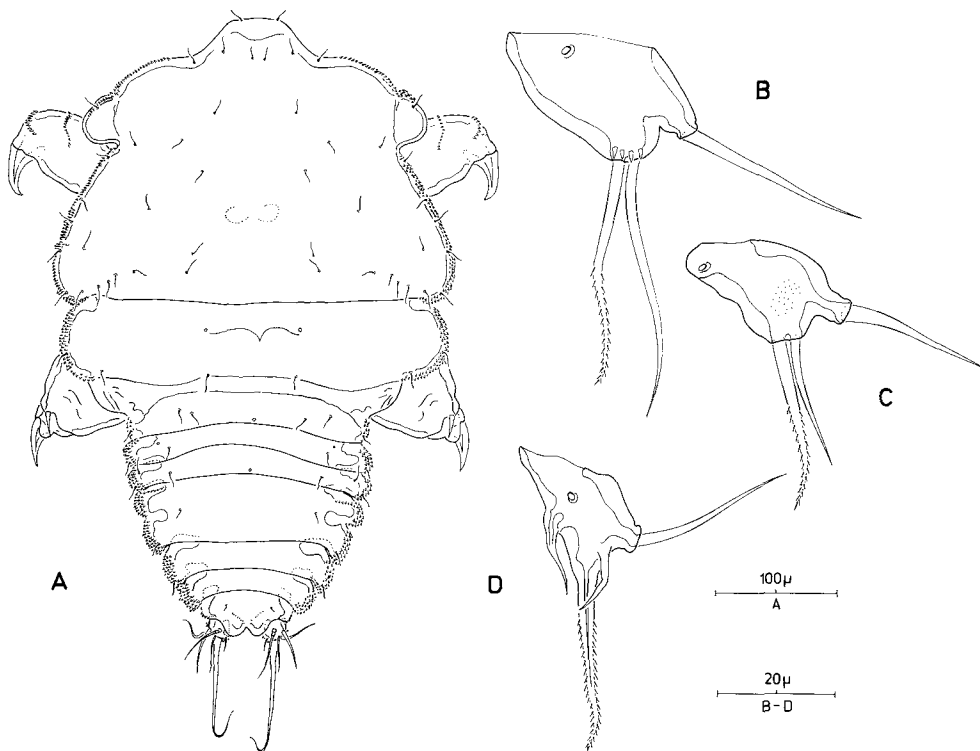


FIG. 2. *Namakosiramia californiensis* Ho & Perkins 1977 (♀). A. Habitus, dorsal view. B. P3. C. P4. D. P5.

can provide clues as to the relationships of the genus. Unfortunately, subsequent attempts to collect males were unsuccessful (Ho, pers. comm.).

Except for the maxilliped, P1 and P2 – all being powerful anchoring appendages – all postantennal appendages of *Namakosiramia* are strongly reduced in size and structure. Several laophontid genera (e.g. *Laophontina*, *Klieonychocamptoides*) show similar profound reductions (however, in relation to an interstitial life-style) in the swimming legs, yet none of them has such reductions in the cephalic appendages. Ho & Perkins (1977; fig. 13) apparently have transposed the maxilla and maxillula; the mandibular palp is represented by only 2 setae. The fifth leg bears 4 armature elements instead of 2.

The anterior margin of the antennal endopodite is provided with 6 setae or spines, the innermost of which is spiniform, short, and free at the base. In all Laophontinae this element is minute, setiform and in most cases fused at the base with the innermost geniculate seta. The endopodal claw of the maxilliped has two accompanying dwarfed setae in contrast to one in other Laophontinae.

Despite the aberrant morphology it seems appropriate to include the genus in the Laophontinae and to nullify the family name Namakosiramiidae. The description of the male probably will solve the question whether a separate subfamily has to be recognized or not.

Although the Copepoda have succeeded in developing more associations with the Cnidaria than with any other group of invertebrates, over 230 species are known to live

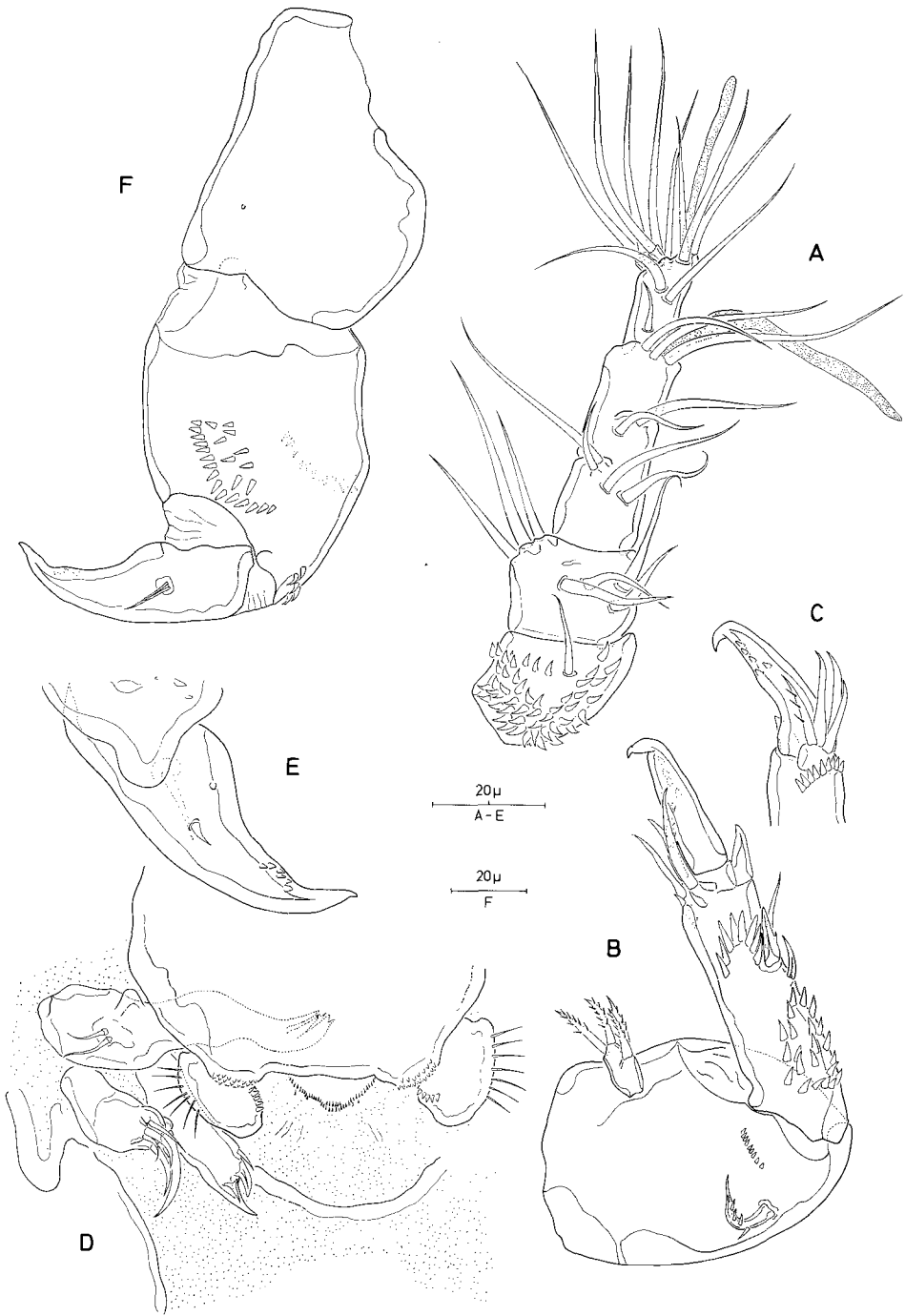


FIG. 3. *Namakosiramia californiensis* Ho & Perkins 1977 (♀). A. Antennula. B. Antenna. C. Antenna, distal part of endopodite, other view. D. Oral area, showing labrum, mandible, maxillula, paragnaths and maxilla. E. Maxilliped, posterior view of endopodite. F. Maxilliped, anterior view.

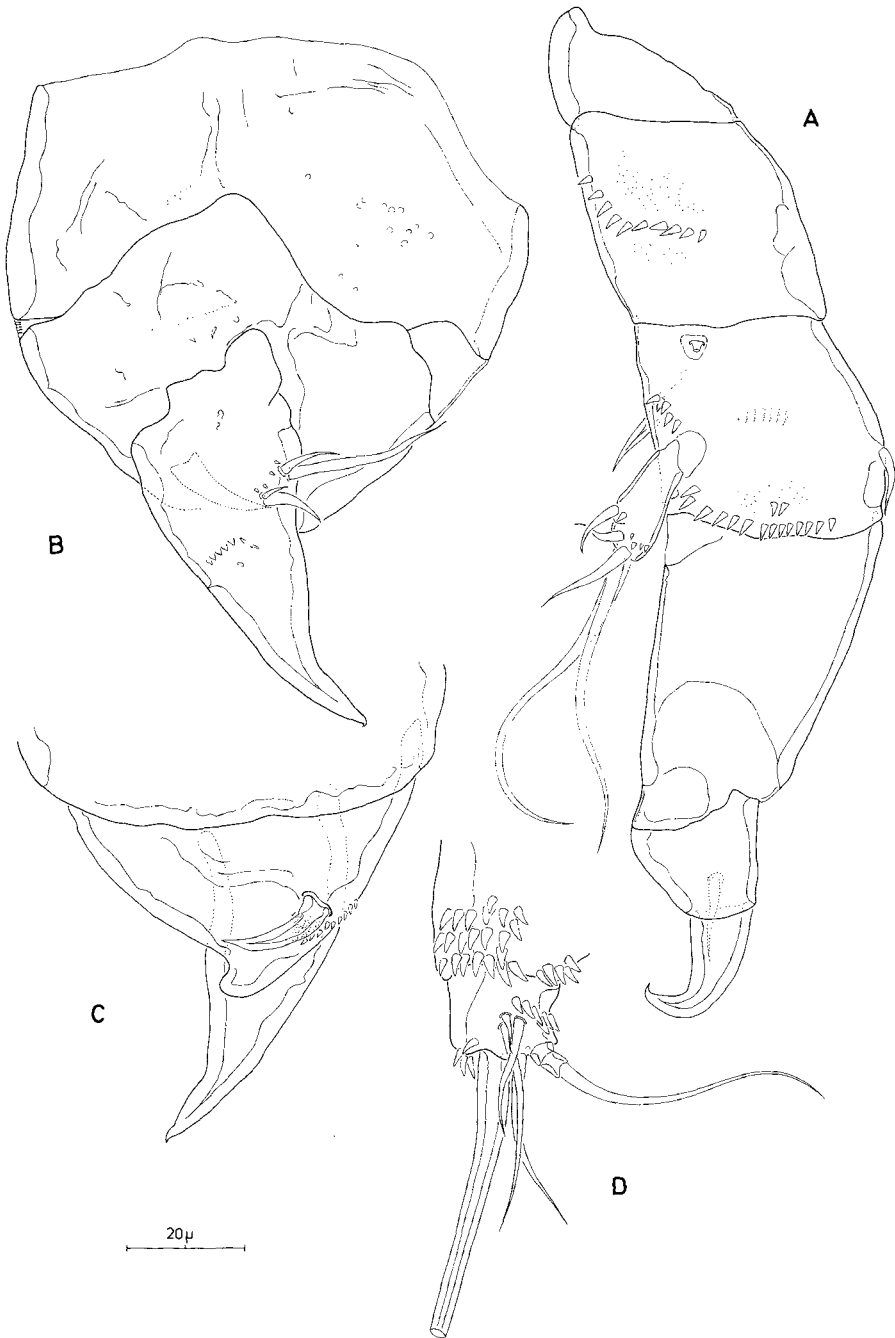


FIG. 4. *Namakosiramia californiensis* Ho & Perkins 1977 (♀). A. P1. B. P2, inner side. C. P2 outer side of exopodite and basis. D. Caudal ramus, lateral view.

in various degrees of association with Echinodermata (Humes, 1985). Of the various orders of Copepoda, the Siphonostomatoida and Poecilostomatoida contain by far the greatest number of species associated with echinoderms (e.g. Barel & Kramers, 1977). Harpacticoids are represented by relatively small numbers; however, they have developed associations with all classes of Echinodermata except the Crinoidea.

Thus far, only one harpacticoid associate has been reported from Asterozoa. Recently, Ho (1982) recovered *Tisbe japonica* from washings of the bat-star *Asterina*

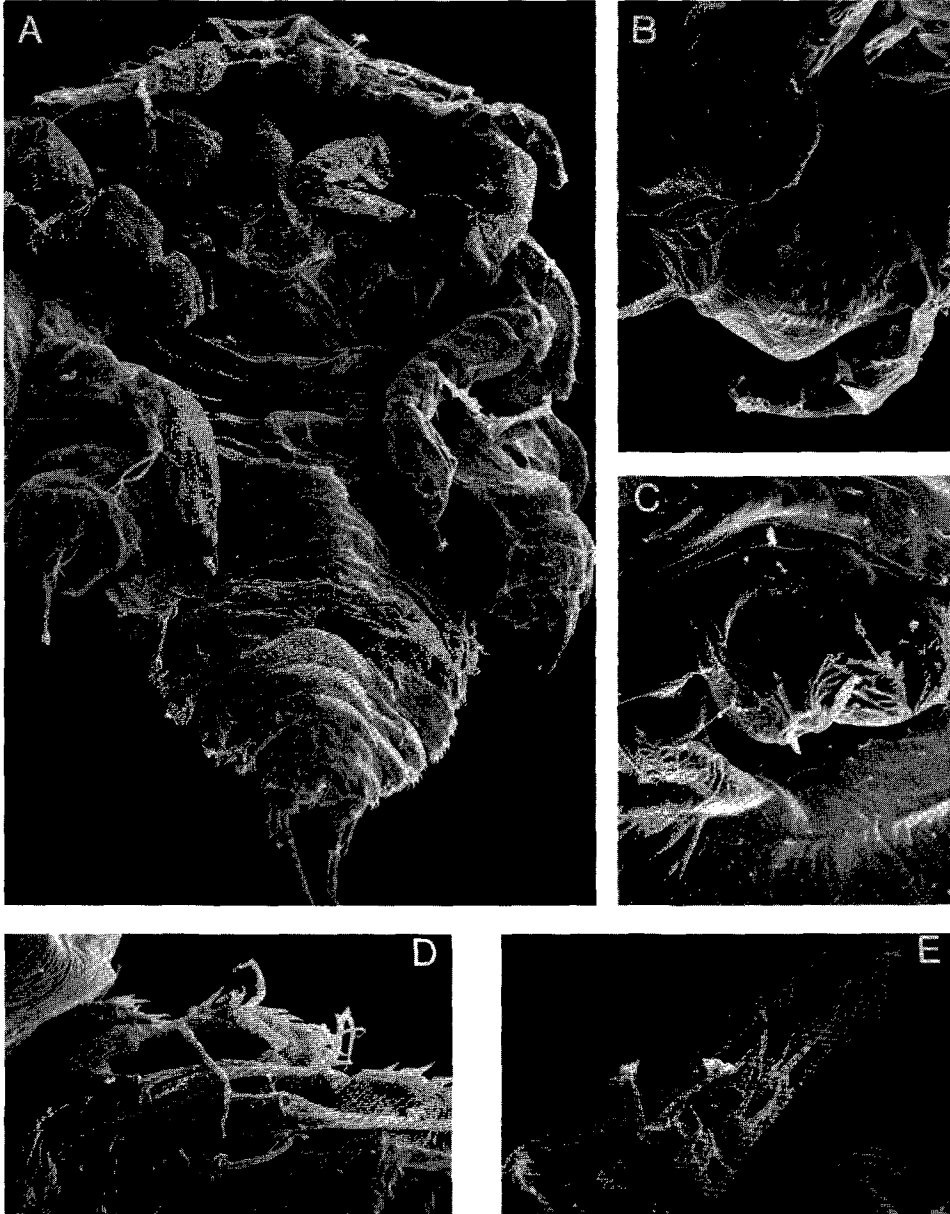


FIG. 5. *Namakosiramia californiensis* Ho & Perkins 1977 (♀). SEM-photography. A. Habitus, ventral view. B. Maxilliped, anterior view (arrow indicating small seta). C. Detail of genital complex with remnants of P6. D. P4 and P5. E. Distal part of antennula.

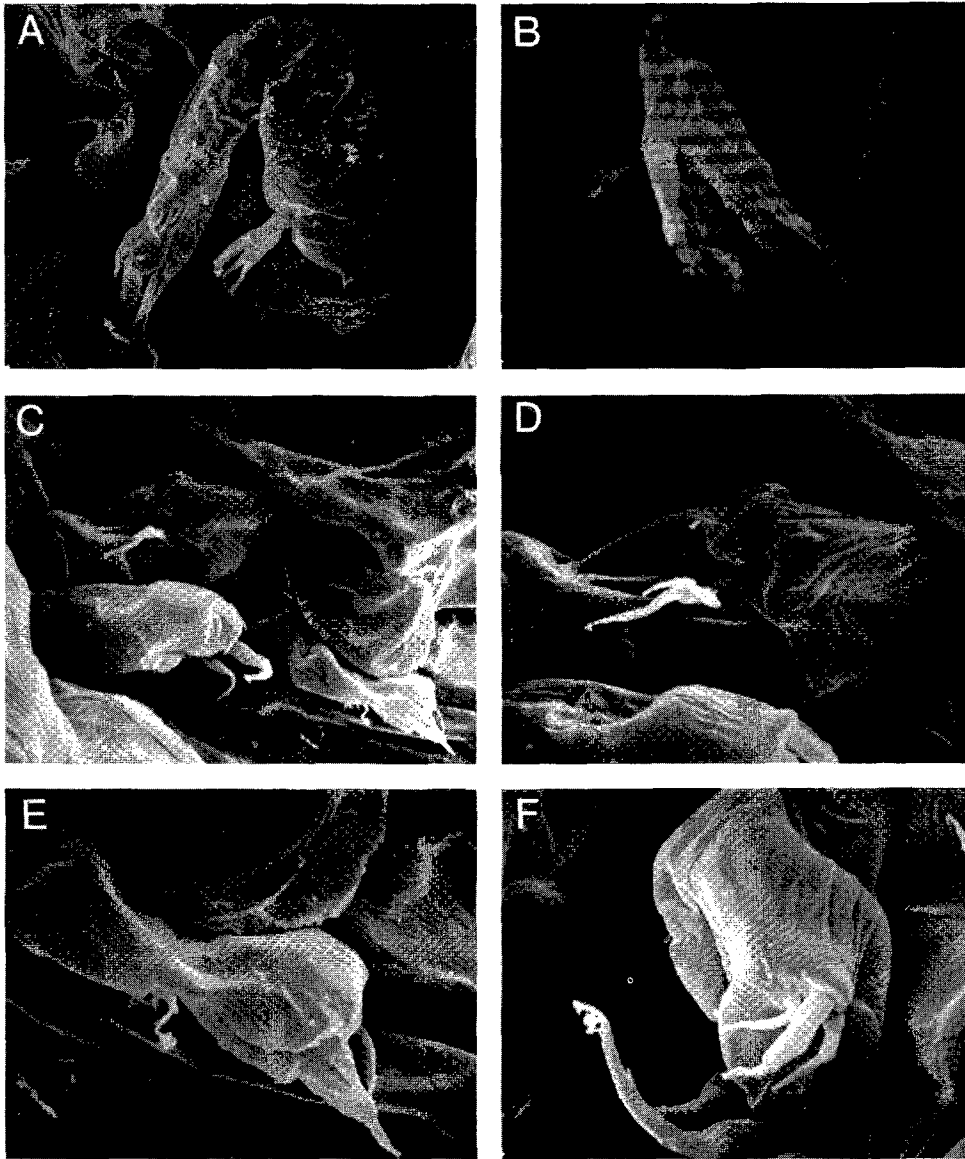


FIG. 6. *Namakosiramia californiensis* Ho & Perkins 1977 (♀); SEM-photography. A. Antenna. B. Antennal exopodite. C. Labrum, mandible, maxillula, paragnath and maxilla. D. Palp of mandible. E. Maxillula. F. Maxilla.

pectinifera collected off Tassha Bay on the west coast of Sado Island, Japan. Bresciani & Lützen (1962) encountered *Euterpina acutifrons* in the slimy covering of *Astropecten irregularis* and both *Parathalestris harpacticoides* and *Stenhelia gibba* on *Solaster papposus*; however, these species are better known as free-living forms, or as Gotto (1979) put it: "... their *bona fides* as associated copepods must therefore remain in doubt".

Porcellidium echinophilum is an associate of the sea-urchin *Echinometra mathaei* near Nossi Bé, Madagascar (Humes & Gelerman, 1962). All copepod stages occur in

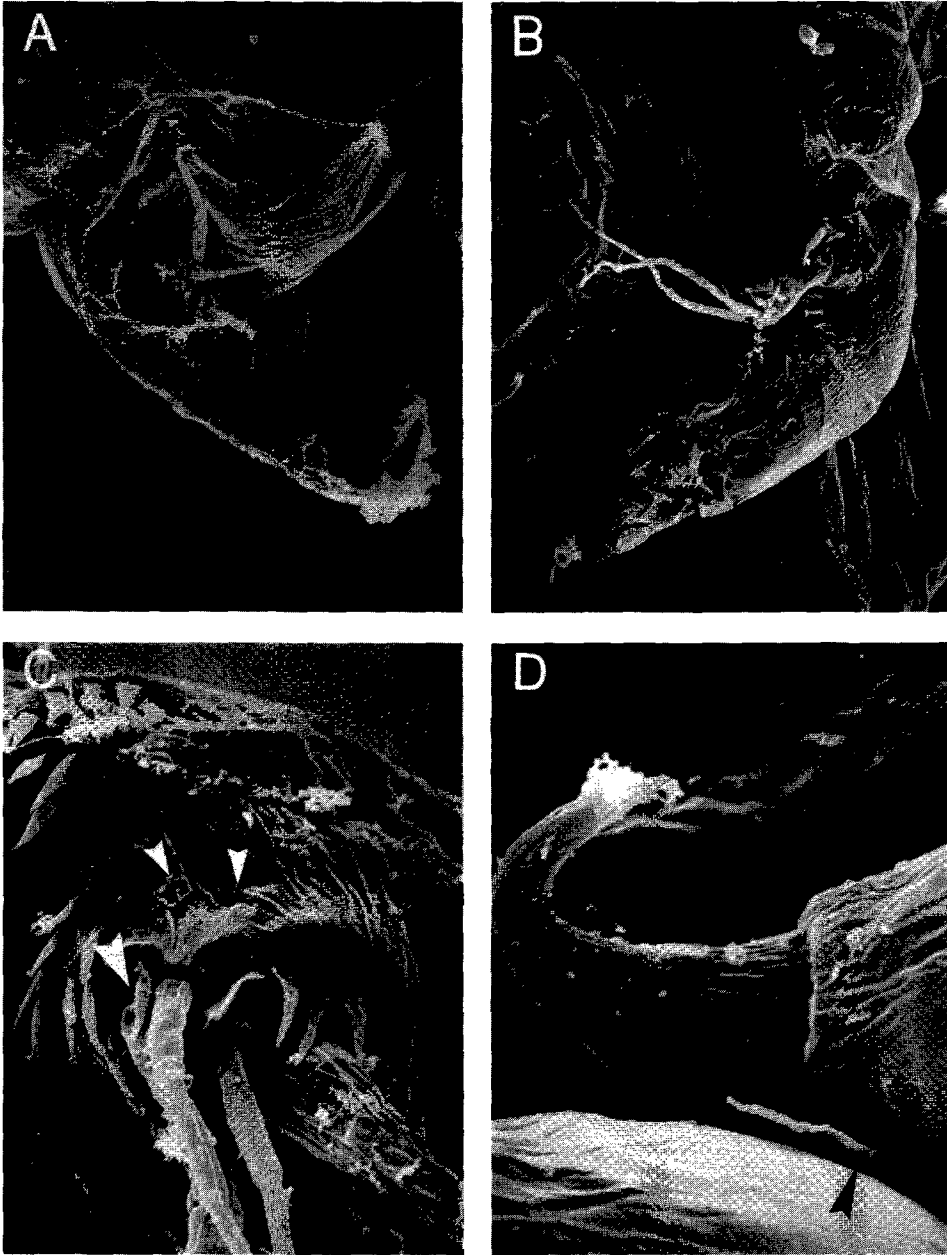


FIG. 7. *Namakosiramia californiensis* Ho & Perkins 1977 (♀); SEM-photography. A. Inner side of P2. B. P1. C. Caudal ramus, dorsolateral view (arrows indicating 2 tubular pores and diminutive anterolateral accessory seta I). D. Distal endopodite segment P1 (arrow indicating small seta).

dense assemblages on the host surface. Adherence to the host is facilitated by the ventral sucking-disc formed by the postantennal appendages of the cephalosome (Bocquet, 1948; Tiemann, 1986). A similar, but not homologous, mechanism is described in *Discoharpacticus mirabilis*, occurring, in addition to *Tisbe* sp, and *Amonardia pentasetosa*, on the echinoid *Loxechinus albus* collected from the Chilean

coast (Noodt, 1954); for the latter two copepod species a specific association remains to be proved. Willey (1930) reported *Laophontodes armatus* and many other species among material collected from the spines of the sea-urchin *Arbacia* (= probably *Lytechinus* since *Arbacia* does not occur in Bermuda; *vide* Volkmann, 1979a: p. 19). *Tisbe biminiensis* was recovered from the test of *Meomia* by Volkmann (1979b: p. 178). In an earlier study of *Tisbe* species from Beaufort, North Carolina (Volkmann-Rocco, 1972b) she stated that these were particularly abundant when new material (e.g. *Arbacia*) was introduced into the aquaria.

In all probability the records (Bresciani & Lützen, 1962) of *Thalestris longimana* on the brittle stars *Ophiothrix fragilis* and *Ophiopholis aculeata* are merely accidental.

Apart from *Namakosiramia* holothurians serve as host for at least 4 other harpacticoid species; however, since the original description they all have turned out to be only loose associates. *Metis holothuriae* has been described in association with *Actinopyga agassizii* on Great Abaco Island, Bahamas (Edwards, 1891). All subsequent records, however, substantiate a free-living life-style for the species (e.g. Lang, 1948). Stock (1961) noted *Sacodiscus humesi* in washings of *Holothuria tubulosa* in the Western Mediterranean, but it remains uncertain whether it is a real associate. *Tisbe holothuriae* has been found in very large numbers in the anterior part of the digestive tube of *Holothuria stellati* near Banyuls-sur-Mer, France (Humes, 1957). Later records proved this find to be rather exceptional as the species is commonly found free-living among algae on both sides of the Atlantic (e.g. Volkmann-Rocco, 1971, 1972a; Bergmans, 1979). In the same area *Cucumaria planci* harbours a second species *Tisbe cucumariae* on its body surface (Humes, 1957). The species, however, seems to be only a facultative associate, often found with tunicates and molluscs but usually free-living among algae in the warm temperate region of the northern hemisphere (Volkmann, 1979b). In this context it should be stressed that many Tisbinae exhibit a tendency towards a loose form of association with other invertebrates (e.g. *T. wilsoni* in the ascidian *Amaroucium*; *T. elongata* in *Homarus vulgaris*; *T. celata* in *Mytilus edulis*; *Sacodiscus ovalis* on *Homarus americanus*).

Though very few harpacticoids are known to be commensals, parasites or otherwise associated, recent studies indicate that they may be more frequent associates than previously believed (Humes, 1985). Within the order, the Laophontidae in their evolutionary history, have succeeded in developing an impressive number of associations and the continuing discovery of new taxa gives evidence that this number represents only the tip of the iceberg.

With respect to the genus *Laophonte*, the first association was mentioned by Jakubisiak (1932) who found *L. royi* (*species incerta sedis* in Lang, 1948) on the spider crab *Maia squinado* from Roscoff. This record as well as his find of *Hemilaophonte janinae* are probably accidental as this is certainly the case for 26 other (mostly phytal) species. The only published record of *L. dominicalis* is that of Monard (1935) who found the species (in laboratory conditions!) on *Ascidia* (= *Phallusia*) *mentula* from Roscoff. Raibaut (1962, 1963) reported *L. commensalis* among the pilose setae of three species of xanthid crabs (*Xantho*) from the Atlantic and Mediterranean coasts of France. Since all stages from the first nauplius to the adult (Raibaut, 1963) can be found on the host, it seems likely that the complete life cycle takes place on the host. An interesting case of inquilinism is described by Raibaut (1966), whose careful examination revealed an inquilinous laophontid *L. adamsiae*, occupying membranous expansions of the basal disc of *Adamsia palliata* which itself lives in association with the pagurid *Pagurus prideauxi*. The actinian host seems to offer a suitable refuge

since larval stages (nauplii and copepodites) were noted, as well as adults, in the enveloping folds of the base. *Laophonte? drachi*, described from the French Catalanian coast, lives in small numbers on the bryozoan *Schismopora armata* (see Médioni & Soyer, 1966).

A number of Laophontidae (all normally free-living) have been observed in accidental association with other animals: *Laophonte similis* (= *L. setosa*) on *Hyas araneus* (T. Scott, 1902), both *L. propinqua* (= *L. serrata*) and *L. intermedia* (= *Asellopsis intermedia*) on sponges from Port Erin, Isle of Man (A. Scott, 1896) and *L. curticauda* (= *Heterolaophonte stromi*) on *Carcinus maenas* (T. Scott, 1902). C. B. Wilson (in Pearse, 1934) identified two species of *Laophonte* found in a loggerhead sponge *Speciospongia vespara* at Dry Tortugas, Florida. Vervoort (1964) recovered *Microlaophonte spongicola* from sponges from the lagoon at Ifaluk Atoll (Caroline Islands). Chislenko (1977) found *Laophonte inopinata* and *L. aldonae* to be associated with the sponge *Phakellia cribrosa* (Axinellida) collected from Franz Josef Land.

Esola hirsuta is described from Muttuvaratu, Sri Lanka (Thompson & A. Scott, 1903) where it was found in washings of pearl oysters together with the calanoid *Ridgewayia typica*.

The genus *Paralaophonte* includes certain species exhibiting a rather loose form of association (*P. congenera congenera* associated with *Limnoria* burrows; see Sleeter & Coull, 1973) or inhabiting the gill chambers of *Maia squinado* (*P. majae*, see Petkovski, 1964; *P. ormieresi*, see Raibaut, 1968). Yeatman (1970) recovered both *P. congenera* and *P. brevirostris* from Chesapeake Bay sponges, however, no recognizable sponge cells were found in the gut contents. The author does not exclude the possibility that the species may feed on dead or decaying sponge fragments. *Paralaophonte macera*, *P. innae* and *P. hyperborea* were encountered on the axinellid *Phakellia cribrosa* by Chislenko (1977); the latter two species were also recovered from the Arctic decapods *Sabinea septemcarinata* and *Lebbeus polaris*.

Nicholls (1957) described two new species of *Mictyricola* being commensal with land crabs on the coasts of Australia and Tasmania. Both *M. typica* (on *Mictyris platycheles*) and *M. proxima* (on *M. longicarpus*) are not inhabitants of the branchial chambers but live on the ventral surface of the crab in the space enclosed between the thorax and the reflexed abdomen or occasionally on the setae of the host's maxillipeds. According to Nicholls (1957) the complete life cycle takes place on *Mictyris* since all stages were obtained from the host.

The monotypic genus *Harrietella* is an associate of wood-infesting Isopoda of the genus *Limnoria*. *H. simulans* has been observed on both *Limnoria lignorum* (Stephenson, 1936, as *Laophonte (brevifurca?)*; Vervoort, 1950; Wells, 1964; Pinkster, 1968) and *L. tripunctata* (Coull & Lindgren, 1969; Sleeter & Coull, 1973) or in wood infested by *Limnoria* species (Pinkster, 1968; Boer, 1971). According to Vervoort (1950) the species attaches itself to the host's telson, or (less frequently) to the host's legs and cephalic appendages, by means of the powerful maxillipeds and P1 endopodites. Both sexes and some developmental stages have been observed clinging to the isopod; attachment probably takes place after the metamorphosis of the nauplius. Boer (1971) questioned the relation between *Harrietella* and *Limnoria*; the use of the isopod-made holes as a hiding place might be a factor of at least equal importance.

Finally, Pinkster (1968) clearly showed that adult *Donsiella limnoriae* are constant associates of *Limnoria* while larval stages are free-living. The 'laophontid' (in my opinion the genus *Donsiella* can hardly be considered a member of the Laophontidae *sensu lato*; several characters allude to a pseudotachidiid relationship) is usually found

on the ventral side of the gribble, where it occupies the angles formed by the sternites and epimerites on either side of the bases of the legs (Krishnaswamy & Jones, 1962). The European distribution of *D. limnoriae* is confined to Norway (Stephensen, 1936; on *L. lignorum*), England (Krishnaswamy & Jones, 1958, 1962; on *L. lignorum*, *L. tripunctata* and *L. quadripunctata*) and the Atlantic and Mediterranean coasts of France (Pinkster, 1968; on *L. lignorum* and *L. tripunctata*). Brunel (1963) observed *D. limnoriae* and a second unidentified laophontid clinging to *L. japonica* in the arctic waters of the Gulf of St. Lawrence, Canada, whilst Gooding (in Krishnaswamy & Jones, 1962) found the species along the U.S. Pacific coast.

Note added in proof.

Hicks (1988, *Journal of Natural History*, **22** (3), 639–684) revised the genus *Donsiella* and described four new genera (*Apodonsiella*, *Pseudonsiella*, *Xylora*, *Oligoxylora*) from intertidal wharf piles and subtidal decomposing wood. It is concluded that the genus *Donsiella* is misplaced within the Laophoridae and that the subfamily Donsiellinae is closely related to the Thalestridae, particularly to the Pseudotachidiinae.

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