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# THE PARASITIC ISOPOD *HOLOPHRYXUS ACANTHEPHYRAE* STEPHENSEN (EPICARIDEA: DAJIDAE) FROM THE SUBANTARCTIC SOUTH PACIFIC, WITH NOTES ON ITS SYNONYMY AND HOST

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*Abstract.*—The dajid isopod *Holophryxus acanthephyrae* Stephensen, 1912a, is newly reported from the subantarctic South Pacific. A female of the species, and the male recovered from her marsupium, collected attached to the carapace of a specimen of the oplophorid shrimp *Acanthephyra pelagica* (Risso) are described. It is concluded that *Isophryxus concavus* Schultz, 1977, the type species of the genus *Isophryxus,* recorded from the antarctic and subantarctic South Pacific, is a junior synonym of *Holophryxus acanthephyrae.* The three other known species of *Isophryxus, I. quadratohumerale* Schultz, 1978, *I. polyandrus* Schultz, 1978, and *I. septapodus* Schultz, 1978, are transferred to *Holophryxus.* Physical damage caused to the host shrimp by *H. acanthephyrae* is discussed. A list of the known species of *Holophryxus,* their distributions, and known host species is presented.

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During a study of the pelagic caridean shrimps belonging to the family Oplophoridae collected by the USNS *Eltanin* from the antarctic and subantarctic South Pacific during the U.S. Antarctic Research Program (Wasmer 1986), I found an ovigerous female dajid isopod loose among specimens of the oplophorid *Acanthephyra pelagica* (Risso) collected at station 1723 of *Eltanin* cruise 24. A note in the sample bottle indicated that the isopod was collected attached to one of the shrimps in the sample, and a male specimen of *A. pelagica* in the bottle was found to have marks on the dorsal surface of its carapace which appeared to have been made by the mandibles and pereopods of the isopod. An additional male specimen of *A. pelagica* from *Eltanin* cruise 19, station 1480 was noted to have marks on its carapace similar to those on the shrimp from station 1723 of cruise 24, although no isopod was present in the sample bottle when it was obtained from the Smithsonian Oceanographic Sorting Center (SOSC).

I tentatively identified the female isopod (and the male found enclosed in her marsupium) from station 1723 as a member of the genus *Holophryxus* Richardson, based on the redescription by Butler (1964) of *H. alaskensis* Richardson, 1905 (the type species of the genus) and my examination, 1966, of the type specimens of *H. californiensis* Richardson, 1908 (synonymized with *H. alaskensis* by Butler in 1964) and of *H. giardi* Richardson, 1908. The examination of the types of these latter two species was made in conjunction with the identification of several dajids from shrimps collected off the coast of Oregon by oceanographic vessels of Oregon State University.

Of the five previously recognized species of *Holophryxus,* only one has been recorded from an oplophorid shrimp. Stephensen (1912a) described *H. acanthephyrae* based on a mature female collected off Greenland attached to the carapace on an oplophorid he identified as *Acanthephyra purpurea,* but which he later concluded (1912b) was *A. multispina,* a synonym of *A. pelagica* (see Wasmer 1986). The recent redescription of the female and the first description of the male of *H. acanthephyrae* by Jones & Smaldon (1986), published while the current work was in an early draft stage, strengthened my conclusion that the female and male isopod from *Eltanin* station 1723 are *H. acanthephyrae* Stephensen.

The dajid genus *Isophryxus* was established by Schultz (1977), with the type species *I. concavus.* The description was based on the holotype female and the allotype male found enclosed in her marsupium collected by a midwater trawl at station 1480 of *Eltanin* cruise 19. Eight additional specimens (six females and two males) of the species were recorded (Schultz 1977) from six midwater trawl stations occupied by the *Eltanin* during cruises 11, 15, and 19 in the antarctic and subantarctic South Pacific. The host species of none of these specimens was known to Schultz. Schultz pointed out that *I. concavus* is similar to the type species of the genus *Holophryxus,* from which it otherwise differs by having the pereonal segments indicated on the dorsal surface of the female. Schultz (1978) subsequently described three additional species of *Isophryxus* (*I. quadratohumerale, I. polyandrus,* and *I. septapodus*) from specimens collected by midwater trawls during *Eltanin* cruises 24, 25, and 35 in the antarctic and subantarctic South Pacific. Again, the host species is not known for these three species.

The purpose of this paper is to describe the female and male *Holophryxus acanthephyrae* from *Eltanin* station 1723, and to propose, based on examination of the pertinent types, that *Isophryxus concavus* Schultz is a synonym of *Holophryxus acanthephyrae* Stephensen. Evidence of physical damage caused to the host shrimp by *H. acanthephyrae* is also discussed. Lastly, a list of the known species of *Holophryxus,* their distributions, and known host species is presented.

Suborder Epicaridea

Family Dajidae

*Holophryxus acanthephyrae* Stephensen

Fig. 1A–D

*Holophryxus acanthephyrae* Stephensen, 1912a:112, figs. 13, 15–21.—Jones & Smaldon, 1986:303, figs. 1–6.

*Isophryxus concavus* Schultz, 1977:93, figs. 17A–17I, 18A–18H, 18O, 18P.

*Material.*—Ovigerous female (22.7 mm long and 10.7 mm wide), and male (2.3 mm long, 1.1 mm wide) from marsupium of female, collected attached to a male specimen of the oplophorid shrimp *Acanthephyra pelagica* (Risso), cl. 26.0 mm, from USNS *Eltanin* cruise 24, sta 1723 (18 Jul 1966, 40°01′S, 149°57′W to 40°05′S, 149°55′W, 880 m), USNM 233550.

*Description.*—Adult female: Body symmetrical, oblong-ovate, dorsal surface convex, ventral surface strongly concave anteriorly. Color in alcohol light yellow.

Dorsal prominence of cephalon slightly bilobed, not visible from below. Cephalic ridge narrow in dorsal view, anterior margin sinuous. Eyes absent.

True segmentation of pereon evident only in lateral view, indicated by posterior 4 pairs of 5 coxal plates; first pair of coxal plates fused with cephalic ridge, forming anterior boundary of oral area; fifth pair small, separated from fourth by distinct space. Dorsal surface of pereon with 3 shallow transverse furrows in integument behind rounded prominence of cephalon.

Pleon continuous with but narrower than pereon, tapering posteriorly to rounded extremity, unsegmented, lacking pleopods and uropods. Dorsal surface of pleon deeply excavated on both sides of midline near junction with pereon.

Oral area bounded anteriorly and laterally by flattened flange-like cephalic ridge.

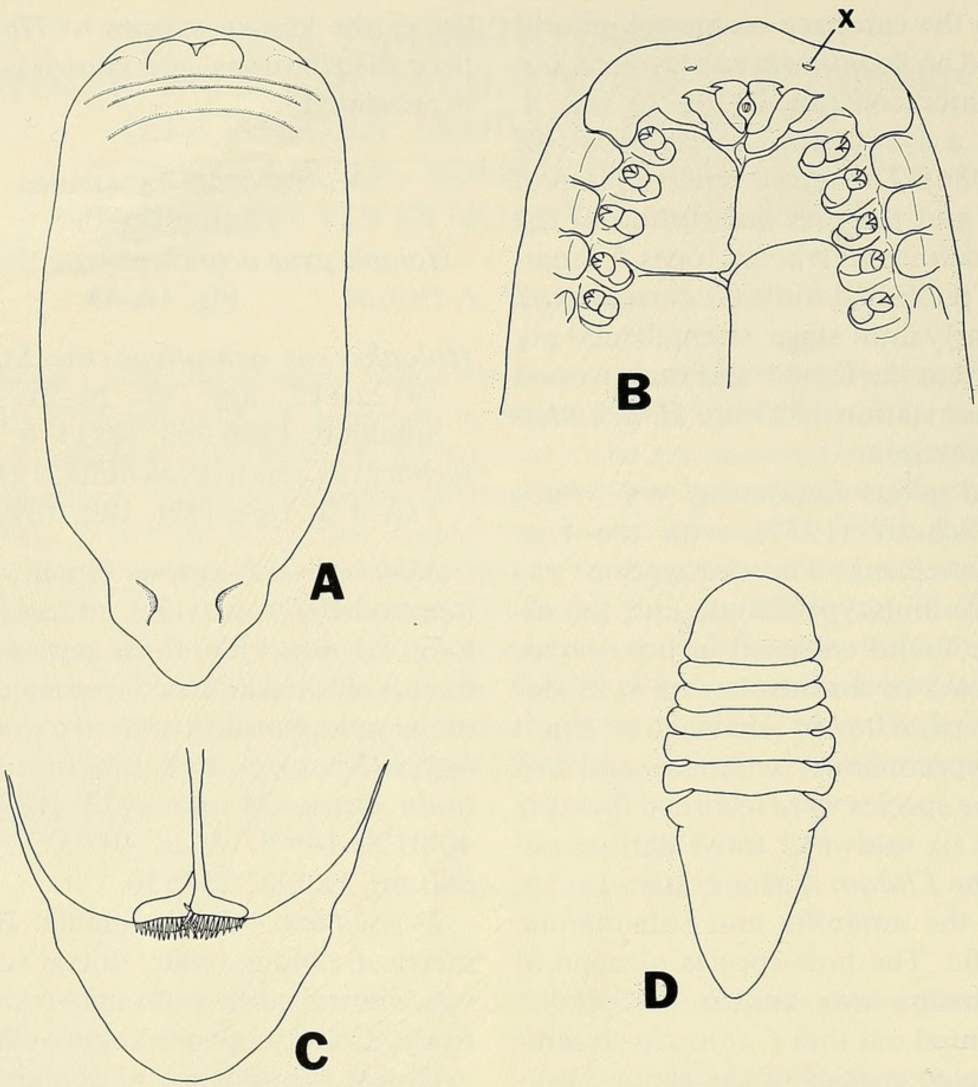


Fig. 1. *Holophryxus acanthephyrae, Eltanin* station 1723: A, Dorsal view, mature female; B, Ventral view, anterior part of pereon, mature female, x = pit organ; C, Ventral view, posterior part of pereon and pleon, mature female; D, Dorsal view, male.

Cephalic ridge with pair of narrow, slit-like pores or pit organs (Fig. 1B, x) about halfway from midline to lateral edge. First and second pairs of antennae unsegmented and flattened, with elongate lobe-like peduncles surrounding oral area. Tips of mandibles styliform, visible in central part of oral area; remaining mouthparts not visible without dissection. Five pairs of short pereopods present (pereopods 6 & 7 lacking), posterior 4 pairs arising from bases near separate coxal plates. Pereopods prehensile, all of similar size and shape, with dactyls strongly recurved and clawlike.

Five pairs of incubatory plates (oostegites) arising from bases of pereopods; only first and fifth pairs visible, covering other 3 pairs. Fifth pair of plates largest, extending to posterior end of pleon and forming largest part of marsupium, medial edges overlapping slightly; posterior margin of each ending in flattened crest just before pleon, each fringed with long spines (12 on left, 13 on right) above posterior end of marsupium.

Male: Elongate, symmetrical, dorsal surface slightly convex, ventral surface concave. Color in alcohol yellowish white.

Cephalon large, rounded anteriorly, completely fused with pereonite 1, lateral margin slightly indented posteriorly, indicating anterior limit of first pereonite. Eyes absent. First antennae short, composed of 3 articles;

second antennae somewhat longer (composed of 3 articles?), directed posteriorly; neither pair visible in dorsal view. Mandible tips projecting from oral area.

Pereonites 2–6 distinctly separated from each other, pereonite 7 almost completely fused with pleon; lateral margins of second through sixth rounded, lateral margins of seventh conical. Seven pairs of prehensile pereopods present.

Pleon conical, slightly longer than pereonites 1–6 combined, longer than wide, unsegmented, tapering posteriorly to narrowly rounded extremity. Pleopods and uropods absent.

*Remarks.*—Based on my comparison of the female and male dajid specimens and their host (*Acanthephyra pelagica*) from *Eltanin* station 1723 with the female holotype of *Holophryxus acanthephyrae* Stephensen, and its type host (*Acanthephyra pelagica*) obtained on loan from the Universitetets Zoologiske Museum in Copenhagen, as well as the description of the species given by Jones & Smaldon (1986), it is concluded that these specimens are identical with *H. acanthephyrae.*

There appear to be no significant differences between the holotype of *H. acanthephyrae* and the specimen from the *Eltanin* oplophorid. Both specimens are ovigerous females of comparable size and shape. The morphological details visible in dorsal, ventral, and lateral views of the two specimens are in very good agreement, although there is a minor difference in the number of spines on the posterior marginal crests of the fifth incubatory plates of the two specimens (14 on each in the case of the holotype, but only 12 and 13 on the specimen from the *Eltanin*).

The female described here is also in essential agreement with the female *H. acanthephyrae* redescribed and illustrated by Jones & Smaldon (1986), although that specimen is smaller and somewhat more deformed. The cephalic pores, first pointed out by Jones & Smaldon (1986), are also easily seen on the female described here. I was unable to see the pores on the holotype of *H. acanthephyrae* or on other members of the genus examined in the course of this study; perhaps the opening to the pore, which may be a sense organ of some type, can be contracted or closed off by the isopod so that it would be especially hard to see on some preserved specimens.

It is unfortunate that Stephensen did not have a male specimen of *H. acanthephyrae* with which the present male specimen can be compared. It is very likely that his holotype female has a male in her marsupium; several of the previously recorded males of other *Holophryxus* species have been taken from ovigerous females on which the medial margins of the fifth incubatory plates are close together or from females which have recently emptied marsupia (Rustad 1935, Butler 1964, Jones & Smaldon 1986).

The male described here is very similar to the male described by Jones & Smaldon (1986). The shape of the lateral margins of the seventh pereonites differ in the two specimens, being more conical in the present specimen. However, as pointed out by Jones & Smaldon (1986), there are few diagnostic characters separating the males known for the different species of *Holophryxus,* as well as evidence of some variation in body form between males of the same species.

The fact that the holotype of *H. acanthephyrae* and one of the four specimens of the species reported by Jones & Smaldon (1986), as well as the present female, were collected on specimens of the oplophorid shrimp *Acanthephyra pelagica* is strong evidence that the dajid from the *Eltanin* material is *Holophryxus acanthephyrae.* Each of the five species of *Holophryxus* for which the host is known occurs on only a single species of pelagic decapod shrimp (see below).

*Holophryxus acanthephyrae* has been recorded previously from the type locality in Davis Strait west of Greenland (60°07′N, 48°26′W) and from the Western Approaches and Bay of Biscay (Stephensen

1912a, Jones & Smaldon 1986). The present record from the subantarctic South Pacific thus considerably extends the known distribution of the species. This new record is not totally unexpected when the wide distribution of its host in the North Atlantic from about 13°N northward, the Mediterranean, the South Atlantic from 24°S southward, and the Indo-Pacific between 32°S and 57°S (Wasmer 1986) is considered.

## Discussion

*Notes on synonymy.*—Comparison of the holotype and allotype of *Isophryxus concavus* Schultz in the National Museum of Natural History with the holotype of *Holophryxus acanthephyrae* and with the female and male dajids from *Eltanin* station 1723 identified herein as *H. acanthephyrae,* has convinced me that Schultz (1977) mistakenly separated *Isophryxus* from *Holophryxus* and that *Isophryxus concavus* and *Holophryxus acanthephyrae* are in fact the same species. By the rule of priority, *Isophryxus concavus* should therefore be considered a junior synonym of *Holophryxus acanthephyrae* and *Isophryxus* becomes a junior synonym of *Holophryxus.*

Schultz (1977) appears to have overlooked Butler's 1964 redescription of *Holophryxus alaskensis* Richardson, 1905, the type species of the genus. Butler pointed out that folds in the dorsal integument of the pereon of several specimens of that species give the impression of segmentation, but that the folds are not related to segmentation. Richardson did not mention well defined transverse folds in her description or show them in her figures of *H. alaskensis*; however, the specimens were apparently somewhat stout and irregularly shaped when preserved (Butler 1964), and for that reason the folds are probably not so evident. Folds or furrows are also present on the dorsal integument of the pereon of *Hypodajus georgiensis* Nierstrasz & Brender à Brandis (1931:212, figs. 106–108), synonymized with *Holophryxus alaskensis* by Butler (1964). Anterior dorsal integumentary furrows of the pereon are present to some extent on all other known species of *Holophryxus* and have been noted in descriptions or are visible on figures of those species, as indicated in the following citations: *H. giardi* Richardson, 1908:fig. 1; *H. richardi,* Stephensen, 1912a:fig. 11; Rustad, 1935:16, fig. 4; *H. acanthephyrae* Stephensen, 1912a:113, fig. 15; Jones & Smaldon, 1986:309, fig. 2A and 2B; and *H. fusiformis* Shiino, 1937:188, fig. 1A and 1B.

The flattened posterior marginal crests armed with long fringing spines on the fifth incubatory plates of the holotype and paratype females of *I. concavus* (not mentioned in Schultz's description of the species but visible in his figs. 17A and 18B) also indicate that these specimens belong to the genus *Holophryxus.* Such crests are apparently present on mature females of the other species of the genus. Although Richardson (1905) does not specifically mention the crests and spines in her diagnosis of the genus or in her description of *H. alaskensis,* her fig. 8c seems to indicate the presence of spines on the posterior part of the fifth incubatory plates. Butler (1964), in his redescription of *H. alaskensis,* mentions the presence of such fringed crests on the fifth incubatory plates on mature females of the species, although his fig. 1c curiously does not show them. The crests are also drawn and described by Nierstrasz & Brender à Brandis (1931:212, fig. 108) in their description of *Hypodajus georgiensis.* Richardson (1908) does not mention the fringed crests in her description of *Holophryxus giardi* and they do not show on her fig. 1, but in my examination of the syntypes I found that they are in fact present on the mature female but folded downward and under the posterior edge of the fifth incubatory plates so as to be hidden from view; this is the result of the specimen being somewhat deformed when preserved. For the other species in the genus, the following citations show the pres-

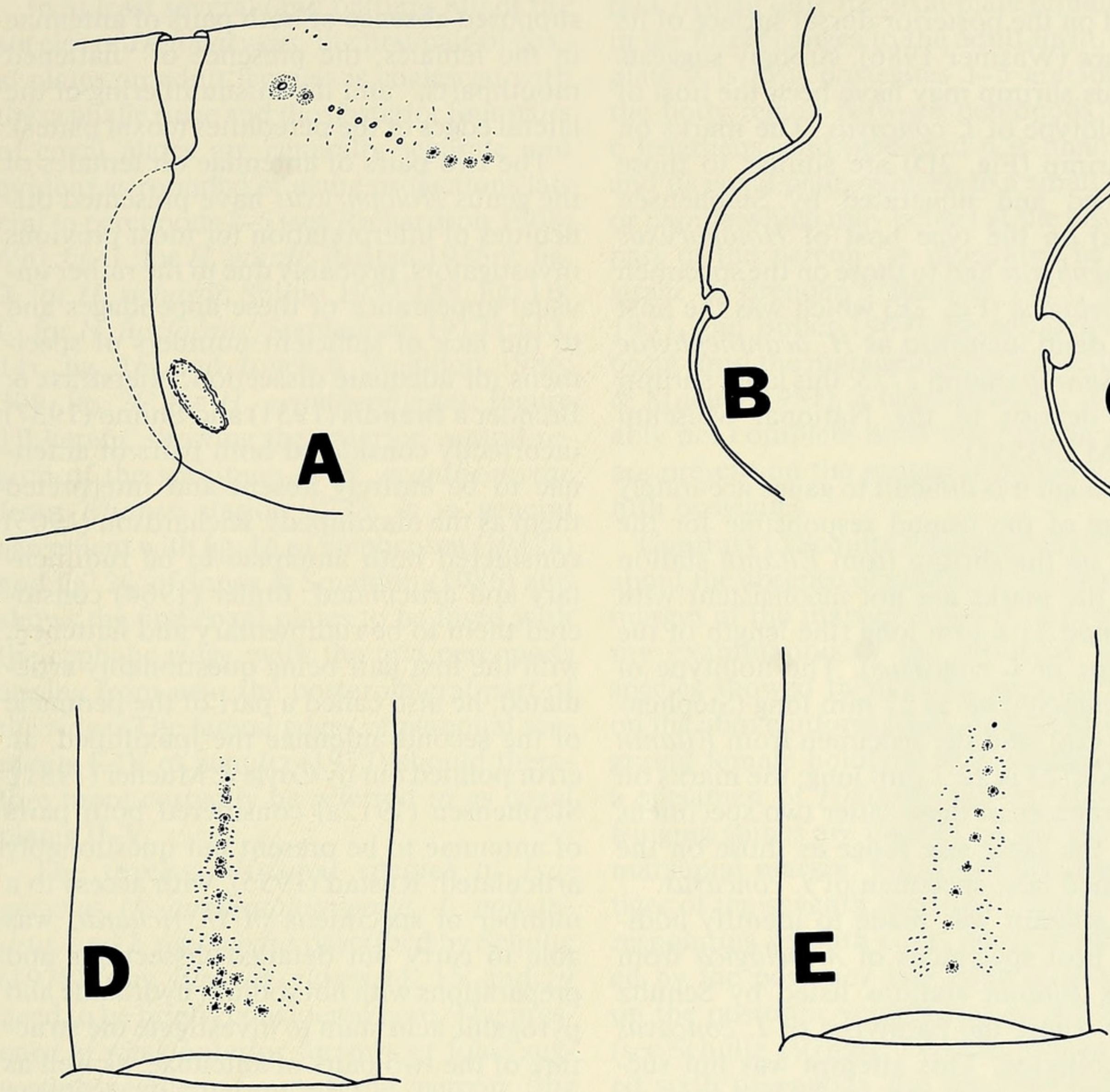


Fig. 2. *Acanthephyra pelagica*: A, Type host to *Holophryxus acanthephyrae* Stephensen, from *Tjalfe* station 322, view of posterior right carapace; B, Posterior right carapace edge of specimen from *Eltanin* station 1723; C, Posterior right carapace edge of specimen from *Eltanin* station 1480; D, Posterior dorsal surface of carapace of specimen from *Eltanin* station 1480, showing marks caused by mandibles and pereopods of isopod; E, Posterior dorsal surface of carapace of specimen from *Eltanin* station 1723, showing marks caused by mandibles and pereopods of isopod.

ence of this morphological feature: *H. richardi,* Stephensen, 1912a:109, 110, figs. 9, 11; Rustad, 1935:26, fig. 14; *H. acanthephyrae* Stephensen, 1912a:115, figs. 15, 17; Jones & Smaldon, 1986:309, figs. 2C and 2D; and *H. fusiformis* Shiino, 1937:190, figs. 1B, C.

The allotype male and other males recovered by Schultz (1977) from females of *I. concavus* show no apparent morphological differences between the male *H. acanthephyrae* described here and that described by Jones and Smaldon (1986).

The host of *Isophryxus concavus* was unknown to Schultz (1977) because the isopods apparently fell off the hosts at the time of collection. The presence of a male specimen of the oplophorid *Acanthephyra pelagica* (carapace length 26.5 mm), USNM 233552, from *Eltanin* station 1480 (the type locality station for *I. concavus*) with marks from the pereopods and mandibles of an isopod on the posterior dorsal surface of its carapace (Wasmer 1986), strongly suggests that this shrimp may have been the host of the holotype of *I. concavus.* The marks on the shrimp (Fig. 2D) are similar to those described and illustrated by Stephensen (1912a) on the type host of *Holophryxus acanthephyrae* and to those on the specimen of *A. pelagica* (Fig. 2E) which was the host of the dajid identified as *H. acanthephyrae* from *Eltanin* station 1723; this latter shrimp is on deposit in the National Museum (USNM 233551).

Although it is difficult to gauge accurately the size of the isopod responsible for the marks on the shrimp from *Eltanin* station 1480, the marks are not inconsistent with an isopod 21.6 mm long (the length of the holotype of *I. concavus*). The holotype of *H. acanthephyrae* is 22 mm long (Stephensen 1912a), and the specimen from *Eltanin* station 1723 is 22.7 mm long; the marks on the carapaces of these latter two specimens are in the same size range as those on the presumed host specimen of *I. concavus.*

An attempt was made to identify additional host specimens of *A. pelagica* from the six *Eltanin* stations listed by Schultz (1977) where the paratypes of *I. concavus* were collected. This attempt was not successful; none of the 14 specimens of *A. pelagica* from five of the stations have any marks indicating they served as hosts to isopods, and no specimens of *A. pelagica* were reported from the sixth station. However, if the specimen of *A. pelagica* from *Eltanin* station 1480 is assumed to be the type host of *I. concavus,* then the evidence becomes stronger that the specimens described as *I. concavus* are in reality *H. acanthephyrae.*

In addition to the undue significance attached by Schultz (1977) to the presence of the dorsal integumentary folds on the pereon of the genus *Isophryxus,* several other, more minor, erroneous interpretations of morphology are present in his diagnosis of the genus and in the description of *I. concavus.* These misinterpretations involve the supposed absence of both pairs of antennae in the females, the presence of "flattened mouthparts," and the misnumbering of the lateral edges of the pereonites (coxal plates).

The two pairs of antennae on females of the genus *Holophryxus* have presented difficulties of interpretation for most previous investigators, probably due to the rather unusual appearance of these appendages and to the lack of sufficient numbers of specimens for adequate dissection. Nierstrasz & Brender à Brandis (1931) and Shiino (1937) incorrectly considered both pairs of antennae to be entirely absent and interpreted them as the maxillipeds. Richardson (1905) considered both antennae to be rudimentary and articulated. Butler (1964) considered them to be rudimentary and flattened, with the first pair being questionably articulated; he also called a part of the peduncle of the second antennae the maxilliped, an error pointed out by Coyle & Mueller (1981). Stephensen (1912a) considered both pairs of antennae to be present but questionably articulated. Rustad (1935), with access to a number of specimens of *H. richardi,* was able to carry out detailed dissections and preparations with hot sodium hydroxide and pyrogallic acid stain to investigate the structure of the two pairs of antennae, as well as the mouthparts. Of the mouthparts, only the tips of the mandibles and part of the maxillipeds were normally visible without dissection. The two pairs of antennae were described by Rustad as being more or less deformed and "cushiony," and encircling the oral cone; even though they occasionally appeared to be articulated, the special preparative techniques used showed them to be unjointed.

Comparison of Schultz's (1977) fig. 17B of the anterior ventral part of *I. concavus* with fig. 16 of Stephensen (1912a) and figs. 2 and 7 of Rustad (1935) leads to the conclusion that what Schultz refers to as flattened mouthparts on his specimens represent the first and second pairs of antennae of Stephensen and Rustad.

In at least several (and perhaps all) of the species of *Holophryxus,* the first pair of coxal plates on adult females is coalesced with the cephalic ridge and the posterior four pairs of coxal plates are generally separate and evident as rounded or acute projections lateral to pereopods 2–5 (see Richardson 1908: 690, fig. 1, for *H. giardi*; Rustad 1935:9, fig. 2, for *H. richardi*; Shiino 1937:188, fig. 1B, C, for *H. fusiformis*; Stephensen 1912a:113, 11r, fig. 16, and Jones & Smaldon 1986: 309, fig. 2C for *H. acanthephyrae*). Figure 1B herein, showing the anterior ventral region of the specimen of *H. acanthephyrae* from *Eltanin* station 1723, is in general agreement with fig. 16 of Stephensen (1912a) and fig. 2C of Jones & Smaldon (1986) and shows the first coxal plates to be fused with the cephalic ridge, with the first pereopods arising from near the posterolateral part of the ridge. The lateral edges of pereonal segments I–IV of Schultz (1977) should therefore more correctly be referred to as coxal plates II–V.

The three additional species of *Isophryxus* (*I. quadratohumerale, I. polyandrus,* and *I. septapodus* described by Schultz (1978) from *Eltanin* cruises 11, 15, and 19 need to be briefly considered here. The presence of weak anterior furrows or folds suggesting segmentation of the pereon, the presence of fringing spines on the posterior margin of the fifth oostegites, and the form of the males clearly indicate that *I. quadratohumerale* and *I. polyandrus* represent species of *Holophryxus.* The situation with *I. septapodus* is perhaps less clear-cut than that with the other described species of *Isophryxus.*

Rustad (1935), Butler (1964), and especially Coyle & Mueller (1981) have shown that the development of the juvenile female stage into the mature *Holophryxus* female involves loss of pleopods, uropods, abdominal segmentation, a change in the mandibles from the sagittate form of the cryptoniscid to a rasplike organ capable of drilling into the carapace, and a reduction of pereopod 7 (with only its coxal plate remaining); in the final changes to the adult form, coxal plate 7 is lost, oostegites 1–5 are formed, the body region between pereopods 5 and 6 lengthens, and pereopod 6 is finally lost and its coxal plate reduced to a small bump or papilla which may persist at the posterior part of the pereon (as illustrated in Nierstrasz & Brender à Brandis 1913, Shiino 1937, and Butler 1964). Breeding does not occur until the marsupium is formed (Coyle & Mueller 1981), a condition that is probably not complete until the fringing spines are present on the posterior margins of the fifth oostegites.

Contrary to Schultz's statement (1978:83) about the absence of spines on the posterior margin of the marsupium of *I. septapodus,* my examination of the holotype of this species showed them to be present. Based on the above information, I suggest that the gravid female holotype of *I. septapodus* is a specimen of *Holophryxus* on which the fringing spines are present on the posterior marsupial margin, but which still has vestiges of the seventh pereopods and the corresponding seventh coxal plates, represented by the posterior two pairs of processes on the posterior ventral part of the pereon (see Schultz 1978:fig. 11A), as well as jointed sixth pereopods and the corresponding sixth coxal plates, represented by the more anterior two pairs of processes on the posterior ventral part of the pereon.

Whether these posterior appendages are retained much beyond maturity in *H. septapodus* (Schultz) can be determined only when additional mature specimens come to hand. Rustad (1935:16–17, figs. 3, 6) has shown that at least in *H. richardi* there is some individual variation in regard to the stage of development at which the sixth pereopods finally disappear (being absent on a specimen of 11.2 mm total length, but still present on another of about 12.9 mm total length); in both these cases, fringing spines are already present on the fifth oostegites. He also suggests (Rustad 1935:12) that the entire genus *Holophryxus* is possibly exceptional among the Dajidae in having the oostegites developed before the sixth pereopods have completely disappeared.

It is significant to note that Schultz (1978) considered the first pereonal segment to be completely fused with the cephalon in the latter three *Isophryxus* species.

*Damage to host.*—The holotype of *H. acanthephyrae* was collected and photographed attached to the posterior surface of the carapace of its host, with its cephalon directed posteriorly (Stephensen 1912a:fig. 13); one of the four specimens of the species reported by Jones & Smaldon (1986:fig. 1) was collected attached to its host in the same position. Three other species of *Holophryxus* (*H. alaskensis, H. giardi,* and *H. richardi*) have been found similarly attached to their hosts (Richardson 1908:figs. 2, 4; Stephensen 1912a:fig. 13; Rustad 1935; Butler 1964, 1980:fig. 7B). The pereopods and mandibles of the isopod leave marks on the carapace of the host as the isopod grows, moves, and feeds (Stephensen 1912a: figs. 14, 18). The mandibles perforate the carapace to the epithelial and connective tissues underneath, but the clawlike dactyls of the pereopods do not completely perforate the carapace (Rustad 1935).

Figure 2E shows the marks made by the pereopods and mandibles of the specimen of *H. acanthephyrae* collected attached to the specimen of *Acanthephyra pelagica* from *Eltanin* station 1723; Fig. 2D shows similar marks on the specimen of *A. pelagica* from *Eltanin* station 1480, the presumed host to *I. concavus.* The holes left by the mandibles tend to be larger than those of the pereopods and surrounded by a large ring of darkly stained tissue. The marks present on both shrimps indicate that the isopods progressively moved posteriorly on the carapaces as the isopods increased in size.

Coyle & Mueller (1981) provided complete descriptions of the larval and juvenile stages of *Holophryxus alaskensis.* The epicarid stage of *H. alaskensis* uses stage V of the copepod *Euchaeta elongata* as an intermediate host, on which it metamorphoses through the microniscid stage to the cryptoniscid stage, which then seeks out the shrimp final host (*Pasiphaea pacifica*). The cryptoniscid crawls beneath the carapace of the shrimp and attaches to the body wall in the branchial chamber above the gills, where it metamorphoses to the juvenile stage. It then moves out of the branchial chamber, up the side of the first abdominal somite and onto the dorsal surface of the carapace, where it attaches and assumes the mature adult form.

Few details of the life cycle of *H. acanthephyrae* are known, although Stephensen (1912a) described an epicarid larval stage from the marsupium of the holotype. From marks and damage (described below) to the carapaces of the two host specimens of *A. pelagica* at hand, and to the type host of *H. acanthephyrae* (which accompanied the holotype when it was obtained on loan from the Universitetets Zoologiske Museum), I suggest that the cryptoniscid stage of *H. acanthephyrae* also attaches inside the branchial chamber of the host. The juvenile female then apparently burrows through the branchial region of the carapace and gains access directly to the outer surface of the carapace, from whence it moves dorsally, begins to feed, and develops into the mature female.

While I was examining the type host of *H. acanthephyrae,* I noticed an oblong, depressed scar on the posterior part of the right branchial region of the shrimp (Fig. 2A). The same area is visible in Stephensen's (1912a:fig. 13) photograph as a darkened area, although over the years the darkened color has apparently become much less evident. The two *Eltanin* specimens of *A. pelagica* which served as hosts for *H. acanthephyrae* show evidence of damage to the right branchial region of their carapaces (Fig. 2B, C), as if something ate or burrowed through at these locations. The damage is contiguous with the posterior edge of the carapaces of these specimens and the edges of the wounds are rounded and partly healed, as if they are of some age.

A small male specimen of *A. pelagica,* carapace length 11.5 mm, from station 1204 of *Eltanin* cruise 14 has two relatively fresh, unhealed holes in the left branchial region of its carapace. Schultz (1977) recorded two small (2.2 and 2.5 mm long) female dajids from the same *Eltanin* station; the specimens were not given a formal species name at the time, but were identified simply as dajid species. Since the specimens bear some resemblance to the immature female of *H. giardi* described and illustrated by Richardson (1908), I suggest that these small dajids may represent a species of *Holophryxus,* and that it is probable, based on the damage to the specimen of *A. pelagica* from station 1204, that they represent juvenile females of *H. acanthephyrae* which had only recently burrowed from the branchial chamber of the host shrimp to the outside of the carapace, from where they were dislodged upon collection or subsequent handling.

*Distributions and hosts of* Holophryxus *species.*—Eight species of *Holophryxus* are currently recognized. The final host species is known for only five of the eight, and the intermediate host is known for only one of these five. Each of the five species for which the final host is known apparently uses a single species of pelagic decapod shrimp as a host. It is expected that the distributions of the various *Holophryxus* species would therefore be limited to those of their single host shrimps. The currently recognized *Holophryxus* species, their distributions, and known hosts are as follows (in chronological order);

1. *H. alaskensis* Richardson, 1905. Northeastern North Pacific, Santa Barbara Channel, California to Prince William Sound, Alaska. Intermediate host, stage V of the copepod *Euchaeta elongata*; final host *Pasiphaea pacifica* Rathbun.
2. *H. giardi* Richardson, 1908. Northwestern North Pacific, off Bering Island (54°48′N, 164°54′E). Final host, *Bentheogennema borealis* (Rathbun).
3. *H. richardi* Koehler, 1911. Central North Atlantic (33°41′N, 36°55′W) north to Davis Strait west of Greenland (66°21′N, 57°04′W), in Denmark Strait between Iceland and Greenland, south of Iceland, to west coast of Norway, and to south of England. Final host, *Sergestes arcticus* Krøyer.
4. *H. acanthephyrae* Stephensen, 1912a. North Atlantic from Davis Strait (60°07′N, 48°26′W) west of Greenland and to south of England, and subantarctic and antarctic waters of South Pacific. Final host, *Acanthephyra pelagica* (Risso).
5. *H. fusiformis* Shiino, 1937. Northwestern North Pacific off east coast of Japan. Final host, *Sergia prehensilis* (Bate).
6. *H. quadratohumerale* (Schultz, 1978). Subantarctic waters of southeastern South Pacific. Final host not known.
7. *H. polyandrus* (Schultz, 1978). Subantarctic waters of southeastern South Pacific. Final host not known.
8. *H. septapodus* (Schultz, 1978). Subantarctic waters of southeastern South Pacific. Final host not known.

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