

A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific

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The cymothoid isopods (Isopoda: Flabellifera: Cymothoidae) of the eastern Pacific are presented, with descriptions, figures, ranges and comments on their host relationships. Fourteen species are treated, two of which are described as new species of *Lironeca*. *Anilocra laevis* Miers, 1877 is synonymized with *A. laticauda* M. Milne-Edwards, 1840. *Nerocila californica* Schioedte & Meinert, 1881 and *Pterisopodus bartschi* Boone, 1918, are synonymized with *N. acuta* Schioedte & Meinert, 1881, and two morphological forms designated. Neotypes are designated for *Lironeca convexa* Richardson, 1905. Expanded generic diagnoses are provided for eastern Pacific taxa. An introductory section presents a review of the world literature on the family Cymothoidae, including discussions of morphology, taxonomy, natural history, evolution, and zoogeography. Confusion regarding the genus *Ichthyoxenos* is discussed, and several species removed to *Lironeca*. A phylogeny for the family is proposed.

KEY WORDS:—Cymothoidae – fish parasites – eastern Pacific – phylogeny.

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INTRODUCTION

“Several of the species treat their fellow inhabitants of the sea with little ceremony, and make up for smallness of size by ferocity of behavior. It is only to be hoped, as indeed it may be considered certain, that their living victims are immeasurably less sensitive to pain than ourselves.”

The Rev. Thomas R. R. Stebbing
A History of Crustacea, 1893

This monograph is the first in a series of studies intended to describe the systematics and natural history of the shallow-water marine isopod fauna of the Tropical Eastern Pacific Zoogeographic Region of the west coast of the Americas (Briggs, 1974; Brusca & Wallerstein, 1979a; Fig. 1). Within the family Cymothoidae, only a single west American species (*Lironeca californica* Schioedte & Meinert, 1893) does not range into this region. Inclusion of this species in the present monograph makes it operationally useful for the entire Pacific coastal region of the New World. This monograph series supersedes an earlier series embracing the Gulf of California in which the family Idoteidae has already been treated (Brusca & Wallerstein, 1977, 1979a,b).

Morphology and taxonomy of the Cymothoidae

The Cymothoidae Leach, 1818 is taxonomically the least understood family within the suborder Flabellifera and is one of the most troublesome of all isopod taxa with which to work. Of the flabelliferan Isopoda, this family is second only to the Sphaeromatidae in numbers of described genera and species (about 42 genera and 250 species). These figures are estimates, as numerous nominal species and a few genera are at present of questionable validity. Excluding the present work, all species known from the eastern Pacific were described between 1766 and 1918. The only attempt to monograph the family was by Schioedte & Meinert (1879–1884), who proposed many of the cymothoid genera. Publications subsequent to their work have consisted of scattered new records and species descriptions. Prior to 1950 cymothoid taxonomists largely followed a typological approach, most new species being described from a single female specimen. The conceptual basis of these older typological descriptions was not consistent with modern population biology (the “new systematics” of Huxley, 1940, and Mayr, 1969), and did not consider species polymorphism or the future discovery of new congeners and/or siblings. Most of these older published descriptions (and illustrations) were cursory or superficial. In most cases, characters now thought to be of considerable taxonomic importance were overlooked and highly variable or polymorphic features used to characterize the species. The pleopods and mouth parts were rarely figured or described. Of the eastern Pacific species, only four have been properly redescribed and figured: *Renocila thresherorum* Williams & Williams, 1980; *Lironeca convexa* Richardson, 1905 (Menzies, Bowman & Alverson, 1955); *L. vulgaris* Stimpson, 1857 (Brusca, 1978b); and *Nerocila acuminata* (as *N. californica*) Schioedte & Meinert, 1881 (Brusca, 1978a). The result is that many species are extremely difficult to distinguish from one another, some appear to be comprised of sibling species clusters, and most are now in need of formal redescription. Undoubtedly, many synonymies exist within the older literature. For example, Brusca (1978b) found the most commonly collected cymothoid in the east Pacific, *Lironeca vulgaris*, to be synonymous with its nominal southern congener *L. panamensis* Schioedte & Meinert, 1884, while the present publication recognizes a complex of five species in this genus in the eastern Pacific (two of which are described for the first time). Many of the species described in the nineteenth and early twentieth centuries have not been reported subsequently, the original descriptions being so brief as to make positive identification impossible. Unless type-material can be located, many of these older names may eventually be relegated to the status of *species inquirenda*.

Similar problems exist at the generic level. Most genera are so similar that they would be considered "over split" by non-peracarid arthropod specialists. There appear to be three rather distinct lineages within the family Cymothoidae (see following discussions), the genera within each differing in only subtle ways.

All cymothoids adhere in large part to the primitive cirolanid ancestral form and possess an unfused pleon of five free segments. In addition, most Cymothoidae possess nearly identical mouth parts, making these structures of little use in species or generic identification. Not only is there consistency in numbers of palp articles on the mouth parts, but in most genera there is little variation in numbers of spines on these appendages. Perhaps most remarkable, however, is that every known species of Cymothoidae except one (*Artystone trysibia* Schioedte, 1866) bears seven pairs of prehensile legs. As yet, an intermediate form between the modern cymothoid (with seven pairs of prehensile legs) and its supposed ancestral forms, the Aegiidae (with only three pairs), is not known. As Fryer (1965, 1968) has pointed out, many cymothoid genera are presently separated on unreliable features, thus it is often possible to refer a given specimen to any of several genera. In many cases, one is clearly faced with genera that simply cannot be defined precisely by unique characters. This situation is not unlike that seen in another major peracarid taxon, the gammarid amphipods (e.g. Karaman & Barnard, 1979).

The cymothoids include some of the largest living isopods, reaching 75 mm in length. The body is often slightly (but rarely grossly) twisted to one side or another, probably the result of a growth response to position on the host fish. It is probable that all are protandric hermaphrodites.

The mouth appendages are strongly modified for the parasitic habit. The maxillipeds are reduced to small palps of two or three articles, the distal being manifestly smaller than the proximal. In ovigerous females the basis of the maxilliped is often enlarged into a flattened plate; this article is, however, rarely removed with the maxilliped when the latter is dissected. The first maxillae (=maxillules) are reduced to slender, uniarticulate styles, which lie adjacent to one another in such a manner as to facilitate transfer of the host's blood toward the mouth. The second maxillae are small, bilobed appendages. All these appendages bear strong, recurved, terminal or subterminal spines that serve to hold the buccal region strongly affixed to the flesh of the host fish. According to Schioedte (1868), the teeth of the maxillae may assist the mandible in rasping the host's flesh. The first maxillae, with few exceptions, bear four terminal spines. The mandibles have lost the lacinia mobilis, setal row, and molar process, and the incisor region is modified into a sharp, blade-like cutting process presumably capable of slicing through the host's epidermis. The mandibular palp is of three articles. The labrum is lamellar and well developed, perhaps aiding in preventing loss of the host's blood from the buccal field. The bilobed paragnath is often inflated and fleshy or sac-like, generally lying in close approximation with the mandibles where it may rest tightly against their inner margins, below the incisor region. Because of this position and because on removal the mandible is often accompanied by removal of one lobe of the paragnath, these lobes have occasionally been mistaken as a structure of the mandible itself (e.g. Trilles, 1972a: fig. 75, *Meinertia parallela* (Otto, 1828); Hale, 1929: fig. 263d, *Ourozeuktes owenii* H. Milne Edwards, 1840; Lincoln, 1972: fig. 2d, *Lironeca africana* Lincoln, 1972; Bowman, 1960: fig. 1h, *Lironeca puhi* Bowman, 1960). The compound eyes

are typically large and well pigmented in juveniles but become increasingly reduced as the individual matures through the male and female phases. Reduction of the eyes is generally accompanied by loss of pigmentation and opacity of the cuticular covering. In contrast to other flabelliferan taxa the antennae are reduced in size and article number and little or no distinction can be made between peduncular and flagellar articles.

The inner margin of at least some of the pereopods of juveniles and males typically bears stout spines which occasionally persist into female instars, particularly on the seventh pair of legs. The dactyls of all seven pereopods form large, recurved, spine-like structures capable of firmly grasping the host fish. The posterior pereopods often are capable of folding back against themselves in a manner not unlike the raptorial second thoracopods of mantis shrimps. The basis of these pereopods may be grooved to receive the ischium-merus part of the leg. In some species of some genera the outer margin of this groove is produced or elevated to form a distinct carina. The presence of this carina results in a greater basis volume and development of considerably greater musculature within that article, which consists of adductors and abductors of the ischium. In some species the size of the carina decreases from male to female life stages (e.g. many species of *Lironeca* Leach). The coxae of cymothoids do not form ventrally expanded plates (as in various idoteid genera, for example) but expand only dorsolaterally to form typical dorsal coxal plates. These plates generally remain largely free from their respective pereonal segment, only the first being fused. In at least some species (e.g. *Idusa carinata* Richardson, 1904), fusion of the first dorsal coxal plate with its pereonite is incomplete.

The pleopods of cymothoid species tend to possess expanded surface areas (relative to other flabelliferan families); probably an adaptation serving to increase respiratory capabilities in these relatively large isopods in response to their immobile adult, parasitic lifestyle. Thus, the lamellae and/or bases may bear expanded lobes or accessory lamellae (e.g. Fig. 26K–O), whereas the endopods may be pleated (thrown into deep folds or pockets, e.g. Fig. 18K–N). The “three-branched” pleopod of many cymothoids appears to be homologous to the pleopods of several genera of parasitic Bopyridae (Isopoda), and selection pressure on these appendages was probably operationally identical in these taxa. In addition, some species (e.g. *Lironeca bowmani* sp. nov.) have finger-like projections on the proximal region of the pleopods (e.g. Fig. 16J–N), not unlike those of *Bathynomus* A. Milne-Edwards. The occurrence of these pleopodal structures is discussed in the section on evolution. The appendix masculinum of cymothoids is reduced and simplified, without spines, denticles or grooves, suggesting that this structure may no longer function in copulation. In some species (e.g. several *Ceratothoa*) it has been lost altogether.

The basic six-segmented pleon is found in all but two genera. In *Ourozeuktes* M. Milne-Edwards, comprised of only four known species, all pleonites are fused with the telson to form a single piece. In *Asotana splendida* (Leigh-Sharpe, 1937) the pleon is said to comprise four segments plus the pleotelson. Leigh-Sharpe originally placed this animal in his monotypic genus *Badroulboudour* based on a single female specimen taken from an unidentified fish in the Rio Napo, Ecuador. This isopod was unique in several regards. In addition to the five-segmented pleon, Leigh-Sharpe (1937) described it as having denticulate patches upon pereonites I and II, three pairs of “lateral horns” on the cephalon, antenna

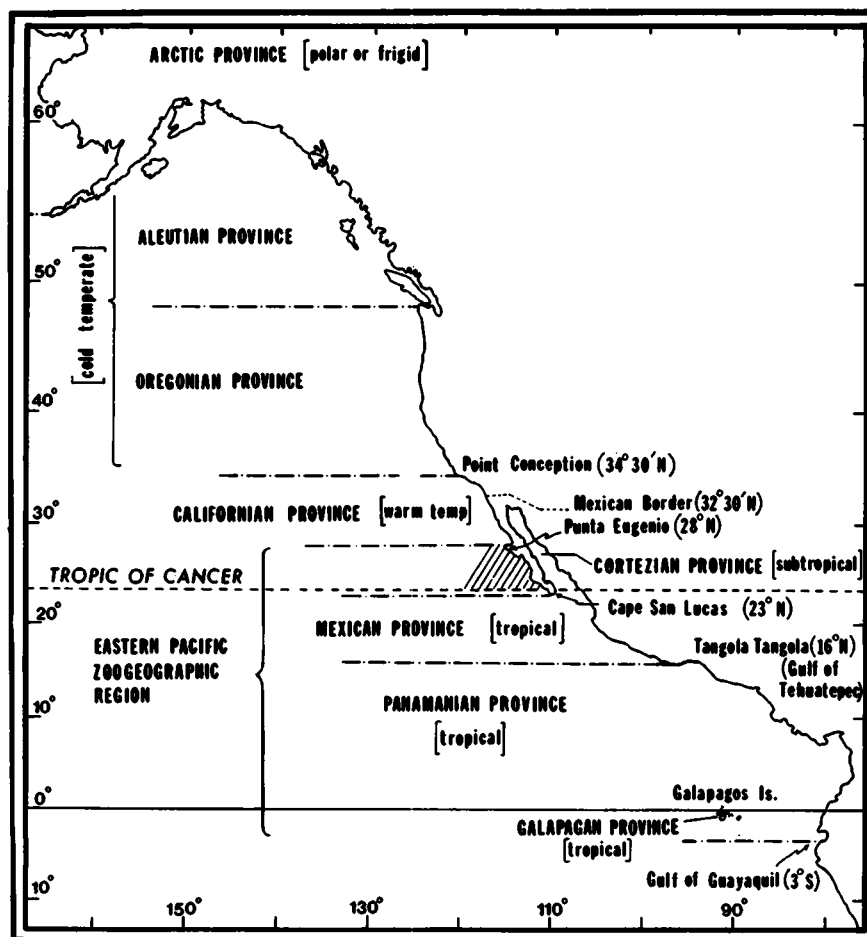


Figure 1. Zoogeographic regions and provinces referred to in the text. (From Brusca & Wallerstein, 1979a).

one of only four articles, and an outward-curving uropodal exopod. These remarkable features should distinguish this animal from any other known cymothoid. Unfortunately, the status of *A. splendida* is still uncertain and Leigh-Sharpe's description of a five-segmented pleon remains to be confirmed. Monod (1937) removed this species to the then monotypic genus *Asotana* Schioedte & Meinert, 1881, and suggested it may be synonymous with the type-species *A. formosa* Schioedte & Meinert, 1881. Van Name (1940) agreed with Monod's generic placement but left open the question of species synonymy. *Asotana formosa*, which has a normal six-segmented pleon, is known only from the Pacific drainage of Peru, while *A. splendida* has been reported only from the Atlantic (Amazonian) drainage of Ecuador.

Traditionally, researchers have emphasized the following characters in descriptions of cymothoid species: length and width of the cephalon, pereonites and pleotelson; shape of the cephalon and pleotelson; size and position of the eyes; number of articles in the antennae; shape and size of the coxal plates (and their visibility in the dorsal aspect); configuration of the posterolateral angles of the pereonites; relative length of the uropodal rami; and presence or absence of

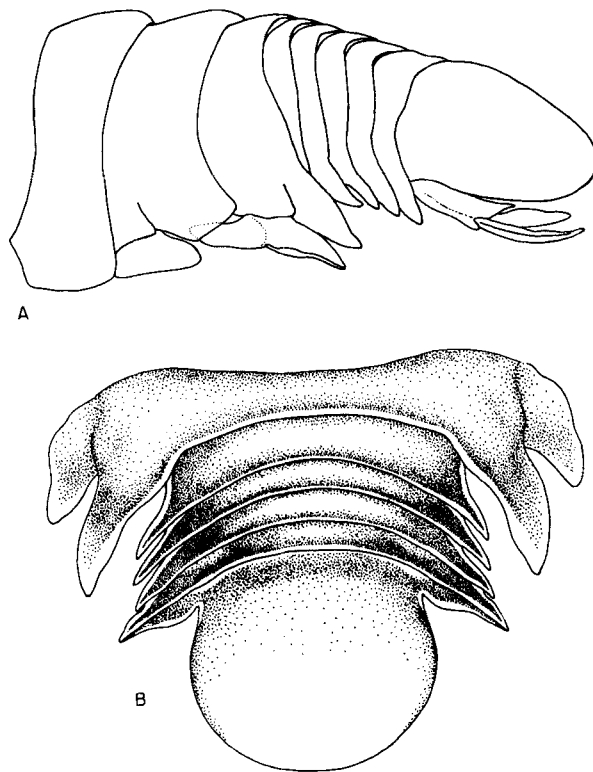


Figure 2. *Renocila thresherorum* Williams & Williams. A, Specimen with coxal plate of pereonite VII directed anteriorly; B, specimen with complete fusion of pleonite 5 to pleotelson.

carinae on the pereopodal bases. Virtually all of these characters show polymorphism within species of Cymothoidae and therefore must be used with caution. Due to the extreme variability of many morphological features of cymothoids, examination of a large series of specimens is crucial in species descriptions, to recognize polymorphism and sibling species. As Lincoln (1972) pointed out with regard to this family, "It is important to appreciate this variability when attempting to identify material such as this, and the lack of such appreciation has undoubtedly been partly responsible for the very large number of species which have been described in the past." In addition to the usual range of polymorphism, occasional specimens show evidence of growth mishaps (e.g. partial or complete fusion of two adjacent pleonites, or unusual growth of a coxal plate, Fig. 2). Further, it is not uncommon to find individuals with what appears to be damage due to attempted predation (by cleaner fishes, etc.), such as missing antennal articles or misshapen uropods or pleotelson margins. The habitat these isopods exploit and their parasitic lifestyle clearly make them vulnerable to such damage.

In the following chapters, taxonomic criteria and characters that I have found reliable for individual genera are presented. In general, morphology of the coxal plates must still be considered a useful feature at the specific level, despite variability. In addition, certain attributes of the pereopods, pleopods, uropods,

and second maxillae have been found to be more useful than most previous workers had anticipated. I regard the pleopods as possessing the single most useful set of taxonomic characters.

Natural history of the Cymothoidae

Cymothoids are ectosymbionts on marine, freshwater, and brackish-water fishes. They parasitize numerous marine species of commercial importance, including members of the families Mugilidae, Atherinidae, Serranidae, Carangidae, Sciaenidae, Embiotocidae, Bothidae, Clupeidae, Pleuronectidae, Scombridae and Haemulidae. They also are important parasites in certain freshwater environments such as South American rivers where they infest fishes used locally for food (Lemos de Castro & Filho, 1946). Marine cymothoids are almost exclusively inhabitants of shallow water, few being known from bathypelagic or greater depths.

The position of the isopod upon its host is reasonably species-specific. Most species attach either epidermally, in the gill chamber, or in the buccal region. However, some species, representing several genera, burrow beneath the skin where they live in a pocket or capsule formed within the musculature of the host (*Artystone* Schioedte and *Riggia* Szidat in freshwater of the New World; *Ichthyoxenos* Herklots and *Ourozeuktes* in fresh and marine waters, respectively, of the Old World). New World freshwater genera not possessing species that burrow beneath the host's skin are *Asotana* Schioedte and Meinert, *Braga* Schioedte & Meinert, *Telotha* Schioedte & Meinert, *Philostomella* Szidat & Schubart, *Paracymothoa* Lemos de Castro, and a few species of *Lironeca*. The freshwater habitat and the burrowing habit may be correlated within the family (see following discussion on evolution). The family as a whole is almost exclusively tropical-subtropical in distribution, throughout the world's oceans. No species are known from European or North American freshwaters.

In general, specific host and ecological data are almost nonexistent in the older literature. Much of the information that does exist is of little use owing to local, vernacular, or incorrect host fish names (e.g. Moreira & Sadowsky, 1978). Cymothoids are generally described as being "parasitic on fishes and certain invertebrates." In at least some species of some genera, it appears that females are largely (or perhaps entirely) nonfeeding, and hence are best considered as obligate commensals. In such cases, these females presumably rely on stored nutritional reserves (from previous male instars) for reproductive energy. In at least two species females appear to be capable of destroying or causing atrophy of the host's tongue: *Cymothoa exigua* Schioedte & Meinert, 1884, and *Ceratothoa* (= *Meinertia*) *oestroides* (Risso, 1826) respectively. In contrast males are apparently always parasitic. Collection records naming squids as hosts, and reports of adult cymothoid host abandonment from formalin-treated pompanos used in fugitive isopods that have abandoned their dying or stressed hosts (a phenomenon first recorded by Goode, 1879, and subsequently by several other workers). I have often seen such fugitives in beach seines, otter trawls, and Isaacs-Kidd midwater trawls (see Brusca, 1977, 1978b). Williams (1974) has reported cymothoid host abandonment from formalin-treated pompanos used in mariculture experiments. Keusink (1979) reports that juveniles and males, and to a lesser extent females, of *Lironeca vulgaris* tend to abandon the host's gill cavity within a few minutes after the host is removed from the water.

Evidence indicates that species of some genera are highly host-specific (e.g. some species of *Cymothoa* Fabricius and *Idusa* Schioedte & Meinert), whereas others are catholic in their host choice (e.g. some species of *Anilocra* Leach, *Nerocila* Leach, and *Lironeca*). However, no clear relationship exists between degree of host specificity and phylogeny within the family, and within any genus one will usually find species that are highly specific, and others that are not. For example, while most species of *Lironeca* possess fairly low host specificity, a number (e.g. *L. caudata* Schioedte & Meinert, 1884, *L. propinqua* Richardson, 1908, *L. puhi*, and *L. sacciger* Richardson, 1909) are presently known from only a single host species. Similarly, while most *Cymothoa* have been recorded from a single host species, several are known to infest numerous species (e.g. *C. exigua* and *C. oestrum* (L., 1758)). Contrary to the opinion of Avdeev (1978), my studies suggest that data on isopod-host fish biology are still far too sketchy or in many cases unreliable to draw meaningful conclusions regarding phylogenetic host specificity trends (if such trends indeed exist). Trilles (1964a, 1969) has come to a similar conclusion from his studies of host specificity among the Mediterranean Cymothoidae. The clearest general trend seen among the eastern Pacific cymothoids is the positive relationship between geographic distribution of the isopod and the number of host fishes used; the greater the range of the isopod, the more host species it is likely to infest. These data are presented in Table 1 for those species for which reasonable host knowledge exists. While these host data are certain to increase as additional collections are made, there is no reason to expect their general relationship to be radically altered.

At least some species of Cymothoidae show a preference for "ecological" host fish categories, such as demersal and/or schooling species (Brusca, 1978a). This situation is similar to that of digenetic trematode parasites of embiotocid fishes which are associated with ecological host fish types, rather than displaying any taxonomic or phyletic host relationship (Arai, 1967). Ecological (as opposed to taxonomic) host preference has also been described for terrestrial arthropod parasites (e.g. mites, Wharton, 1957).

The pereopods and mouth parts of the Cymothoidae are especially modified to facilitate their parasitic lifestyle (see previous section). Rondelet recognized the blood-feeding nature of cymothoids over 400 years ago (see Schioedte, 1868:2). Gunther (1931) discussed the mouth appendages of aegiids and cymothoids,

Table 1. Relationship of distribution (given in numbers of biogeographic provinces inhabited) to numbers of host fish species

Species	No. of biogeographic provinces inhabited	No. of host species utilized
<i>Ceratothoa gaudichaudii</i>	6	11
<i>Lironeca vulgaris</i>	5	30
<i>Nerocila acuminata</i> (E. Pacific only)	4	40
<i>Lironeca convexa</i>	4	3
<i>Lironeca californica</i>	3	7
<i>Cymothoa exigua</i>	3	6
<i>Lironeca bowmani</i>	3	1
<i>Ceratothoa gilberti</i>	1	2
<i>Lironeca menzeisi</i>	1	1

pointing out similarities in both form and function. Romestand (1978) and Romestand & Trilles (1974, 1975, 1976) have shown that cymothoids produce anticoagulants in esophageal side glands that assist in feeding on blood, but that host-parasite immunological reactions (when they exist) are fairly weak. Most recently these workers have described various biochemical, histological, and hematological manifestations of parasitized host fishes, including anemia resulting from decreased erythrocyte count in host circulation (Romestand & Trilles, 1977, 1979; Romestand, 1979).

In most cases, workers have been hard-pressed to recognize deleterious effects of cymothoids on their hosts. Behavior of infested fishes usually does not differ significantly from that of uninfested fishes. Confronted with this, Keys (1928) placed infested and noninfested California killifishes (*Fundulus parvipinnis*) under conditions of thermal and osmotic stress, recording significantly increased mortality among parasitized individuals. He concluded, with regard to the permanence of the deleterious effects produced by a limited period of attachment of the isopod, that no serious injury is involved. Westman & Nigrelli (1955) came to similar conclusions with regard to *Olencira praegustator* (Latrobe, 1802) on Atlantic menhaden, stating that infestation could fatally lower the host's resistance under conditions of unusual environmental stress. Lewis & Hettler (1968) showed that non-parasitized menhaden can survive high temperatures better than individuals infested with *O. praegustator*. Weinstein & Heck (1977) found no significant differences between coefficients of condition calculated for parasitized and unparasitized host fishes, and concluded that the Caribbean species *Cymothoa excisa* Perty, 1830 does little, if any, damage to snappers (Lutjanidae). Lanzing & O'Conner (1975) found that luderick, *Girella tricuspidata*, along the southeast coast of Australia showed no outward signs of aberrant growth or behavior when parasitized by *Ceratothoa imbricatus* (Fabricius, 1787) or *Irona renaudii* (Bleeker, 1857). However, statistical analyses of length-weight relationships of infested and noninfested fishes revealed the latter to be in better overall condition (greater weight per given length). Interestingly, their analyses suggested that fishes infested by a single isopod were not significantly "less healthy" than non-infested individuals; only hosts carrying two or more isopods tended to be underweight. Romestand & Trilles (1979) found that several species of European cymothoids were capable of slowing growth in their hosts, although they did not apparently affect weight-size ratios of the fish. Romestand (1978) discussed several pathogenic effects of cymothoids upon the organs and growth rates of infested hosts. Turner *et al.* (1969) stated that fishes "heavily parasitized" by *Lironeca vulgaris* in southern California appeared "gaunt and barely able to swim." Kaczynski & Cannon (1974) found that white perch parasitized by *Lironeca ovalis* (Say, 1818) in the Hudson River weigh less than comparable nonparasitized individuals. Sadzikowski & Wallace (1974) found similar conditions in the Delaware River. Vũ-Tan-Tuê (1963) reported on the increased likelihood of the sparid *Boops boops* to grow vomerine teeth when parasitized by the buccal parasite *Meinertia oestroides*.

In most species that have been studied closely, physical damage to the host has been evident. Comeaux (1942) reported breaking of host gill filaments and the formation of scar tissue at the place of attachment for various species of "Aegathoa", *Nerocila*, *Lironeca* and *Cymothoa*. Bowman & Mariscal (1968) reported that *Renocila heterozota* Bowman & Mariscal, 1960 was responsible for considerable tissue damage to the anemone fish *Amphiprion akallopisos*, including erosion down

to the myomerites. Brusca (1978a) reported similar damage from *Nerocila acuminata* (as *N. californica*). Bowman (1960) observed that nearly all the gill filaments of the Hawaiian moray eel, *Gymnothorax eurostus*, are missing on the side parasitized by *Lironeca puhi*.

Kroger & Guthrie (1972) stated that male *Olencira praegustator* damaged the gills of juvenile Atlantic menhaden, *Brevoortia tyrannus*, which sustain infestation levels up to 40%. They concluded, in agreement with Goode (1879) and Richardson (1904b), that females were commensal rather than parasitic. Turner & Roe (1967) reported infestation rates of 65% in *Brevoortia smithi* off the Florida panhandle. Guthrie & Kroger (1974) showed that menhaden parasitized by this cymothoid had difficulty avoiding surface trawls, even during daylight hours.

Lincoln (1971) suggested that *Lironeca convexa* may use food particles trapped by the gill-rakers of the jack *Chloroscombrus orqueta*, a suggestion I find unlikely in view of cymothoid mouth part morphology. Menzies *et al.* (1955) stated for *Lironeca convexa* that "whether the male eats fish flesh is not known and the examinations made of the stomachs of males, and females as well, give no clues as to their food habits." They also noted, however, that the gills of the host fish are considerably "eroded" by males, but females located on the tongue appear to cause no direct injury. Hochberg & Ellis (1972) reported some pathogenicity associated with *Anilocra* sp. in the West Indies, although presence of the parasite did not appear to alter the host's behavior noticeably. Brusca (1978b) found that male *Lironeca vulgaris* unquestionably feed on their host's blood, damaging the gills and/or inner opercular surface while doing so; females appear to be either nonfeeding or may also feed upon blood within the gill chamber.

Species that burrow beneath the host's skin obviously do considerable damage. Akhmerov (1939) found that *Ichthyoxenos amurensis* Garstfeldt, 1858 feeds on the blood of the host fish *Leuciscus waleckii*. A number of workers have reported on the deleterious effects of *I. amurensis* in east Asia (Dogiel *et al.*, 1961; Akhmerov, 1939, 1941; Krykhtin, 1951). The latter author estimated that 13% of the *Leuciscus waleckii*, a valuable coregonid food fish of the Amur River, die before reaching a marketable size due to infestation by this isopod. Huizinga (1972) reviewed the pathobiology of *Artystone trysibia* from South America. Monod (1976) discussed the deleterious effects of *Ourozeuktes bopyroides* (Lesueur, 1814) on its host, the triggerfish *Balistes stellaris*.

Morton (1974) partly reviewed the subject of position on the host fish and suggested a rather sophisticated and directed mode of attachment for *Nerocila phaeopleura* Bleeker, 1857. Brusca (1978b) discussed host attachment behavior of *Lironeca vulgaris*.

Host-parasite data for eastern Pacific cymothoid species are included in this monograph under their respective taxa. Overall, it would appear that most cymothoids, like other external fish parasites, only slightly lower the general well-being of their hosts. Exceptional cases occur, such as bilateral or multiple infestations of the gills or situations in which the host fish is placed in physically stressful environments. Injured fishes may facilitate their healing process by utilizing warm shallow waters as "recovery wards" (Gunter & Ward, 1961). Kroger & Guthrie (1972; also Guthrie & Kroger, 1974) have provided evidence that adult menhaden parasitized by *O. praegustator* migrate into estuaries to recuperate, where they can school with slower-swimming juveniles. This hypothesis is supported by data in the present study, which suggest that cymothoids occur in

greater abundance in California estuaries and bays than in offshore waters. However, these distributional data also support the alternate hypothesis that the physical constraints of these semi-enclosed habitats may in themselves facilitate relatively greater spread of the isopods, thus producing generally higher infestation rates.

Available data suggest that infestation levels vary greatly for a given host species and locality. Further, occurrence of infested host fishes is extremely patchy. The only observable trends appear to be increased rates of infestation in coastal bays and lagoons, and decreased levels in larger host individuals. Based on decreasing infestation rates on larger host fishes several workers have suggested that the isopods in question could be responsible for early death of the fish (e.g. Krykhtin, 1951; Lanzing & O'Conner, 1975). Trilles (1964b) has shown that (in some species of European Cymothoidae) a correlation exists between size of the isopod and size of the host, while in other species no such correlation exists. Trilles hypothesized that the former situation is common in cymothoid species that lose their ability to swim at an early age (e.g. *Anilocra physodes* (L., 1758), *Mothocya epimerica*, *Ceratothoa parallela*, *Emetha audouinii* M. Milne-Edwards, 1840), and that the latter situation occurs in species that retain their swimming ability well into the adult male stage (e.g. *Nerocila orbigny* Schioedte & Meinert, 1881).

One might assume that secondary infections by microorganisms at the site of attachment would be common on cymothoid hosts; however, this has been recorded in the literature only once. Lawler *et al.* (1974) found lymphocystis associated with the gills of silver perch (*Bairdiella chrysura*) infested by *Lironeca ovalis*. Of the 21 fish with gill lymphocystis lesions examined, 20 had one or more *L. ovalis* associated with the lesion. The existence of bacterial and fungal infections has been widely assumed for other crustacean-fish associations and such references occur throughout the literature (see Kabata, 1970). Fungi best known as secondary invaders belong to the Saprolegniaceae which are saprophytic, though capable of developing on the damaged and necrotic tissues of living fishes. Infections by these fungi are frequently reported in association with wounds caused by parasitic copepods.

The development and life history of several cymothoid species have been described (e.g., Legrand, 1951, 1952; Menzies *et al.*, 1955; Nair, 1956; Trilles, 1968; Kroger & Guthrie, 1972; Brusca, 1978a,b). Fain-Maurel (1966) has reported on the reproductive anatomy, meiotic cycle, karyology, and biology of several Mediterranean species of *Meinertia* Stebbing, *Anilocra*, and *Nerocila*, and given the first descriptions of gametogenesis for the family. Eggs are centrolecithal, oval and enclosed in a chorion and vitelline membrane, the latter not being readily visible until the first few divisions have taken place. Development progresses through a number of distinct stages within the marsupium. Brusca (1978b) described five visible marsupial stages for *Lironeca vulgaris*. Gastrulation proceeds by migration of cells from the blastoporal area towards the yolk. It is believed that the chorion of isopods is derived from follicle cells and is therefore a "true" chorion, although this has not been fully established (Shiino, 1957). Nair (1956) claims that, unlike most crustaceans, including terrestrial isopods, the gut of at least some cymothoids (*Irona robusta* and *I. far* Nair, 1950) is derived solely from the ectoderm. The number of eggs carried in the marsupium varies directly with body length within a given species, ranging from about 200 to 1600, most being in the range of 300–600. In mouth/gill inhabiting species, the hatching manca appear

always to be released via the gill chamber and opercular opening of the host. Manca and juvenile stages (the latter referred to by Brusca, 1978b, as the "aegathoid" stage) typically bear large eyes, spinose pereopods, and setose pleonal appendages to facilitate swimming. The distinct morphology of the juveniles led Dana (1852) to establish a separate genus for this life stage, *Aegathoa*. Both Dana and Harger (see Stebbing, 1893:353) noted with a prophetic sense of phylogenetic insight the strong similarity between members of this "genus" and species of the closely related family Aegiidae. Juveniles and young males typically attach for short periods to almost any convenient fish. Little is known regarding these temporary attachments, although some workers have referred to juveniles and young males as "facultative parasites" on "intermediate hosts" (e.g. Lindsay & Moran, 1976). Whether or not the isopod actively feeds on the fish at this point is not known. As the juvenile matures, it eventually finds an acceptable "definitive" host fish upon which to attach permanently. Upon attachment to this host and transition into a functional male, the natatory setae are lost. With the exception of the prehensile legs, juveniles strongly resemble a typical cirrolanid in body form, and are strikingly similar among species and throughout most genera. Reliable characters to distinguish species in the juvenile stage are not yet known, although the spination of the pereopods may eventually prove useful.

Probably all members of the family Cymothoidae are protandrous hermaphrodites, a phenomenon first observed by Bullar (1876) and confirmed by Mayer (1879). More recently, this phenomenon has been discussed by Montalenti (1941), Legrand (1952), Trilles (1964b, 1969), and Fryer (1968). Romestand (1971) has carried out electrophoretic studies of cymothoid hemolymph proteins in relation to the phases of sexual development. As in the Anthuridae, which are largely protogynic hermaphrodites, sex reversal usually takes place, at least superficially, in a single molt.

The exact stimulus initiating the sex change has not been elucidated. Brusca (1978b) states for *Lironeca vulgaris*, that "The stimulus for the sex reversal may be either the presence of a new male entering the gill chamber or the absence of a resident female on the host fish when the young male first attaches (or subsequent death of the resident female). Size alone cannot account for the timing of the sex change, as large males do exist, albeit in relatively low numbers. It is not uncommon to find fishes infested with isopods of only one sex. The fact that adult females (and males) vary so greatly in size suggest that the male grows and remains masculine until a second male attempts to establish residence on the same host. The first male may then, regardless of its size, undergo the sex change molt." After the change, the continuing presence of a female appears to prolong the new male's masculine stage, at least in *Anilocra physodes* (Legrand, 1951, 1952), and perhaps in *Lironeca puhi* (Bowman, 1960). In any event, the sex change appears to be under neuroendocrine control (Trilles, 1968).

Midmolt individuals, having a masculine anterior region and feminine posterior region, are not uncommon. In many species the female stages retain vestiges of the male appendix masculinum which often decreases in size in succeeding instars. Thus, mere presence of an appendix masculinum should not be taken as evidence that a specimen is male, but rather presence or absence of the penes should be used to sex individuals lacking developed oostegites.

Most species probably live only one year or occasionally two years. The question of whether a single brood or several broods are produced by a female remains

unanswered. Data in support of both possibilities exist. In those species in which the females do not feed, a single brood might be predicted; in others two or three broods may be postulated.

Evolution and zoogeography of the Cymothoidae

Although 100 years have elapsed since Schioedte & Meinert's monograph and over 200 studies dealing with this taxon have been published, the systematics of the Cymothoidae is still too poorly understood to propose a detailed phylogeny of the genera. Nevertheless, in view of the ways in which the theories of continental drift and vicariance biogeography have altered our interpretation of the Earth's biotic history, it is appropriate to summarize our present state of knowledge regarding the evolution of this family.

Menzies *et al.* (1955) have suggested that the Cirolanidae, Aegiidae, and Cymothoidae form a "phylogenetic and ecological lineage" stemming from a primitive flabelliferan stock. While I am not in full agreement with their assessment of the habits of the species in these three families, comparative behavioral and morphological data do strongly support their proposed evolutionary sequence. The three families are very similar morphologically and show a distinct trend from a general scavenging-predatory lifestyle to increasingly parasitic and specialized existence. These adaptations are most clearly seen in the mouth parts, pereopods and pleopods. The structure of these appendages in the Cymothoidae was discussed above. Aegiid mouth appendages are manifestly more similar to those of the Cymothoidae than the Cirolanidae. As in the cymothoids, aegiids have lost the lacinia mobilis and molar process of the mandible and transformed the incisor region into a blade-like slicing or cutting structure. Aegiid mouthparts also possess the robust recurved spines and styliform first maxillae seen in cymothoids, but wanting in cirolanids. Only pereopods I-III are "prehensile" in the aegiids. Cirolanids are primarily benthic scavengers and predators, and they are for the most part excellent swimmers. Many species are known occasionally to feed upon pelagic and demersal fishes in shallow waters; they may best be regarded in that mode as "micropredators." Aegiids are also primarily benthic forms but leave the bottom to attach temporarily to passing fishes from which they extract a meal; aegiids may thus be considered as "micropredators" or "temporary parasites." Cymothoids are good swimmers only during the manca, juvenile and early male stages, during which they resemble a typical cirolanid in body form and pleopodal setation. Adults are obligate symbionts on marine and freshwater fishes and lack directed swimming ability. In *Lironeca vulgaris*, for example, females are unable to move at all while males have only limited crawling and short-distance swimming abilities (Brusca, 1978b).

One is tempted to ascribe the closely related families Corallanidae and Excorallanidae a position in the above evolutionary lineage, most logically between the Cirolanidae and Aegiidae. In the two former families the mandibles also lack fully developed laciniae mobili and molar processes, while pereopods I-III bear dactyls that are elongated and recurved, but not to the extent seen in species of Aegiidae. Loss of the lacinia mobilis and molar process has, however, occurred in several unrelated isopod genera, throughout the order. The taxonomy of these two small families is uncertain and most genera of Corallanidae should probably be removed to other families (e.g. Excorallanidae, Cirolanidae). Little is known of

the habits of corallanid and excorallanid species. For these reasons, I have taken the conservative course and refrained from speculating on where, if at all, these taxa may fit into the phylogeny presented in Fig. 4B.

The above morphological and ecological data are corroborated by Fain-Maurel's (1966) karyological studies on Mediterranean cymothoids, which attest to the significant genetic distance of this family from other flabelliferan taxa and further suggest that they possess both a considerable phyletic independence and considerable age. The size of the family, the large number of genera relative to the number of species (42: 250), and its zoogeographic patterns provide additional data in support of the Cymothoidae being pre-drift in origin (i.e. at least 180 M years old). This timing is consistent with Schram's (1977) analysis of the Malacostraca, in which he describes the Mesozoic as a period dominated by a tremendous radiation of anatomically-advanced Peracarida and Eucarida. Indeed, the limited Triassic fossil record points to this period as a time of major flabelliferan radiation throughout warm Pangaeian seas. It is remarkable, almost enigmatic, that a species-rich family of this age has not evolved a greater morphological diversity or generic endemism. Certainly the adoption of a parasitic life style has greatly influenced the conservative nature of cymothoid morphological evolution, while their relatively high dispersal potential may play a major role in reducing generic endemism.

Three separate evolutionary lines are discernible within the family Cymothoidae. One has led to a strategy of superficial (epidermal) attachment on the host fish (e.g. *Renocila* Leach, *Nerocila*, *Anilocra*, etc.), while a second has produced a more intimate, buccal-gill chamber strategy of infestation (e.g. *Lironeca*, *Idusa*, *Irona*, *Cymothoa*, *Ceratothoa* Dana, *Codonophilus* Haswell, etc.). These two lineages have genera of a typical Tethyan distribution, restricted almost entirely to the tropics, subtropics, and warm temperate regions of the world's oceans. If a Tethyan origin is inferred for these two lineages one sees their invasion of the warm-temperate latitudes to be a more recent event, presumably beginning sometime during the early Cenozoic or late Mesozoic. Like other modern descendants of the warm-water Tethyan biota (i.e. the "pantropical marine component" of Rosen's (1975) Gondwanian track biota), species of the family Cymothoidae are rarely encountered in the cool and cold temperate latitudes.

In addition to the distinct ecological (host-parasite) differences between these two Tethyan lineages, several morphological trends are also discernible. Genera of the buccal-gill lineage are characterized by having the cephalon more-or-less immersed in the pereon, a more convex body than other genera, possibly reduced calcification of the exoskeleton (see Trilles, 1972b), achievement of increased pleopodal surface area by formation of sheet-like lamellae or digitiform accessory gills (only occasionally by pocketing or sac-like folding of the pleopods), and thin, relatively weakly attached oostegites. The lamellar accessory gills may, in some species, be as large as the exopods and endopods themselves, giving the appearance of a trilamellar pleopod (e.g. *Cymothoa exigua*). Limited published data and personal observations indicate species of this lineage copulate in the buccal cavity or less frequently within the gill chamber of the host.

In the superficially attaching genera, the cephalon is not immersed in the pereon (or only weakly so), the body is generally more depressed and perhaps more heavily calcified, increase in pleopodal surface area is accomplished by the

formation of small accessory lamellae and sac-like folds or pleats (generally on the endopod), and the oostegites are more robust, thicker and firmly attached to the coxae (see Lagarrigue & Trilles, 1969, and Trilles, 1972b, for a discussion of some of these morphological trends). Species in this lineage copulate upon the external surface of their host fish.

The third cymothoid "lineage" is less distinct and, in fact, almost certainly polyphyletic. This group is represented by nine genera of freshwater and fish burrowing taxa. The paleozoogeographic origins of these genera are not immediately clear from the distributional data of extant species, and there are no certain fossil records for these or any other cymothoid genera¹. This lack of clarity is partly due to confusion created by unstable taxonomy within the family.

The freshwater genus *Ichthyoxenos* cannot be distinguished from *Lironeca* on morphological criteria, and several species have been shuffled back and forth between these two taxa. Miers (1880) recognized this and stated that the two genera were identical, excepting one (*Ichthyoxenos*) was freshwater and the other marine, a condition that no longer prevails. Van Name (1920) considered the wide geographic disparity of *Ichthyoxenos* records as evidence that the genus was not monophyletic, but representative of convergent evolution among a number of *Lironeca*-descended species. Most recently Fryer (1965) has considered *Ichthyoxenos* (*sensu* Herklots, 1878) to be the junior synonym of *Lironeca* Leach, 1818.

In fact, confusion regarding the taxonomy of the *Lironeca-Ichthyoxenos* complex is alleviated when the host-parasite relationships of the taxa are considered. Two very distinct modes of attachment exist within this complex of species. One is a simple buccal-gill infestation identical to that seen in the marine species of *Lironeca* and other genera in the "buccal-gill lineage." The other involves a strikingly different, flesh-burrowing strategy, in which the isopod buries itself beneath the host epidermis, forming a capsule within the tissue of the myomeres, with only a small opening near the pleopods for a respiratory current. The type species of *Ichthyoxenos* (*I. jellinghausii* Herklots, 1870) is such a burrower. If this species, and the other six flesh-burrowing species are considered a monophyletic taxon — *Ichthyoxenos* — their distribution is seen to be restricted to a relatively small, freshwater biotope in the Far East. These six species are:

- I. jellinghausii* Herklots, 1870. Java, Sumatra, Batavia.
- I. geei* Boone, 1920. China.
- I. japonensis* Richardson, 1913. Japan.
- I. montanus* Schioedte & Meinert, 1884. Himalayan Mts.
- I. opisthopterygium* Ishii, 1916. Japan.
- I. amurensis* Garstfeldt, 1858. Far eastern U.S.S.R.

The remaining 11 species in this group, the buccal-gill inhabitants, should be restricted to the genus *Lironeca*. This requires removal of the following from *Ichthyoxenos*: *L. asymmetrica* (Ahmed, 1970), *L. expansus* (Van Name, 1920), and *L. lazzari* (Pearse, 1921). This relegates the freshwater species of *Lironeca* to two geographically discrete and biogeographically related regions, the freshwater biotopes of central Africa (the Congo River Basin) and South America. Thus, it is seen that vicariance models could probably be applied, at least in part, to both

¹Bowman (1971) reported a possible cymothoid from an upper Cretaceous formation in Texas. The single specimen was recovered from the matrix surrounding the fossil remains of a large mackerel shark (*Lamna* sp.). Bowman's reconstruction suggests it may have been a *Cymothoa*- or *Lironeca*-like species.

groups: the South American–African species of *Lironeca* being possible descendants of the large and well-documented Neotropical–Ethiopian freshwater track¹.

All genera of burrowing species are strictly freshwater, excepting *Ourozeuktes* which is strictly marine. A few species belonging to the marine genera *Anilocra*, *Nerocila*, *Irona* and *Olencira* have been reported on occasion from freshwater habitats. However, these have all been shown to be “good” marine species that are capable of occasionally penetrating into estuarine and brackish-water conditions. These four genera are thus excluded from the immediate analysis. The frequent occurrence of species of *Lironeca* in freshwater is evidence that this genus, one of the largest, most widespread, and presumably one of the oldest in the family, may have arisen from the same stock that originally gave rise to the freshwater/burrowing line. Morphological considerations also support the hypothesis that many freshwater species and genera (excepting perhaps *Asotana* and *Braga*) may have evolved from a *Lironeca*-like ancestor.

If the modern distributions of the nine genera in this freshwater/burrowing lineage are plotted, it is seen that nearly all (excepting *Lironeca* and *Ichthyoxenos*) are restricted to South America (Fig. 3). This fauna has recently been reviewed by Trilles (1973). The marine burrowing genus *Ourozeuktes* occurs in the Indo-west Pacific region and a single questionable species of *Telotha* (*T. indica* Nierstrasz 1915) has been reported from the west coast of Java. Nierstrasz described *T. indica* from a single specimen; the species has not been reported since. Further, his comments suggest it was a marine form, not freshwater as are all its supposed congeners in South America. Hence, by excluding *T. indica* as a possible mistaken generic placement, all the known strictly freshwater genera (excepting *Ichthyoxenos*) occur in South America and are austral in distribution.

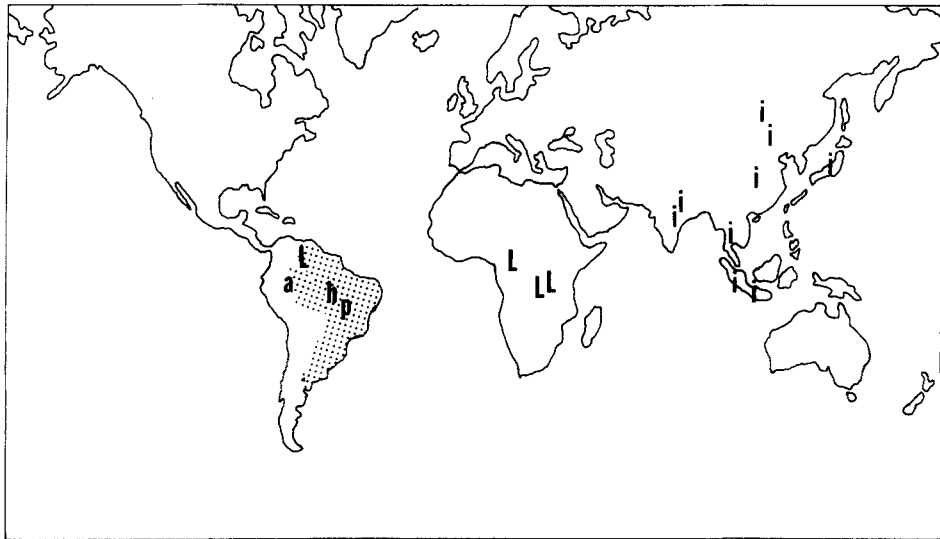


Figure 3. Modern distributions of freshwater-fish burrowing genera and species. a, *Asotana*; p, *Paracymothoa*; h, *Philostomella*; L, *Lironeca*; i, *Ichthyoxenos*. *Artystone*, *Braga*, *Riggia* and *Telotha* are represented by the stippling.

¹Several species of freshwater *Lironeca* appear questionable. *L. asymmetrica* may be a marine species; it is impossible to tell from the published data. *L. enigmatica* Fryer, 1968 was described from juveniles.

Three hypotheses to explain such a distributional pattern appear logical. (1) The group represents a facet of the Gondwanian Track biota, placing its probable origin in the Mesozoic. The presence of only *Lironeca* in Africa, and the lack of freshwater representatives in India and Australia–New Zealand do not support this hypothesis. (2) Each genus can be considered to have arisen independently by invasion of the freshwater biotope via estuaries (i.e. dispersal). (3) The South American fauna arose in concert (with the possible exception of *Lironeca*) as a result of a correlated series of vicariant biogeographic events, presumably subsequent to the splitting of South America from Africa (i.e. Late Cretaceous/Early Paleocene).

Szidat (1944, 1955) has provided considerable data favoring the third hypothesis. He considers the freshwater isopod (and trematode) parasites of South America to be relicts derived from an original Tethyan stock during massive geotectonic events in that continent. Fryer (1965, 1968) appears to agree with Szidat's analysis, and further states that the relict concept may also apply to the *Lironeca* of Lake Tanganyika. Szidat places the timing of the South American events as Tertiary, further ruling out a direct Gondwanian association. The timing of Szidat's theory is, however, based largely on "pre-drift" concepts (i.e. the work of von Ihering, 1902, 1907, 1927; Camp, 1952; and Eigenmann, 1905).

My concept of phylogeny within the Cymothoidae is presented in Fig. 4B. It is based on the above considerations and the cladogram presented in Fig. 4A. It seems probable from morphological, zoogeographic, and ecological data that a *Lironeca*-like ancestral form gave rise to all but two of the freshwater/burrowing genera (i.e. *Asotana* and *Braga*). The evolution of the burrowing habit may have occurred independently several times (e.g. in the genus *Ichthyoxenos*, several South American freshwater genera, and in the marine genus *Ourozeuktes*). The South American fauna probably represents the most recent freshwater representatives of this lineage. While the origins of the buccal-gill chamber genera are depicted in Fig. 4 as a single event, it is understood that these numerous genera arose through a large number and variety of vicariant and/or dispersal events over a considerable period of time. The same holds true for the externally attaching line leading to *Nerocila*, *Anilocra*, and others. There is no evidence that the family Cymothoidae suffered from the massive extinction of species that predominated in other groups during the Cretaceous-Tertiary transition.

The phylogeny proposed in Fig. 4 does not vary greatly from that of Schioedte & Meinert's (1879–1884) original taxonomic divisions within the Cymothoidae as interpreted today. Their Anilocridae corresponds to my "externally attaching lineage," while their remaining groups (Saophridae, Ceratothoinae, Cymothoinae and Lironecinae) are together analogous to my "buccal-gill chamber lineage." Both Schioedte & Meinert's classification and my proposed phylogeny suggest that the South American freshwater genera do not represent a monophyletic group. If this is indeed the case, then their origins cannot be considered in the light of generalized track theory unless the genera of each subfamily are first evaluated independently of one another.

If the above phylogenetic analysis is correct, *Nerocila* and its allied genera constitute the most primitive extant taxa in the family. Further, apomorphic features of the Cymothoidae are clearly seen to be the immersed cephalon and pleon, thin oostegites, convex body form, and buccal-gill chamber habit. Taxa such as *Cymothoa* and *Idusa*, which share the synapomorphic trait of deep pleonal

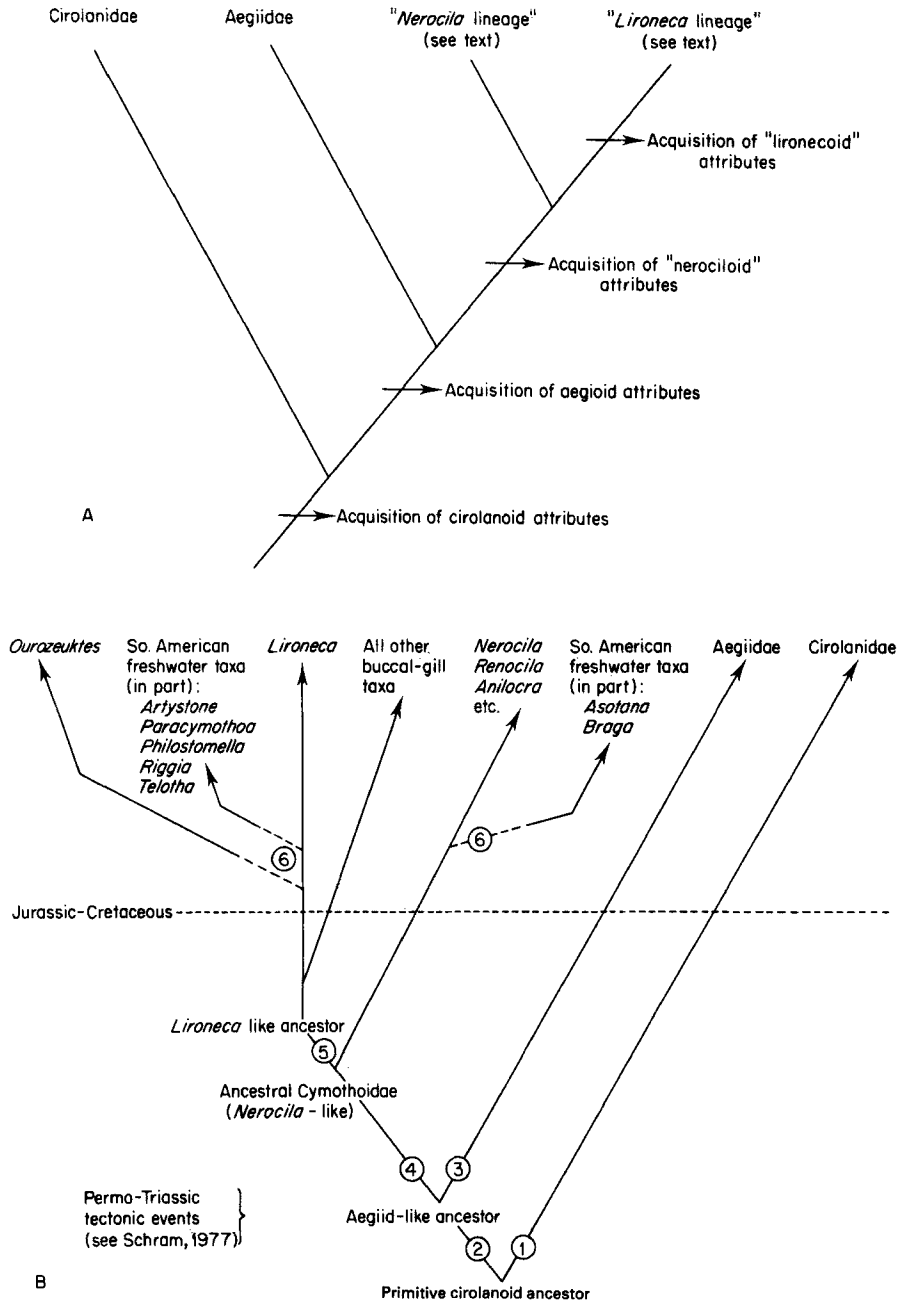


Figure 4A. Cladogram depicting the proposed origins of the families Cirolanidae, Aegiidae, and Cymothoidae (see text for further details). B. Proposed phylogeny of the Cymothoidae. 1. Acquisition of cirolanid familial attributes. 2. Increasing specialization for feeding upon living fishes, including development of prehensile pereopods and modifications of mouth parts. 3. Pereopods I-III prehensile; no obligatory or permanent dependence upon host fish in adult stage. 4. Acquisition of cymothoid familial attributes, including obligatory parasitism, pereopods IV-VIII prehensile, reduction in appendage setation (in adults), and modification of antennae and pleopods. 5. Acquisition of the gill chamber-buccal habit, and associated morphological attributes; pan-Tethyan distribution of family. 6. Adaptations to and invasions of freshwater biotopes (see text for further details).

immersion into the pereon may be considered, in this light, to represent two of the most recently derived marine cymothoid genera. *A priori*, one would expect species of the less derived cymothoid taxa to possess relatively lower host specificity. While accurate host data are wanting for most species, a review of the world literature suggests that indeed, species of *Nerocila*, *Anilocra* and *Renocila* appear to infest more species of host fishes than do species in other cymothoid genera. Among eastern Pacific species *Nerocila acuminata* infests the greatest spectrum of host fish species (Table 1).

Due to the overall poor taxonomic understanding of cymothoid genera and species, the zoogeographic history and phylogenetic relationships of the New World fauna are difficult to assess. There are no marine genera endemic to the New World. There may be two reasons for this. First, as discussed above, most marine genera of this family appear to have become established during the Permo-Triassic Tethyan Sea radiation. Second, due to the nature of their host associations most species tend to be widely distributed. This second factor (lack of geographic isolation) may be partly responsible for the apparently slow rate of morphological evolution in this family. The eastern Pacific cymothoid fauna contains fewer species than that of the western Atlantic (14 *v.* approximately 25). The New World, in turn, has far fewer known species than the Old World (*c.* 39 *v.* *c.* 210).

The low number of species in the New World may suggest to some an alternate hypothesis — that this family was more recently (*i.e.* post-drift) established in the Western Hemisphere, and hence primarily the product of dispersal events, rather than vicariance. Two facts, however, provide compelling evidence against this alternative. The first is the great age ascribed to the family. The second is the absence of any endemic New World marine genera.

The eastern Pacific does not possess a truly coastal *Anilocra* fauna. The two eastern Pacific records of the Caribbean species *A. laticauda* Milne Edwards, 1840 may be in error, while records of the Pacific *A. meridionalis* suggest that this species is an offshore, oceanic, epipelagic-mesopelagic form. Further collecting may show *A. meridionalis* to be distributed throughout the equatorial oceanic Pacific.

The eastern Pacific coastal *Nerocila* fauna is presently restricted to a single species, the amphi-American *N. acuminata*. This species' known range includes the Hawaiian Islands, suggesting that it may be circumtropical. Unfortunately, the genus is so large that only a detailed generic revision could properly determine if *N. acuminata* has Indo-West Pacific relationships or conspecifics. The only other eastern Pacific *Nerocila* (*N. excisa*) is a known Indo-Pacific species recorded so far only from the vicinity of offshore islands in the New World.

Only a single species of *Renocila* is known from the eastern Pacific, *R. thresherorum* Williams & Williams, 1980. Records of this species are all from the central-southern Gulf of California. T. E. Bowman (*pers. commn*) has indicated that E. Williams is presently describing several new species in this genus from the Caribbean region.

The genus *Lironeca* is represented in the eastern Pacific by five species, plus occasional occurrence of the Australasian/Indo-Pacific *L. raynaudii* Milne Edwards, 1840 in Chile. Nowhere in the eastern Pacific do more than three of these five species occur sympatrically. *Lironeca californica* is restricted to north temperate latitudes, while *L. convexa* and *L. vulgaris* range from temperate waters

all the way to Peru. The other two species are restricted to warm waters, one restricted to the Gulf and outer Baja coast (*L. menziesi*), and the second (*L. bowmani*) ranging throughout the tropical eastern Pacific. These data are summarized in Table 2.

The genus *Ceratothoa* is represented by two species in the eastern Pacific. *Ceratothoa gilberti* is essentially a Gulf of California endemic. *Ceratothoa gaudichaudii* possesses a distribution that is the austral equivalent to that seen in *Lironeca vulgaris*, ranging from southern California to the tip of South America.

Only one species of *Cymothoa* exists in the eastern Pacific, *C. exigua*. It possesses a typical "Panamic" distribution, ranging throughout the Tropical Eastern Pacific zoogeographic Region.

Unlike most other marine taxa, clear faunal relationships are not evident within the eastern Pacific Cymothoidae. The presence of *Anilocra laticauda* and *Nerocila acuminata* in this region is clearly tied to the former Tertiary Caribbean Province of Woodring (1966), more recently described as the Panamanian Track (Croizat *et al.*, 1974). The latter species, however, may eventually be shown to be circumtropical. The amphi-American distribution of these two species is herein interpreted as the product of low level, current dispersal events, rather than strictly slow evolutionary rates (Rosen, 1975). *Anilocra meridionalis* most likely is Indo-West Pacific in origin.

Species of the genus *Braga* Schioedte & Meinert, 1881 probably do not occur in the eastern Pacific. See Thun & Brusca (in press) for a discussion of this genus, and synonymy of *B. occidentalis* Boone, 1918 with *B. patagonica* Schioedte & Meinert, 1884.

Of the eastern Pacific cymothoid fauna, only one species (7%) is entirely restricted to temperate latitudes, although five (36%) of the remaining species have ranges that extend significantly into these colder waters. Eight species (57%) occur in the Gulf of California, and three (21% of the eastern Pacific fauna; 38% of the Gulf fauna) of these are essentially endemic to that body of water. The questionable Mexican and Panamanian Provinces of Briggs (1974) contain no endemic species of Cymothoidae.

METHODS AND MATERIALS

The materials upon which this monograph is based were obtained from a variety of sources. The cymothoid holdings of the Allan Hancock Foundation constitute the core material and now include the author's personal collections made over the past ten years. In addition, considerable material was borrowed from other museums; these are listed below with their abbreviated designation as used in the text following. Primary types of all species except *Lironeca californica*, *Anilocra laticauda* and *Ceratothoa gaudichaudii* were examined. Authors are provided following the first use of each taxon throughout the text.

- AHF Allan Hancock Foundation, University of Southern California, Los Angeles, California.
- AMNH American Museum of Natural History, New York, New York.
- BMNH British Museum (Natural History), London.
- CAS California Academy of Sciences, San Francisco, California.
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Table 2. Summary of provincial distribution of eastern Pacific Cymothoidae. Dots represent minimal or rare occurrence in a province*

Species	Distribution (by province)†							
	Arctic	Aleutian	Oregonian	Californian	Cortezian	Mexican	Panamanian	Oceanic distribution
<i>Anilocra meridionalis</i>								-----
<i>laticauda</i>						-----		-----
<i>Nerocila acuminata</i>								-----
<i>excisa</i>								-----
<i>Renocila thresherorum</i>					-----			-----
<i>Lironeca bowmani</i>								-----
<i>californica</i>								-----
<i>convexa</i>								-----
<i>menziesi</i>								-----
<i>vulgaris</i>								-----
<i>Ceratothoa gilberti</i>								-----
<i>gaudichaudii</i> ‡								-----
<i>Cymothoa exigua</i>								-----

* *Lironeca baynaudi* is not plotted, but included in discussion.

† See Briggs, 1974, and Brusca & Wallerstein, 1979a.

‡ *Ceratothoa gaudichaudii* ranges south to Patagonia.

- MNHN Muséum National d'Histoire Naturelle, Paris.
USNM National Museum of Natural History, Washington, D.C.
YPM Peabody Museum of Natural History, Yale University, New Haven, Connecticut.
SIO Scripps Institution of Oceanography, University of California, San Diego, California.
UW Thomas Burke Memorial Washington State Museum, Seattle, Washington.

All material was examined using a Wild M-5 stereomicroscope with both transmitted and reflected light sources, a Zeiss phase-contrast compound microscope, and a Labsource QH-150 Quartz/Halogen Illuminator and Spectral Irradiator.

The terminology used is not new, and has its basis in contemporary isopod literature. Segments of the pereon (pereonites), coxae (coxal plates), and pereopods are numbered with roman numerals. Segments of the pleon (pleonites) and pleopods are numbered with arabic numerals. "Body index" refers to the ratio of the body length to width (length divided by width). Length is measured from the anterior margin of the cephalon to the posterior margin of the pleotelson with the specimen held flat against a glass dish. In most species of Cymothoidae the body index decreases with maturity, females being relatively broader than males. The coxae never form ventral plates in the Cymothoidae and hence in the descriptions the term "coxal plates" is used, rather than the more lengthy (but in this family synonymous) phrase "dorsal coxal plates" (see Sheppard, 1957; and Brusca & Wallerstein, 1979b, for discussions of these structures). The terminal and subterminal spines of the maxillipedal palp, maxilla 1 and maxilla 2 are always very sharp and more-or-less recurved. References to these spines in the descriptions do not repeatedly describe this "prehensile" nature, but merely refer to them as "spines." The outer lobe of the second maxilla in cymothoids is almost always the larger; the inner, the smaller. The anterior (or ventral) lamella of the pleopods is taken to be the exopod; the posterior (or dorsal) lamella, the endopod. Illustrations are from female specimens unless otherwise indicated. Sizes, size ranges, and size ratios of important structures are given in the descriptions.

The generic diagnoses are somewhat expanded in comparison to those traditional in the literature. The single largest problem preventing a thorough evolutionary understanding of this family is uncertain generic definitions and boundaries. I have attempted to enlarge upon and/or amend the descriptions of the genera treated. These redescriptions are based upon a critical review of the world literature, and examination of most New World (and many Old World) marine species. Complete synonymies, geographic ranges and discussions of distribution patterns are provided for all species treated. Complete lists of locality collection data are not given. These data are voluminous and recorded on index cards kept current by the author; copies are available from the author or AHF upon request. Zoogeographic and phylogenetic analyses follow the hypothetico-deductive method of Popper (1959, 1965) as seen in the light of Morse & White (1979) and Settle (1980), and utilize the terminology of Brusca & Wallerstein (1979a). Common names of fishes are based upon Miller & Lea (1972), Thomson & McKibbin (1976), Thomson *et al.* (1979), and Shiino (1976). The first reference cited following a specific name in the synonymy section is the

author of that name; subsequent published references to that name follow, separated by semicolons.

KEY TO THE CYMOTHOID GENERA KNOWN FROM THE EASTERN PACIFIC

1. Uropods and pleopods heavily setose juveniles (*i.e.* "aegathoid" stages)
 - Uropods and pleopods not setose 2
2. Antenna 1 broader and usually longer than antenna 2; cephalon very weakly immersed (posteriorly sunk) in pereonite I; anterior margin of pereonite I not trisinate *Renocila*
 - Antenna 1 not broader or longer than antenna 2, usually the reverse; cephalon distinctly immersed in pereonite I OR not at all immersed; anterior margin of pereonite I distinctly trisinate, OR not at all trisinate 3
3. Cephalon not immersed in pereonite I; posterior margin of cephalon distinctly trisinate (*e.g.* Figs 5, 7, 11) 4
 - Cephalon more-or-less immersed in pereonite I; posterior margin of cephalon not trisinate (*e.g.* Figs 15, 21, 23) 5
4. Cephalon generally narrowing anteriorly forming an acute projection produced ventrally between first antennae; postero-lateral angles of pereonites II-VI not produced; coxal plates short, barely reaching or falling short of posterior border of respective segments (Figs 5, 7) *Anilocra*
 - Cephalon not as above, frontal margin without acute projection; bases of antenna 1 separated by clypeus; postero-lateral angles of pereonites II-VI manifestly produced, increasingly so posteriorly; coxal plates long, usually extended to or falling just short of posterior border of respective segment (Fig. 11) *Nerocila*
5. Basal articles of antennae 1 expanded and touching
Ceratothoa (= *Codonophilus* and *Meinertia*, in part)
 - Basal articles of antennae 1 not expanded and touching, although they may be nearly touching 6
6. Pleon continuous with lateral margins of pereon, forming a more-or-less continuous and symmetrical body margin; pleonites 1-2 occasionally somewhat immersed in pereon (Fig. 15) *Lironeca*
 - Pleon slightly or abruptly narrower than pereon, disrupting continuity of body margins; pleon generally deeply immersed in pereon (Figs 25, 27) 7
7. Body compressed laterally, dorsum strongly convex ("hunched"); bases of antenna 1 nearly touching; pleon weakly but distinctly narrower than pereon (Fig. 27) *Idusa*
 - Body not compressed laterally; bases of antenna 1 widely separated; pleon strongly and abruptly narrower than pereon (Fig. 25) *Cymothoa*

Genus *Anilocra* Leach, 1818

Diagnosis. Body narrow, somewhat more compressed and dorsally convex than in *Nerocila*. Cephalon usually narrows anteriorly to triangular apex folded down (ventrally) between bases of first antennae; downward folding gives anterior margin of cephalon truncate appearance in dorsal aspect. Cephalon with posterior border forming three weak lobes, not nearly as prominent as in *Nerocila*; cephalon not immersed, or only weakly immersed, in pereonite I. Anterior border of pereonite I more-or-less weakly trisinate, matching posterior border of cephalon. Posterolateral angle of pereonite I usually not produced or prominent; those of II–VI never produced or prominent; those of VII always more-or-less produced. Coxal plates small and compact, failing to reach posterior margins of their respective pereonites by a considerable distance (although in a few species coxal plates extend almost to pereonal margins). Pereopods gradually increasing in length posteriorly, seventh often manifestly longer than sixth. Pleon not at all, or only slightly immersed in pereonite VII. Pleopods 3–5 often thrown into deep pockets or pleats. Uropods often extended beyond posterior margin of pleotelson.

Remarks. New World species of *Anilocra* are easy to recognize by the presence of the ventrally folded anterior margin of the cephalon. There are presently about 23 valid species of *Anilocra*, five of which are now known from the Americas. *Anilocra acuta* Richardson, 1910 occurs along the eastern seaboard of the United States. *Anilocra plebia* Schioedte & Meinert, 1881 and *A. laticauda* Milne-Edwards, 1840 are tropical west Atlantic species. Hochberg & Ellis (1972) reported an undescribed species of *Anilocra* as occurring commonly on longjaw squirrelfish in the West Indies. *Anilocra meridionalis* Richardson, 1914 is known only from the tropical eastern Pacific. *Anilocra leavis*, *sensu* Miers, 1877 from Peru and Martinique, is herein synonymized with *A. laticauda*. The eastern Pacific species of *Anilocra* are exceedingly rare and are not represented in most museum collections.

Key to the species of Anilocra known from the east Pacific

1. Width of pleotelson subequal to pleonite 5; pleopods narrow, not visible in dorsal view; uropodal endopod subequal to, or shorter than exopod; pleopods 3–4 without marginal venation (Fig. 6J–M) *A. meridionalis*
- Width of pleotelson much greater than pleonite 5; pleopods wide, visible in dorsal view; uropodal endopod longer than exopod; pleopods 3–4 with marginal venation (Fig. 8F–K) *A. laticauda*

Anilocra meridionalis Richardson, 1914

(Figs 5, 6)

Anilocra meridionalis Richardson, 1914: 362. Nierstrasz, 1931: 129; Trilles, 1972c: 11.

Description (female). Body: width 4.0 mm, length 11.2 mm; narrow, body index 2.80 for midmolt female (holotype). General color (in alcohol) diffuse brown (Fig. 5).

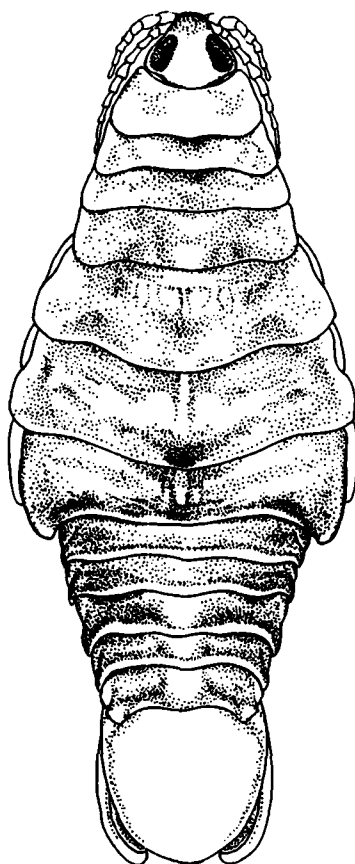


Figure 5. *Anilocra meridionalis* Richardson. Type.

Cephalon: Subtriangular, narrowing anteriorly; greatest width (along posterior margin) 1.4 times length. Front folded ventrally (see generic diagnosis); posterior margin weakly trisinate, and weakly immersed in pereonite I. Eyes moderately large, width of each $1/4$ greatest width of cephalon (Fig. 5). Antenna 1 reaching about midline of pereonite I; of eight articles, the distal five bearing short setae; proximal three articles not manifestly larger than remaining articles (Fig. 6A). Antenna 2 reaching posterior margin of pereonite II; laterally compressed; of 11 articles (Fig. 6B). Mandible with terminal palp article setose (Fig. 6E). Maxilla 2 with two spines each on inner and outer lobes; outer with pectinate scales (Fig. 6D). Maxilliped with one small terminal and two small subterminal spines (Fig. 6F).

Pereon: Posterolateral angles of all pereonites evenly rounded, not extended. Coxal plates small, compact, none reaching posterior margin of their respective segments; those of III–VII falling considerably short of posterior margins of respective segments (Fig. 5). Pereopods increase gradually in length from I to VII; without carinae, although bases of posteriormost legs with shallow groove to receive ischium-merus.

Pleon: Not immersed in pereonite VII. Pleonites decreasing gradually in width posteriorly; subequal in length. Pleotelson slightly longer than wide (width/length ratio 1:1.4); posterior margin evenly rounded (Fig. 5); pleotelson

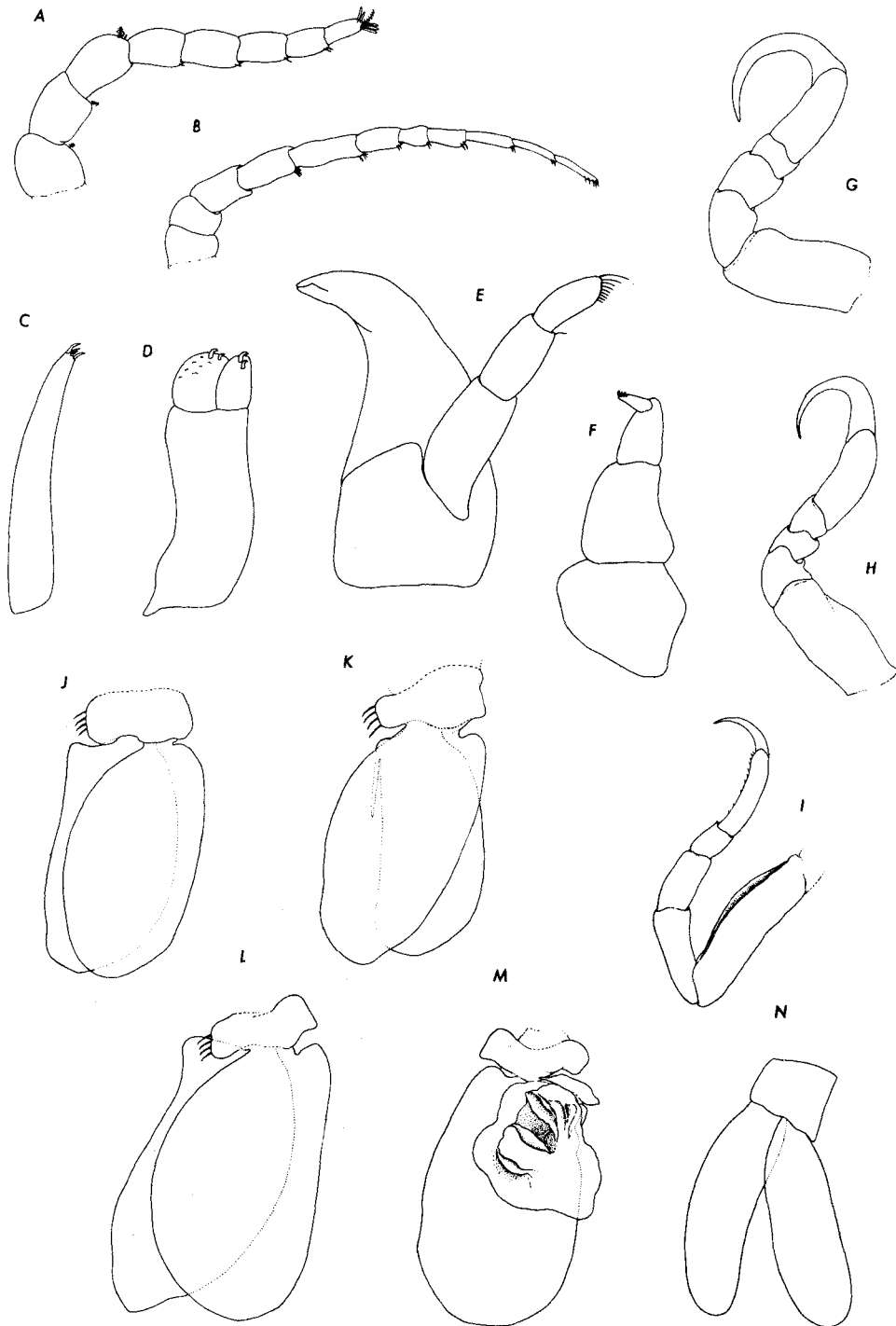


Figure 6. *Anilocra meridionalis* Richardson. Type. A, Antenna 1; B, antenna 2; C, maxilla 1 (R); D, maxilla 2 (R); E, mandible (R); F, maxilliped (R); G, pereopod I; H, pereopod IV; I, pereopod VII; J, pleopod 1; K, pleopod 2; L, pleopod 4; M, pleopod 5; N, uropod.

and pleonite 5 subequal in width. Pleopods simple, without well developed accessory lamellae; endopod of pleopod 5 strongly pleated; appendix masculinum persists into female stage (Fig. 6J–M). Uropodal rami evenly ovate, subequal in size or endopod barely shorter than exopod, rami reaching barely beyond posterior margin of pleotelson (Fig. 6N).

Remarks. Only the holotype (a midmolt female) and two juveniles were available for study. The description and figures are based on the holotype.

Type deposition. USNM 46400.

Distribution. Richardson reported the single female specimen from which the species was described (from near the Galapagos Islands, 9°31'N, 106°30'5"W) from a depth of 1923 fathoms on a rocky bottom. However, the original label accompanying this specimen gives a depth range of "300 fms [ca. 600 m] to surf." The label data are probably correct as it is highly unlikely the *Albatross* was capable of sampling a "rocky bottom" at a depth of 1923 fathoms. In addition, Richardson gave the size of the type as 9.5 × 28 mm, twice the actual size of the specimen. The two juveniles deposited at AHF were collected between the islands of Hawaii and Clipperton (10°0'N, 142°50'W) by the National Marine Fisheries Service. They were taken in a midwater trawl of unknown depth. The absence of this species from the extensive inshore collections available for the present study suggests that it is an offshore or oceanic species. Its rarity is attested by its absence from the numerous *Anton Dohrn* and *Velero III* and *IV* collections from the tropical eastern Pacific.

Host data. The host of this enigmatic species is not known.

Anilocra laticauda M. Milne-Edwards, 1840
(Figs 7, 8)

Anilocra laticauda Milne-Edwards, 1840: 259. Schioedte, 1868: 12; Schioedte & Meinert, 1881: 126; Moore, 1902: 172; Richardson, 1900: 221; 1901b: 528; 1905: 227; 1912: 190; Gerstaecker, 1901: 263; Nierstrasz, 1915: 81; 1918: 114; 1931: 130; Boone, 1921: 94; 1927: 139; 1930: 16; Coventry, 1944: 533; Bowman & Diaz-Ungria, 1957: 112; Menzies & Glynn, 1968: 46; Schultz, 1969: 153; Gosner, 1971: 476; Hochberg & Ellis, 1972: 84; Trilles, 1975: 306; Trilles & Valla, 1975: 967; Bowman, Grabe & Hecht, 1977: 393; Kussakin, 1979: 283 (Not Pearse, 1952: 39 or Causey, 1956: 10).

Anilocra mexicana de Saussure, 1857: 505. de Saussure, 1858: 484; Haller, 1880: 388.

Anilocra leachii Schioedte, 1866: 205. Schioedte, 1868: 12.

Anilocra laevis Miers, 1877: 672. Gerstaecker, 1901: 264; Richardson, 1910: 85; Nierstrasz, 1931: 129.

Description (female). Cephalon: Small narrowed anteriorly; front folded ventrally (see generic diagnosis). Antennae 1 of eight articles; nearly reaching anterior margin of pereonite I; proximal three articles manifestly larger than remaining articles (Fig. 8A). Antenna 2 of 8–10 articles; nearly reaching posterior margin of pereonite I; articles 5–6 longest (Fig. 8B). Mouth parts missing from specimen.

Pereon: Pereonites IV–VI widest; pereonite VI longest; pereonite VII manifestly shorter and narrower than VI. Pereonite I with anterolateral angles not produced; VII with posterolateral angles produced, but broadly rounded. Coxal plates small, compact, posterior angle of coxae II–IV obtuse; V–VII with

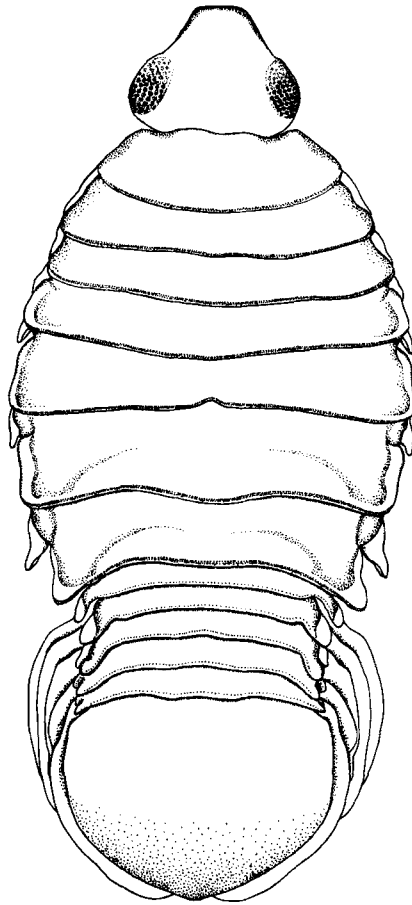


Figure 7. *Anilocra laticauda* Milne Edwards. Syntype (*A. laevis* Miers, 1877).

posterior portion free from pereonite, angle subacute (Fig. 7). Pereopods with weak carinae (Fig. 8C–E).

Pleon: Pleonites decrease slightly in width posteriorly; subequal in length. Pleotelson wider than pleonites and broadly rounded along posterior border; wider than long. Pleopods very large, extended beyond lateral margins of pleon and visible in dorsal aspect (Fig. 7). Pleopods with accessory lamellae as figured (Fig. 8F–K); pleopods 3–4 with strong folding and lateral venation (Fig. 8I–K). Uropods fail to reach distal margin of pleotelson; evenly rounded; endopod longer than exopod (Fig. 8H).

Remarks. Miers' original description of *A. laevis* was based upon two specimens collected by Prof. A. Wrzesniowsky of the University of Warsaw, one from Peru (Pacific) and the other from Martinique (Atlantic). Miers stated that Wrzesniowsky forwarded these specimens to Dr Gunther, who in turn entrusted them to him for identification. No type deposition was provided by Miers and I have been able to locate only one of these syntypes, the Martinique specimen (BMNH). Trilles & Vala (1975) suggested that *A. laevis* might be a synonym of *A.*

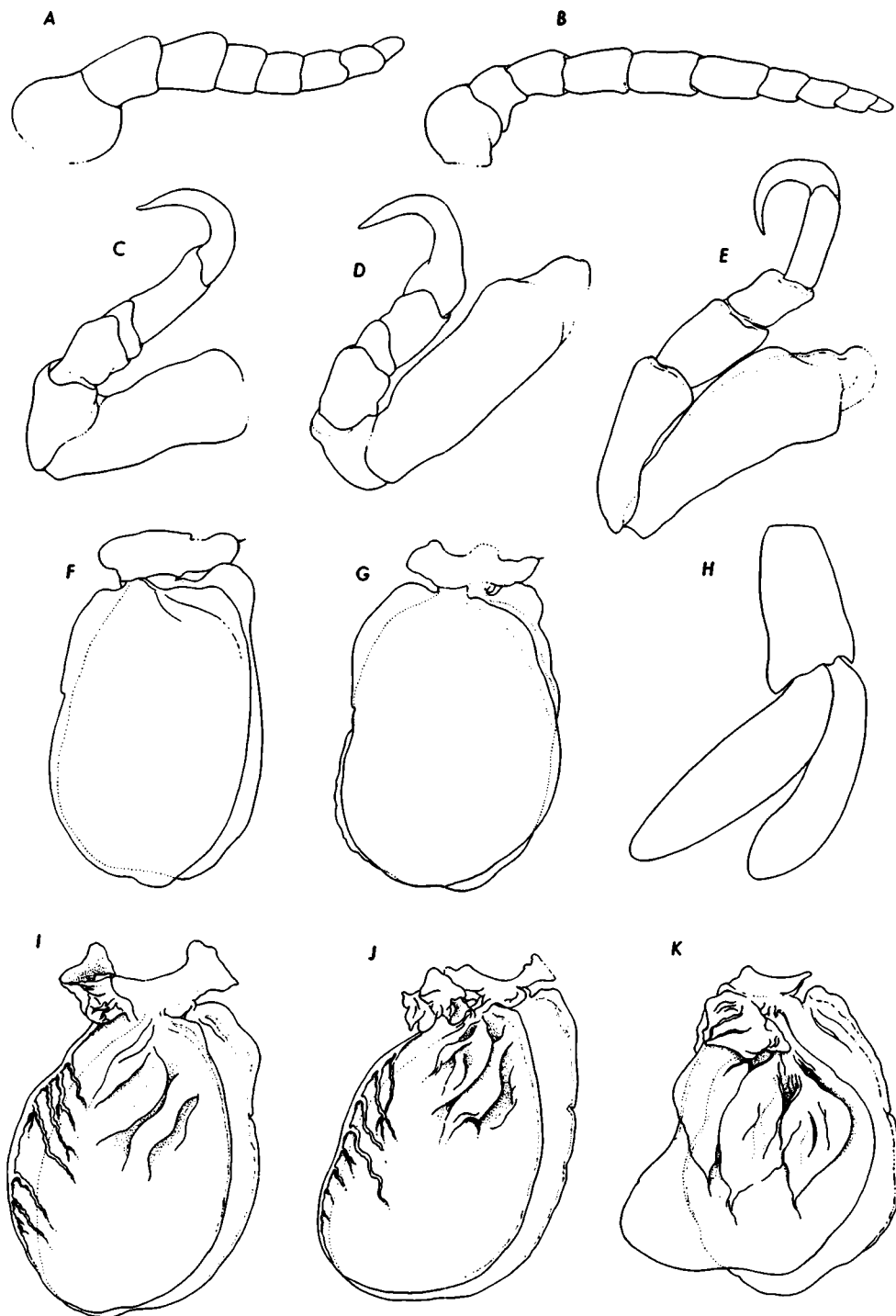


Figure 8. *Anilocra laticauda* Milne Edwards. Syntype (*A. laevis* Miers, 1877). A, Antenna 1; B, antenna 2; C, pereopod I; D, pereopod IV; E, pereopod VII; F, pleopod 1; G, pleopod 2; H, uropod; I, pleopod 3; J, pleopod 4; K, pleopod 5.

laticauda by including it in the latter species' "Synonymie et mentions successives" (accompanied by a question mark). They did not discuss the possible synonymy and apparently did not examine any type material. Trilles (1975) also commented on this possible synonymy. Miers (1877) claimed *A. laevis* differed from *A. laticauda* only in the length of its first antennae and uropodal rami. Examination of Miers' Martinique type and specimens of *A. laticauda* (USNM) has revealed that both of these characters are variable within the species, and that no other constant morphological differences exist. Despite the lengthy list of references to this species, an expanded description has not yet been published; hence that given here, based upon the Martinique syntype (BMNH 1879-21), which is herein synonymized with *A. laticauda*.

Type deposition. *Anilocra laevis*, syntype, BMNH 1879-21; *Anilocra laticauda*, MNHN.

Distribution. Only two eastern Pacific records exist. Miers (1877) originally reported it from "Peru," providing no further data. Coventry (1944) reported it from 250 miles WSW of Acapulco, Mexico. His record was of a single specimen taken from the left dorsal surface of *Oxyporhamphus micropterus*. I have been unable to locate either of these specimens. The single available specimen allegedly of Pacific origin suggests that presence of *A. laticauda* in the eastern Pacific is questionable, and that it rarely (if ever) obtains and/or survives passage through the Panama Canal. Its distribution in the western Atlantic was discussed by Menzies & Glynn (1968) and Bowman *et al.* (1977). The latter authors stated that *A. laticauda* probably does not occur in the United States except in the Florida Keys, although it is common throughout the Caribbean. This species is presently being examined by E. H. Williams, who feels it may be represented by a "species complex" in the West Atlantic (T. Bowman, pers. comm).

Host data. *Anilocra laticauda* has been reported from over 15 host species in the Caribbean; see Trilles & Vala (1975) for a recent review. In the Pacific it is reported only from *Oxyporhamphus micropterus*.

Genus *Renocila* Miers, 1880

Diagnosis. Body generally more depressed than in most other cymothoid genera, rarely twisted to one side. Cephalon strongly to weakly truncate anteriorly; posterior margin only slightly overlapped by pereonite I. Antennae 1 and 2 rather flattened, widely separated at base; antenna 1 broader and usually longer than antenna 2, sometimes markedly so. Anterior margin of pereonite I not trisinate. Posterolateral angles of pereonites V-VII more-or-less strongly produced; all coxal plates more-or-less strongly produced posteriorly. Pereopods of females without carinae on bases. Pleonites not laterally incised (after Bowman & Mariscal, 1968).

Remarks. In general appearance species of *Renocila* resemble *Anilocra*, however some (e.g. *R. thresherorum*) also bear a striking superficial resemblance to some *Lironeca*. One of the diagnostic features of *Renocila* is the relative lengths of antennae 1 and 2, which is just the reverse of that in most cymothoid isopods. See Bowman & Mariscal (1968) for further comments and a key to the species of *Renocila* known to that date. Only a single species of *Renocila* is known from the eastern Pacific.

Renocila thresherorum Williams & Williams, 1980
(Figs 9, 10)

Description (female). Body: Width 7.0–14.0 mm, length 12.0–30.5 mm; body index 1.8–2.5 (mean 2.15) for non-ovigerous females, 1.7–2.3 (mean 1.82) for ovigerous females. General color (in alcohol) dark tan or purple, dorsal surface with scattered chromatophores, concentrated on posterior borders of segments (Fig. 9).

Cephalon: Width 1.35–1.65 times length; posterior border weakly crenulate and weakly immersed in pereonite I (Fig. 9). Eyes well developed. Antenna 1 of eight articles, barely reaching anterior margin of pereonite I; antenna 2 of eight articles, barely reaching anterior quarter of pereonite I (Fig. 10A, B). Maxilliped with two terminal, and one subterminal spines (Fig. 10F). Maxilla 1 with four terminal spines (Fig. 10C). Maxilla 2 with semilunar pectinate scales; each lobe with two terminal spines (Fig. 10D). Mandible as figured (Fig. 10E). Free margin of labrum strongly crenulate.

Pereon: Pereonites I and V longest; II and VII shortest, or II–III and VII shortest; IV–VI subequal in length. Pereonites V and VI widest. Pereonite VII often covering lateral margins of pleonite 1. In dorsal aspect, coxae II and III barely reaching posterior margins of their respective pereonites; coxae IV–VII reaching one-half distance to posterior margins of respective pereonites (Fig. 9). Posterior angles of coxae II–III rounded; of IV rounded or subacute; of V–VII subacute (Fig. 9). Pereopods increasing gradually in length posteriorly. Pereopod I with or without a single spine on outside of merus (Fig. 10G); pereopods II–VII with one or two spines on outside of merus; pereopods V–VII with small spines on inside border of propus and carpus, absent on V–VI in larger specimens (Fig. 10H, I). Posterior pereopods more spinose than anterior pereopods; all pereopods without carinae.

Pleon: Pleonites subequal in width and length. All pleopods with stout setae on medial margins of bases; pleopods 3–5 with small lamellar accessory gill on proximal region of endopod; pleopod 2 with or without remnant of appendix masculinum (Fig. 10J–N). Posterior margin of pleotelson evenly rounded; width subequal to length; width/length = 1.1 (Fig. 9). Uropodal endopod ovate; exopod elongate, longer than endopod; uropods extended beyond posterior margin of pleotelson (Fig. 10O).

Male. Width 3.0–5.0 mm, length 8.0–12.5 mm; body index 2.5–3.3 (mean 2.81). Similar to female except for the following: lateral margins of pereon nearly parallel; coxae II–VII with posterior angles broadly rounded; pereopods V–VII with distinct carinae.

Remarks. *Renocila thresherorum* can be quickly distinguished from all other eastern Pacific cymothoids by its broad, darkly pigmented body, lack of accessory lamellae on the pleopodal bases, and the general features of pereonites and coxal plates. Unlike most species of *Renocila*, the first antennae of *R. thresherorum* are not manifestly longer than the second. Almost all specimens made available for this study were collected by personnel of Scripps Institution of Oceanography, and are now deposited in the invertebrate collections of that institution. Some specimens from San Jose del Cabo Bay and Santa Cruz Island (Mexico) have attached algae and ciliate protozoans on the exoskeleton. This species was recently described by E. and L. Williams, and was "in press" when the present

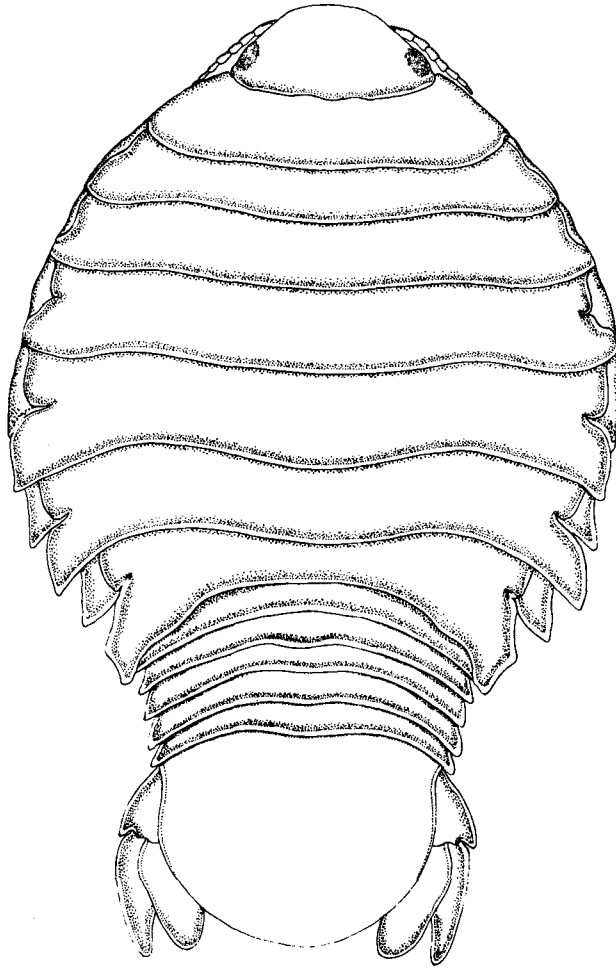


Figure 9. *Renocila thresherorum* Williams & Williams. Female.

manuscript was accepted for publication. E. Williams was kind enough to furnish me with copies of page proofs of their paper.

Type deposition. Holotype and allotype deposited in USNM; type numbers not yet assigned.

Distribution. *Renocila thresherorum* appears to be endemic to the central and southern Gulf of California. Of more than 350 individuals I have examined, from 42 lots, only three records were outside the Gulf. Two of these records are from Magdalena Bay, a large mangrove estuary that is known to serve as an "extra-Gulf" refugium for numerous other Gulf endemic invertebrates (Brusca, 1980). The third record is of a female and associated juvenile from 1.6 km off Corona del Mar, southern California. These distributional data suggest the single California record was a case of chance dispersion. The type specimens are from Loreto, Baja California Sur, Mexico (13 October 1978).

Host data. Only two host associations have been made for *R. thresherorum*. The

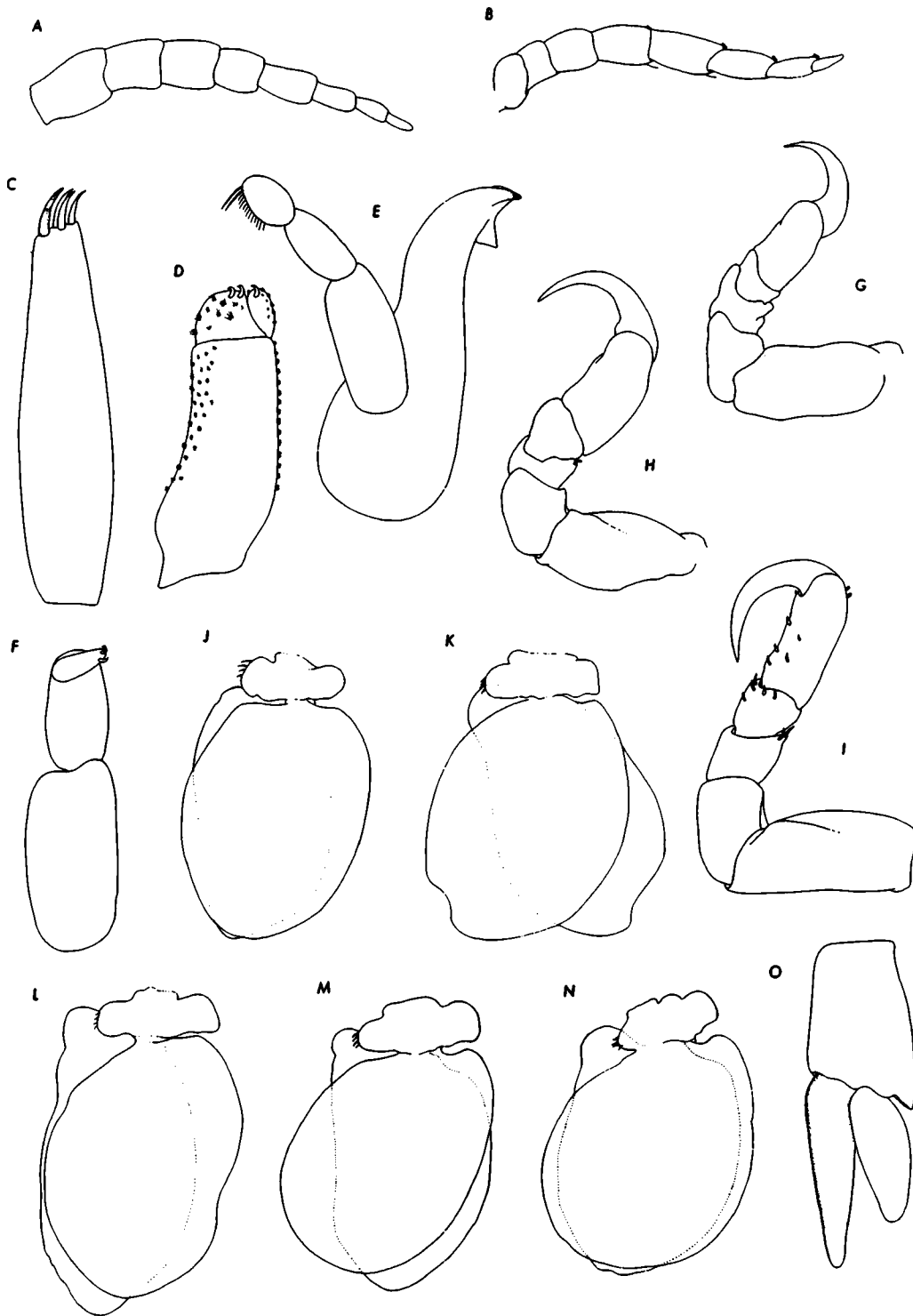


Figure 10. *Renocila thresherorum* Williams & Williams. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (R); F, maxilliped; G, pereopod I; H, pereopod IV; I, pereopod VII; J, pleopod 1; K, pleopod 2; L, pleopod 3; M, pleopod 4; N, pleopod 5; O, uropod.

holotype and allotype were taken from the dorsal surface (“... along side of the dorsal fin. Male and female on either side of the dorsal fin”) of a barspot cardinalfish, *Apogon retrosella* (Gill, 1863). This fish ranges throughout the Gulf of California and south at least to Oaxaca. I have recorded it from the side of a panamic fanged blenny, *Ophioblennius steindachneri* Jordan & Evermann, 1898 from Isla Coronado, in the southern Gulf of California. The isopods, one male and one female, were attached one each behind the pectoral fins. Slight tissue damage was evident. *Ophioblennius steindachneri* ranges from the upper Gulf of California to Peru, and is the most abundant combtooth blenny along rocky coasts in the tropical eastern Pacific. Its Atlantic twin is the redlip blenny, *O. atlanticus* Silvester. Both known hosts inhabit exposed rocky shores, *O. steindachneri* being typical of surge-swept unprotected rocky headlands (Thomson *et al.*, 1979). Almost all specimens of *R. thresherorum* have been taken by use of rotenone-based ichthyocides in rocky subtidal habitats shallower than 35 m. The above data suggest that this species is most common on rocky-shore fishes of central-southern Gulf of California coasts, and further, that it may dislodge from its host rather easily. This particular habitat preference is probably the reason it has not been reported earlier, since traditional collection techniques have not sample subtidal rocky habitats.

Genus *Nerocila* Leach, 1818

Diagnosis. Body generally more depressed than in most other cymothoid genera, rarely twisted to one side; chromatophores of dorsum often arranged in three longitudinal rows. Cephalon not acute and projected anteriorly (as in *Anilocra*), but with anterior margin convex, acutely convex or concave. Cephalon not immersed in pereon or only slightly immersed; posterior border produced into three lobes; anterior border of pereonite I correspondingly trilobate. First pair of antennae nearly contiguous to moderately separated at bases, separated by clypeus¹; mandibular palp of three articles. Posterolateral angles of pereonites weakly to strongly produced, usually increasingly so posteriorly. Coxal plates well developed and prominent, generally extended almost to, or to (but rarely beyond) posterolateral angles of their respective pereonites. Pleon not at all immersed in pereon; pleonites subequal in length; pleonites 1 and 2 generally extended posterolaterally. Pleopods typically with small lamellar accessory gills; pleopods 3–5 often thrown into deep pockets or folds. Uropods generally extended beyond posterior border of pleotelson. Appendix masculinum of male generally persists in female stage, reduced in size.

Remarks. The genus *Nerocila* is easily distinguished from all other cymothoid genera by the preceding combination of characters. Species limits within the genus, however, are difficult to define precisely. Most species are highly polymorphic or variable in most morphological characters, while characters that are reasonably fixed are not distinctly different from one species to another, giving them limited taxonomic value. The results of this dilemma are that older descriptions are generally useless for species identification, while newer

¹ In the subgenus *Emphyllia* Koelbel, represented by the single species *N. (Emphyllia) sundaica* Bleeker, the basal articles of antenna 1 are inflated and may be in contact with one another (Bowman, 1978a).

descriptions and diagnoses which are more comprehensive must define species by "combinations of characters," rather than by a suite of distinct and unvarying character states.

The mouthparts, for example, are of little or no taxonomic value, being more or less identical in all species. Similarly, there is little difference in pereopodal morphology between the species. Juvenile and male stages of most (if not all) species bear pereopodal spines on the posterior legs that are progressively lost with succeeding instars. Old males and females possess few or no pereopodal spines. Literature in which presence or absence of pereopodal spination is mentioned should be used with caution, particularly if information on sex is not provided.

The general body form is variable, particularly in width/length ratios, and degree of development of the posterolateral angles of pereonites and coxal plates. Despite variations within a given species these two morphological features have some diagnostic value. In addition to normal variations in body morphology due to genetic polymorphism and environmental influences during growth, damage to the appendages and even the extended angles of the pereonites and coxae is common. The stout setae on the medial margins of the pleopodal bases are often partly or entirely eroded away. The antennae often have fewer than the normal number of articles. The uropodal rami and posterior margin of the pleotelson are commonly disfigured and in varying states of regeneration. It seems highly likely, though not yet proved, that these injuries are the results of predation attempts by conspecific hosts or cleaner fishes. Adult *Nerocila* are ectoparasites, and in most cases may be too large to be removed by a cleaner fish, although they do remain susceptible to limited predatory damage by cleaners. Finally, a study of a large series of *Nerocila acuminata* indicates that both the number of facets in the eye and the length of the appendix masculinum (in females) decrease with age, indicating that these characters are of little taxonomic value. The pleopods are of some value, most species typically bearing small lamellar accessory gills on the outer and/or inner margin of the basis, and the inner margin of the rami.

Species in this genus tend to show a broad host preference, apparently based more on their life history strategies and ecological preferences than on taxonomic specificity, with most preferring demersal and/or schooling fishes (see discussion of *N. acuminata*). Published host data reveals that most species are associated with three to ten species of fishes, in several families. Future studies of this genus may show most to be as catholic in their host preference as *N. acuminata*, which is recorded from 39 different host species in the eastern Pacific alone. The literature, as well as my field studies, indicate that the principal locations of attachment by species of *Nerocila* are, (1) on a fin, most often the caudal or dorsal fin, (2) at the base of a fin, most often the dorsal or pectoral fin, and (3) on the isthmus. Several exceptions are known.

About 40 species of *Nerocila* are known. Only five of these occur in the New World: *N. excisa* (Richardson, 1901); *N. acuminata* Schoiedte & Meinert, 1881 (= *N. californica* Schioedte & Meinert, 1881, *syn. nov.*; *N. fluviatilis* Dana, 1853 (see Van Name, 1940: 123); *N. munda* Harger, 1873; and *N. lanceolata* (Say, 1818). Of these, only the first two are known from the east Pacific. *Nerocila acuminata* is a widespread species, presently known from the west Atlantic, east Pacific (formerly as *N. californica*) and Hawaii. *Nerocila excisa* is an Indo-Pacific species not known from mainland America.

Key to the species of Nerocila known from the east Pacific

1. Anterior margin of cephalon concave (medially excavate); posterolateral angles of pereonites I–VI rounded, not produced into acute angles (Fig. 14A, B) *N. excisa*
- Anterior margin of cephalon convex; posterolateral angles of all, or just posterior pereonites produced into acute or subacute angles (Fig. 11) *N. acuminata*, 2
2. Posterolateral angles of all pereonites strongly produced and acute, reaching beyond posterior borders of their respective segments; coxal plate of pereonite II strongly produced, with acute posterior angle; cephalon considerably wider than long (Fig. 11C, D) *N. acuminata*, aster form
- Posterolateral angles of all, or just posterior pereonites weakly produced, those of I–V never reaching beyond posterior borders of their respective segments; coxal plate of pereonite II not produced, posterior angle rounded; cephalon barely wider than long, or width subequal to length (Fig. 11A, B) *N. acuminata*, *acuminata* form

Nerocila acuminata Schioedte & Meinert, 1881

(Figs 11, 12, 13)

Nerocila acuminata Schioedte & Meinert, 1881: 48. Richardson, 1900: 220; 1901b: 527; 1902: 291; 1905: 220; Comeaux, 1942: 86; Pearse, 1947: 326; 1952: 39; Hutton, 1964: 447; Schultz, 1969: 152; Briggs, 1970: 55; Gosner, 1971: 476; Hastings, 1972: 274; Brusca, 1978a: 152; Williams & Williams, 1978: 122; Moreira & Sadowsky, 1978: 100; Kussakin, 1979: 278.

Nerocila californica Schioedte & Meinert, 1881: 72. Richardson, 1899a: 172; 1899b: 830; 1900: 220; 1905: 211; Nierstrasz, 1915: 73; 1931: 126; Hale, 1926: 208; Gurjanova, 1936: 83; Schultz, 1969: 151; Olson, 1972: 1203; Brusca, 1977: 129; 1978a: 141; 1980: 231; Valentine & Phelps, 1977: 129; Moreira & Sadowsky, 1978: 100; Kussakin, 1979: 276.

Pterisopodus bartschi Boone, 1918: 596.

Description (female). Body: Width 7.0–13.0 mm, length 14.0–25.0 mm. Body index 1.85–2.51 (mean 2.08) for non-ovigerous females; 1.75–2.26 mm (mean 1.99) for ovigerous females. General color tan, yellowish or lavender, usually with three longitudinal rows of dense chromatophores on dorsum (Fig. 11).

Cephalon: Width greater than length or rarely approximating length; frontal margin convex, evenly to acutely rounded; eyes oval, moderately large to small; large females occasionally with eyes so reduced as to be apparently wanting (Fig. 11A–C). Antenna 1 of eight articles, first two expanded but not touching (Fig. 12A); antenna 2 of 9–11 articles, first two weakly expanded, but not touching; about 1 mm longer than antenna 1 (Fig. 12B). Maxilliped with 2–4 terminal spines (Fig. 12F). Maxilla 1 with four apical spines (Fig. 12C). Lobes of maxilla 2 with two spines each, and numerous, semilunar, pectinate scales (Fig. 12D). Mandibles simple; palp with one to several setae on distal articles, and fewer setae on middle article (Fig. 12E).

Pereon: Pereonite I, V and VI longest, subequal in length; II–IV shortest; V–VI widest (Fig. 11A–C). Posterolateral angles of all, or only posterior pereonites produced, subacute or acute, increasing in length posteriorly, those of VII

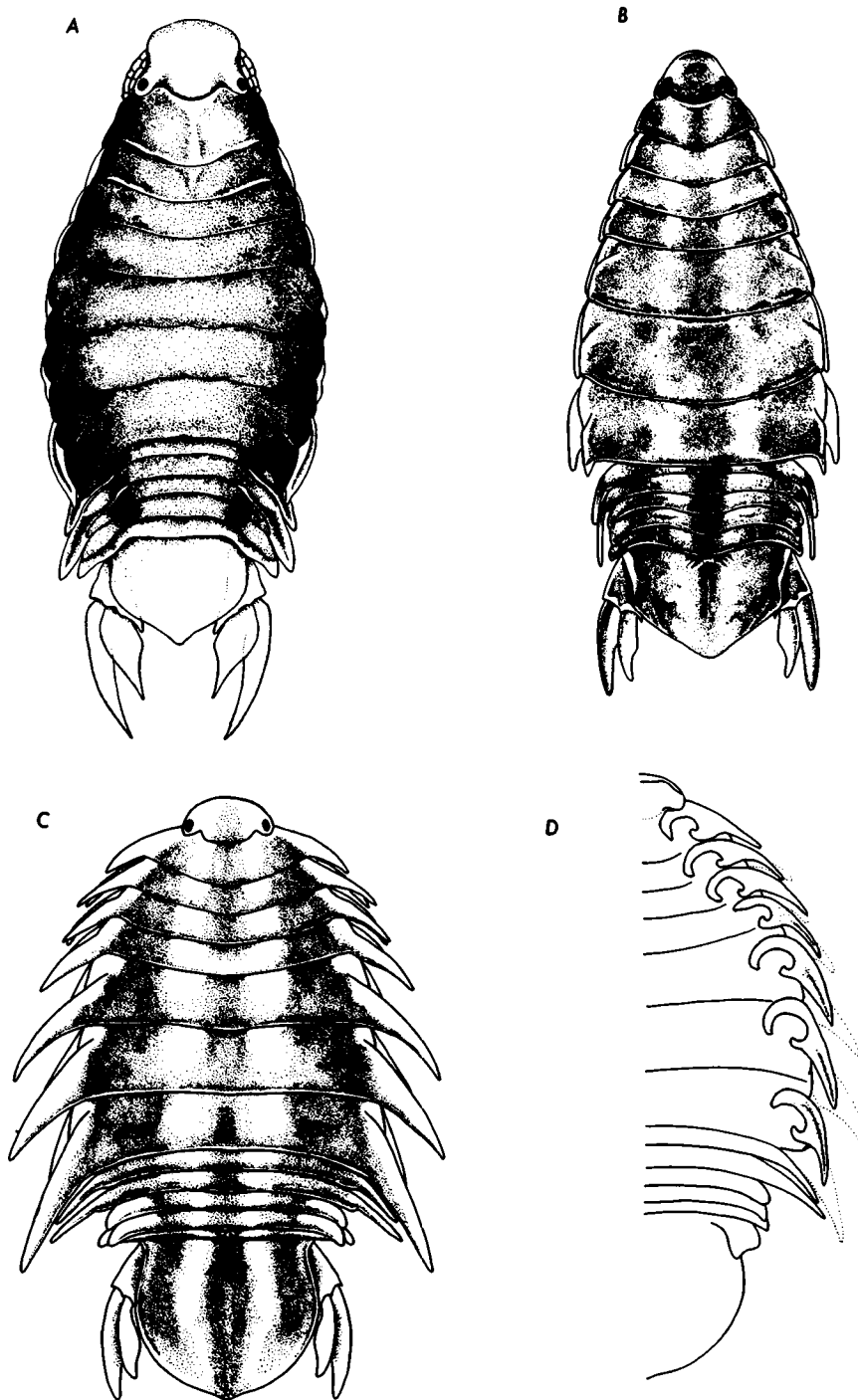


Figure 11. *Nerocila acuminata* Schioedte & Meinert; from the eastern Pacific. A, *N. acuminata, acuminata* form, female; B, *N. acuminata, acuminata* form, male; C, *N. acuminata, aster* form, female, dorsal aspect; D, *N. acuminata, aster* form, female, ventral aspect showing coxal morphology.

may be extended up to $3/4$ length of pleon. Coxal plates usually all visible in dorsal aspect, although if body is strongly convex coxae tend to be directed more ventrally and less easily seen in dorsal aspect. Posterior angles of all, or only posterior coxae produced; subacute or acute (Fig. 11). Posterior pereopods with basis flattened and somewhat grooved, without carinae (Fig. 13B–D); young females retain masculine spination on pereopod VII (Fig. 13D).

Pleon: Pleonites subequal in length. Pleonites 1 and 2 with long posterolateral processes, those of pleonite 1 extended at least to pleonite 3, usually to anterior margin of pleotelson; those of pleonite 2 usually extended to midline of pleotelson (Fig. 11). Pleopods with lamellar accessory gill on lateral margin of basis (usually folded in midline) and on medial proximal margin of endopod, the latter being considerably folded on pleopods 3–5 (Fig. 12I–K); bases with four stout setae on medial margin, often reduced or absent on posterior pleopods. Pleopod 4 often with endopod thrown into single large, transverse fold or pocket (Fig. 12J); pleopod 5 with endopod always pleated (thrown into 3–4, strong, well defined transverse folds) (Fig. 12K). Female retains appendix masculinum, which becomes smaller with successive molts. Pleotelson shield-shaped, posterior margin slightly acuminate (Fig. 11). Uropodal peduncle distally crenulate, inner border forming a large spine; exopod lanceolate, distal end narrowly rounded; endopod subpyriform, shorter than exopod; both uropodal rami extended beyond posterior border of pleotelson (Fig. 13E).

Description (male). Width 3–10 mm, length 10–20 mm; body index 1.87–2.61 (mean 2.26). Similar to female except for following: usually considerably smaller and more slender (note body indices); anterior margin of cephalon somewhat more acute; eyes larger; body more heavily pigmented; body generally more convex, making coxal plates less easily visible in dorsal aspect. Young males have spines on pereopods III–VII (Fig. 13C); older males have reduced spination.

Remarks. Brusca (1978a) discussed Richardson's (1905) description of this species (as *N. californica*) as well as its development and life history, providing descriptions and figures of the juvenile or "aegathoid" stages. In recognition of their apparent phyletic proximity he designated the west Atlantic *N. acuminata* as the Caribbean analog of *N. californica*. However, after examination of extensive collections recently made available from SIO, CAS, UA, USNM and Hawaii, it has become apparent that there is no reason to continue regarding these two nominal species as distinct and they are herein synonymized, as is Boone's *Pterisopodus bartschi*. Boone (1918) erected a new family (the Pterisopodidae) for her single specimen from Honda Bay, Cuba. Both Richardson and J. Maloney apparently recognized the specimen as *Nerocila acuminata*, as they both placed labels in the jar with Boone's holotype indicating its true identity. I have examined the holotype of *P. bartschi* and over 400 additional specimens, from 130 collections, from throughout the west Atlantic, east Pacific and Hawaii. No significant morphological differences exist among specimens within or between any of these localities.

Richardson (1905) distinguished *N. californica* from *N. acuminata* on the basis of width-length ratios of the body and cephalon, and the degree to which the pereonites and coxae are extended. The extent of variation in specimens of this species that I have examined, often from a single host, encompasses the entire range of these highly variable characters. Further evidence that these west Atlantic and east Pacific nominal species are synonymous comes from the

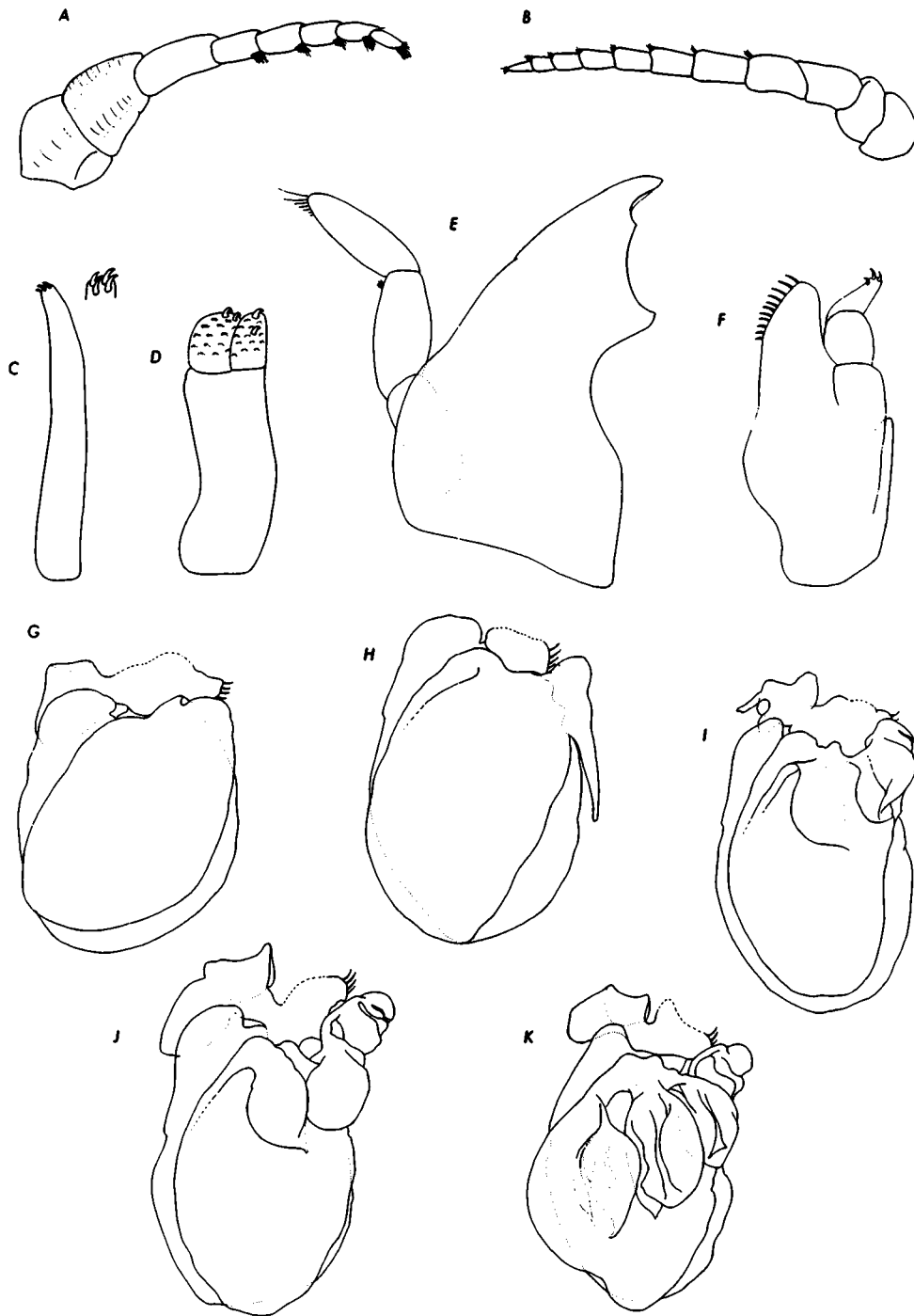


Figure 12. *Nerocila acuminata*, *acuminata* form. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (R); F, maxilliped; G, pleopod 1; H, pleopod 2; I, pleopod 3; J, pleopod 4; K, pleopod 5.

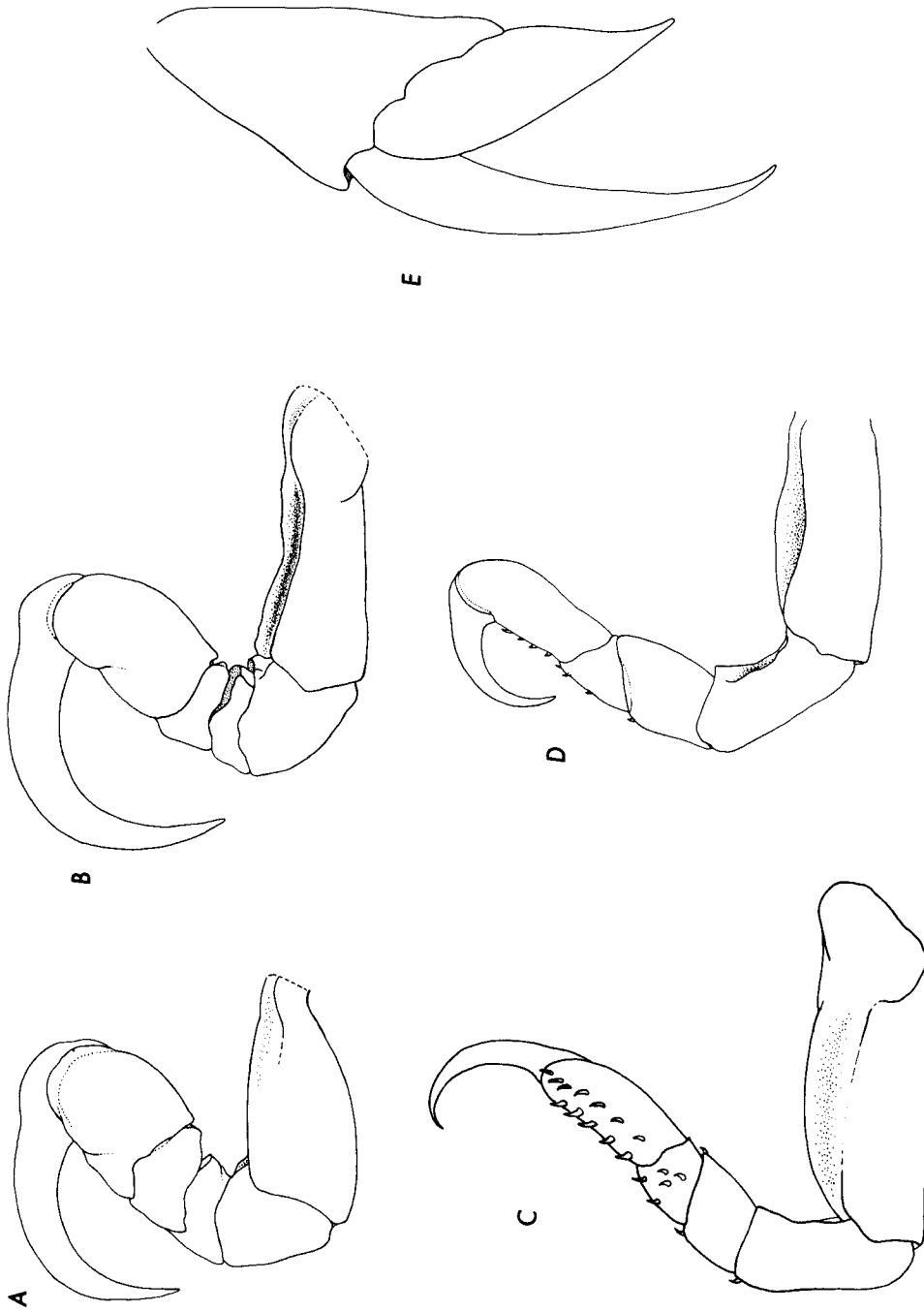


Figure 13. *Nerocila acuminata, acuminata* form. A, Pereopod I; B, pereopod IV; C, pereopod VII (male); D, pereopod VII (young female); E, uropod.

existence of two distinct morphological forms of *N. acuminata*, both of which are amphi-American in distribution. Based upon these zoogeographical data it appears probable that some level of gene mixture must occur between the east Pacific and west Atlantic populations via the Panama Canal. Evidence that *N. acuminata* can tolerate freshwater for short periods of time, and brackish water for long periods of time, exists in the form of collection records and specimens collected at the turn of this century in the region of the mouth of the Colorado River which at that time was an area of nearly pure fresh water (Brusca, 1980, and references therein). *Nerocila orbigny* (= *N. fluvialis*) is also known to penetrate into freshwater along the Atlantic seaboard of South America. Bowman *et al.* (1977) stated that *Anilocra acuta* occurs in oligohaline and mesohaline waters, and they report its presence in waters with salinities as low as 2‰ suggesting that this species could also tolerate freshwater, at least for short periods. Barnard (1925) came to the conclusion that *Nerocila rhabdota*, *N. cephalotes* and *N. armata* were one and the same species after many years of collecting and examining specimens from a wide geographic area. He hence designated a *cephalotes* form and a *rhabdota* form of *N. armata*, based upon the same principal morphological features I have used to distinguish the *aster* form of *N. acuminata* (i.e. the extent to which the posterior angles of the pereonites and coxae are produced).

Specimens of *N. acuminata* are frequently found with various attached epibionts, particularly hydroids (*Clytia* sp.) and the barnacle *Conchoderma virgatum* (Spengler). See Hastings (1972) and Brusca (1978a) for Atlantic and Pacific *C. virgatum* records, respectively.

Type deposition. *Nerocila acuminata* and *N. californica*, MNHN; *Pterisopodus bartschi*, USNM 50406

Nerocila acuminata, *acuminata* form

Diagnosis. Cephalon width equal to or greater than length; front acutely rounded. Posterolateral angles of any or only posterior pereonites produced, those of the anterior pereonites weakly produced and rounded or subacute; those of the posterior pereonites more strongly produced and subacute to acute; posterolateral angles of pereonites I–V not reaching beyond posterior borders of their respective segments. Coxal plates III–VII, IV–VII, or V–VII with acute posterolateral angles; coxae rarely reaching beyond posterior borders of respective segments.

Nerocila acuminata, *aster* form

Diagnosis. Cephalon always wider than long; frontal margin evenly rounded. Posterolateral angles of all pereonites strongly produced, acute; all reaching well beyond posterior borders of their respective pereonites; those of VII typically reaching at least to anterior border of pleotelson. Coxal plates II–VII with strongly produced, acute posterior angles; subequal in size; coxae II (and sometimes III) reaching to or slightly beyond distal angle of their pereonite; III–VII falling progressively shorter of distal angles of respective pereonites. (= *Pterisopodus bartschi* Boone, 1918).

Remarks. The most striking diagnostic features of the *aster* form of *N. acuminata* are its greatly extended, sharply pointed pereonites and coxae, giving the animal

a starlike appearance, hence the choice of the form designation (Fig. 11C, D). Morphological intermediates between the two forms occur, but are rare. Only three host identifications have been made for this form: the oval flounder, *Syacium ovale* (from San Carlos Bay, near Guaymas, Sonora, Mexico), a "papio" (probably *Caranx ignobilis*) from Kaneohe Bay, Hawaii, and a "pargo" (Lutjanidae) from the Gulf of Nicoya, Pacific Costa Rica. In addition, W. J. Cooke (pers. commn) reports the possible occurrence of this form, in Hawaii, on a sharpnose puffer, *Canthigaster jactator*, an unidentified holocentrid soldierfish ("menpachi"), and an unidentified acanthurid (surgeonfish). The difference in body morphology between the two forms of *N. acuminata* may be an expression of a rare gene combination, or may be the product of nonadaptive responses or allometry resulting from environmental conditions during growth of post-juvenile instars. An overview of the broad range of nongenetic morphological variations in marine invertebrates has been stated eloquently by Vermeij (1978). As yet available data are insufficient to provide evidence in favor of or against these possibilities.

Distribution. The distribution of *N. acuminata* in the eastern Pacific is from southern California (Los Angeles–Long Beach areas) to Peru, including the Gulf of California, and the offshore islands of Las Tres Marias and the Galapagos. It is especially common in coastal lagoons and bays, such as Newport Bay and Mission Bay in California, Estero de Punta Banda and Magdalena Bay on the west coast of Baja California, and throughout the shallow waters of the Gulf of California (Mexico) and Gulf of Nicoya (Costa Rica). Specimens of the *aster* form has been recovered from throughout this range (only the *aster* form has thus far been collected from the Hawaiian Islands). This broad distribution, with both forms occurring sympatrically in the Atlantic and the Pacific, and the occurrence of morphological intermediates, precludes the designation of subspecies within the complex. There is no reason to suspect strong genetic or geographic isolation between the forms. Considering the extremely broad spectrum of host fishes utilized by this species, a reasonable degree of gene mixing throughout the range should be expected, including the possible transgression of the Panama Canal. However, given the apparent slow rate of evolutionary change in the morphology of cymothoids (see introductory section) gene flow through the canal need not necessarily exist to maintain similar (ancestral) gene pools in the Atlantic and Pacific Oceans.

Host data. As a result of this study, *Nerocila acuminata* is now known from about 40 host fish species in the Pacific (see Table 3). It has also been reported from a large number of hosts in the Atlantic portion of its range. Brusca (1977, 1978a) provided data on hosts and general isopod/host biology of this species. *Nerocila acuminata* clearly is less host-specific than most cymothoid species. Nevertheless, some comments on the host records in Table 3 are in order. While many of these new host records are based upon collections made by me, most are from the literature or from labels with specimens from the USNM, SIO, CAS and AHF collections. The older records contain no information regarding host fish damage associated with the isopod. Further, a number of host records appear rather unlikely, possibly accidental records of "fugitive" isopods from a trawl catch. Others are undoubtedly records of temporarily attached young isopods. For example, Pearse (1947) reported *N. acuminata* from the mouths and gill chambers of a number of fishes in the vicinity of the Duke University Marine

Laboratory, Beaufort, North Carolina. It is clear that schooling and demersal fishes are preferred hosts of *N. acuminata*, the most common being members of the families Engraulidae, Atherinidae, Serranidae, Mugilidae, and Embiotocidae. Hosts in these families are often found suffering high infestation rates. Maximum infestations range from 85–90% of a catch for some engraulids, and to 57% of a catch for some embiotocids. Parasitized individuals typically have both a male and a female isopod attached to the isthmus, at the base of a fin, or on the fin proper. Records from hosts such as puffers, sculpins, skipjacks, sea robins, most croakers, sharks and rays usually consist of a single record of one individual on a fish. These isolated records are most probably of either temporarily attached young, or fugitives in trawl catches. If an actual host-parasite relationship existed in these cases it probably represented an individual effectively lost from the gene pool and hence of little biological significance. Also, it seems reasonable to assume that the durable placoid scales and tough skin of sharks and rays would preclude penetration by the mouthparts of Cymothoidae.

Considerable tissue damage to the host may occur. In heavy infestations, such as upon the anchovy population (*Cetengraulis mysticetus*) of the northern Gulf of California, multiple infestations are common. In this region, I have found as many as four isopods on one host, while two to three per fish is common. Each isopod is usually responsible for considerable tissue damage (e.g. erosion down to the myomeres). In many cases, 10–80% erosion of fin has been observed. Valentine & Phelps (1977), reporting this isopod on barred surfperch (*Amphistichus argenteus*) in southern California, found it attached only at the base of the caudal fin, where multiple scars were common. In the Belmont Shores area they found the incidence of parasitized fish to be random, even when hosts were divided into age (size) classes. Further, they found no evidence of a preference to attach to either the right or left sides of the host.

Table 3. Annotated list of host records for *Nerocila acuminata* in the eastern Pacific*

Family Heterodontidae (bullhead sharks)

Heterodontus francisci, horn shark. Monterey Bay, California to Gulf of California; one record, from San Diego (Richardson, 1905, as *Gypropleurodus francisci*).

Family Carcharhinidae

Triakis semifasciata, leopard shark. Oregon to Gulf of California; one record (Schioedte & Meinert, 1881).

Family Myliobatidae (eagle rays)

Myliobatis sp., probably *M. californica*, bat ray. Oregon to Gulf of California; one record (Schioedte & Meinert, 1881).

Family Engraulidae (anchovies)

Cetengraulis mysticetus, anchoveta. Los Angeles to Peru (rare north of Magdalena Bay); more records exist from this pelagic, schooling anchovy than any other host; infestation rates from the northern Gulf of California range to 90%.

Anchoa sp., probably *A. helleri*, Gulf anchovy. Common throughout the Gulf of California; one record, from El Golfo de Santa Clara, Sonora.

Family Ariidae (marine catfishes)

"Cat fish." Richardson (1905) was probably referring to the chihuil (*Bagre panamensis*) when she reported this host. The chihuil ranges from southern California to Peru, including the Gulf of California. No subsequent records from this fish exist.

* Range of host fish and indication of damage to host (when known) follows common name. References indicate source of host data (from literature); records without references are the authors personal records.

Table 3 *continued*

-
- Family Atherinidae (silversides)
- Leuresthes tenuis*, California grunion. Endemic to southern California and northwest Baja California; Olson (1972) reported this association from San Diego, California (Mission Bay).
- Leuresthes sardina*, Gulf grunion. Endemic to northern Gulf of California; numerous records; considerable host damage usually present.
- Atherinops affinis*, topsmelt. Vancouver Island, Canada to Gulf of California; several records, particularly from shallow bays and lagoons of southern California; tissue damage has been noted.
- Atherinopsis californiensis*, jacksnelt. Oregon to southwest Baja California; one record; no tissue damage evident.
- Family Scorpaenidae (rockfishes and scorpionfishes)
- Scorpaena guttata*, spotted scorpionfish (or sculpin). Santa Cruz, California to Baja California, and in northern Gulf of California; one record (Schioedte & Meinert, 1881, and Richardson, 1905). No other species in this abundant and species-rich family have been implicated as hosts.
- Family Percichthyidae (temperate basses)
- Stereolepis gigas*, giant sea bass. Northern California to Gulf of California; one record (collected by inter-American Tropical Tuna Commission from "gills" of one individual off Cape San Lucas, Baja California).
- Family Serranidae (sea basses)
- Epinephelus* sp. (?). Richardson (1905) reported two juveniles from "*Promicrops guttatus*"; this would appear to be a misidentification of a member of the similar *Epinephelus*; no subsequent records from this genus.
- Roccus saxatilis*, striped bass. British Columbia to northwestern Baja California; several records, all from Newport Bay, California; tissue damage common. (= *Morone saxatilis*, by Moyle, 1976.)
- Mycteroperca xenarcha*, broomtail grouper. Northern California to Peru; several records.
- Mycteroperca rosacea*, leopard grouper. Throughout Gulf of California south at least to Jalisco, Mexico; one record (from mouth), southwest Baja California.
- Paralabrax clathratus*, kelp bass. Oregon/Washington border to Magdalena Bay, Baja California; two records from San Diego (Mission Bay), California.
- Family Carangidae (jacks)
- Oligoplites altus*, leatherjacket (= *O. mundus*). Southern California to Peru; several records; tissue damage consistently present.
- Caranx ignobilis* (?); "papio" Hawaii; tissue damage present; *aster* form.
- Family Sciaenidae (croakers)
- Cynoscion macdonaldi*, totuava. Endemic to the north-central Gulf of California; several records.
- Cynoscion orthonotus*, Gulf corvina. Endemic to upper Gulf of California; one record.
- Menticirrhus nasus*, highfin corbina. Southwest Baja California and throughout Gulf, south to Panama; one record, from Magdalena Bay, Baja California.
- Umbrina roncadorensis*, yellowfin croaker. Point Conception, California to the Gulf of California; one record, from San Diego (Mission Bay), California.
- Micropogon megalops*, Gulf croaker. A northern Gulf of California endemic; one record.
- Family Lutjanidae (snappers)
- "Pargo." One record, from Gulf of Nicoya, Costa Rica; *aster* form.
- Family Embiotocidae (surfperches)
- Embiotoca jacksoni*, black surfperch. Northern California to Point Abrejos, Baja California; several records from San Diego (Mission Bay), California.
- Amphistichus argenteus*, barred surfperch. Bodega Bay, California to southwest Baja California; numerous records; tissue damage common.
- Cymatogaster aggregata*, shiner surfperch. Alaska to San Quintin Bay, Baja California; one record, from Newport Bay, California.
- Micrometrus minimus*, dwarf surfperch. Bodega Bay, California to Cedros Island, Baja California; one record.
- Phanerodon furcatus*, white surfperch. Vancouver Island, Canada to Point Cabras, Baja California; several records; fairly common association in Newport Bay, California; tissue damage common.
- Family Mugilidae (mulletts)
- Mugil cephalus*, striped mullet. Cosmopolitan in warm seas; Monterey, California to Chile in eastern Pacific; numerous records from southern California to Peru; tissue damage common; Nierstrasz (1915) reports it as *M. mexicana*.
- Family Istiophoridae (billfishes)
- Istiophorus platypterus*, sailfish. Cosmopolitan; San Diego to Chile in east Pacific; several records from the Mazatlan area; early records cite host as *I. greyi*, a junior synonym; several records with epizoic barnacle *Conchoderma virgatum*.
- Tetrapturus audax*, striped marlin. Throughout warmer waters in Pacific; Point Conception to Chile in eastern Pacific; one record.
- Family Tetraodontidae (puffers)
- Sphoeroides annulatus*, bullseye puffer. San Diego, California to Peru; one record, from northern Gulf of California; no tissue damage evident.
-

Table 3 *continued*

Family Bothidae (lefteye flounders)
<i>Syacium ovale</i> , oval flounder. Gulf of California to Panama; several records; tissue damage common; both <i>acuminata</i> and <i>aster</i> forms.
Family Triglidae (searobins)
<i>Prionotus quiescens</i> , Gulf searobin. Southern California to Galapagos Islands. One record, from El Golfo de Santa Clara, Sonora; no tissue damage evident; isopod with thick growth of hydroid (<i>Clytia</i>) on dorsum.
Family Haemulidae (grunts)
<i>Orthopristis reddingi</i> , bronze striped grunt. Central west Baja California and throughout Gulf of California; one record, from northern Gulf.
Family Scombridae (mackerels and tunas)
<i>Euthynnus lineatus</i> , black skipjack. Southern California to Colombia; one record from mouth of fish, from El Salvador.
<i>Scomber japonicus</i> , Pacific mackerel. One record (reported as <i>S. sarda</i> , a junior synonym of <i>S. japonicus</i>), from Panama.

Nerocila excisa (Richardson, 1901)

(Fig. 14)

Aegathoa excisa Richardson, 1901a: 567. Nierstrasz, 1915: 103; 1931: 146; Monod, 1922: 409; Van Name, 1924: 184.

Nerocila excisa Richardson, 1914; 363. Nierstrasz, 1931: 126; Trilles, 1972c: 11; 1975: 324.

Diagnosis. Cephalon with frontal margin distinctly excavate or concave; (according to Trilles, 1972c, females occasionally lack this concavity). Posterolateral angles of pereonites I-VI rounded, never produced into acute angles (Fig. 14A,B). Coxal plates of pereonites reaching posterior margin of their respective segment, or nearly so; those of V-VII with posterior portions free from body margin; posterior angles of all coxae evenly rounded to subacute, never extended sharply beyond posterior borders of respective pereonites (Fig. 14A,B). Pereopods without carinae (Fig. 14G,H). Uropods extended beyond posterior margin of pleotelson (Fig. 14A).

Remarks. *Nerocila excisa* is principally an Indo-Pacific species, not known from the mainland coast of America. It has been reported from the Cocos Islands (off Costa Rica) and from several open ocean stations west of the Galapagos Islands (5°N 90°W, Richardson's original description; 9°57'N 137°47'W; 160°40'S 163°30'E) and for this reason is included here. Trilles (1972c) comments on Richardson's description and provides new figures.

Type deposition. *Aegathoa excisa*, USNM 25173. *Nerocila excisa*, USNM 46435,

Host data. *Nerocila excisa* has been reported from the fin of a dolphinfish (*Coryphaena hippurus*), from the stomach of the same species, and from *Grammistes* sp. (a member of the soapfish family, Grammistidae).

Genus *Lironeca* Leach, 1818

Diagnosis. Body often twisted to one side; color generally diffuse. Cephalon weakly to deeply immersed in pereonite I; posterior border not trisinate, or very weakly so. Anterior border of pereonite I broadly excavated to receive cephalon. Antennae 1 widely separated at base, basal articles not expanded. Pereopods subequal or increasing slightly in length posteriorly. Males usually with carinae or bases of posterior pereopods; females with or without carinae. Coxal plates usually clearly visible in dorsal aspect. Pleon not much narrower

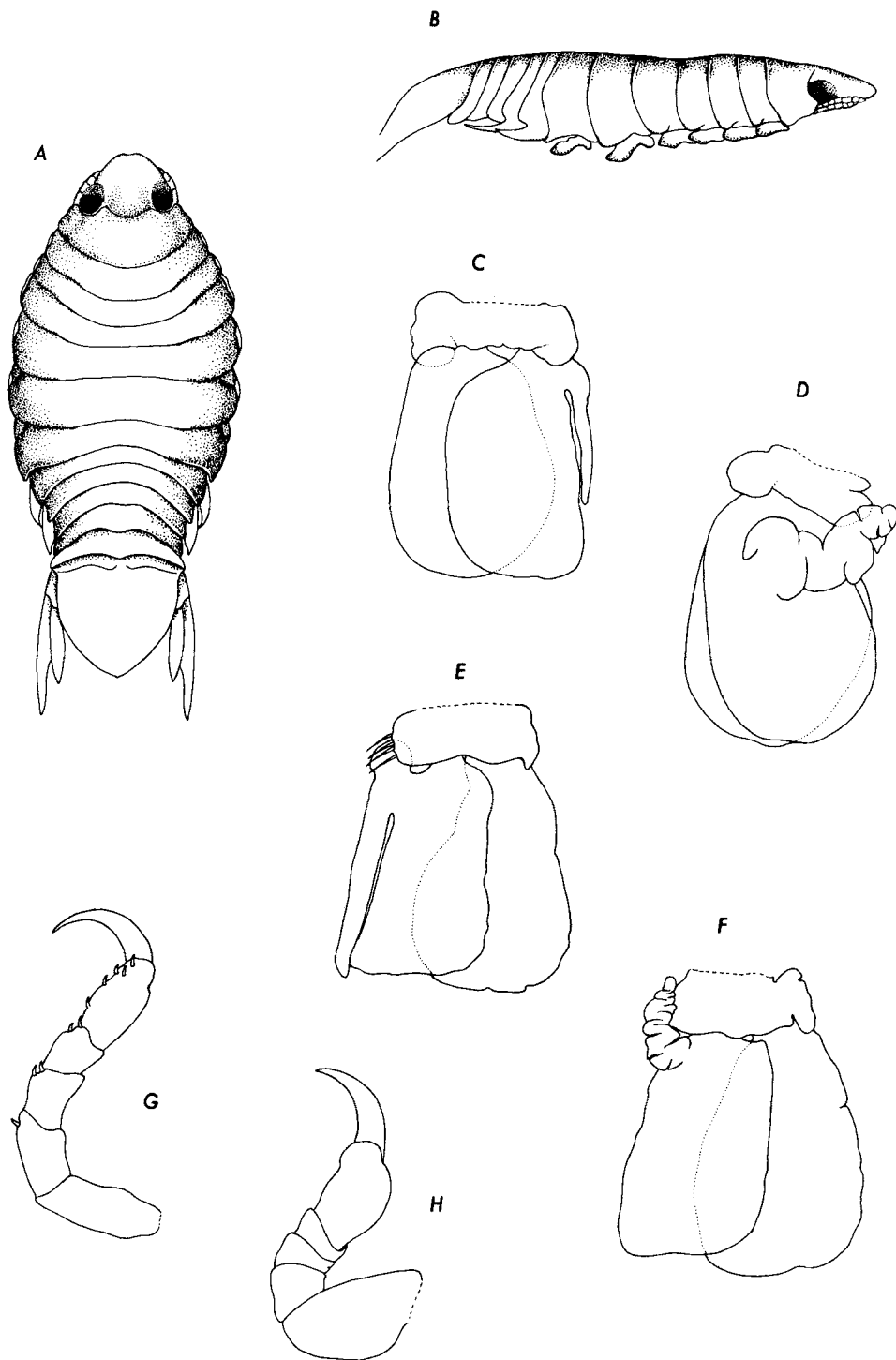


Figure 14. *Nerocila excisa* (Richardson). A, dorsal view; B, lateral view; C, pleopod 2 (female); D, pleopod 3 (female); E, pleopod 2 (male); F, pleopod 3 (male); G, pereopod VII (Male); H, pereopod I (male). All figures after Trilles, 1972c.

than pereon. Pleonites subequal in width; 1-2 only rarely narrow or weakly immersed into pereonite VII. Pleopods often highly folded and/or with lamellar or digitiform accessory gills. Appendix masculinum of male generally persists, reduced in size, into female stage. Uropods occasionally reach beyond posterior border of pleotelson, but in most species fall short of it.

Remarks. Relative to other eastern Pacific genera, *Lironeca* has enjoyed a considerable amount of recent study. An excellent paper by Menzies *et al.* (1955) on *L. convexa* represents the first modern (re)description of a New World cymothoid. Their efforts were clearly aimed towards the discovery of new taxonomic characters for the species of this genus. In addition, their paper represents the first attempt to describe the life history of a New World cymothoid. The general life history of *L. vulgaris* has been described by Brusca (1978b). Species of *Lironeca* are all buccal and/or gill chamber parasites. In some species both male and female inhabit the gill chamber, feeding either on the gills or upon the epithelium of the inner surface of the operculum (*e.g. L. puhi* Bowman and *L. bowmani* sp. nov.). In other species the male infests the gill chamber whereas the female inhabits the buccal region, generally attaching near the base of the host's tongue. In some species females live in either the mouth or the gill chamber (*e.g. L. vulgaris, L. ovalis*).

At present there are 12 described marine species of *Lironeca* in the New World, five of which are herein reported from the eastern Pacific. Menzies (1962) reported specimens of an unidentified species from San Quintin Bay, Baja California. These specimens, and additional material, have been examined and found to represent a new species, herein named in his honour, *Lironeca menziesi* sp. nov. The Indo-West Pacific species *L. raynaudii* Edwards, 1840 occasionally has been reported from southern Chile and the Straits of Magellan. Curiously, it does not occur in the tropical east Pacific.

Brusca (1978b) discussed the morphological features useful in distinguishing species of *Lironeca*. Reliable taxonomic characters include: width vs. length ratios of cephalon and pleotelson; shape and size of coxal plates; morphology of pereopodal articles; and pleopod morphology. As in most other flabelliferan genera, the pleopods provide one of the most stable and easily recognized character sets for reliably distinguishing species of east Pacific *Lironeca*. Unfortunately, these appendages have not been figured or described for most Atlantic American forms. Species-specific pleopodal attributes include pleating, especially on the posterior pleopods, and the presence of accessory gills. The latter may be simple lamellar plates, or complex digitiform processes. Generally only a small percentage of a *Lironeca* population parasitizing a single host species are laterally twisted. Twisting can be either to the right or the left but may eventually be shown to be correlated to place or position of attachment on the fish. Twisting produces minor degrees of asymmetry, particularly in regard to lengths of the uropods and pleonites relative to the pleotelson and adjacent body somites.

Juvenile and male stages of most *Lironeca* species bear pereopodal spines. In some species these are restricted to the posterior pereopods. The spines are progressively lost with succeeding instars and older males and females possess few or no spines, or have the spines restricted to pereopod VII. Alterations in morphology due to predation, as seen in *Nerocila*, are apparently rare in *Lironeca* and other buccal-gill inhabiting cymothoid genera. The stout setae on the medial

margin of the pleopodal bases are often partially or entirely eroded away. Older females tend to have more opaque exoskeletal coverings over the compound eyes, partly obscuring the ommatidia. Morphologically, the genus *Lironeca* appears closely related to *Irona* (= *Mothocya*).

Key to the species of Lironeca known from the east Pacific

- 1 Body strongly convex dorsally; cephalon subquadrate (Fig. 15A,B); pleotelson narrowing abruptly posteriorly (Fig. 15A); pereonites II-VI of female with anterolateral bosses (Fig. 15A); maxilla 2 with 7-11 terminal spines (Fig. 18D) . . . *Lironeca convexa*
- Body not strongly convex dorsally; cephalon not subquadrate (Fig. 15C-G); pleotelson not narrowing abruptly posteriorly (Fig. 15C-G); pereonites II-IV of female without anterolateral bosses (Fig. 15C-G); maxilla 2 with 1-4 terminal spines 2
- 2 Uropods reaching considerably beyond posterior margin of pleotelson (Fig. 15F); pleopods 1-5 with dendritic accessory gills (Figs. 16J-N); endopods of pleopod 5 pleated (Fig. 16N); females without carinae on bases of posterior pereopods (Fig. 16H,I) *Lironeca boumani* sp. nov.
- Uropods falling short, or reaching barely beyond posterior margin of pleotelson (Fig. 15C-E); pleopods 2-5 without dendritic accessory gills; endopod of pleopods not pleated; females with or without carinae on bases of posterior pereopods 3
- 3 Cephalon with frontal margin not produced (Fig. 15E); bases of posterior pereopods with distinct carinae (Fig. 20F,G); maxilliped with 2-4 terminal spines (Fig. 20J); coxae VI-VII extended to, and usually beyond posterior margins of respective pereonites (Fig. 15E) *Lironeca vulgaris*
- Cephalon with frontal margin produced (Fig. 15C,D); bases of posterior pereopods of females without distinct carinae; maxilliped with 1-5 terminal spines; coxae VI-VII not reaching posterior margins of respective pereonites 4
- 4 Merus and carpus of pereopod IV expanded (Fig. 19H); accessory lamellae of pleopodal bases well developed (Fig. 19J-N); maxilla 1 with one large and three small terminal spines (Fig. 19C); males with coxal carinae on pereopods IV-VII; maxilliped with 1-5 terminal spines (Fig. 19F); anterior margin of pereonite I weakly trilobate or sinuate (Fig. 15C); free margin of labrum with deep medial incision *Lironeca menziesi* sp. nov.
- Merus and carpus of pereopod IV not expanded (Fig. 17H); accessory lamellae of pleopodal bases not well developed (Fig. 17J-N); maxilla 1 with two large and two small terminal spines (Fig. 17C); males without coxal carinae; maxilliped with three terminal spines (Fig. 17F); anterior margin of pereonite 1 not trilobate or sinuate (Fig. 15D); free margin of labrum without deep medial incision *Lironeca californica*

Lironeca bowmani sp. nov.

(Figs 15, 16)

Description (female). Body: Width 5.5–10.0 mm, length 11.2–17.0 mm; body index 2.03 for non-ovigerous females, 1.63–1.86 (mean 1.72) for ovigerous females. General color (in alcohol) tan; dorsal surface with randomly scattered chromatophores (Fig. 15F).

Cephalon: Width 1.3–1.5 times length; posterior border moderately to strongly trisinate, weakly to moderately inserted into pereonite I (Fig. 15F). Eyes distinct. Antennae 1 of eight articles, reaching anterior third of pereonite I (Fig. 16A). Antennae 2 of 7–10 articles, extended to, or barely beyond anterior third of pereonite I (Fig. 16B). Maxilliped with two terminal and one subterminal spines (Fig. 16F). Maxilla 1 with four terminal spines (Fig. 16C). Maxilla 2 with semilunar, pectinate scales; one spine on inner lobe, two spines on outer lobe (Fig. 16D). Mandible as figured (Fig. 16E). Free margin of labrum strongly crenulate.

Pereon: Pereonite I longest; pereonites VI–VII shortest in smaller individuals, VI subequal to II–V in larger specimens. Pereonites V–VI widest in smaller individuals, IV–V widest in larger specimens. Coxae II–III with posterior angles rounded or acute; IV–VII acute; II–III or II–IV extended barely past posterior margin of respective pereonites; V–VIII extended well beyond posterior border of respective pereonites (in dorsal aspect). Pereopods increase gradually in length posteriorly; pereopods without spines on inside border of propus and carpus, with or without spines on outside of merus (Fig. 16G–I). Pereopodal bases lack carinae.

Pleon: Pleonites subequal in width and length (Fig. 15F). Pleopods 1–5 with or without stout setae on medial border of basis. Pleopod 1 with lamellar accessory gill on lateral margin of basis and dendritic accessory gill on medial proximal region of endopod (Fig. 16J). Pleopod 2 with dendritic accessory gills on lateral margin of basis and on medioproximal region of endopod; appendix masculinum of variable size. Pleopods 3–5 with dendritic accessory gills on lateral part of basis and lamellar accessory gill on medioproximal region of endopod (Fig. 16L–N); pleopods 3–4 with single medioproximal fold on endopod; 5 with 3–5 proximal folds on endopod. Pleotelson shieldshaped, posterior margin subacuminate, width slightly greater than length (Fig. 15F). Uropodal endopod and exopod tapering distally, extended beyond posterior border of pleotelson; exopod shorter and broader than endopod (Fig. 16O).

Male (not available).

Remarks. *Lironeca bowmani* is strikingly different from all eastern Pacific congeners in its possession of complex digitate accessory gills on the pleopods. In addition, the uropods are manifestly longer than any other eastern Pacific *Lironeca*, extending well beyond the posterior margin of the pleotelson. *Lironeca bowmani* is named for Dr Thomas E. Bowman (USNM) in recognition of his important contribution to cymothoid taxonomy and biology.

Type deposition. Holotype (female), AHF 791. Mexico, Sinaloa, Mazatlan Bay, 22 August 1979. Paratypes, USNM, SIO, Estación Mazatlan, Univ. Nacional Autónoma México (Sinaloa, México).

Distribution. Records are from throughout the Gulf of California, near the Tres Marias Islands (20°40'N 105°20'W), and near Malpelo Island (3°24'N 80°45'W). The absence of records between central west Mexico and Panama is most likely due to inadequate sampling. Existing collections are from "shallow water" to 80 m.

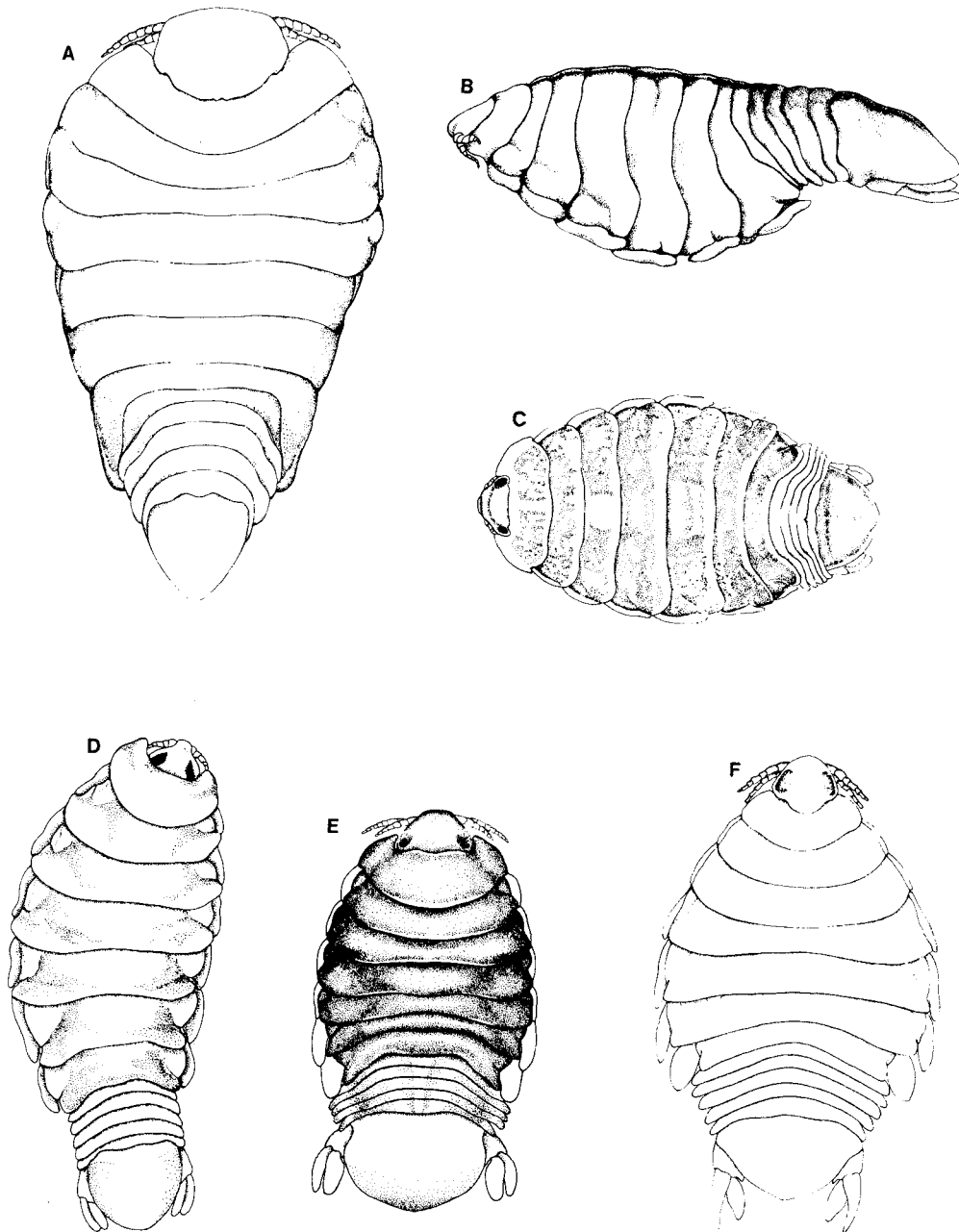


Figure 15. *Lironeca* species of the eastern Pacific (females). A, *L. convexa*; B, *L. convexa* (lateral view); C, *L. menziesi* sp. nov.; D, *L. californica*; E, *L. vulgaris*; F, *L. bowmani* sp. nov.

Host data. *Lironeca bowmani* has been recovered from three species of fishes: the Gulf croaker, *Micropogon megalops*; the Gulf grunion *Leuresthes sardina*; and a herring, *Clupea* sp. The two former fishes (both northern Gulf of California endemics) had clearly sustained damage to the gills. Data on the latter species are insufficient to indicate if gill damage had occurred. In all cases females have been found only within the gill chamber.

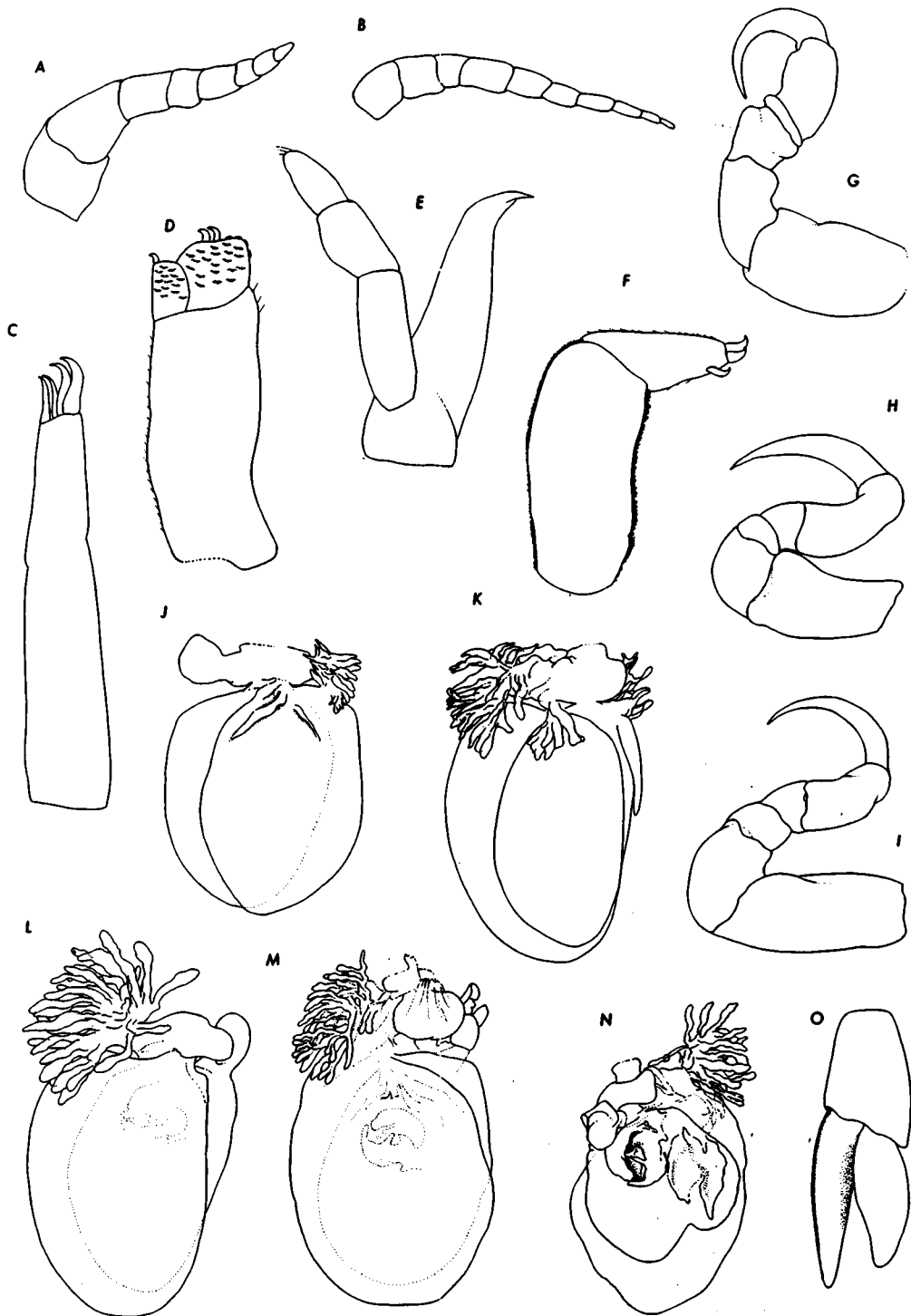


Figure 16. *Lironeca boumani* sp. nov. A, antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (R); F, maxilliped; G, pereopod 1; H, pereopod 4; I, pereopod VII; J, pleopod 1 (R); K, pleopod 2 (L); L, pleopod 3 (L); M, pleopod 4 (L); N, pleopod 5 (R); O, uropod.

Lironeca californica Schioedte & Meinert, 1883
(Figs 15, 17)

Lironeca californica Schioedte & Meinert, 1883: 372. Richardson, 1899a: 172; 1899b: 829; 1900: 221; 1905: 260; Fee, 1926: 26; Keys, 1928: 279; Nierstrasz, 1931: 144; Gurjanova, 1936: 92; Hatch, 1947: 211; Menzies, 1962: 345; Arai, 1967: 2166; Schultz, 1969: 166; Olson, 1972: 1204; Iverson, 1974: 166; Kussakin, 1979: 298.

Description (female). Body: Width 4.5–7.0 mm, length 9.0–15.0 mm; body index 2–2.4 (mean 2.2) for ovigerous females. General color (in alcohol) tan, dorsal surface with or without distinct chromatophores.

Cephalon: Width 1.2–1.6 times length; deeply immersed in pereonite I; frontal margin extended, narrow, bluntly round or truncate. Eyes well developed (Fig. 15D). Antennae 1 separated by approximately 0.5 mm; of eight articles; reaching anterior 1/3 of pereonite I (Fig. 17A). Antennae 2 of 9–10 articles; subequal to antenna 1 in length (Fig. 17B). Maxilliped with three terminal spines (Fig. 17F). Maxilla 1 with two large, and two manifestly smaller terminal spines (Fig. 17C). Maxilla 2 with two terminal spines and semilunar pectinate setae on each lobe (Fig. 17D). Mandible as figured (Fig. 17E). Free margin of labrum smooth or slightly concave medially; not crenulate or incised.

Pereon: Moderately convex dorsally. Pereonite I longest, anterolateral angles produced forward to border posterior 1/3 to 1/2 of cephalon; anterior margin not trilobate. Pereonite VII shortest. Pereonites III–VI (or III–V) widest; V–VII narrowing posteriorly (Fig. 15D). All coxae with subacute posterior angles. In dorsal aspect, coxae II–III extended 1/2 – 2/3 distance to posterior margins of their respective pereonites; coxa IV extended 2/3 to just short of posterior margin of its pereonite; coxae V–VII not quite reaching posterior margins of their respective pereonites (Fig. 15D). Pereopods similar, increasing gradually in length posteriorly, due almost entirely to increase in length of ischium; inside borders without spines; bases without well developed carinae (Fig. 17G–I).

Pleon: Pleonites subequal in width and length. Lateral margins of pleonite I occasionally covered by pereonite VII. Posterior margin of pleotelson rounded, maximum width 1–1.2 times length (Fig. 15D). Pleopods 1–5 with small accessory lamella on medioproximal margin of endopod, often increasing in size posteriorly, and occasionally absent on pleopods 1–3 (Fig. 17J–N). Pleopodal bases with or without medial setae, basis of 5 with weakly developed lateral accessory lamella. Pleopod 2 with or without remnant of appendix masculinum. Uropods large; endopod and exopod ovate, extended just beyond or falling barely short of terminal margin of pleotelson; exopod slightly larger than endopod.

Male. Width 2.5–5.0 mm; length 9.0–12.0 mm; body index 2.65–3.60 (mean 3.0). Similar to female except for the following: cephalon not immersed in pereonite I in smaller instars, weakly immersed in larger instars. Pereonites II–IV widest. All coxae extending approximately 3/4 length of their respective pereonites. Pereopods I–VII with or without spines on propus and carpus. Lateral margins of pleonite I rarely covered by pereonite VII; all pleopods with stout setae on inner margins of bases.

Remarks. *Lironeca californica* is the only North American cymothoid whose principal range is within temperate waters, and the only New World cymothoid that is strictly temperate in distribution. It is easily distinguished from *L. vulgaris*,

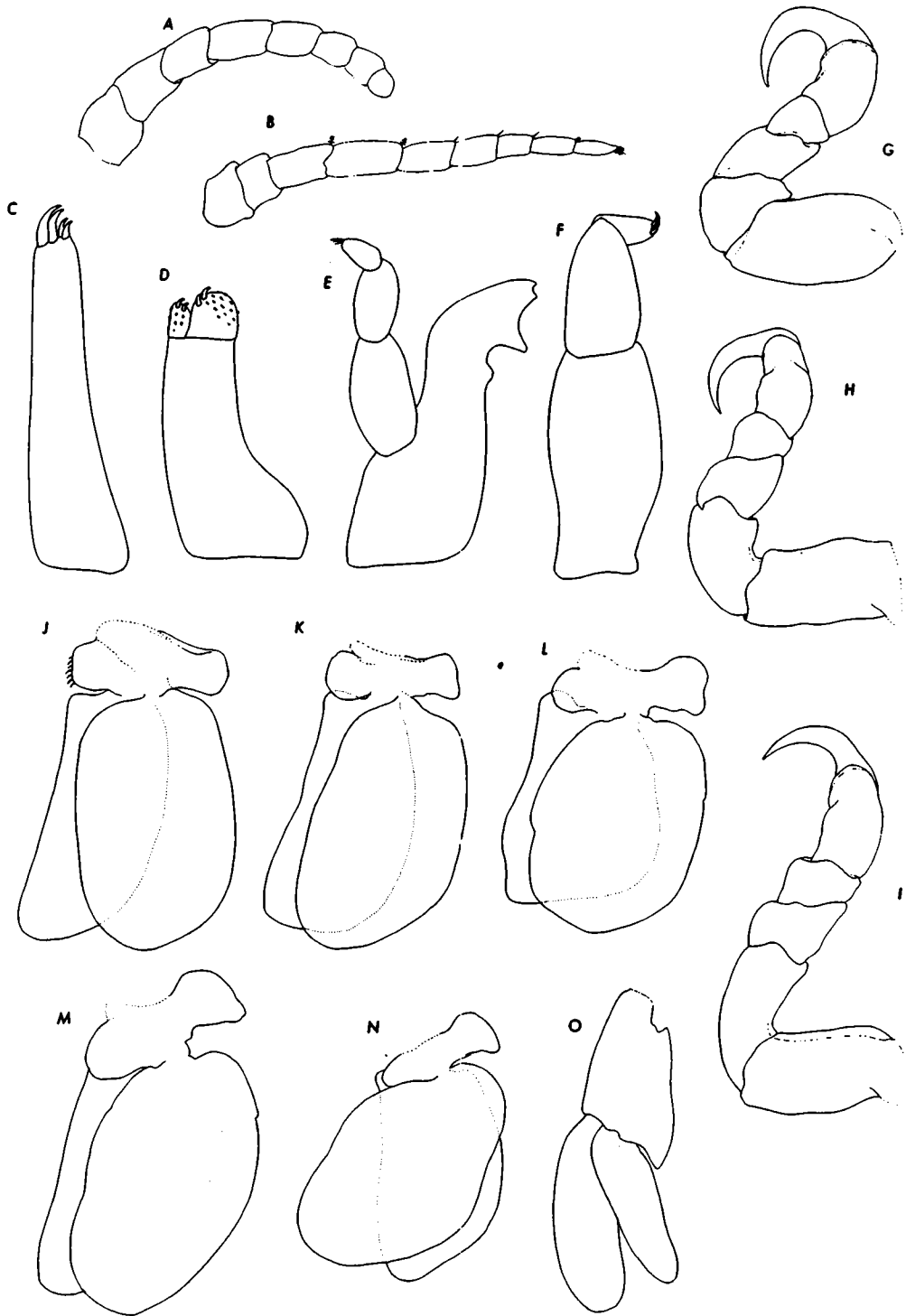


Figure 17. *Lironeca californica* Schioedte & Meinert. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (L); F, maxilliped; G, pereopod 1; H, pereopod IV; I, pereopod VII; J, pleopod 1; K, pleopod 2; L, pleopod 3; M, pleopod 4; N, pleopod 5; O, uropod.

with which it is partially sympatric, by the lack of pereopodal carinae in females.

Type deposition. Unknown.

Distribution. Alaska to Punta Eugenio, west coast of Baja California; uncommon south of San Diego, California and north of Washington State. *Lironeca californica* is particularly common in bays and lagoons. Its depth range is shore to 90 m.

Host data. *Lironeca californica* is collected regularly in California from dwarf surfperch (*Micrometrus minimus*) and shiner surfperch (*Cymatogaster aggregata*). There are also records from surf smelt, *Hypomesus pretiosus* (see Hatch, 1947), topsmelt (*Atherinops affinis*), arrow goby (*Clevelandia ios*), and California killifish, *Fundulus parvipinnis*. Keys (1928) reported that samples of *F. parvipinnis* taken in southern California were regularly infested with small numbers of *L. californica*. I have collected this fish from the marine canals of Venice, Los Angeles, and have not found it associated with this isopod. Olson (1972) reported specimens from gill chambers of the California grunion, *Leuresthes tenuis*, from Coronado Strand and San Diego Bay.

Dr J. Carlton has deposited (USNM) numerous specimens of *L. californica* collected from Lake Merritt. This is a brackish-water lake connected by a channel to the Oakland Estuary, and thence to San Francisco Bay. Its salinity varies greatly through the year. Carlton reports (pers. commn) numerous records (from Lake Merritt) of this isopod on the threespine stickleback *Gasterosteus aculeatus microcephalus*, with infestations ranging from common to abundant. He has recorded it with less frequency from the introduced rainwater fish *Lucania parva*, and has recorded single males, once each from northern anchovy (*Engraulis mordax*) and Pacific herring (*Clupea harengus*) that had been stranded on a beach after a large fish kill. Carlton reports infested sticklebacks behaving in a sluggish manner, tending to swim erratically, and occurring (at times) nearer to the surface, in contrast to noninfested fish.

Lironeca convexa Richardson, 1905

(Figs 15, 18)

Lironeca convexa Richardson, 1905: 445. Nierstrasz, 1931: 144; Menzies, Bowman & Alverson, 1955: 277; Schultz, 1969: 167; Lincoln, 1971: 185; Brusca, 1973: 205; 1977: 129; 1980: 231.

Description (female). Body: Width 5.0–13.0 mm, length 13.0–26.0 mm; body index 2.6–3.0 (mean 2.7) for non-ovigerous females, 1.83–2.7 (mean 2.2) for ovigerous females. General color (in alcohol) tan, dorsal surface with or without obvious chromatophores (Fig. 15A, B).

Cephalon: Subquadrate, width 1.3–1.6 times length; posterior border weakly trisinate and deeply immersed into pereonite I; frontal margin broad, weakly convex. Eyes distinct (Fig. 15A). Antennae 1 separated by approximately 1.5 mm; of eight articles (Fig. 18A); nearly reaching midline of pereonite I. Antennae 2 of 8–11 articles (Fig. 18B); extended nearly to, or barely past, midline of pereonite I. Maxilliped with 2–3 terminal spines (Fig. 18F). Maxilla 1 with one large, and three manifestly smaller terminal spines (Fig. 18C). Lobes of maxilla 2 with semilunar pectinate scales; outer lobe with 3–6 terminal spines; inner lobe with 4–5 terminal spines (Fig. 18D). Mandible as figured (Fig. 18E). Free margin of labrum strongly crenulate, with deep medial incision.

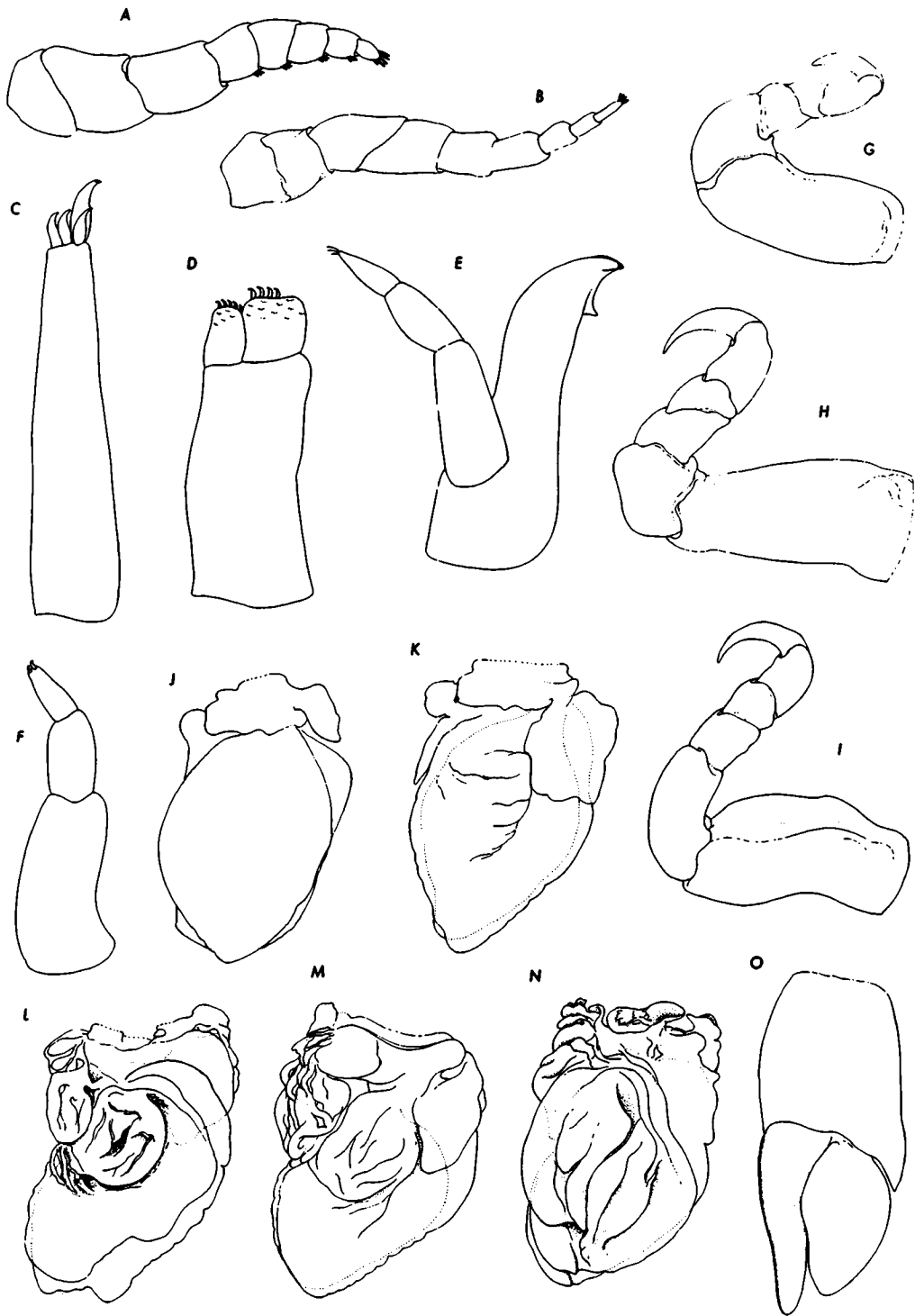


Figure 18. *Lironeca convexa* Richardson. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (R); F, maxilliped; G, pereopod 1; H, pereopod IV; I, pereopod VII; J, pleopod 1; K, pleopod 2; L, pleopod 3; M, pleopod 4; N, pleopod 5, O, Uropod.

Pereon: Strongly convex dorsally, degree of convexity increasing with size. Pereonite I longest, anterior margin weakly crenulate; anterolateral angles broadly rounded, produced forward to border posterior 2/3 of cephalon. Pereonite VII usually shortest (occasionally II and VII); pereonites III, IV and V widest. Pereonites II–IV with anterolateral bosses (Fig. 15A, B). Coxae of pereonites II–VII occupy entire lateral margins of respective pereonites, VII often extended barely beyond posterior border of its somite in lateral view; posterior angles of coxae II–IV abruptly rounded, those of V–VI broadly rounded, VII rounded or subacute. Pereopods similar, increasing gradually in length posteriorly; inside borders without spines (Fig. 18G–I). Pereopods I–VI without carinae; VII with weakly developed carina on basis (Fig. 18I).

Pleon: Pleonites subequal in length; decreasing gradually in width posteriorly. Lateral margins of pleonite I usually obscured by pereonite VI. Pleotelson tapers strongly posteriorly, apex acutely rounded; maximum width subequal to length. Pleopods 1–5 with lateral margin of basis bearing accessory lamella; endopod with medioproximal accessory lamella, large and folded on 3–5; exopod with lateral accessory lamella (Fig. 18J–N). Pleopod 2 with appendix masculinum (often reduced). Pleopods 3–5 with endopod produced into large medial folds, these folds occasionally pushing against exopod to produce distinct bulge in latter. Uropods large, extended to or past posterior margin of pleotelson; endopod wider, but shorter than exopod (Fig. 18O).

Description (male). Body width 5.0–6.0 mm, length 12.5–15.0 mm; body index 2.5–3.0 (mean 2.7). Similar to female except for the following: body not so convex; cephalon not immersed, or only slightly immersed in pereonite I, posterior border strongly trisinate; antennae 1 of 7–8 articles, separated by 1 mm or less, reaching anterior third of pereonite I; pereonites II–IV without anterolateral bosses; pereopods IV–VII with distinct carinae.

Remarks. The original description of this distinctive cymothoid was based upon a single specimen collected in 1885 by Dr W. L. Jones. The host was not recorded. Richardson deposited the holotype in the collection of the University of Pennsylvania; it has subsequently been lost. Despite the fact that no records of this species were published between the time of its original description and 1955, *L. convexa* is a common isopod in the tropical eastern Pacific. Menzies *et al.* (1955) reviewed the life history and host-parasite relationship of this species in some detail.

Type deposition. Neotypes herein designated. Female (neotype), AHF 734; neotype (male), AHF 734a. Both from Mexico, Nayarit, Playa Novilla, west of Tecuala; 26 April 1973; in gills (male) and mouth (female) of *Serranus* sp.; from a beach seine.

Distribution. Southern California to the Gulf of Guayaquil, Ecuador; uncommon north of Nayarit, Mexico. No records of this species exist from the Gulf of California.

Host data. Nearly all records for *L. convexa* have been from Pacific bumper, *Chloroscombrus orqueta*, a common carangid in the eastern Pacific, ranging from San Diego to Peru, including the Gulf of California. *Chloroscombrus orqueta* is a bait species of minor importance to the California-based tuna fleet. In addition, I have examined one collection of six specimens taken from the gills of pompanos (either *Trachinotus rhodopus* or *T. paitensis*); one collection from unidentified carangids, collected by night light in Juanico Bay, Baja California;

and a male and female from an unidentified species of *Serranus* (probably *S. fasciatus*, the barred serrano) from the state of Nayarit, Mexico. The latter two appear to be valid host records. Both species of pompano occur in the Gulf of California. Female specimens are invariably found in the host's mouth; males in the gill chamber.

***Lironeca menziesi* sp. nov.**

(Figs 15, 19)

Lironeca n. sp. Menzies, 1962: 345.

Description (female). Body: Width 5.0–12.0 mm, length 7.5–21.0 mm; body index 1.67–2.2 (mean 1.9) for non-ovigerous females, 1.5–1.8 (mean 1.6) for ovigerous females. Chromatophores diffuse (Fig. 15C).

Cephalon: Width 1.4–2.0 times length; deeply immersed in pereonite I. Frontal margin produced, dorsally depressed, broadly truncate (Fig. 15C). Eyes distinct. Antennae 1 of 6–8 articles; separated by 1 mm or less; reaching anterior third of pereonite I (Fig. 19A). Antennae 2 of 9–11 articles; reaching to or beyond midline of pereonite I (Fig. 19B). Maxilliped with 1–5 terminal spines (Fig. 19F). Maxilla 1 with one large and 2–3 smaller terminal spines (Fig. 19C). Maxilla 2 with semilunar, pectinate scales; outer lobe with 1–2 spines; inner lobe with 0–2 spines (Fig. 19D). Mandible as figured (Fig. 19E). Free margin of labrum bilobed, with deep medial incision.

Pereon: Pereonites I and V longest; anterolateral angles produced forward to border posterior third of cephalon. Pereonite VII shortest; IV–V widest. In the dorsal aspect, coxae II–VII with subacute posterior angles, II–III not quite reaching posterior margins of respective pereonites; IV–VII extended about 2/3 length of respective pereonite (Fig. 15C). Pereopods similar, increasing gradually in length posteriorly; inside margins without spines; merus and carpus of IV expanded; carinae wanting (Fig. 19G–I).

Pleon: Pleonites subequal in length, but decreasing slightly in width posteriorly. Pleonite 1, and sometimes 2, obscured in dorsolateral aspect by pereonite VII. Pleopods 1–5 with stout setae on medial margin of basis, and lamellar accessory gill on lateral margin of basis; endopods with small medioproximal accessory lamella, increasing in size posteriorly (Fig. 19J–N). Pleopod 2 with at least a remnant of appendix masculinum. Pleotelson broadly rounded, width approximately 1.5–2.0 times length (Fig. 15C). Uropods small, not quite reaching posterior margin of pleotelson; endopod and exopod ovate; exopod slightly larger than endopod (Fig. 19O).

Male. Body width 3.0–5.0 mm, length 7.0–12.0 mm; body index 1.8–2.40 (mean 2.17). Similar to female except for the following: posterior angles of coxae generally less acute; pereopods with spines on propus, carpus and merus; posterior pereopods with distinct carinae on bases.

Remarks. *Lironeca menziesi* is similar to *L. californica*, but can be distinguished by the expanded merus and carpus of pereopod IV, the well-developed accessory lamellae on the pleopodal bases, the spination of the maxilliped and second maxilla, the trisinate cephalon-pereonite I margin and the lack of a deep medial incision on the labrum. Menzies (1962) recognized the similarity when he stated that, "This probable new species is somewhat intermediate between *Lironeca californica* and *Lironeca panamensis* [= *Lironeca vulgaris*] ..." *Lironeca*



Figure 19. *Lironeca menziesi* sp. nov. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (R); F, maxilliped; G, pereopod I; H, pereopod IV; I, pereopod VII; J, pleopod 1; K, pleopod 2; L, pleopod 3; M, pleopod 4; N, pleopod 5; O, uropod.

menziesi can be distinguished from *L. vulgaris* by its lack of pereopodal carinae in females, and produced frontal margin of the cephalon. This species is named in honor of Robert J. Menzies, for his extensive contributions to isopod systematics and his initial recognition of this particular species.

Type deposition. Holotype (female) AHF 4924; Allotype (male) AHF 4924a. Mexico, off Baja California Norte, Guadalupe Island, Melpomene Cove; shore collection; 17 December 1949. Paratypes, USNM, SIO, CAS.

Distribution. Western Baja California and the Gulf of California, including the offshore Pacific Baja islands of Coronados, Guadalupe and Alijos; to a depth of 30 m. Collections have been made from sand and mud bottoms, rocky subtidal habitats and tidepools.

Host data. The only host record for *L. menziesi* is from the gill cavity of the woolly sculpin, *Clinocottus analis*. The fish was taken from a tidepool on Guadalupe Island by Carl Hubbs (Zaca Expedition, 1946).

Lironeca vulgaris Stimpson, 1857

(Figs 15, 20)

Lironeca panamensis Schioedte & Meinert, 1884:349. Richardson, 1899a:172; 1899b: 830; 1905:257; Nierstrasz, 1915:85; 1931: 144; Shen, 1936-38: 5; Menzies, 1962: 345; Schultz, 1969: 167; Brusca, 1973: 205; 1977: 128; 1978b: 3; 1980: 231; Trilles, 1976: 783.

Anilocra occidentalis Richardson, 1899a: 172. Richardson, 1899b: 830; 1900: 220.

Lironeca vulgaris Stimpson, 1857: 508. Stimpson, 1859: 88; Schioedte & Meinert, 1884: 344; Calman, 1898: 261; Richardson, 1899a: 172; 1899b: 830; 1900: 221; 1904a: 214; 1904c: 659; 1905: 285; Nierstrasz, 1915: 99; 1917: 90; 1931: 144; Gerstaecker, 1901: 86; Gurjanova, 1936: 92; Hatch, 1947: 211; Menzies *et al.*, 1955: 288; Schultz, 1969: 165; Turner *et al.*, 1969: 89; Hobson, 1971: 504; Crane, 1972: 152; Brusca, 1973: 205; 1978b: 3; 1980: 231; Ho, 1975: 71; Miller, 1975: 297; Trilles, 1976: 780; Kussakin, 1979: 298.

Description (female). Body: Width 6.3-19.1 mm (mean=9.0); length 11.4-43.0 mm (mean=18.5); body index 1.6-2.18 (mean, non-ovigerous females 1.91; standard deviation 0.13; mean, ovigerous females 1.84; standard deviation 0.12); body occasionally twisted to right or left. Chromatophores diffuse (Fig. 15E).

Cephalon: About two-thirds as wide as long (length to width ratio 0.41-0.73; mean 0.66); frontal margin weakly truncate. Eyes well developed. Antennae 1 separated by approximately 1 mm; of eight articles; reaching posterior border of cephalon (Fig. 20A). Antennae 2 of 10-11 articles; reaching 1/3 to 1/2 distance into first pereonite (Fig. 20B). Maxilliped with 2-4 terminal spines (Fig. 20J). Maxilla 1 with one large and three smaller terminal spines (Fig. 20C). Exopod of maxilla 2 with 2-4 terminal spines; endopod with 2-4 terminal spines (Fig. 20D). Mandible as figured (Fig. 20I). Free margin of labrum bilobed, with deep medial incision.

Pereon: Pereonite I longest; anterolateral angles produced forward to border posterior quarter of cephalon (Fig. 15E). Pereonites IV-V widest. Coxal plates II-VII visible in dorsal aspect; IV-VII or V-VII free distally, with posteriorly directed subacute angles; all reaching at least posterior margins of respective pereonites, and occasionally beyond (Fig. 15E). Pereopods similar, increasing

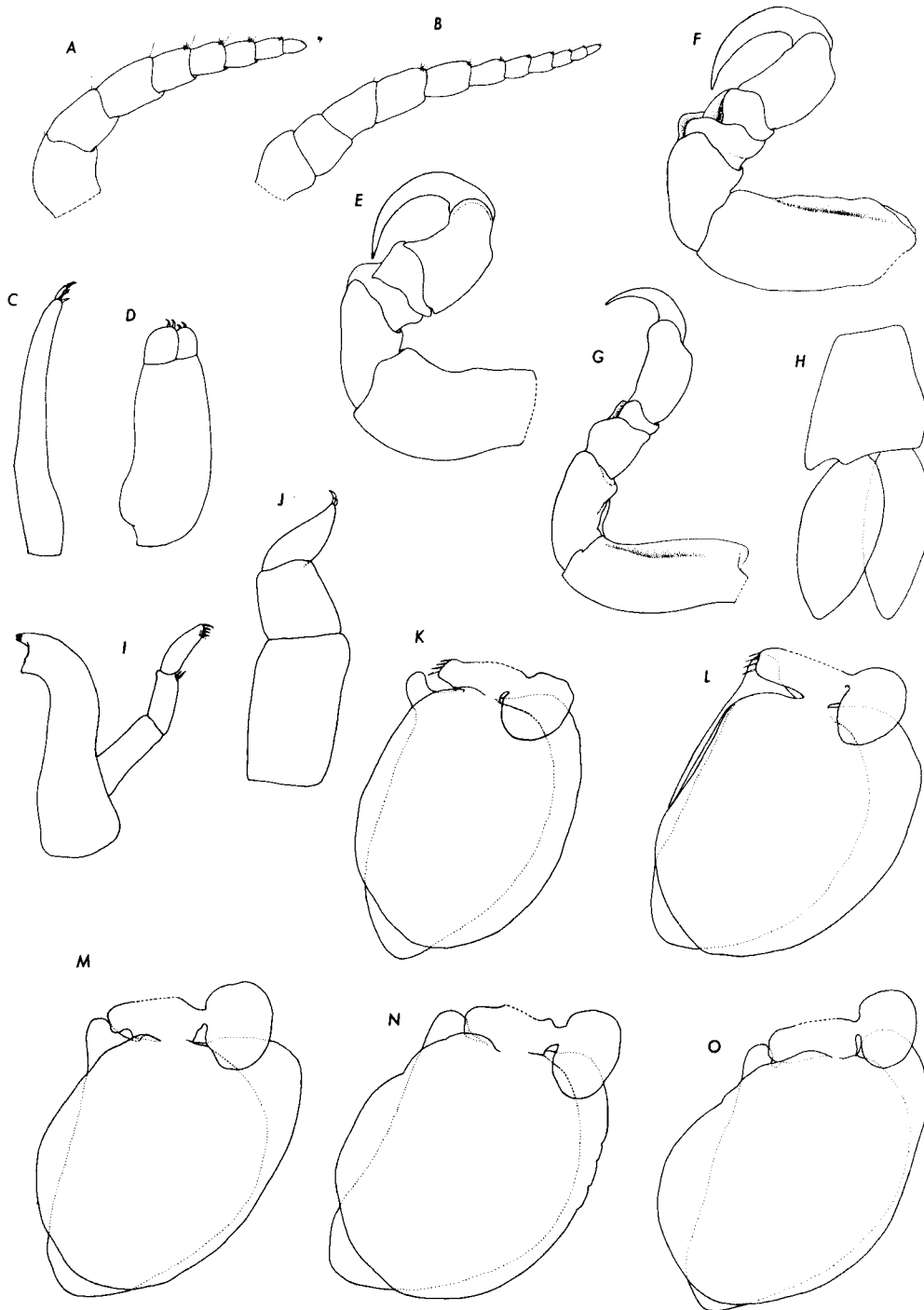


Figure 20. *Lironeca vulgaris* Stimpson. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, pereopod 1; F, pereopod IV; G, pereopod VII; H, uropod; I, mandible (R); J, maxilliped; K, pleopod 1; L, pleopod 2; M, pleopod 3; N, pleopod 4; O, pleopod 5.

gradually in length posteriorly; inside borders without spines (Fig. 20E–G); IV–VII with carina on basis, increasing in size posteriorly (Fig. 20F–G).

Pleon: Pleonites subequal in length; all more-or-less visible in dorsal aspect; strongly twisted individuals may have parts of one or more pleonites hidden under pereon. Midline of pleon more-or-less elevated, forming a slight median rise (Fig. 15E). Pleotelson evenly rounded; width approximately twice length (length to width ratio 0.47–0.78; mean 0.52). Bases of pleopods 1–5 with or without stout medial setae, with lateral accessory lamella of variable size. Pleopods 1–5 with medioproximal accessory lamellae on endopod (Fig. 20K–N); pleopod 2 with at least a remnant of male appendix masculinum (Fig. 20L). Exopod and endopod of uropod subequal (Fig. 20O).

Description (male). Width 3.2–16.2 (mean 6.5; standard deviation 2.5); length 6.9–31.0 (mean 11.9; standard deviation 4.2); body index 1.7–2.2 (mean 1.97; standard deviation 0.14). Similar to female except for the following: body smaller and narrower; cephalon more distinctly truncate; coxal plates less acute; young males with spines on propus and carpus of pereopods; posterior pereopods with somewhat more distinct carinae on bases.

Remarks. Brusca (1978b) discussed this species at some length, including its synonymy with *L. panamensis*, descriptions and figures of brood and juvenile stages, fecundity, and host-parasite relationships. Keusink (1979) has compiled considerable data on the ecology of this species.

Type deposition. *Anilocra occidentalis*, USNM 22567; *Lironeca panamanensis*, MCZ 1077 (2 syntypes); *Lironeca vulgaris*, USNM.

Distribution. Coos Bay, Oregon to Colombia, South America (near Malpelo Island); common from San Francisco south. *Lironeca vulgaris* has been collected from depths of 1–311 m, most often by otter trawl and beach seine.

Host data. Brusca (1978b) reported this isopod from 24 species of host fishes. The following new records are herein reported: *Cymatogaster aggregata* (shiner surfperch), commonly found infested in San Francisco Bay, California; *Scorpaenichthys marmoratus* (Cabezon), from La Jolla (Scripps Canyon), California; *Serranus aequidens* (a tropical sea bass), from 112 fathoms in the south-central Gulf of California; *Hippoglossina stomata* (bigmouth sole), off Newport, California; *Cetengraulis mysticetus* (anchoveta), from the Rio Colorado Delta, northern Gulf of California; "salmon" (sic), Coos Bay, Oregon; *Leptocottus armatus* (staghorn sculpin), San Francisco Bay. While *Lironeca vulgaris* obviously possesses a very low level of host selectivity, it does show a strong preference for bottom fishes of the families Bothidae and Synodontidae, and schooling fishes of the family Embiotocidae. It is recovered regularly from surfperch, lingcod, sand-dabs and lizard-fish. In southern California, infestation levels (per trawl) as high as 3% have been noted on sand-dabs, and up to 80% in lizard-fishes. Female specimens are more commonly encountered in the gill chamber than in the buccal region, and when both male and female are present they are generally located in opposite gill chambers.

Genus *Ceratothoa* Dana, 1853

Diagnosis. Cephalon more-or-less immersed in pereonite I. Pereonite I with anterolateral angles extended and anterior margin broadly excavated to receive cephalon; not trisinuate. Antennae 1 with basal articles expanded and touching.

Coxal plates compact. Anterior coxal plates never extended beyond posterior borders of their respective pereonites; posterior coxal plates nearly reach, or extend slightly beyond posterior borders of their respective pereonites. Pereopods I–III more-or-less manifestly shorter than IV–VII; IV–VII with or without carina on basis. Pleon with anterior somites narrower than and immersed in pereon. Some species lacking appendix masculina on the second pleopods.

Remarks. Bowman (1978b) discussed nomenclatural problems with the genera *Ceratothoa*, *Codonophilus*, *Glossobius* Schioedte & Meinert and *Meinertia*. By applying the law of priority he showed that both *Meinertia* and *Codonophilus* should be considered synonyms of *Ceratothoa*. Dana (1852) erected the latter genus based on two species, "*Cymothoa Gaudichaudii* et *C. parallela* hic pertinent." If a type were chosen for *Ceratothoa*, it would have to be one of these species, which have been referred to until now as *Meinertia gaudichaudii* (Milne-Edwards, 1840) and *Meinertia parallela* (Otto, 1828). The present monograph follows Bowman's recommendations and considers *Ceratothoa* to be the senior synonym of both *Meinertia* and *Codonophilus*. Bowman further recommended that species of *Ceratothoa* that are parasites on flying fishes should be returned to *Glossobius* Schioedte & Meinert, 1883. These actions restore the nomenclature of Schioedte & Meinert (1883).

Trilles (1964c) pointed out that some species in the genus *Ceratothoa* (i.e. *Meinertia*) lack appendix masculina on the second pleopods of the male. He cited three Old World species possessing this remarkable character state: *C. oestroides* (Risso), *C. italica* (Schioedte and Meinert), and *C. capri* (Trilles). I have found both eastern Pacific members of this genus also to lack appendix masculina (*C. gilberti* and *C. gaudichaudii*). It appears, based upon a review of the literature, that there is a trend in this genus towards reduction (and loss) of this structure, although no particular pattern is clear.

Four species of *Ceratothoa* are presently known from the New World: *C. gaudichaudii*, *C. gilberti*, *C. deplanata* (Bovallius, 1885) and *C. transversa* (Richardson, 1900). The last two are west Atlantic species. *C. transversa* was described from a single juvenile specimen and is in need of redescription. There is a single record of the enigmatic austral species *Ceratothoa laticauda* (Milne Edwards), which according to Bowman (1978b) should not be called *Glossobius laticauda* (Schioedte & Meinert's original nomenclature, 1883:309), from the oceanic eastern Pacific (also see Trilles, 1972d: 1252). It was taken from the stomach of the dolphin-fish *Coryphaena hippurus* off southern Mexico (USNM 104866).

Key to the species of Ceratothoa known from the east Pacific

- 1 Pereopods IV–VII without carinae (Fig. 21B,D); posterior margin of pleonite 5 smooth, not trisinate (Fig. 21C); labrum with wavy free margin, with wide medial notch *C. gilberti*
- Pereopods IV–VII with carinae (Fig. 23C,D); posterior margin of pleonite 5 trisinate (except in occasional males) (Fig. 23B,E); labrum with free margin broadly excavate, without medial notch

C. gaudichaudii

Ceratothoa gilberti Richardson, 1904

(Fig. 21, 22)

Meinertia gilberti Richardson, 1904:53. Richardson, 1905:241; Nierstrasz, 1931: 132; Schultz, 1969: 158; Brusca, 1973: 205.

Meinertia n. sp. MacGinitie, 1937: 103.

Codonophilus gilberti Brusca, 1980: 232.

Description (female). Body: Width 8.0–14.0 mm, length 16.0–29.0 mm; body index 1.78–2.67 (mean, 2.05). Lateral margins of body convex; often twisted somewhat to one side. Color (in alcohol) tan with diffuse black or purple chromatophores, occasionally concentrated in posterior half of segments (Fig. 21C).

Cephalon: Width 1.6–2.9 times length (mean, 1.9); deeply immersed in pereonite I. Frontal margin subacute, sides straight. Eyes well developed (Fig. 21C). Antennae short, failing to reach midline of pereonite I, often falling short of posterior border of cephalon itself; antenna 1 of seven articles; antenna 2 of 8–9 articles (Fig. 22A,B). Maxilla 1 with two large and two small terminal spines (Fig. 22C). Outer lobe of maxilla 2 with four spines; inner lobe with 3–10 spines; margin of inner lobe with numerous large denticles; both lobes with pectinate setae (Fig. 22D). Maxilliped with three terminal spines (Fig. 22F). Mandible simple (Fig. 22E). Labrum with free margin wavy, with a wide medial notch.

Pereon: Dorsal surface moderately to strongly convex. Lateral regions of pereonite I swollen and raised into a broad boss above coxal area; II and III with weak lateral swelling; VI–VII with or without weak lateral swelling (Fig. 21C). Pereonite I longest; IV next longest; VII manifestly shorter than I–VI. Pereonites IV and V widest. Posterolateral angles of all pereonites unproduced, smoothly rounded. All coxae compact, rounded, never produced, failing to reach posterior margins of their respective segments (Fig. 21C). Vestige of penes persisting on non-ovigerous females. Pereopods increasing gradually in length posteriorly. All pereopods with grooved bases, increasingly developed posteriorward, those of IV–VII quite deep. Pereopods without carinae (Fig. 21A,B,D).

Pleon: Pleonite 1 narrow; 2–5 manifestly wider than 1; 3–5 subequal in width. Pleonite 5 with posterior margin smooth, not trisinate or undulate (Fig. 21C). Pleotelson subequal in width to pleonites 3–5, wider than long; width 1.5–2.1 times length (mean, 1.8); posterior margin evenly rounded (Fig. 21C). Pleopods simple, without accessory gills or folds (Fig. 22G–I). Uropods short, not reaching posterior border of pleotelson; exopod and endopod similar in shape; exopod slightly larger than endopod (Fig. 22L).

Description (male). Body 5.0–8.0 mm wide; 12.0–19.0 mm long; body index 2.27–2.60 (mean, 2.45). Pleopod 2 without appendix masculinum. Similar to female except for the following: cephalon width 1.9–2.5 times length (mean 2.2); penes large, about 0.5 mm long; pleotelson width 1.7–2.1 times length (mean 1.9).

Remarks. Specimens examined agree well with Richardson's (1904b) original description, except for her comment that the body is reddish brown. Richardson's description was based on three specimens, two males and a female, taken from the mouth of the mullet, *Mugil hospes*, at Mazatlan, Sinaloa, Mexico.

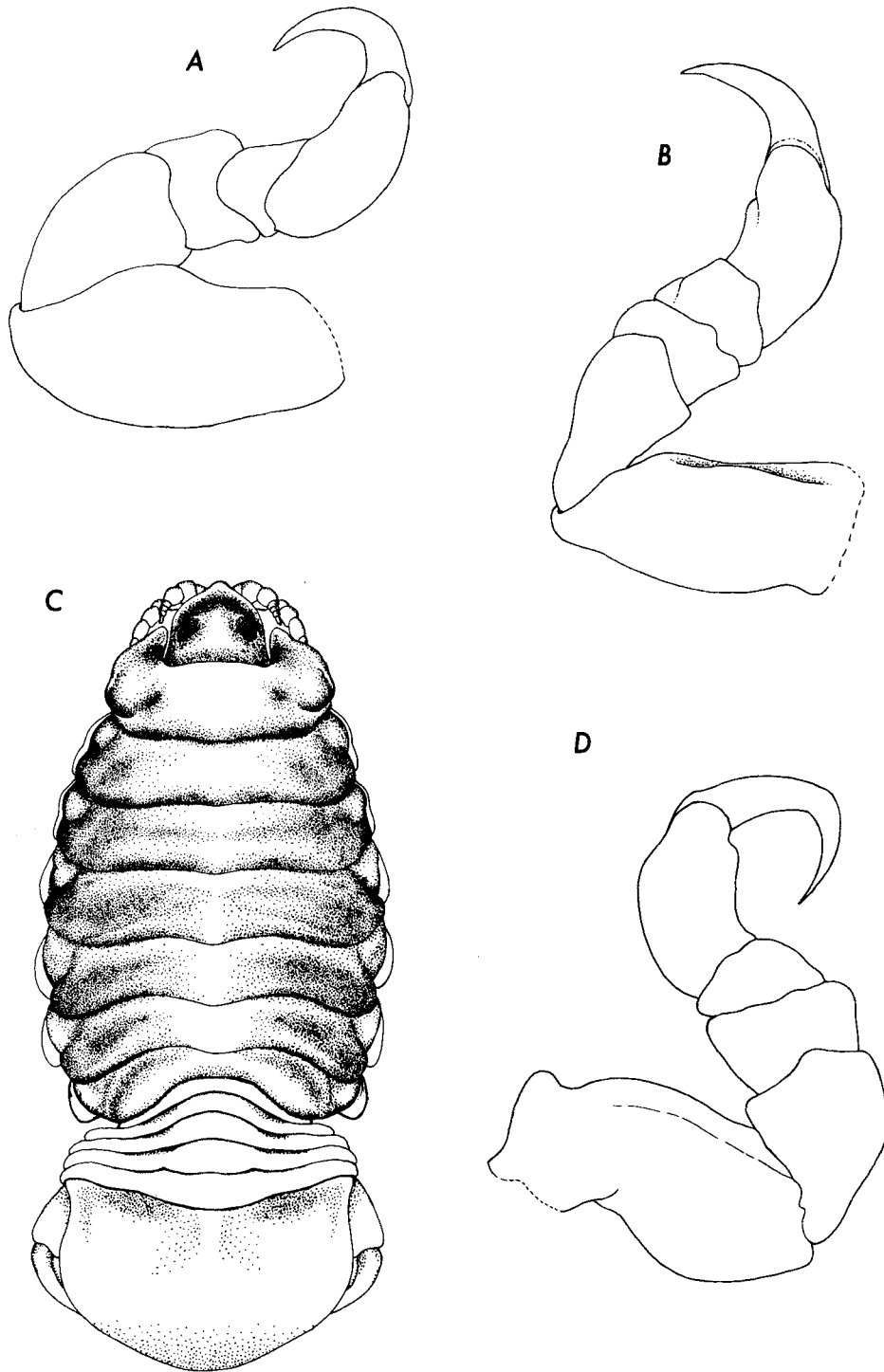


Figure 21. *Ceratothoa gilberti* Richardson. A, Pereopod I; B, pereopod IV; C, dorsal view (female); D, pereopod VII.

Ceratotha gilberti is easily distinguished from its only eastern Pacific congener, *C. gaudichaudii*, by its possession of shorter uropods, distinct pereonal bosses, lack of carinae on pereopods IV–VII, and smooth posterior margin of pleonite 5. *Ceratotha gilberti* and *C. gaudichaudii* are similar in general appearance and share a unique feature known from only a few other species of *Ceratotha*, this being the absence of an appendix masculinum on the males. *C. gilberti* is also similar in appearance to the Atlantic *C. deplanta* but differs in its lack of pereopodal carinae and shorter uropods.

Type deposition. USNM 29080.

Distribution. Southern California to Mazatlan, Sinaloa, Mexico. There are but two California records, both from warm shallow bays (Newport Bay, Orange Co. and Tijuana Estuary, San Diego Co.). West Baja California records are also from warm localities (Estero de Punta Banda, Baja California Norte; and outside Tortugas Bay, off Punta Bartolome, Baja California Sur). Records exist from throughout the Gulf of California, but not south of it. This distribution suggests *C. gilberti* may be essentially a Gulf of California endemic (see Brusca, 1980), able to maintain isolated populations in warm-water refugia of bays and lagoons of west Baja and southern California. This restricted distribution is in contrast to that of *C. gaudichaudii*, which ranges from southern California south to Cape Horn and around to Patagonia, but is notably absent from the Gulf of California. These distributional data, plus similarities in overall morphology suggesting a close phylogenetic relationship between the two species and similarities in host fish preference, all suggest the possibility that *C. gilberti* may be competitively excluding *C. gaudichaudii* from the Gulf of California.

Host data. California records are from the striped mullet, *Mugil cephalus* (Mugilidae), although MacGinitie recorded one from a "flatfish" off Newport Bay (USNM 104278). Gulf of California records are all from the Gulf mullet *Mugil hospes*. No other hosts are known. Both males and females have only been taken from the mouths of their host fishes. One large female from Mazatlan has a luxurious growth of hydroids (*Clytia* sp.) on the dorsum.

Ceratotha gaudichaudii (Milne-Edwards, 1840)

(Figs 23, 24)

Cymothoa gaudichaudii Milne-Edwards, 1840: 271. Nicolet, in Gay, 1849: 3; Dana, 1952: 203; Cunningham, 1869–1871: 499; Gerstaecker, 1901: 264.

Ceratotha rapax Heller, 1865: 146.

Ceratotha gaudichaudii Heller, 1865: 146; Schioedte & Meinert, 1883: 335; Bowman, 1978b: 217.

Meinertia gaudichaudii Stebbing, 1893: 345; 1902: 643; Richardson, 1899a: 171; 1899b: 829; 1901a: 568; 1905: 237; 1910: 79; Van Name, 1924: 183; Nierstrasz, 1931: 171; Menzies, 1962: 116; Szidat, 1965: 84; 1966: 5; Schultz, 1969: 157; Lincoln, 1971: 186; Trilles, 1972d: 1242; Brusca, 1973: 205.

Codonophilus gaudichaudii Nierstrasz, 1931: 131; Brusca, 1977: 130; 1980: 232.

Description (female). Body: width 11.0–22.0 mm, length 27.0–55 mm; body index 1.13–3.00 (mean, 2.48). Sides of body more-or-less parallel, particularly in young individuals; older females broadened posteriorly, pereonite IV widest; rarely twisted to the right or left (Fig. 23B). Color (in alcohol) yellow, usually without obvious chromatophores, or with scattered chromatophores.

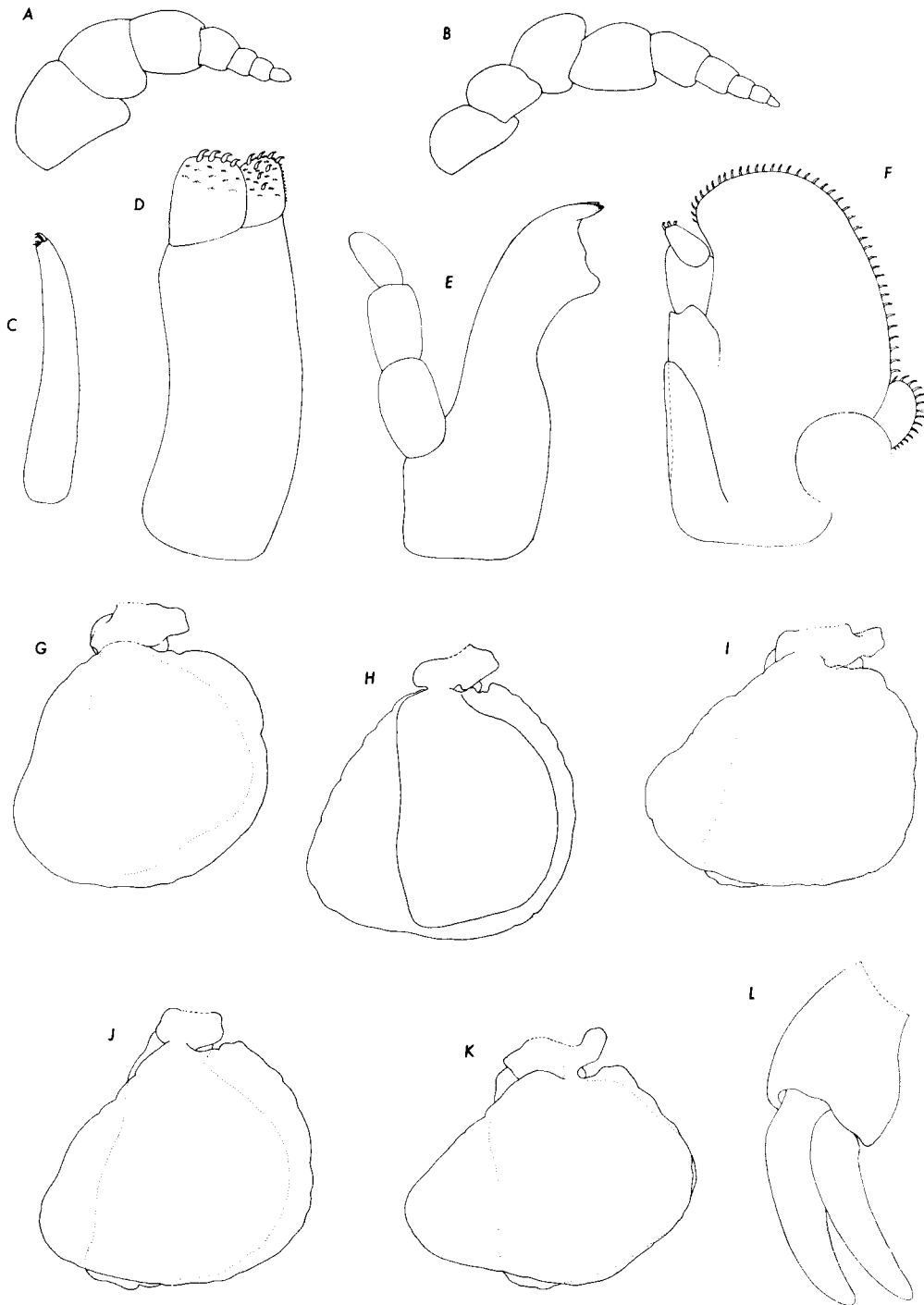


Figure 22. *Ceratothoa gilberti* Richardson. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (R); F, maxilliped; G, pleopod 1; H, pleopod 2; I, pleopod 3; J, pleopod 4; K, pleopod 5; L, uropod.

Cephalon: Width 1.2–2.0 times length (mean 1.65); deeply immersed in pereonite I. Frontal margin subacute to truncate (Fig. 23B). Eyes moderately well developed, partly obscured by cuticle in older individuals. Antennae short, failing to reach midline of pereonite I and often falling short of posterior margin of cephalon. Antenna 1 of 7 articles; antenna 2 of 7–9 articles (Fig. 24A,B). Labrum with free margin broadly excavate and occasionally weakly crenulate; without medial notch. Mandible simple, as figured (Fig. 24E). Maxilla 1 with 4 terminal spines, subequal in size or 1 or 2 larger than others (Fig. 24C). Maxilla 2 with complex setation; outer lobe with pectinate scales and up to 30 spines; inner lobe with pectinate scales and up to 16 spines (Fig. 24D). Maxillipedal palp with 2–8 terminal spines (Fig. 24F).

Pereon: Dorsal surface moderately to strongly convex. Lateral regions of all pereonites weakly swollen above coxae, but never raised into distinct bosses (Fig. 23B). Pereonite I longest; IV next longest; VII manifestly shorter than I–VI. Pereonites IV–V widest. Posterolateral angles of all pereonites unproduced, smoothly rounded. All coxae compact, rounded, never produced; all coxae fail to reach, or barely reach posterior margins of respective pereonites (Fig. 23B). Pereopods with shallow grooves on basis; IV–VII with basis produced into large carina. Pereopods with merus expanded, increasingly so on more posterior legs (Fig. 23A,C,D).

Pleon: Pleonite 1 narrow; 4–5 manifestly wider than 1; 3–5 subequal in width. Posterior margin of pleonite 5 trisinate (Fig. 23B). Pleotelson subequal in width to pleonites 3–5, and wider than long (width 1.6–2.2 times length; mean 1.8); posterior margin evenly rounded. Pleopods simple; 1–2 without accessory gills or folds; 3–5 with small accessory lobe on endopod; lamellae of 4–5 occasionally thrown into one or two shallow pockets (but never folded strongly, as in *Nerocila* or *Anilocra*) (Figs. 25G–K). Uropods extended slightly beyond posterior margin of pleotelson; exopod and endopod similar in shape; exopod slightly larger than endopod (Fig. 24L).

Description (male). Body more symmetrical than females, sides very straight (parallel). Body 5.5–12.0 mm wide, 11.0–34.0 mm long; body index 2.24–3.09 (mean, 2.65). Cephalon 1.25–2.28 times wider than long (mean, 1.80). Eyes large and dark. Pleotelson 1.30–2.07 times wider than long (mean, 1.77). Penes large, about 0.4 mm long. Pleonite 5 not trisinate, or weakly trisinate. Pleopod 2 lacking appendix masculinum (Fig. 23E).

Remarks. *Ceratothoa gaudichaudii* resembles the west Atlantic *C. deplanta* in having pereopodal carinae, expanded pereopodal meri, and in overall body form. It can be most easily distinguished from *C. deplanta* by its trisinate posterior border on pleonite 5. See *C. gilberti* for further remarks.

Type deposition. Unknown.

Distribution. Southern California to Cape Horn, and around to southern Patagonia, South America. Although there are but few records from southern California, numerous records exist for west Baja California. There are no records, however, from the Gulf of California or the Magdalena Bay-Cabo San Lucas region. *Ceratothoa gaudichaudii* appears to be common to abundant in waters of the Galapagos, Ecuador, Peru, and Chile (south to Valparaiso). Only a single record exists south of Valparaiso (from Patagonia). Richardson (1905: 237) reported "Panaieti, Louisiade Archipelago, New Guinea" (sic) as one of the localities for this species. Menzies (1962) felt records of *C. gaudichaudii* from

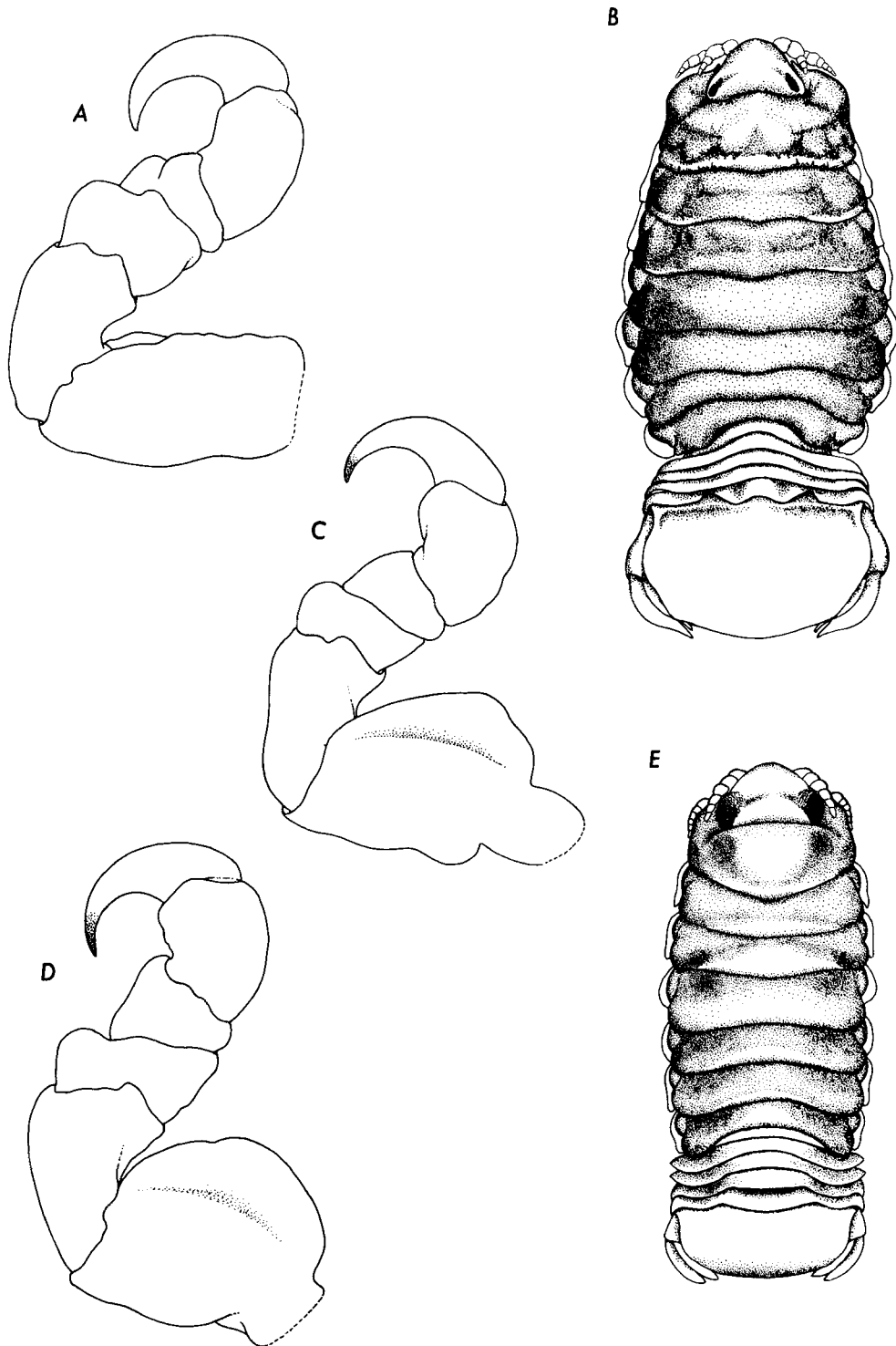


Figure 23. *Ceratothoa gaudichaudii* (Milne Edwards). A, Pereopod I; B, dorsal view (female); C, pereopod IV; D, pereopod VII; E, dorsal view (male).

Chile should be regarded as "contaminants, being transported to there from elsewhere." I have found it, however, to be common throughout the coastal region of Chile (north of Valparaiso), and *C. gaudichaudii* can be considered as a regular member of both the warm and cold water ecosystems of that area. *Ceratohoa gaudichaudii* is, in fact, unique among cymothoids in that it ranges south into the cold Magellan Province (of Briggs, 1974, and others).

Host data. California records are from the striped mullet, *Mugil cephalus* (Mugilidae), and a questionable record from a "Mackerel." Baja California records are from pompano, *Trachinotus* sp. (Carangidae), and herring, *Etrumeus teres* (Clupeidae). Peruvian records are from *Peprilus medius* (Stromateidae), *Neptomenus crassus* (Carangidae), "jurel," and the Pacific bonito, *Sarda chiliensis* (Scombridae). Chilean records are from Pacific bonito, Pacific mackerel, *Scomber japonicus* (Scombridae), *Decapterus* sp. (Carangidae), *Trachurus* sp. (Carangidae), and *Gasterochisma melanopus* (Scombridae). The occurrence of this isopod on numerous species of fishes, in several families, suggests it possesses a fairly low host specificity. Most recorded hosts are pelagic schooling species.

Genus *Cymothoa* Fabricius, 1787

Diagnosis. Body usually not twisted to one side. Cephalon more-or-less immersed in pereonite I (most often deeply immersed); anterior border of pereonite I broadly excavated to receive cephalon. Antennae I widely separated at base; basal articles not expanded. Pereonite I with anterolateral angles more-or-less produced to embrace cephalon. Anterior coxal plates not reaching posterior borders of pereonites; posterior coxal plates nearly reaching, or extending slightly beyond posterior borders of pereonites. Pereopods I–III shorter than IV–VII; IV–VII with carinae on bases. Pleon abruptly narrower than, and deeply immersed in, pereon. Pleonites increasing in length and width from anterior to posterior.

Remarks. The genus *Cymothoa* is one of the most poorly understood of all the cymothoid genera. Only two or three of the more than 30 known species of *Cymothoa* were described in this century. At the present time, species in this genus are distinguished from one another primarily by the shape of pereonites and coxae. Only six species have been reported from the New World: *Cymothoa excisa* ranges from Massachusetts to Brazil, and throughout the Gulf of Mexico and Caribbean; *C. caraibica* Bovallius, 1885 is a West Indies species; *C. oestrum* ranges from Virginia to Venezuela, and throughout the Gulf of Mexico and Caribbean; *C. brasiliensis* Schioedte & Meinert, 1884 has not been reported since its original description from off Rio de Janeiro; Bowman & Diaz-Ungria (1957) reported an undescribed species from Venezuela; and *C. exigua*, the only eastern Pacific species, which ranges from the Gulf of California to Ecuador. Miers' (1877) record of *C. oestrum* from Peru (Pacific) was probably a misidentification (Trilles & Vala, 1975). *Cymothoa recta* Dana, 1853, is known only from Hawaii (Richardson, 1904d).

Cymothoa exigua Schioedte & Meinert, 1884

(Figs 25, 26)

Cymothoa exigua Schioedte & Meinert, 1884: 232. Richardson, 1905: 250; Van Nane, 1924: 184; Schultz, 1969: 161: 123; Brusca, 1980: 232.

Cymothoa exigua (?), Comeaux, 1942: 86; Williams & Williams, 1978: 123.

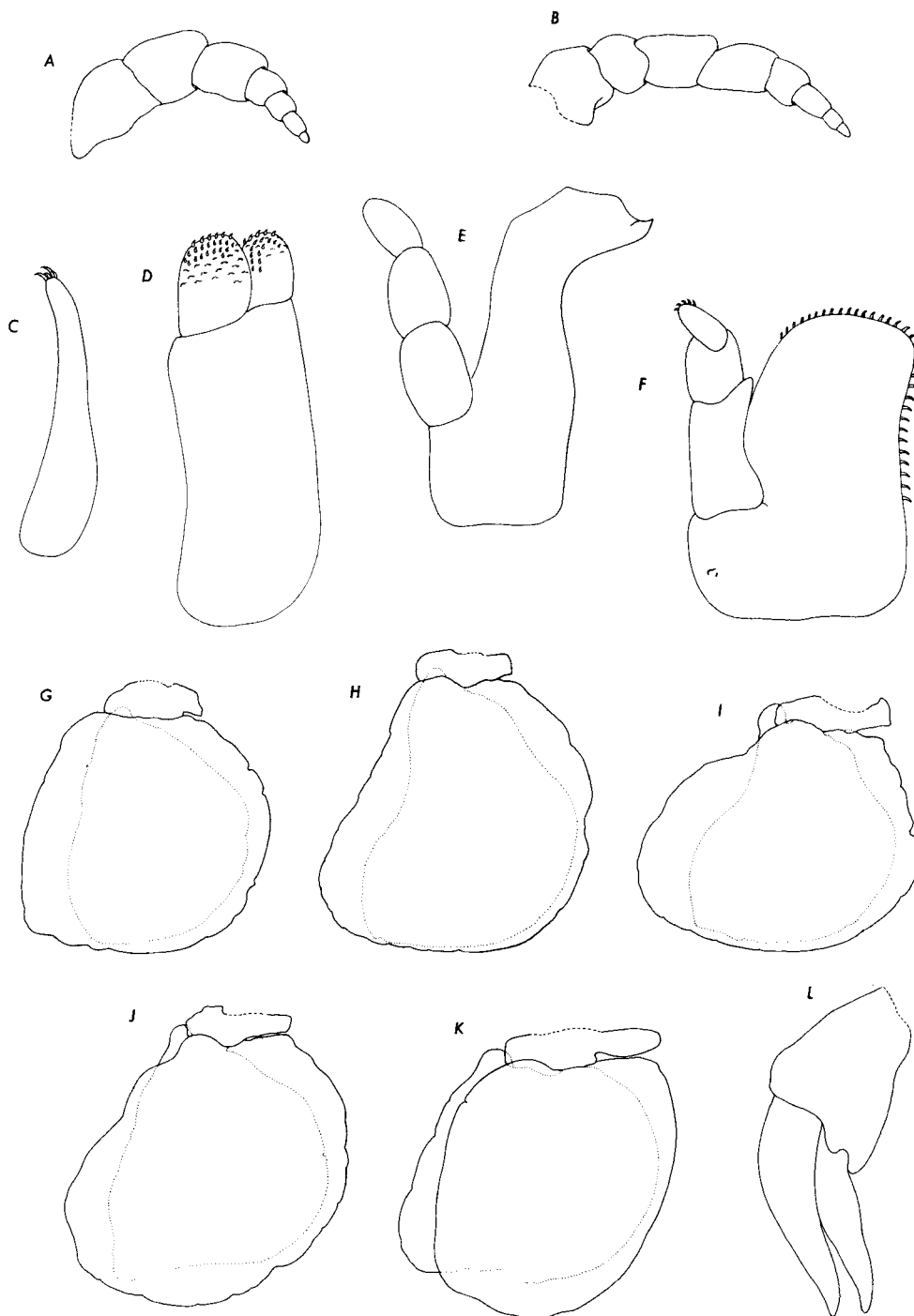


Figure 24. *Ceratohoa gaudichaudii* (Milne Edwards). A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible; F, maxilliped; G, pleopod 1; H, pleopod 2; I, pleopod 3; J, pleopod 4; K, pleopod 5; L, uropod.

Description (female). Body: Width 4.0–14.0 mm, length 8.0–29.0 mm; body index, nonovigerous females 1.71–2.75 (mean 2.23), ovigerous females 1.65–2.38 (mean 1.96). Color tan, dorsal surface usually without scattered chromatophores (Fig. 25).

Cephalon: Width 1.27–2.94 times length; posterior border not trisinate; weakly to moderately immersed into pereonite I (Fig. 25). Eyes well developed. Antennae 1 separated by approximately 0.5–1.5 mm, of 7–9 articles, usually eight; extended to or falling short of anterior third of pereonite I (Fig. 26A). Antennae 2 separated by approximately 1.0–1.75 mm; of 7–10 articles; extended to anterior 1/3 to 1/2 of pereonite I (Fig. 26B). Maxilliped with 4–7 spines on distal article (Fig. 26F). Maxilla 1 with 4, rarely 5, terminal spines (Fig. 26C). Maxilla 2 with denticles along margins, and semilunar pectinate scales on medial surfaces; 7–25 large terminal spines (Fig. 26D). Mandible as figured (Fig. 26E).

Pereon: Pereonite I longest; II–IV subequal in length; V–VII decreasing in length posteriorly; VII shortest. Pereonites V–VI widest. All coxae fail to reach, or barely reach, posterior margins of their respective segments; posterior angles of II–III forming 90° angles; those of IV–VII subacute (Fig. 25). Pereopods I–VII without spines; increasing in length posteriorly; IV–VII with carinae on basis, increasing in size posteriorly (Fig. 26G–I).

Pleon: Pleonites 1–5 with medial elevation; 4–5 widest; 5 longest. All pleopods with lateral accessory lamella on basis, increasing in size posteriorly, subequal to endopod on pleopod 5. Endopod of pleopods 1–5 with medioproximal accessory lamella, increasing in size posteriorly, large and convoluted on 3–5 (Fig. 26K–O). Pleopod 2 with appendix masculinum, variable in size. Pleopods 3–4 usually with a single fold or pocket on medioproximal surface of endopod; 5 with a series of 2–5 such folds. Pleotelson wider than long, width 1.64–2.94 times length; posterior margin concave in larger individuals; straight or slightly convex in smaller individuals. Uropodal rami narrow and elongate, but not extended beyond posterior border of pleotelson (Fig. 26J).

Description (male). Width 3.0–7.0 mm; length 7.5–15.0 mm; body index 2.0–2.5 (mean 2.16). Similar to female except for the following: coxal plate III, and occasionally IV and V, with posterior angles forming right angles; pereopods IV–VII with minute spines on inner margin and lateral surface of carina; lateral margins of pleonites never covered by pereonite VII; accessory lamella of basis, on pleopods 3–5, reduced (relative to exopod and endopod) as compared to females; posterior margin of pleotelson never concave.

Remarks. *Cymothoa exigua* is the only member of the genus known to occur in the tropical eastern Pacific. Its affinities are impossible to assess at this time as both the west Atlantic and Indo-Pacific faunas are poorly known. I have examined Schioedte & Meinert's two types and found them to consist of one ovigerous female (holotype; from the Galapagos Islands; host unknown) and one male (allotype; from Panama). The male possesses what appear to be developing oostegites on pereonites I–III.

Type deposition. Holotype, female, MCZ 3719. Allotype, male, MCZ 3718.

Distribution. *Cymothoa exigua* is strictly Panamic in distribution, ranging throughout the Gulf of California, south to Ecuador. Northernmost records are from the delta of the Colorado River, at the head of the Gulf of California, and in the warm bays of San Juanico, Almejas, and Magdalena on southwest Baja California. Southernmost records are from north of the Gulf of Guayaquil

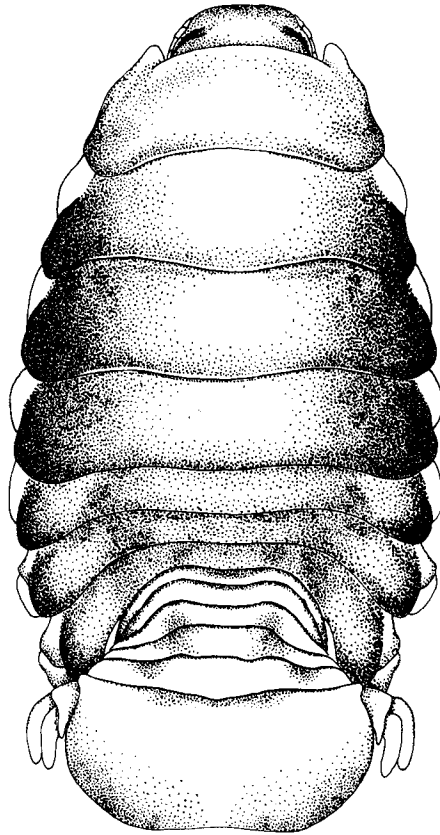


Figure 25. *Cymothoa exigua* Schioedte & Meinert (Female).

(0°56'S, 80°44'W). This isopod is very abundant throughout the Gulf of California. All records are from depths of less than 60 m; most are from depths of 2–20 m; most were collected by otter trawl or fish poison stations. Although Williams & Williams (1978) cited Comeaux's (1942) record from Louisiana, they now agree (pers. commn), that this was most likely a misidentification.

Host data. Richardson (1905) perpetuated Schioedte & Meinert's record of *C. exigua* from the mouth of *Citharichthys sardidus* (Pacific sand-dab), from Panama. This host identification appears to be in error, however, as this fish is not known to occur south of Baja California. Brusca (1977, 1980) reports *C. exigua* as common on *Orthopristis reddingi*, the bronze striped grunt, in the Gulf of California. Additional records subsequent to these are as follows: *Leuresthes sardina* (the Gulf grunion), northern Gulf of California, one record; *Cynoscion orthonopterus* (Gulf corvina), northern Gulf of California, three records; *Lutjanus peru* and *L. guttatus* (red snappers), Gulf of California, several records; *Micropogon megalops* (Gulf croaker), northern Gulf of California, two records; *Menticirrhus nasus* (highfin corbina), northern Gulf of California, one record; *Lutjanus maculatus* (a snapper), Panama, one record. Only in *Orthopristis reddingi* and *Cynoscion orthonopterus* has tissue damage to the gills been noted. However, all of the above records appear to be valid, as females were always reported from the buccal region, attached to the tongue, whereas males were from the gills (except

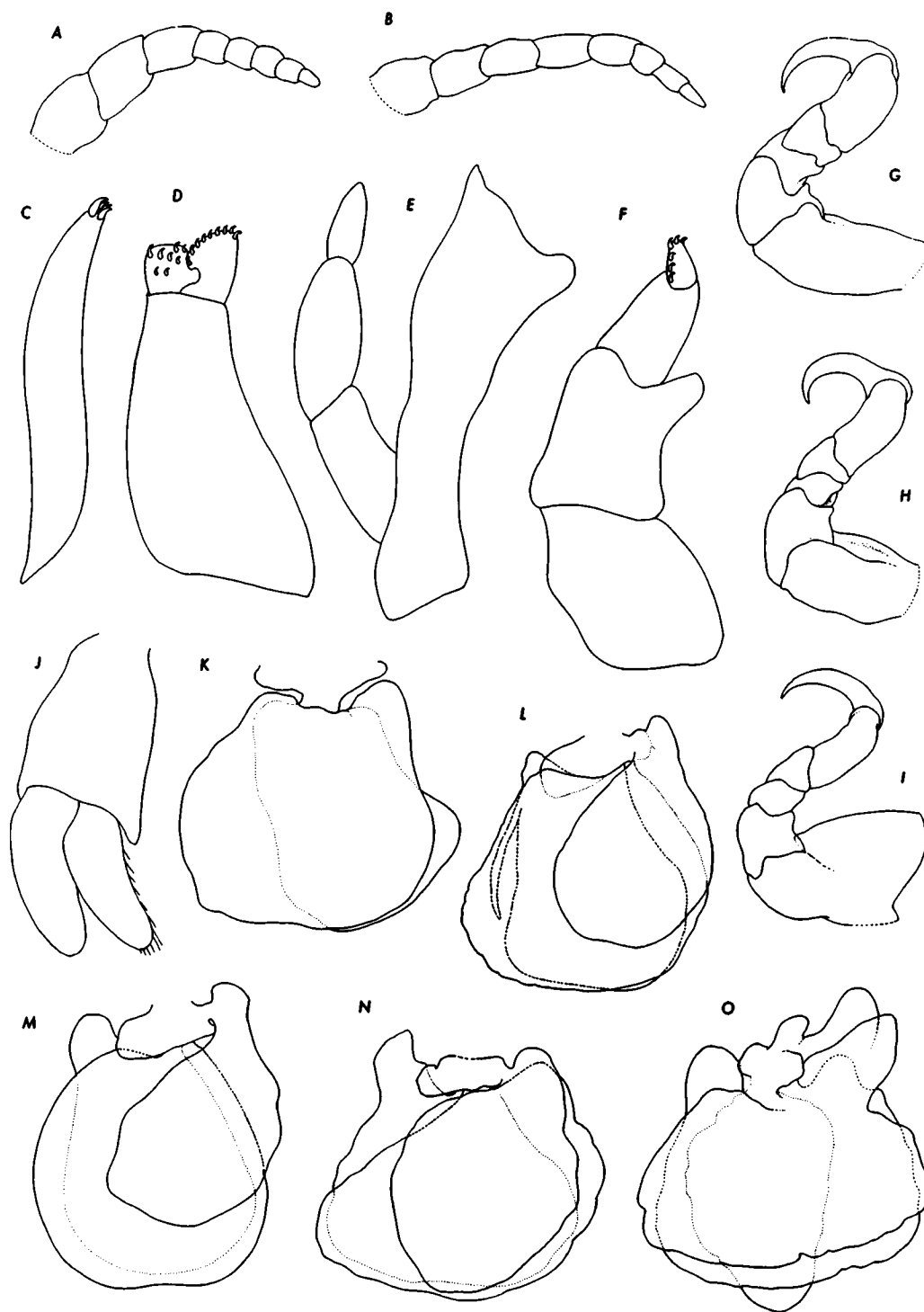


Figure 26. *Cymothoa exigua* Schioedte & Meinert. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (L); F, maxilliped; G, pereopod 1; H, pereopod IV; I, pereopod VII; J, uropod; K, pleopod 1; L, pleopod 2; M, pleopod 3; N, pleopod 4; O, pleopod 5.

when apparently "in copula," venter to venter, with the female, in the mouth). Most records report one individual of each sex per host, although occasional records of single females do exist. No multiple infestations (i.e. two males or two females) have been recorded. In the northern Gulf of California infestation rates on *Orthopristis reddingi* to 75% of a catch have been recorded.

Genus *Idusa* Schioedte & Meinert, 1883

Diagnosis. Body narrow, laterally compressed and dorsally convex. Cephalon immersed in pereonite I; anterior border of pereonite I broadly excavated to receive cephalon. Basal articles of antennae 1 nearly touching at base, but not expanded as in *Ceratothoa*. Posterolateral angles of pereonites not acute or extended. Coxal plates small and compact. Pleon somewhat narrower than, and somewhat immersed in pereon.

Remarks. *Idusa* is a small genus, six species having been described from the east and west Pacific. Only *I. carinata* Richardson is known from the New World.

Idusa carinata Richardson, 1904

(Figs 27, 28)

Idusa carinata Richardson, 1904b: 52. Richardson, 1905: 246; Nierstrasz, 1931: 138.

Description (female). Body: Width 9.0–11.5 mm; length 13.5–20.0 mm; body index 1.42–1.94 (mean 1.69) for ovigerous females. Body twisted to right or left, often grossly distorted. Color (in alcohol) light tan to dark brown; dorsal surface without distinct chromatophore pattern (Fig. 27).

Cephalon: Width 1.2–1.7 times length; anterior margin medially produced, acute; posterior margin straight, deeply immersed into pereonite I (Fig. 27). Eyes weakly to moderately well developed. Antennae 1 of 5–7 articles; extended to anterior margin of pereonite I (Figs 27, 28A). Antennae 2 of 7–9 articles; reaching anterior third of pereonite I (Figs 27, 28B). Maxilliped with 1–4 terminal spines; margin of lamellar plate with minute feathered setae (Fig. 28F). Maxilla 1 with 3–4 terminal spines (Fig. 28C). Maxilla 2 with 5–14 spines; inner lobe with 2–4 spines, outer lobe with 3–9 spines (Fig. 28D); medial margin of inner lobe and basis with numerous minute denticles. Mandible as figured (Fig. 28E).

Pereon: Pereonite I longest, anterolateral angles acute, produced to border eyes; VI and VII shortest; II–V variable. Pereonites IV and V widest. Coxal plates not visible in dorsal aspect due to lateral compression of body; in lateral view II–VI extended $\frac{2}{3}$ to $\frac{3}{4}$ the distance to the posterior borders of their respective pereonites; VII extended to posterior margin of its pereonite; I usually with a deep suture, indicating incomplete fusion with its somite; posterior angles of coxae II–IV or II–V forming right angles, those of V–VII or VI–VII acutely rounded. Pereopods increasing gradually in length posteriorly; all with carina on basis, increasing in size posteriorly; carinae of posterior legs strongly grooved to receive ischium-merus-carpus (Fig. 28G–I).

Pleon: Pleonites increasing gradually in length and width posteriorly. Pleopods lack stout setae on inner margin of bases; 3–5 with small medio-proximal extension on endopod (Fig. 28L–N); 2 with or without remnant of

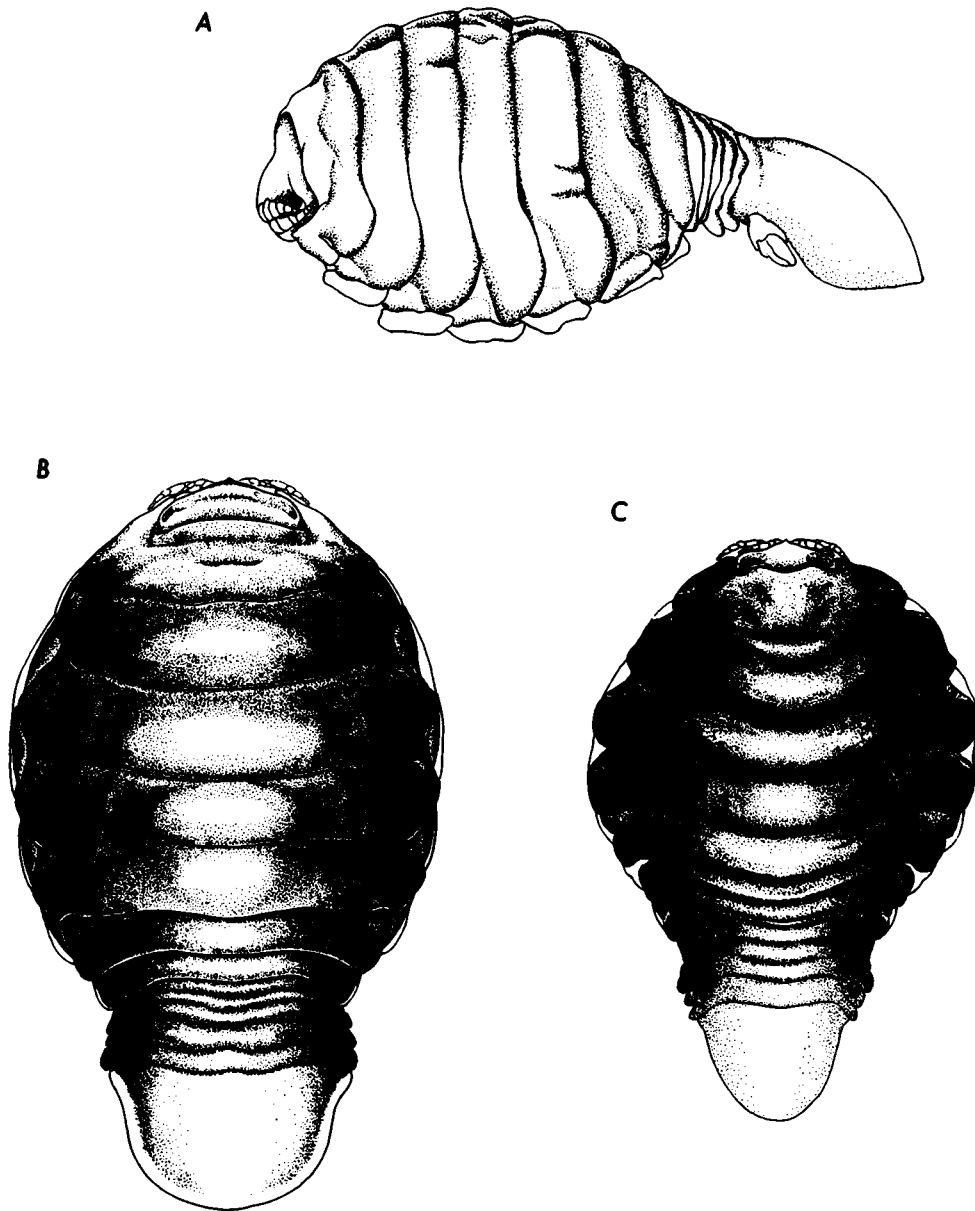


Figure 27. *Idusa carinata* Richardson. A, Lateral view; B, C, dorsal views of two female specimens.

appendix masculinum (Fig. 28K). Posterior margin of pleotelson evenly rounded (Fig. 27B–C); pleotelson often strongly “folded” or compressed laterally (Fig. 27A). Uropodal endopod and exopod minute, substyliform, subequal in length to basis (Fig. 28O).

Male. Similar to female in all regards; with appendix masculinum.

Remarks. Richardson’s description of *I. carinata* (1904b, 1905) agrees well with all specimens I have examined. Her reference to antennal “flagellum” (sic)



Figure 28. *Idusa carinata* Richardson. A, Antenna 1; B, antenna 2; C, maxilla 1; D, maxilla 2; E, mandible (L); F, maxilliped; G, pereopod 1; H, pereopod IV; I, pereopod VII; J, pleopod 1; K, pleopod 2; L, pleopod 3; M, pleopod 4; N, pleopod 5; O, uropod.

apparently refers to the entire antennae, rather than some distal part of these appendages.

Type deposition. Syntypes; one male, one female; USNM 28961.

Distribution. I have recovered only four collections of *I. carinata*; two from the Gulf of Panama and two from Guayaquil, Ecuador.

Host data. Only the type specimens bear host data and include a note (apparently in Richardson's handwriting) stating, "always found in mouth of *Mugil hospes*", a mullet (Mugilidae).

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