



The external morphology of the onychopod 'cladoceran' genus *Bythotrephes* (Crustacea, Branchiopoda, Onychopoda, Cercopagididae), with notes on the morphology and phylogeny of the order Onychopoda

JOEL W. MARTIN and CORA E. CASH-CLARK

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The onychopod 'cladoceran' genus *Bythotrephes* Leydig is reviewed and redescribed based on introduced material of the *B. cederstroemi* 'form' from the Great Lakes of North America. Reviewed briefly are the systematic history, introduction into North America, and natural history of the genus. Using S.E.M. and light microscopy, we then illustrate a mixture of plesiomorphic and (predominantly) derived features, most of which can be explained as modifications for predation. An emended generic diagnosis includes unique and previously poorly known characters that serve to distinguish *Bythotrephes* from the confamilial genus *Cercopagis*, such as a distinctly bilobed labrum, spinose anterior mandibular process, small (exopodal?) spines on the external face of thoracopods 1–3, and a gnathobasic process (proximal endite) on thoracopod 1. A redescription, combined with observations on the external morphology, highlights several morphological peculiarities. These include the strongly bilobed labrum, the loss of one of the original two pairs of maxillae (with a question raised as to which pair has been lost), an unusual point of origin for the 'proximal endite' (termed herein the 'gnathobasic process' because of uncertainty of homology) on thoracopods two and three, a bulbous process of unknown significance located just posterior to the last thoracopod, and the presence of what might be a remnant of the food groove believed to have been present in a hypothesized ancestral group leading to the Onychopoda. The problem of whether *Bythotrephes* contains one dimorphic species or two species, *B. longimanus* and *B. cederstroemi*, is reviewed briefly, and the morphological feature in which these forms differ (the caudal process) is described in detail for the *cederstroemi* form. Comparison with descriptions of other cercopagidids suggests that *Bythotrephes* is a highly derived taxon, with short-abdomen genera of the Podonidae and Polyphacidae (e.g., *Polyphemus*) appearing closer to the onychopod phyletic stem, and with the more closely related genus *Cercopagis* more derived still. Phylogeny within the Cladocera, and the possible origin of the Cladocera from a cyclesteriid-like ancestor among the spinicaudate conchostracans, is reconsidered. A hypothesis of evolutionary relationships is presented that depicts the ctenopods and anomopods as having arisen from a hypothetical *Cyclestheria*-like ancestor, with the predatory cladoceran taxa Haplopoda and Onychopoda being derived from the base of the anomopod lineage. Some of the many problems in the suggested phylogeny are discussed.

Joel W. Martin & Cora E. Cash-Clark, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A.

Introduction

Among the most unusual of all extant crustaceans are those that comprise the branchiopod order Onychopoda. Onychopods are small to relatively large crustaceans (to 12 mm including the length of the caudal process; Martin, 1992) that inhabit freshwater and marine plankton and the vegetated littoral zone of lakes and ponds. The morphology of onychopods very nearly defies categorization, and although historically placed among the 'Cladocera,' onychopods differ from other cladoceran groups in numerous ways (e.g., see Fryer 1987a, b; Martin 1992; and below). As opposed to all other cladoceran orders except the monotypic Haplopoda (*Leptodora kindtii*), all members of the Onychopoda are highly modified predators,

although some may ingest particulate matter as well (Fryer 1987a, b; Martin 1992). It is probable that many of the morphological peculiarities of onychopods reflect their predatory habits. The Onychopoda, as presently recognized, consists of three families and 9 or 10 genera, and is characterized by the following combination of features (from Fryer 1987a, b; reproduced in Martin 1992), several of which are shared with other Branchiopoda:

1. The head and trunk are short, and the original segmentation has been obscured by extensive fusion.
2. The carapace valves (= secondary shield of Walossek 1993) have been reduced to a dorsal brood pouch (in females) that no longer encompasses the body, and on the floor of which is a Nährboden for supplying nutrients to the developing embryos (see Rossi 1980).

3. There is a single, median compound eye, occupying nearly the entire area of the 'head' and composed of numerous ommatidia that may be of several different structural types (e.g., there are 130 ommatidia of four types in *Polyphemus*; Odselius and Nilsson 1983). The external cuticle overlying the eye is not faceted.
4. The labrum is large and bears secretory glands.
5. The antennules are uniramous and more or less tubular.
6. The antennae are biramous and natatory. The endopod has three segments, the exopod has four, and all except the small first segment of the exopod bear plumose natatory setae.
7. The mandibles are more derived than in the relatively primitive grinding/rolling type seen in most branchiopods (e.g., see Fryer 1983, for the anostracan *Branchinecta ferox*) and are modified for biting.
8. The maxillules are reduced.
9. The maxillae are absent (this character and the above character are questioned in this paper).
10. There are four pairs of 'thoracic' (pregenital) limbs, all of which are stenopodous, segmented, grasping appendages. Each bears a medially directed gnathobasic process or 'proximal endite' (see Walossek 1993), which may or may not articulate with the thoracopod (exceptions are mentioned in this paper; e.g., the genus *Cercopagis* lacks a gnathobasic process on leg 1, and homologues of this process on other legs in *Bythotrephes* are uncertain).
11. Each limb lacks an inflated 'branchial' (osmoregulatory) epipod common in most other branchiopods.
12. There is no food groove (a character state that is questioned in this paper).
13. The first leg of the male is often modified for grasping the female (although the various modifications are not always homologous).
14. Penes are occasionally found as paired, external structures located behind the base of the last trunk limb (partially modified in the present paper).
15. The abdomen may be either short or long, and may or may not bear caudal rami. We add to this that a pair of terminal setae, which all branchiopods (or at least non-anostracan branchiopods) seem to have at some point during their development, is found on onychopods as well, serving to demonstrate that they are truly branchiopods, a point that has been questioned in the past (Mordukhai-Boltovskoi 1968; see also Fryer 1987a). These setae have been illustrated for *Bythotrephes* previously (e.g., Müller 1867, pl. 5, fig. 17; Lilljeborg 1901, pl. 80, fig. 10) but to our knowledge have not been used as a branchiopod synapomorphy (see Discussion).

While compiling information for a review of the microscopic anatomy of branchiopod crustaceans (Martin 1992), we were struck by the paucity of basic morphological knowledge concerning species of the Onychopoda (compared to, for example, what is known for other 'cladoceran' taxa such as the daphniids). Most of the above characters have only rarely been illustrated, and almost never by means of scanning electron microscopy (S.E.M.), for any onychopod. Thus, the erection of any phylogenetic hypotheses of 'cladoceran' orders, and indeed of the entire Branchiopoda, is severely hindered.

The present paper attempts to provide a preliminary step toward a better understanding of the relationships of these bizarre animals to other branchiopod Crustacea by more closely examining the external anatomy of a single genus: *Bythotrephes* Leydig, 1860.

Brief systematic history

The order Onychopoda, formerly a subdivision of the Cladocera (see Fryer 1987a, b, for arguments to elevate former cladoceran taxa to ordinal status), currently contains three families: Polyphemidae Baird, 1845 (one genus, *Polyphemus*), Podonidae Mordukhai-Boltovskoi, 1968 (6 or 7 genera), and Cercopagididae Mordukhai-Boltovskoi, 1966 (two genera, *Bythotrephes* and *Cercopagis*) (Fryer 1987b; Mordukhai-Boltovskoi and Rivier 1987; Dodson and Frey 1991; Martin 1992). These families differ in the length and form of the caudal process, the presence and condition of true exopods on the thoracopods, and the relative development of the first thoracopod, among other less obvious differences (see Discussion and Mordukhai-Boltovskoi 1968; Mordukhai-Boltovskoi and Rivier 1987).

The genus *Bythotrephes* was originally erected by Leydig (1860) based on animals taken from the stomachs of fishes from the Bodensee (Lake Constance), a large freshwater lake bordering Switzerland, Austria, and Germany. Placed in the family Polyphemidae Baird, 1845 by most earlier workers, such as Sars (1862), Lilljeborg (1901), and Scourfield and Harding (1966), *Bythotrephes* was transferred to the newly created family Cercopagidae by Mordukhai-Boltovskoi (1968), along with one other genus, *Cercopagis* Sars, 1897. *Bythotrephes* Leydig is today recognized as having either one or two species (see Discussion), and is found in freshwater reservoirs in Europe, Russia, Asia (introduced) and the United States (introduced).

Although the family Cercopagidae was formally erected by Mordukhai-Boltovskoi in 1968, this grouping, containing the same two genera (*Cercopagis* and *Bythotrephes*), was recognized by him earlier (Mordukhai-Boltovskoi 1966) as the subfamily Cercopaginae (treated at that time as being within the family Polyphemidae). Therefore the correct date for the family name should be 1966, rather than 1968 as is most typically used (e.g., Bowman and Abele 1982). Additionally, the correct orthography of the family name derived from *Cercopagis* is Cercopagididae, and not Cercopagidae. According to Brown (1956: 812), 'pagis' derives from the stem pagid, and therefore the family ending -idae has to be added to Cercopagid (see also the International Code of Zoological Nomenclature, Article 29(a) and (b)). Consequently, the correct name and date for this family are hereby corrected to Cercopagididae Mordukhai-Boltovskoi, 1966.

Introduction into North America

Although originally a European genus, *Bythotrephes* has now been found in the Sinkiang region of China (Chiang 1964) and more recently in the United States. Dispersal was almost certainly via the freshwater ballast of ocean freighters (Sprules *et al.* 1990). Limited dispersal by other

means is perhaps possible; Lehman (1987) cited Steinwender (1935) as attributing the spread of resting eggs of *Bythotrephes* in Europe to waterfowl, and Lange and Cap (1986) suggested this mechanism for transport of eggs to North America (see also Evans 1988). However, it is unlikely that this is how *Bythotrephes* arrived in North America, or it would have appeared much earlier than it did, and its distribution would not be restricted to bodies of water large enough to accommodate ocean-going vessels. The source of the North American population was probably ballast water picked up near St Petersburg by Soviet freighters during the late 1970s and early 1980s (see Sprules *et al.* 1990; Raloff 1992).

The first records in North America were from Lakes Erie and Huron in 1984; the entry point into the Great Lakes was probably the southern Lake Huron area (Bur *et al.* 1986; Berg and Garton 1988). Shortly thereafter, *Bythotrephes* was reported from Lake Ontario in 1985 (Lange and Cap 1988), Lake Michigan in 1986 (Lehman 1987; Evans 1988), and Lake Superior in 1987 (Cullis and Johnson 1988; Garton and Berg 1990; Jin and Sprules 1990). Comparisons were provided by Berg and Garton (1988) and Garton and Berg (1990), who noted slight differences in the populations of Lakes Superior and Erie (with a higher percentage of males, greater average weight, and higher number of females carrying sexual resting eggs in the former), and by Jin and Sprules (1990), who surveyed all of the Great Lakes with the exception of Lake Superior.

Natural history

Bythotrephes is a voracious predator (e.g., Mordukhai-Boltovskoi 1958; Monakov 1972; Evans 1988; Sprules *et al.* 1990). Its mode of feeding was compared to that of *Leptodora* and *Polyphemus* by Monakov (1972), who stated that all three genera 'tear up the prey with their mandibles and then suck it in' (Monakov 1972: 372). Because of this mode of feeding, gut contents reveal little about preferred prey items. However, several studies have reported that *Bythotrephes* will readily consume almost any component of the zooplankton, and appears to be an opportunistic predator. Monakov (1972) listed prey that included other Crustacea, rotifers, and planktonic stages of chironomid larvae. Monakov also cited Mordukhai-Boltovskoi (1958, 1960) as saying that *Bythotrephes* prefers *Polyphemus*, *Bosmina*, and *Ceriodaphnia*, with a preference for rotifers and copepods in the spring but preying mostly on other cladocerans in the summer (see Monakov 1972). De Bernardi and Giussani (1975) concluded that *Bythotrephes* and *Leptodora* were responsible for the collapse of certain *Daphnia* populations in Lake Maggiore. De Bernardi *et al.* (1987) noted that *Bythotrephes* can consume up to 30 *Daphnia* per day, and Sprules *et al.* (1990) calculated that a single animal can remove all the daphniids from 0.4 to 1.0 l of water per day. Not surprisingly, there has been some apprehension over introductions of this genus. Raloff (1992) expressed concern over the depletion of daphniids in the Great Lakes of the United States, where it was originally feared that by depleting the *Daphnia* population, the introduced *Bythotrephes* might endanger fish populations (e.g.,

Evans and Jude 1986; Evans 1988; Lehman 1987, 1988; Scavia *et al.* 1988). However, G. Sprules (personal communication, Sprules *et al.* 1990; see also Raloff 1992) is less concerned, noting the much higher rate of population growth in daphniids than in *Bythotrephes*. The introduction of *Bythotrephes* may also present non-ecological problems: Cullis and Johnson (1988) noted that individuals were so numerous that they 'adhered to fishing lines and fouled fishing gear' in Michipicoten Bay, Lake Superior.

Although the general habitat of the genus—freshwater lakes and reservoirs—is well established, there is some confusion or conflict in the literature as to the depth range of *Bythotrephes*. The graph provided by Lindstrom (1955: 139) shows a range from the littoral to deep pelagic waters in Sweden. Evans (1988), working with the introduced Lake Michigan population, and referring to the publications of Lindstrom (1955), Lotmarker (1964), and Zozulya and Mordukhai-Boltovskoi (1977), expressed surprise that *Bythotrephes* turned up in the gut contents of bottom-feeding (approximately 97 m) sculpins, as she considered it 'a surface dwelling genus' (Evans 1988: 238). Evans speculated that the presence of *Bythotrephes* in the sculpin's diet might be explained by sinking of the onychopods after death, rather than occurrence of live *Bythotrephes* at that depth. Lotmarker (1964) also felt that, at least in Sweden, the genus seems 'to prefer the upper layers.' However, Cullis and Johnson (1988) stated that Lake Superior might provide an optimal habitat for *B. cederstroemi* production 'as this species is most abundant at depths greater than 20 meters (Nilsson 1979) in European oligotrophic lakes.'

The long caudal process has been shown by Barnhisel (1991a, b) to be effective in deterring predation by small fish. Nevertheless, *Bythotrephes* has been found in the stomach contents of many fish species, including: chinook salmon and pink salmon (Cullis and Johnson 1988); yellow perch, white perch, white bass, and walleye (Bur *et al.* 1986); species of *Coregonus* in Italy (Guissani 1974) and Sweden (Nilsson 1979); char (Lindstrom 1955); and sculpin (Evans 1988), in addition to the species discussed in Barnhisel (1991a, b). In some studies of gut contents, *Bythotrephes* appears to be a preferred food item. Nilsson (1979) stated that the more pelagic white fish feed 'almost entirely' on *Bythotrephes*, and Lindstrom (1955) noted that char (*Salmo alpinus*) seem to seek out *Bythotrephes* even though they are rare.

Populations of *Bythotrephes* undergo both sexual and asexual reproduction depending upon seasonal cues, producing resting eggs or brooding developing embryos in a dorsal brood pouch (e.g., see Herzig 1985, Andrew and Herzig 1984, Mordukhai-Boltovskoi 1956, 1957). Life history parameters for the Laurentian Great Lakes populations were reviewed by Sprules *et al.* (1990) and Garton *et al.* (1990).

Despite the unusual nature of cercopagidid morphology and its possible ecological importance, few papers have addressed the basic morphology of the family. This is especially true in *Bythotrephes*, where most authors have elected to reproduce the illustrations of Leydig (1860), Müller (1867), or Lilljeborg (1901). These figures were beautifully executed, but are lacking in detail

(or are simply erroneous) concerning some characters now thought to be of taxonomic or phylogenetic significance (discussed later). Additionally, we are aware of only one study (Mordukhai-Boltovskoi and Rivier 1987) that has examined any characters of the genus using electron microscopy.

Material and methods

Material for this study came from two sources. Samples sent to us by Mr Wendell Haag, Ohio State University, were collected by Drs David Berg and David Garton in Batchawana Bay, Lake Superior, Ontario, Canada, on 15 September 1988, at a depth of approximately 30 m. Collections were made using vertical hauls with a 110 µm plankton net and preserved in 10% sugared formalin. We transferred samples to 70% ethanol in 1991. Additional collections of *Bythotrephes cederstroemi*, including males, were sent to us by Dr David Garton, Ohio State University, from collections made by Dr David Berg in the summer of 1988 in Lake Erie, U.S.A. Approximately 60 individuals were dissected and examined, about half of which were prepared for S.E.M.

Illustrations were prepared with the aid of a Wild M5APO stereomicroscope and a Nikon Labophot compound microscope, each equipped with a camera lucida. Details were confirmed by observation using S.E.M. Specimens subjected to S.E.M. were briefly sonicated while still in 70% ethanol, dehydrated in a graded ethanol series, and air dried from HMDS (hexamethyldisilazane; see Nation 1983) or critical-point dried (less frequently used) before sputter coating with gold and viewing on a Cambridge Stereoscan 360 at 10 kV.

There is currently no terminology or classification scheme that is universally accepted for the great diversity of crustacean spines and setae. According to Felgenhauer (1992: 33), 'strict limiting definitions for cuticular surface specializations are difficult to produce and have not really been accurately defined. What one investigator may consider a spine could be a strong seta of another investigator.' Although Felgenhauer was discussing decapods, this is true also for other crustaceans. Some workers have made a distinction on a functional basis, with the word 'seta' restricted to structures having sensory functions. Others employ a structural distinction. For example, Watling (1989: 16), although concerned primarily with malacostracans, distinguished between a spine and a seta by defining the former as a 'non-articulated cuticular extension of the exoskeleton that has a base that is generally not as wide as the structure is long; regardless of its size or shape, a spine has no socket.' In *Bythotrephes* there are large, spinulose setae on each leg that undoubtedly function as spines (that is, they aid in grasping prey) but that originate in well defined cuticular sockets. We have sidestepped the terminology problem by referring to these as 'spine-like setae', and to their various projections as setules or spinules depending upon their relative size.

Voucher specimens, both in ethanol and mounted on S.E.M. stubs, have been deposited in the Crustacea collections of the Natural History Museum of Los Angeles County.

Abbreviations used in the figures

a1	antenna 1 (antennule)
a2	antenna 2
an	anal opening (anus)
bp	bulbous process
bpch	brood pouch
do	dorsal organ
e	compound eye
emb	developing embryos
en	endopod
ex	exopod
fg	sternal food groove
g	gnathobasic process (= proximal endite)
la	labrum
md	mandible
mp	anterior mandibular process
mx	maxilla
Nähr	Nährboden
i1	thoracic leg 1
i2	thoracic leg 2
i3	thoracic leg 3
i4	thoracic leg 4
p	penis

Family Cercopagidae

Genus *Bythotrephes* Leydig, 1860

Emended diagnosis

Compound eye extremely large, composing nearly entire head. Naupliar eye (ocellus) absent. Antennule reduced, slightly dilated distally, most commonly with 6 aesthetascelike setae in two groups of 3 each. Antenna with 8 natatory setae on 4-segmented exopod and 7 natatory setae on 3-segmented endopod. Exopod setation (proximal to distal) 0, 1, 2, 5. Endopod setation 1, 1, 5. Labrum large, fleshy, distinctly bilobed, with anterior lobe conical and extending ventrally and slightly posteriorly beyond flatter posterior lobe. Mandible strongly bilobed, composed of anterior spinose process and posterior bifid tooth. Thoracopod one greatly exceeding length of other thoracopods, with small triangular gnathobasic process on first segment. Thoracopod 2 and 3 with large, denticulate gnathobasic process stemming from, and articulating with, second segment. Thoracopod 4 greatly reduced, with gnathobasic process fused to (not articulating with) thoracopod. Segments of thoracopod 4 condensed (fused). Thoracopods 1–3 with exopod reduced to triangular spine-like process arising from outer face of basal segment and bearing single, distal spine-like seta. Thoracopod 4 with exopod reduced to single seta arising from short, cylindrical, cuticular peduncle. Caudal process extremely long, most often composed of three articles, with pair of ventrally directed spines at leading edge of each article. Functional anal opening located ventrally between these spines. Articles of caudal process covered with minute, posteriorly directed cuticular scales.

Description and external morphology

Head and eye. The head is essentially composed of a single enormous compound eye (Figs 1–3, 4A, B). In adults, the diameter of the eye can be as much as 7% of the length of the entire animal, and if the caudal process is excluded then the eye is fully 1/3 the length of the body (measured from the leading edge of the compound eye's cornea to the front edge of the most proximal article of the caudal appendage). Although lacking external facets (Figs 1, 4A), the individual ommatidia of the eye are visible beneath the thin overlying cuticle in light microscopy (Figs 2, 3). Dissection of the overlying cuticle reveals an eye composed of at least 200 ommatidia; there are 117 visible in Fig. 4B, where approximately half of the ommatidia were removed during the dissection. There is no nauplius eye (= ocellus) visible in external view, but no histological sections were made to determine whether presumed sensory elements representing a nauplius eye have been incorporated into the brain, as appears to be the case in the functionally similar haplopod *Leptodora* (see Martin 1992).

Dorsal organ. The dorsal organ is conspicuous under light microscopy (Fig. 3) but less so under S.E.M. (because of shrinkage of the post-cephalic region; compare Figs 1 and 3). It is situated dorsally and medially, posterior to the eye

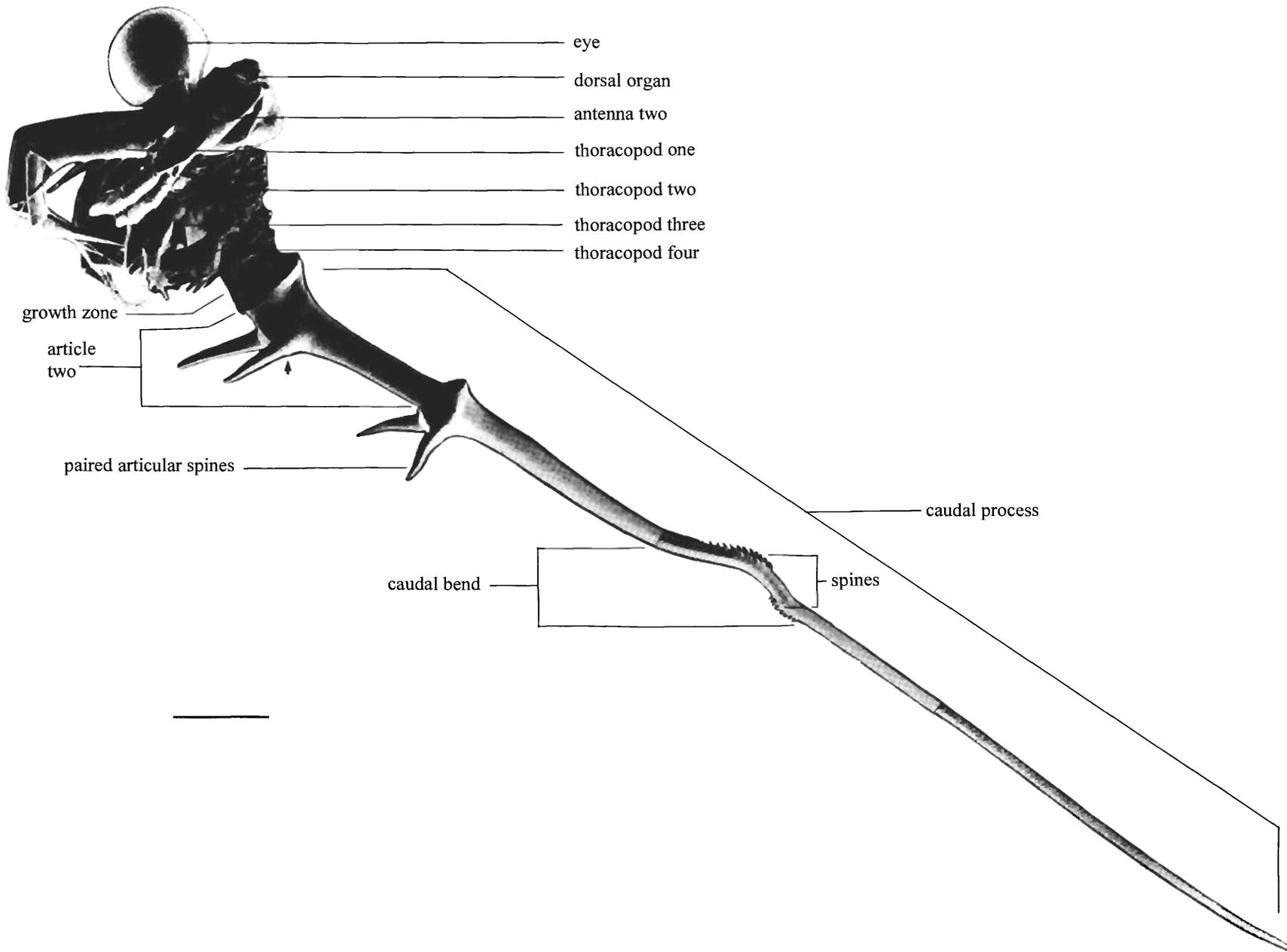


Fig. 1.—S.E.M. montage of *Bythotrephes cederstroemi* 'form' from the Laurentian Great Lakes of the United States. Female, left lateral view. Some distortion of anterior region is evident from shrinkage of tissue during preparation (compare with Fig. 3). Arrow denotes location of functional anal opening. Scale bar 500 μ m.

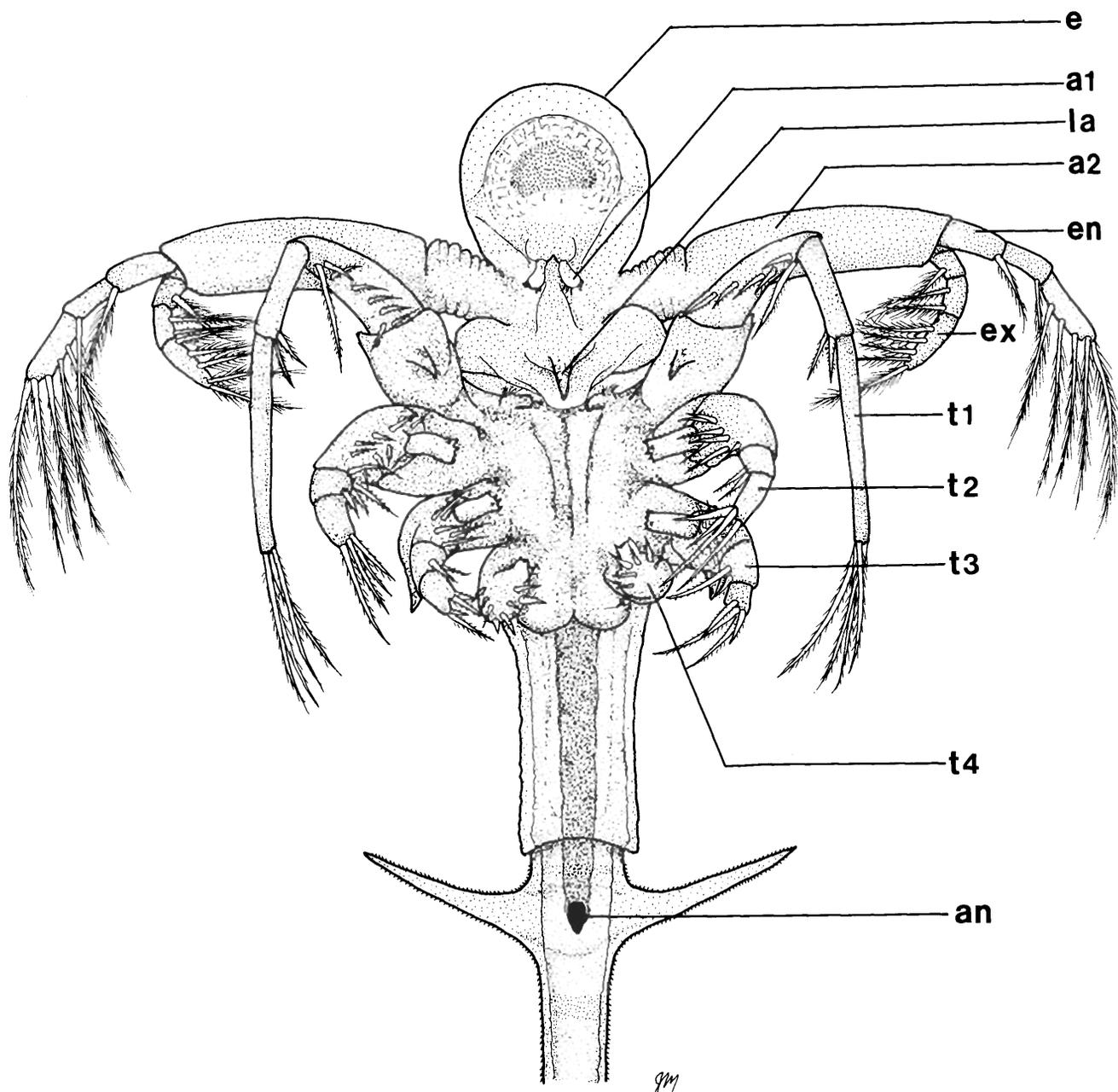


Fig. 2.—*Bythotrephes cederstroemi* 'form', ventral view of anterior region of a 10 mm (total length) female.

and anterior to the region where the reduced carapace valves form the brood pouch (e.g., Leydig 1860; Lilljeborg 1901; Gicklhorn and Keller 1925). Fusion of thoracic components makes it difficult to determine to which somite this organ belongs. As in other branchiopods in which such an organ has been reported, it is delineated from the surrounding cuticle by a raised cuticular border (Fig. 8D), and the difference in thickness between the cuticle overlying the dorsal organ and that of the surrounding cuticle is evidenced by the different degree of distortion of the cuticle caused by preservation and drying (Fig. 8D). The function of the dorsal organ is not known, but we assume that it is primarily an osmoregulatory device, as is the case with most other branchiopods and indeed for other onychopods where known (see Potts and Durning 1980; Martin and Laverack 1992; Martin 1992; Walossek 1993).

Carapace valves and brood pouch. The usual explanation for the lack of a well developed bivalved carapace (= secondary shield of Walossek 1993) in onychopods is that

the valves have been reduced and function only as a dorsal brood pouch in females. This condition is readily visible in adult females (Fig. 3). Its surface is smooth (Fig. 3), but invariably displays wrinkling upon preparation (dehydration) for S.E.M., evidence of the thin nature of the cuticle. The posterior and ventral region always appears to be indented. According to Mordukhai-Boltovskoi (1968), cercopagidids differ from polyphemids and podonids in that in the latter two families there is a true 'shell', which is lost in cercopagidids so that what remains is a thin and very flexible 'chitinous membrane' (Mordukhai-Boltovskoi 1968: 203). This thin cuticular covering expands to accommodate the growing embryos (some visible in Fig. 3), and is shed upon release of the young, after which the female grows a new one (Mordukhai-Boltovskoi 1968, Yurista 1992). The appearance of a similar, but smaller, dorsal outgrowth of the cuticle in males is more difficult to explain, but is possibly a phylogenetic remnant of a time when onychopods exhibited paired carapace valves more in keeping with those seen throughout the non-predatory cladoceran groups.

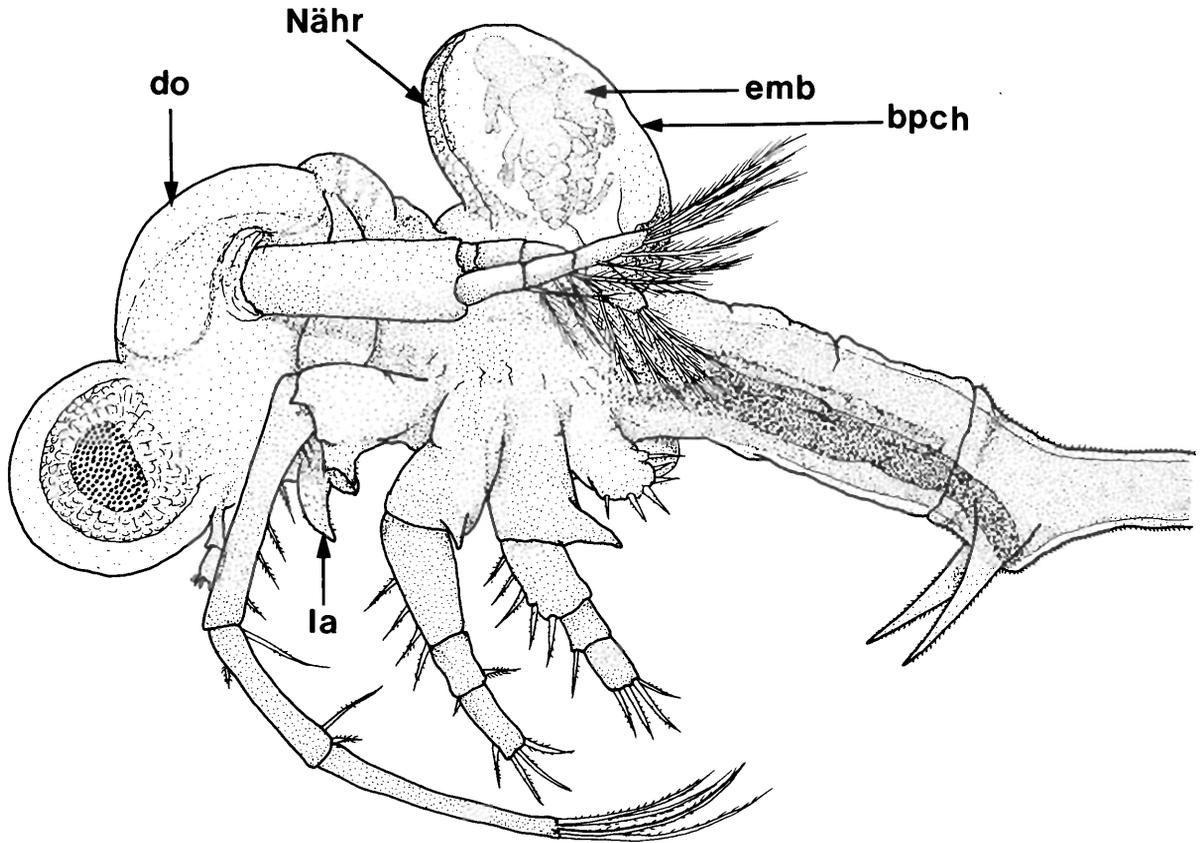


Fig. 3.—Same animal as in Fig. 2, lateral view of anterior region showing dorsal brood pouch containing Nährboden and developing embryos.

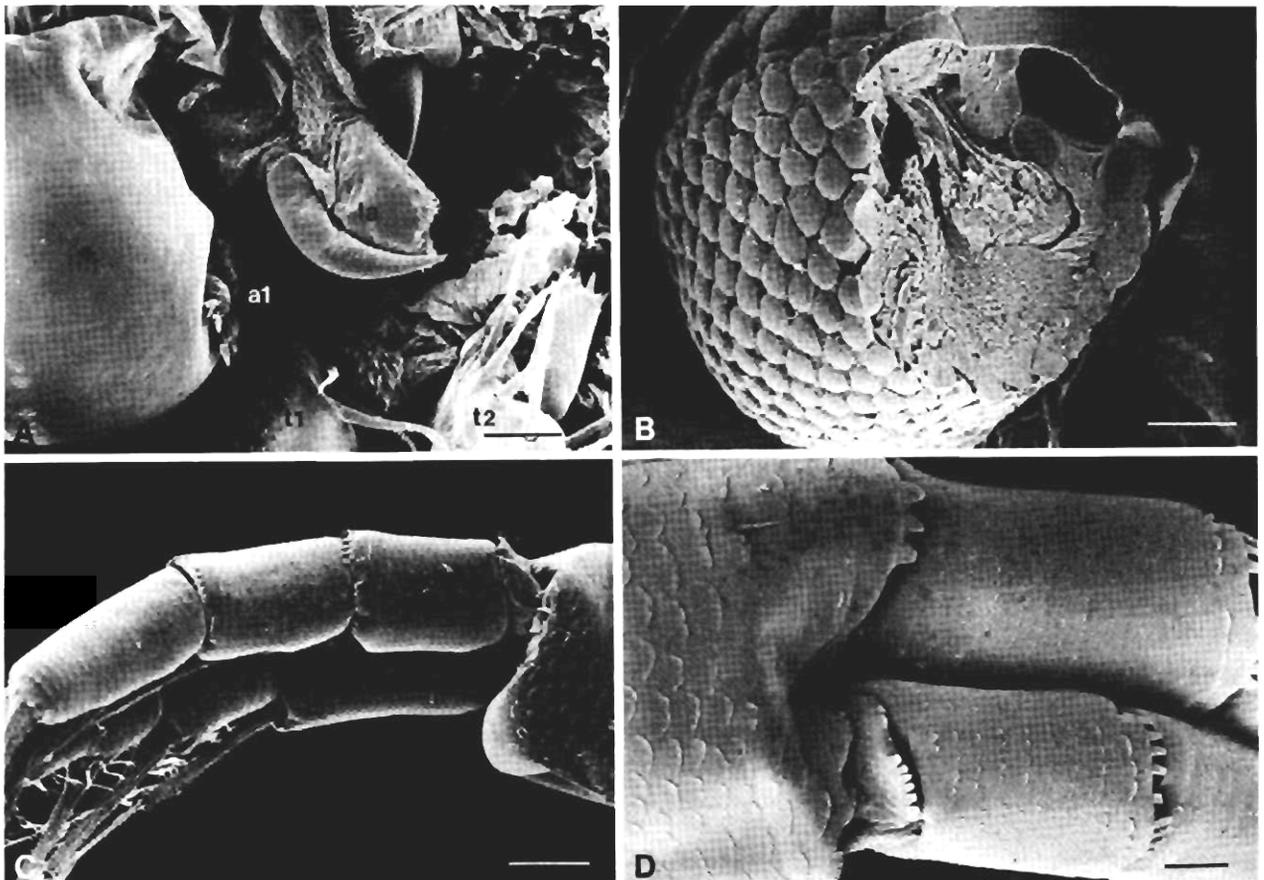


Fig. 4.—A. Anterior region, lateral view of animal showing compound eye (at far left), antennules, bilobed labrum, and gnathobasic process at the base of thoracopods 1 and 2.—B. Compound eye with overlying cuticle removed, exposing ommatidia.—C. Lateral view of base of exopod (foreground) and endopod of left second antenna. Note reduced first segment of exopod.—D. Dorsal view of right second antenna. Note scales occurring around basipod and segments of both exopod (bottom of figure) and endopod. Scale bars: A 100 μ m; B 50 μ m; C 50 μ m; D 25 μ m.

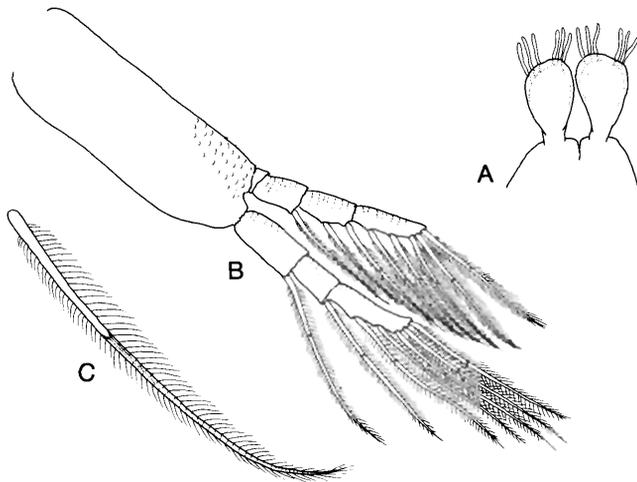


Fig. 5.—A. Antennules.—B. Antenna (4-segmented exopod at top).—C. Natatory seta (from first segment of endopod) enlarged. Figures not to scale.

Antennule. The antennules (Figs 2, 3, 4A, 5A) arise from a small bilobed protrusion of the 'head' cuticle that has been essentially overgrown by the compound eye. Each is pear-shaped, being widest distally, and is covered by very thin cuticle, as evidenced by the extensive shrinkage and distortion in S.E.M.-prepared individuals (e.g., Fig. 4A). The distal surface of each typically bears 6 aesthetascs, arranged in two clumps of 3 setae each (Fig. 5A).

Antenna. The second antenna (Figs 1, 2, 3, 4C, 4D, 5B) is a large, natatory appendage (true for all Onychopoda). Both rami are well developed, the endopod with three and the exopod with four segments. The first article of the exopod is reduced and is visible mostly from a dorsolateral perspective (Figs 3, 4C, D, 5B), as the posterior side of this segment is poorly developed and tends to merge with the articulating soft cuticle of the following segment. Small cuticular scales (Fig. 4D) occur in regular rows around the basipod and around all of the cylindrical segments of the endopod and exopod. Additionally, each segment bears distal blunt, nearly rectangular teeth (Fig. 4C, D), which vary in degree of development, spacing, and number among individuals. (Thoracopods also bear terminal spine-like teeth at the base of the more distal article and are never of the blunt, rectangular type seen on the distal border of all of the antennal segments.)

The natatory setae (Fig. 5B, C) are long and plumose. The number of setae on each ramus (branch) of the antenna has been used as a distinguishing characteristic to separate the genus *Bythotrephes* from *Cercopagis* (e.g., Sars 1897; Mordukhai-Boltovskoi and Rivier 1987). According to the key of Mordukhai-Boltovskoi and Rivier (1987), there are 7 setae on each ramus in *Cercopagis*, but 8 on the outer ramus (exopod) of all species of *Bythotrephes*. In *Bythotrephes*, setation is as follows (proximal to distal): exopod 0, 1, 2, 5; endopod 1, 1, 5. In both rami, the 5 setae of the distalmost segment are arranged as 3 terminal plus 2 subterminal setae.

The difference in number of natatory setae between the genera concerns the third segment of the exopod, which bears one terminal and one subterminal seta in *Bytho-*

trephes vs only one seta in *Cercopagis*. However, in Leydig's (1860) original description of *Bythotrephes* (*B. longimanus*), only 7 setae are illustrated on each branch, and similar inconsistencies in setal number among the many other illustrations of species in these genera have appeared over the years. As noted by Muller (1876) and Lilljeborg (1901), Leydig's illustrations were based on macerated specimens from the stomachs of fishes, and therefore cannot be considered reliable. As we did not examine a large series of individuals in both genera, we cannot comment on the reliability of this character as a generic diagnostic feature, although we include it in our diagnosis of *Bythotrephes*, following the work of Sars (1897) on *Cercopagis* and Mordukhai-Boltovskoi and Rivier (1987) on all predatory cladoceran taxa. In specimens examined by us, number and location of natatory setae did not vary.

Labrum. The labrum is a very distinctive feature of the genus. It is a large, fleshy, bilobed protrusion that extends downward, backward and over the mandibles (see Figs 3, 4A, 6, 7). The anterior lobe is the longer, is basically conical, and extends ventrally and posteriorly past the tip of the posterior lobe (Fig. 7A, B). It bears numerous small spines, often in pairs, scattered along its entire length (Fig. 7A, B). Its tip bears a small pore, probably the exit duct of one of the labral glands (Fig. 7D, E), which is surrounded by teeth that are slightly more stout than the paired setae found along the length of the lobe (Fig. 7C, E).

The posterior lobe is clearly separated from the anterior lobe by a deep indentation of the cuticle (Fig. 7A). It is not conical, but thicker and more flattened in an anterior-posterior direction. Its anterior surface is smooth, and bears a low medial ridge that fits neatly into a corresponding indentation on the posterior side of the anterior lobe. Its posterior (oral) surface, and to some degree the lateral borders, bear a dense covering of setae (Figs 7D, F, 8A). Its lateral margins extend outward, and the medial portion extends backward, such that the mandibles, viewed from below, are completely covered by it (Fig. 6). Its posterior face is deeply indented and bears curved rows of simple spine-like outgrowths of the cuticle (Fig. 8B), all of which are directed upward toward the mouth. Toward the base of this lobe, the spines converge in a whirlpool-like configuration (Fig. 8C); the significance of this arrangement of spines is not known.

Both anterior and posterior lobes contain musculature, readily visible using light microscopy, so independent movement of each is possible (although we have not documented it).

Mandible. The mandible (Figs 6, 8E, F, 9, 10), of which only the coxa remains, is a heavily sclerotized appendage obviously adapted for biting. It is bilobed, with a toothed, blade-like posterior lobe and a heavily armored 'mandibular process' forming the anterior lobe (Figs 9A, 10A).

The posterior lobe is a heavily sclerotized, bifid, tooth-like process. The lower (posterior) branch is the heavier of the two, and bears a smaller tooth about midway along its anterior border (Fig. 9B).

The anterior lobe of the mandible, herein termed the

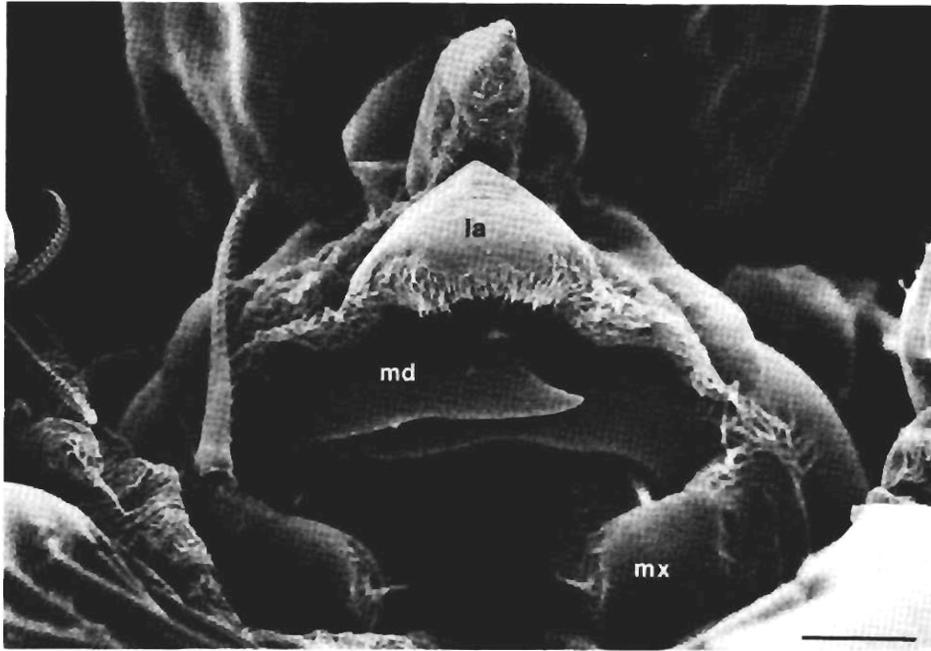


Fig. 6. Posterior view of entire mouthfield, looking anteriorly from sternum and showing anterior and posterior lobes of labrum, overlapping right and left mandibles (lettering is on right mandible), and right and left maxillae or maxillues (?; see text). Large spinulose seta appearing to extend from top of right maxilla is an artifact; this seta broke away from the first thoracopod. Large structure in background is compound eye. Scale bar 50 μm .

mandibular process (mp) (Figs 9A, 10A) (following Lilljeborg, 1901), is a stout, cylindrical outgrowth that bears a cluster of up to 30 strong, heavily toothed spines (Figs 9C, 10C). These spines are almost always slightly curved, and bear strong teeth along the curved portion. All spines are oriented in the same direction—i.e. the axes are more or less parallel—but individual spines may be rotated slightly to different degrees, such that the teeth face in all directions (Figs 9C, 10C).

The inner surface of the mandible bears from 20 to 30 short, simple spines or setae, mostly in a small field at the base of the larger tooth of the posterior lobe (Fig. 10B, D). A few spines continue in a curved line up the base of the weaker (anterior-most) tooth.

The dorsal external extremity of the mandible contacts the head cuticle in the form of a strong conical tip, which is the point of articulation of the mandible in other branchiopods with rolling/grinding types of mandibles (e.g., see Martin 1989 for conchostracans). However, in *Bythotrephes*, this conical tip appears to be fused with the head cuticle (Fig. 8E, F).

Maxilla. We detected a single maxilla (Figs 6, 11A–C). The proximal portion appears flaccid, usually wrinkling somewhat during the drying process, and bears a row of simple setae along the slightly elevated anterior border, where it is in contact with the lateral bend of the mandible (Fig. 11A). More distally, it is somewhat inflated, with its outer (posterior) face completely smooth. Its distalmost tip bears an unusual arrangement of small spines and setae (Fig. 11A, B). The small spines are arranged in a semicircular pattern around the anterior edge of a circular depression, which appears to be weaker or thinner than the surrounding cuticle. Emerging from the center of this depression is an elongate cuticular extension (seta?) that is open at the tip. The entire complex suggests the

possibility of glandular secretion, or perhaps excretion, if what we have found is in fact the opening of the maxillary gland shared by other branchiopods.

The salient question, and one we have not attempted to address, is whether the single existing maxilla is the first maxilla or the second. If this is the first maxilla (maxillule)—as usually assumed, as for example by Fryer (1987b) and Martin (1992)—then there is a question as to what this distal opening is, for the maxillule in branchiopods is not known to contain secretory or excretory components. If, however, it is the second maxilla, then the terminal opening could be that of the efferent duct of the maxillary gland, in which case the genus is unique in the Branchiopoda in the loss of the *first* maxilla and retention of the second. There is also the question of where the opening for the maxillary gland might be if this is *not* the second maxilla. Onychopods possess a maxillary gland (see Martin 1992; 127, fig. 72) which supposedly opens on the maxilla in all groups, but that must, of necessity, open on the body wall if the appendage is lost. We have not located another opening on the body wall, but it is extremely difficult to examine the ventral sternal cuticle between the mandible and single remaining maxillule/maxilla; this area is delicate and subject to distortion, and a single slit-like opening could easily be missed.

Food groove. By definition, onychopods are supposed to lack a true sternal thoracic food groove as is found in non-predatory cladocerans (Fryer 1987a, b) and in the ground pattern of branchiopods in general (Walossek 1993). In *Bythotrephes*, we repeatedly encountered a slight median depression running the length of the thoracic sternal cuticle and leading to the mouth (Fig. 11D). The sternal cuticle is thin and flexible here, and wrinkling caused by drying might explain this feature. However, its constant

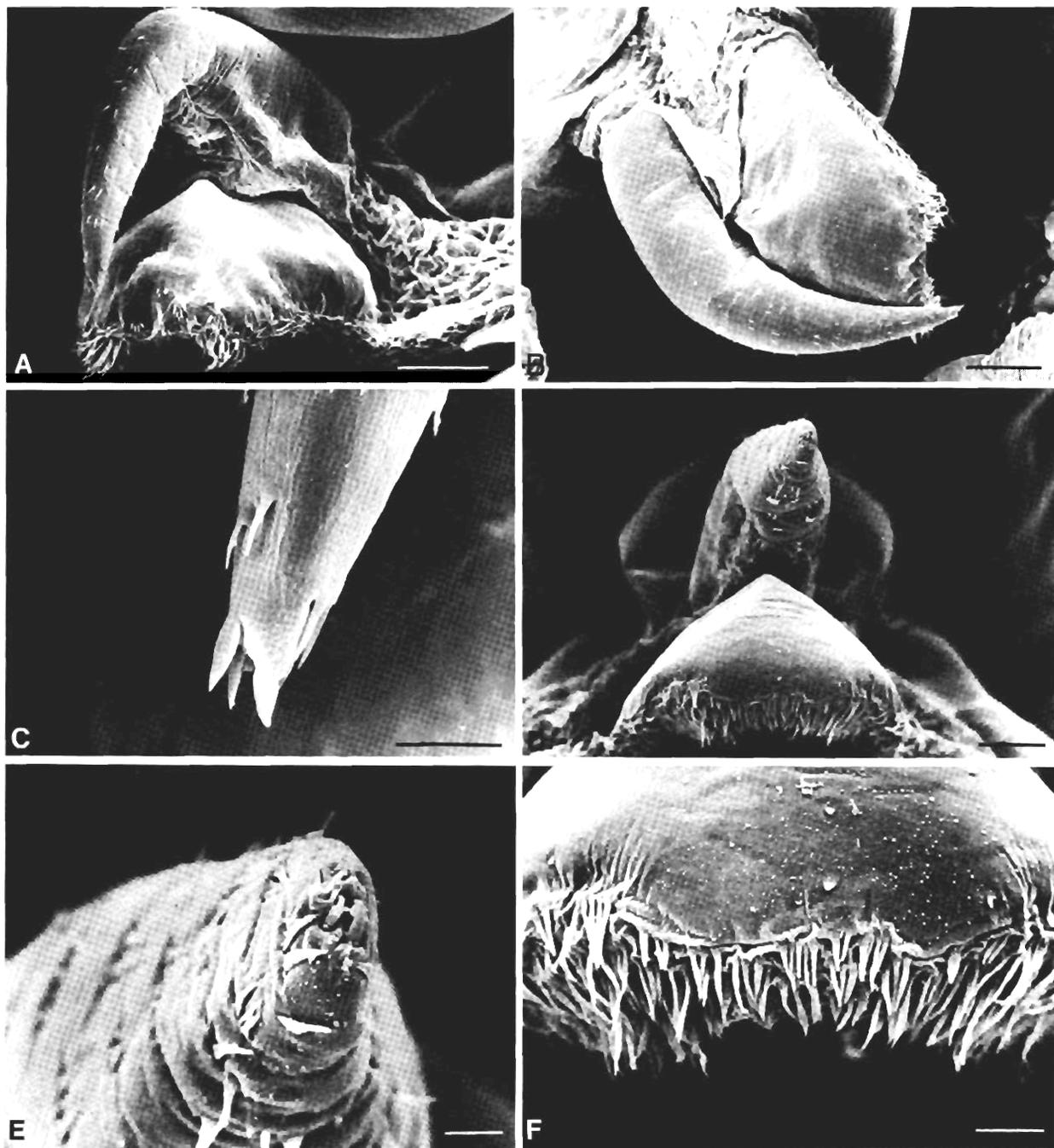


Fig. 7. Labrum.—A. Ventrolateral view of anterior (uppermost) and posterior lobes.—B. Lateral view of both lobes.—C. Tip of anterior lobe showing stout spines.—D. Ventral view showing setation of posterior lobe and opening at tip of anterior lobe. Note conical shape of anterior lobe and thicker and more flattened shape of posterior lobe.—E. Pore at distal tip of anterior lobe.—F. Dense mass of setae covering posterior and lateral borders of posterior lobe shown in D. Scale bars: A 50 μm ; B 50 μm ; C 10 μm ; D 25 μm ; E 5 μm ; F 10 μm .

occurrence in the same location and orientation lead us to believe that this groove is not an artifact of preparation. If we have correctly interpreted this structure as the remnant of a former food groove, almost undoubtedly non-functional in its present state, and considering that this is a strictly predatory species, then it is a character that is supportive of the derivation of the onychopods from non-predatory ancestral 'cladoceran' stock.

First thoracopod. The first thoracopod (Figs 12, 13, 14A–C, 15) is a long, well developed, stenopodous appendage. It is composed of four segments, the second and fourth being the longest. It is possible that another segment, more basal than the one that we are calling the first, exists;

such was tentatively suggested by a number of earlier illustrations (e.g., see figures in Lilljeborg 1901: pl. 82). Because of the wrinkling and other distortion during the drying process of the very thin cuticle that surrounds the base of each leg, it is possible that this segment has been overlooked. We did not detect a more basal segment in either S.E.M. or light microscopy preparations. If such a segment does exist, this would necessitate renumbering the segments of each leg in this paper.

The basal (first) segment (see Fig. 13) is short and apparently covered with slightly softer cuticle than are more distal segments, as it tends to compress more than the latter upon dehydration. Its medial side bears a small, triangular lobe armed distally with short spines and setae

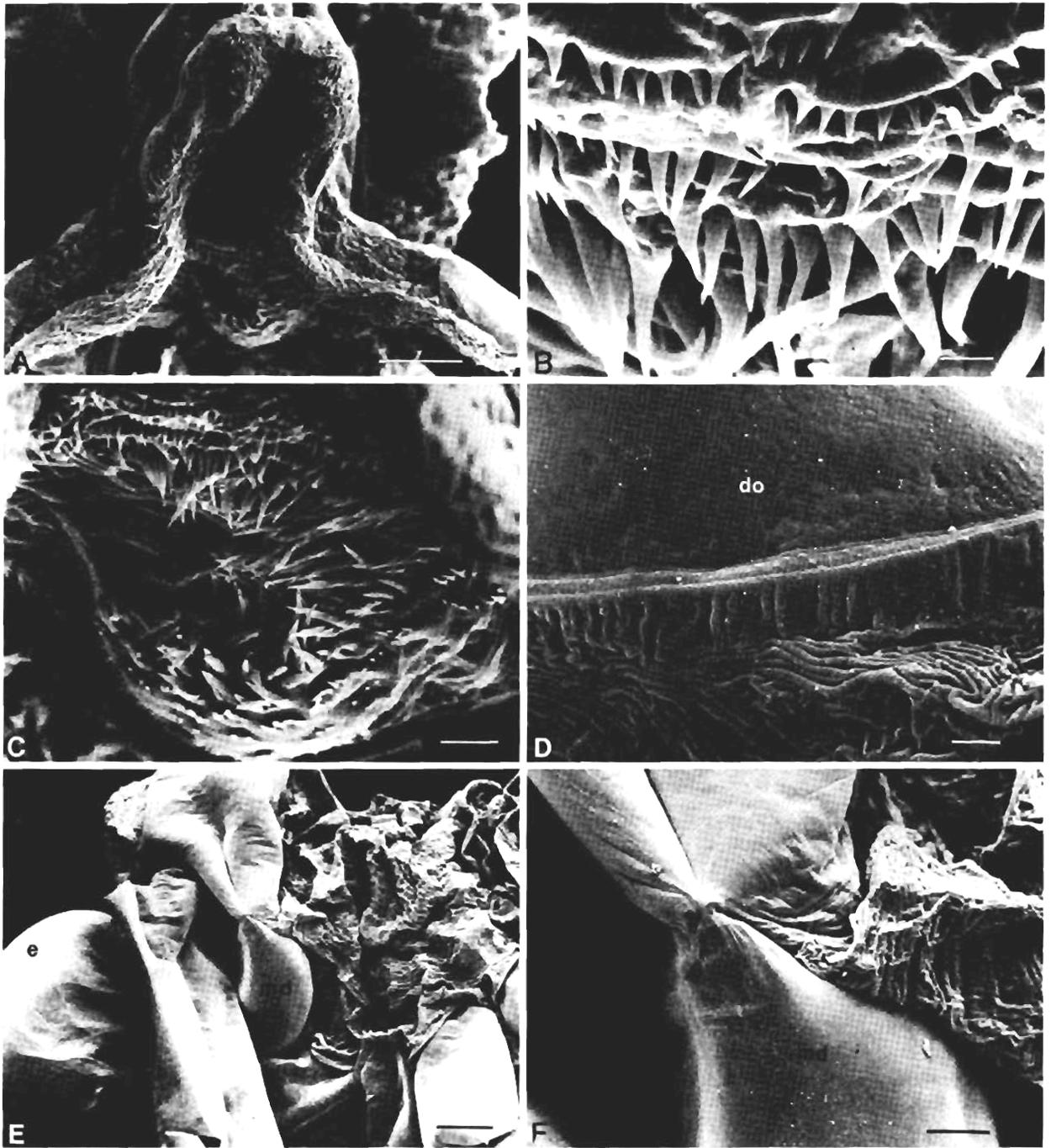


Fig. 8.—A. Labrum, posterior surface of the posterior lobe; orientation of photograph as in Fig. 6.—B. Spine-like outgrowths arranged on deeply indented posterior surface of posterior lobe of labrum.—C. Convergence of spines in whirlpool-like configuration, possibly indicating the mouth opening (see text).—D. Cuticular border of dorsal organ, showing difference in cuticular thickness as evidenced by wrinkling.—E. Anterior region, lateral view of animal showing dorsal external extremity of mandible in contact with cuticle of thorax/head.—F. Higher magnification of external region in which mandible appears to fuse with head cuticle. Scale bars: A 50 μm ; B 2.5 μm ; C 10 μm ; D 5 μm ; E 100 μm ; F 25 μm .

(Figs 13, 14A), just distal to which lies another cluster of small setae. Although this lobe does not appear to be homologous with the stouter proximal endites of the more posterior three pairs of legs, it is probably analogous, functioning in some way to direct food toward the mouth field. If it is to be considered the equivalent of the proximal endite or gnathobasic process seen on more posterior legs, then compression and fusion of thoracopodal segments must have occurred, as the more posterior leg endites clearly arise from a more distal segment (see below). The external face of the basal segment bears a small, ventrally directed, more or less conical spine (Figs 13, 14, 16A), bearing at its tip a minute single seta, which

we are terming the exopod. Although there is room for questioning our identifying this seta-tipped spine as the true exopod (D. Walossek, personal communication), there seems to us to be a rather clear transition within the onychopods from larger, setose exopods, such as those of *Polyphemus*, to smaller exopods bearing a single distal seta (e.g., *Podon* and especially *Evadne*; see Fig. 22, thoracopod 2 comparison).

The second segment is approximately 4 times as long as wide (width measured at midpoint of the segment). Its surface is covered with small cuticular scales (as described previously for the second antenna) and scattered small setae, especially on the dorsolateral surface. The medial

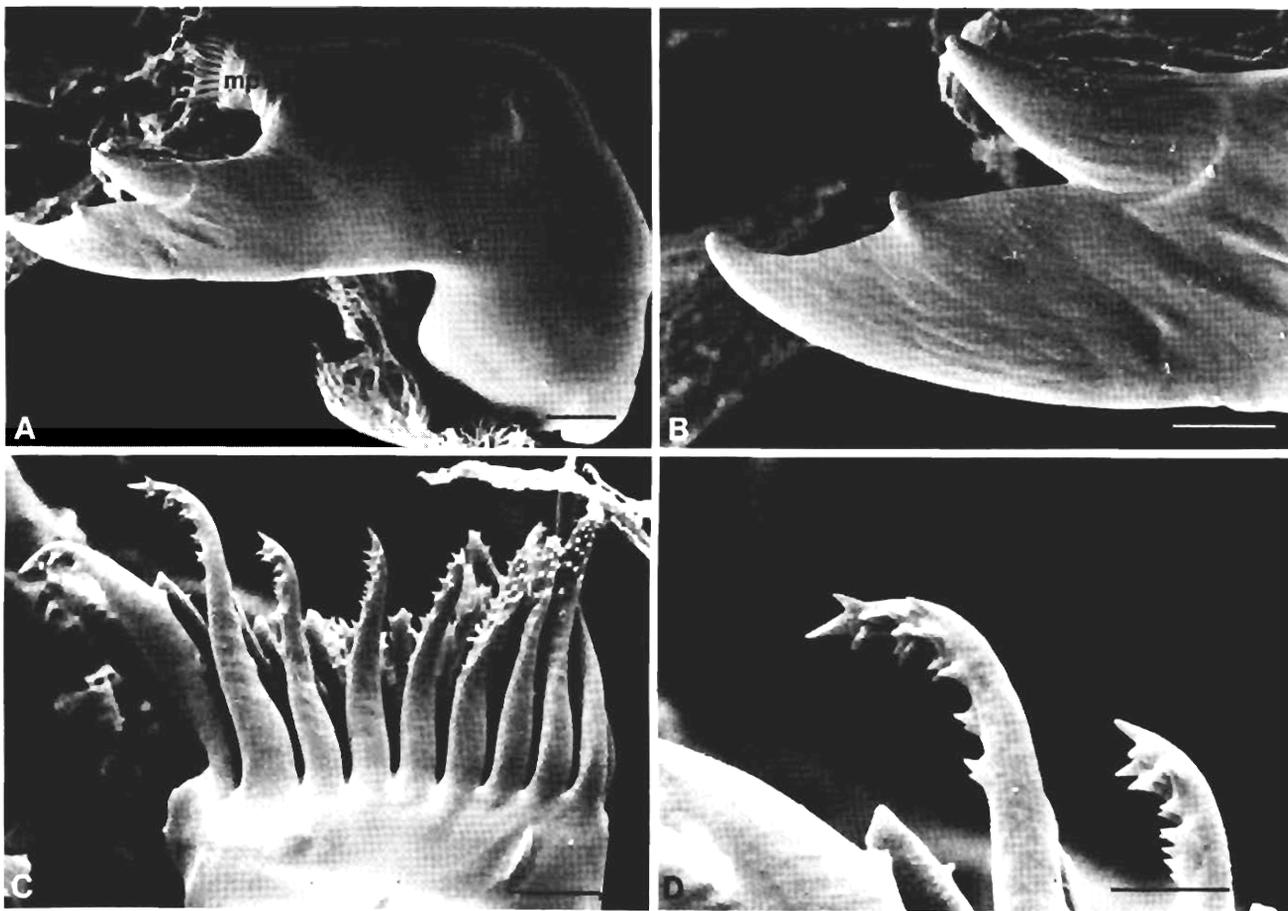


Fig. 9.—A. Outer face of left mandible showing lower blade-like posterior lobe and anterior lobe with spinose mandibular process.—B. Posterior lobe showing bifid toothed blade.—C. Anterior lobe showing heavily armored mandibular process.—D. Heavily toothed spine of mandibular process. Scale bars: A 50 μm ; B 25 μm ; C 10 μm ; D 5 μm .

surface is armed with 7 or 8 well developed spine-like setae, each of which bears numerous spinules (Fig. 15A–D). Two of these setae are located basally, and another two at the distomedial border, such that a row of four large spine-like setae remain along the medial border (Figs 13, 14A). These bear several (usually 4) rows of spinules along the distal half of the setal shaft, and are often slightly sinuate. The central two rows of spinules are stouter than those of the flanking rows, with each stout spinule curving distally, away from the base of the setal shaft (see Fig. 15D). Basally, each spine-like seta is buttressed on the external side by a strong piece of cuticle arising from the appendage surface (Fig. 15C); this arrangement allows movement (flexing) of the seta in a medial plane, but restricts outward movement beyond the position where the shaft is approximately at a 90° angle to the leg. Of the distalmost pair of setae, one is similar to the stout spine-like setae just described, whereas the other is longer, more slender, and nearly smooth (Figs 13, 14B).

The third segment is shorter, is similarly covered with cuticular scales, and bears only two setae located on the distomedial border (Fig. 14B). This pair of setae resembles the distalmost pair of the preceding segment, in that one of these setae is armed with rows of spinules along the distal half of the shaft, whereas the other is long, slender, and nearly smooth.

The fourth segment is nearly equal in length to the second, and bears 4 long setae (2 ultimate, 2 penultimate)

at its terminus. These arise from slight outgrowths of the leg cuticle, and are buttressed on the proximal side by a toothlike process that forms the outer face of the setal socket (Fig. 16C). These four setae are long, occasionally exceeding the length of the fourth segment itself. The proximal half bears minute setules. The distal half, set off from the proximal half by a distinct annulus at the approximate midpoint of the seta, bears heavier, immovable spinules (Fig. 14C and S.E.M. inset). Like segments two and three, the fourth segment is covered with minute cuticular scales (Figs 14C, 16C).

Second thoracopod. The second leg (Figs 13, 14D) is about half as long as the first, and, although stenopodous, differs from the first in a number of respects.

Along the outer face the horizontal line of articulation between the first and second segments is apparent (e.g., Fig. 17B, upper right corner). The basal segment bears a conical exopodal spine on its external face, similar to that of the first thoracopod but slightly larger (Figs 14D, 16A). Like that of thoracopod one, it has a single minute seta at its tip (Fig. 16B). On the medial side of the leg, the suture separating the two segments is more difficult to see, in part because it does not lie in the same horizontal plane as it does externally. Here it extends upward and over the gnathobasic process (proximal endite) (Figs 13, 14D). Most previous authors have illustrated the proximal endite as coming off segment 1 (e.g., Leydig 1860) or arising from somewhere between segments one and two,

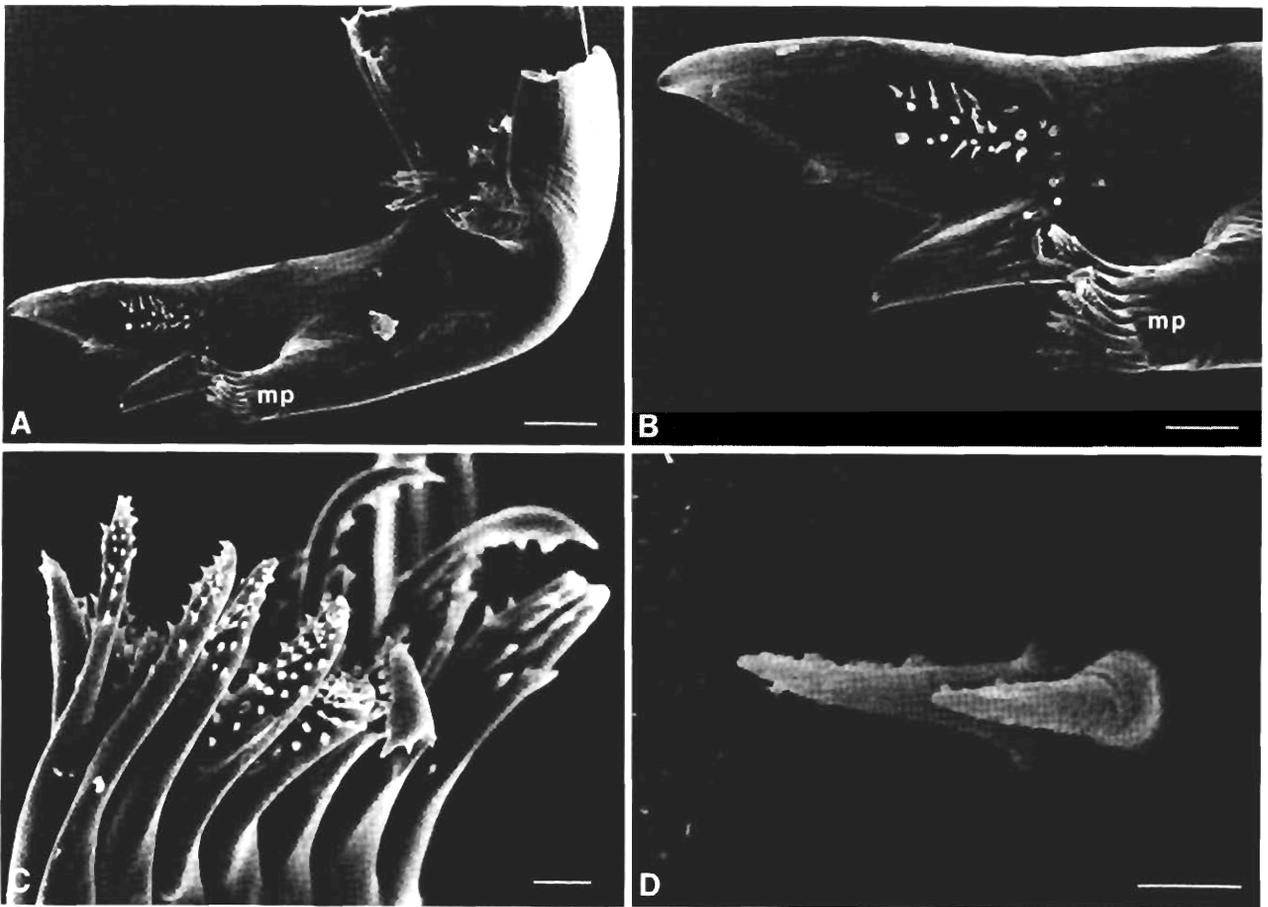


Fig. 10.—A. Inner face of left mandible showing anterior and posterior lobes from an anterior perspective.—B. Small spines on inner face of blade-like posterior lobe.—C. Mandibular process of anterior lobe, inner side.—D. Short simple spines on inner face of posterior lobe (see in B). Scale bars: A 50 μm ; B 25 μm ; C 5 μm ; D 2.5 μm

although Lilljeborg's (1901) Pl. 82, fig. 4 is correct. S.E.M. shows clearly, however, that the gnathobasic process articulates with, and arises from, the more distal segment (segment 2). This means that the gnathobasic process on this leg and the following leg cannot be considered homologous with the triangular lobe that appears to fulfill the same function in leg 1. In thoracopod 2, the process arises from the posteromedial side of a long, low ridge of cuticle, which bears 4 or 5 spine-like setae distal to the process. This very stout gnathobasic process (proximal endite) clearly articulates with segment 2 (Figs 12, 13, 14D, 17A, B), is approximately three-times as long as wide, and bears at its distal (medially directed) end a series of stout, conical spines and teeth (Fig. 17C, D), which are larger toward the posterior side of this biting tip.

The second segment, which again appears almost fused to the basal article when viewed medially (because of the curved suture line) but distinct in lateral (outer) view, bears 9–11 serrate spine-like setae (Figs 13, 14D, 17A, B) along the medial face, similar to those of the first thoracopod. These are buttressed by thickened cuticle to allow flexing only toward the midline, and bear minute spinules in two or three rows along the setal shaft.

The third segment is shorter than the combined first and second segments, and bears but two subterminal spinulose spine-like setae. One of these is shorter and stronger than the other, is different from the previously

mentioned setae, and bears the stout, anteriorly directed setules described for the spine-like setae of thoracopod one (see lower S.E.M. insert, Fig. 13). The other is longer, and is minutely setulose (Fig. 14D).

The distal (fourth) segment (Figs 13, 14D, 16C) bears 4 spinulose setae, 2 terminal and 2 subterminal, each arising from a slight elevation in the surrounding cuticle, and each buttressed by a sharp, triangular spine-like extension of the cuticle (Figs 14D, 16C). Each pair consists of one short seta similar to those on segment 1, and 1 long seta of the same type found on the distal segment of thoracopod 1. All segments, but particularly the distal two, are covered with minute cuticular scales directed distally (Fig. 16C).

Third thoracopod. The third leg differs only slightly from the second. It is slightly shorter, and bears a nearly identical gnathobasic process on the medial face of the second segment (Figs 12, 13, 17B). As in thoracopod two, the suture line separating segment 1 from segment 2 curves up and over the gnathobasic process, making it difficult to distinguish exactly where the dividing line is. The gnathobasic process (proximal endite) articulates with the leg, bears stout spines that increase in size toward the posterior edge of the biting tip, and has approximately the same length/width ratio as in thoracopod 2 (Figs 13, 17B). The number of setae on each segment is also similar to what was described for leg 2, although there are fewer

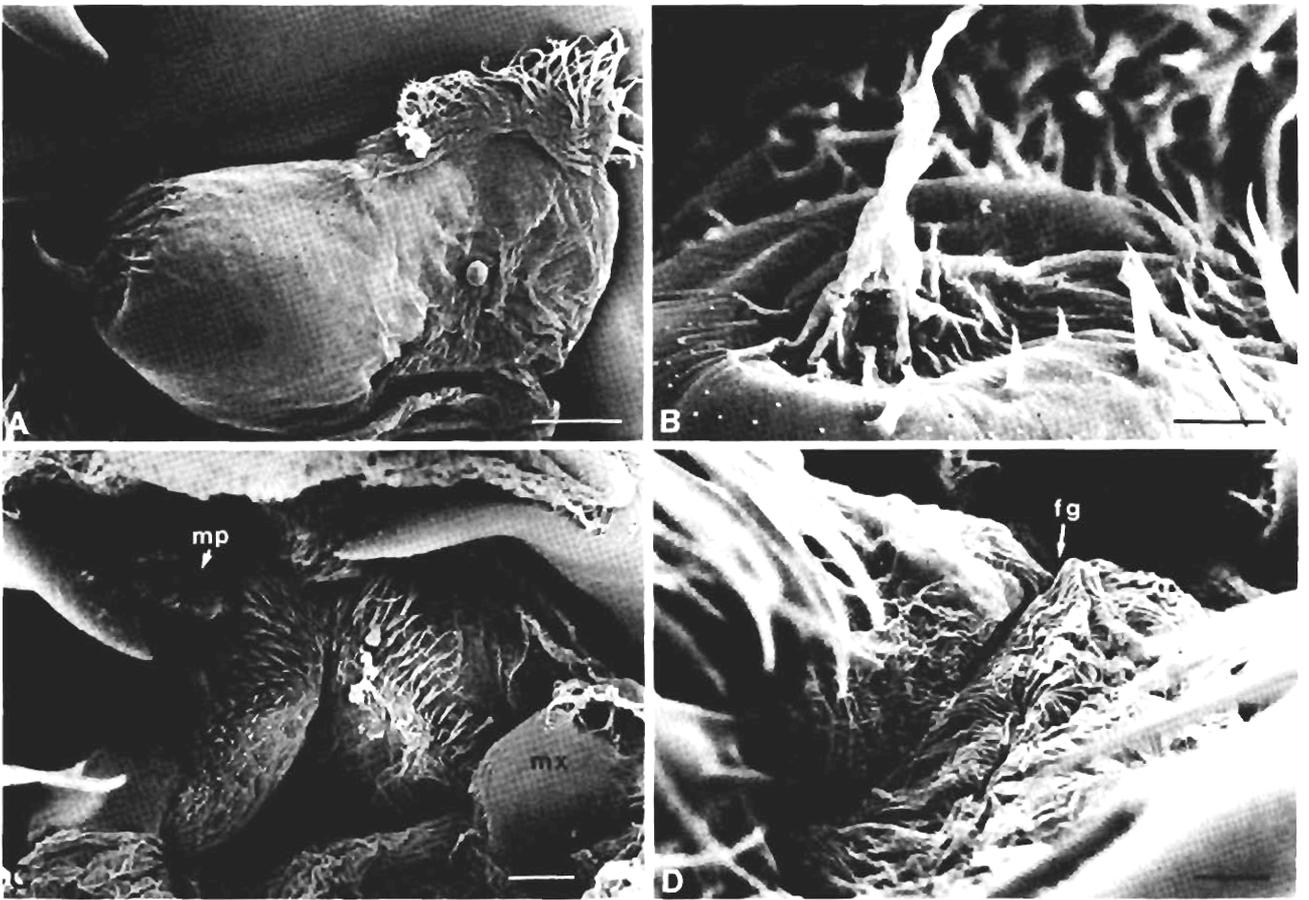


Fig. 11.—A. Left maxilla, postero-ventral view; mandible in background. Note inflated distal region and its circle of spines and setae.—B. Tip of maxilla showing circle of setae and possible exit duct in centre.—C. Opening to mouth.—D. Food groove on ventral surface of thoracic sternum. Scale bars: A 25 μ m; B 5 μ m; C 25 μ m; D 25 μ m.

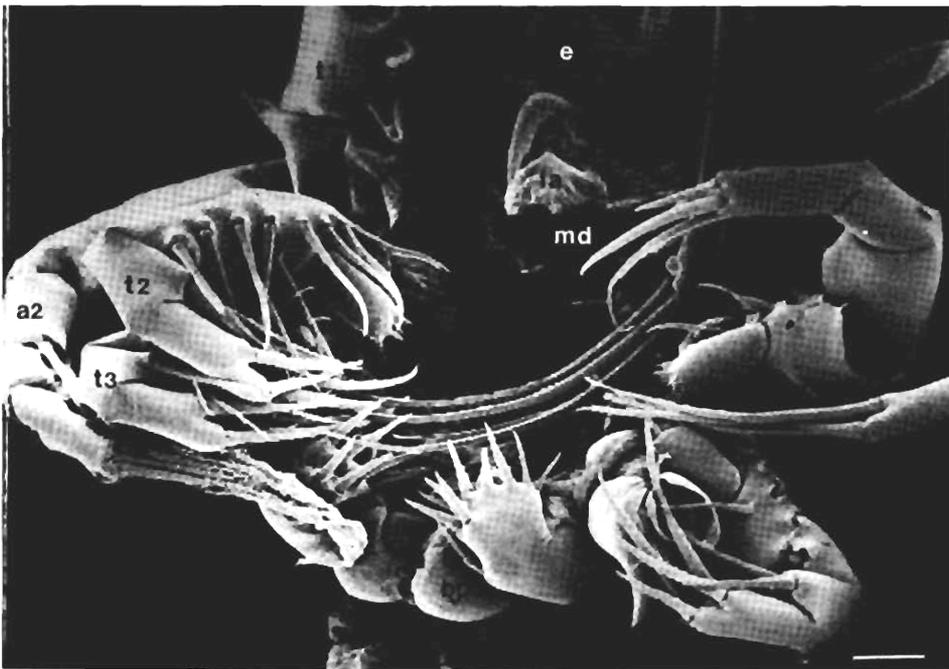


Fig. 12.—Posterior cephalic and thoracic regions, ventral view showing labrum, mandibles, antenna, and thoracopods 1–4 forming 'grasping basket'. Note also bulbous process posterior to thoracopod 4. Scale bar 125 μ m.

setae on segments 1 and 2 (a total of 7 or 8, vs 9–11). The distal two segments are nearly identical in their armature and arrangement and type of setae, buttressing spines, and cuticular scales. One notable distinction is that in the

third leg, the exopodal spine is considerably longer and wider than in either legs 1 or 2 (Figs 3, 13, 17A). Its tip bears a minute but readily seen seta, thus serving to link the more anterior exopodal spines, which bear smaller

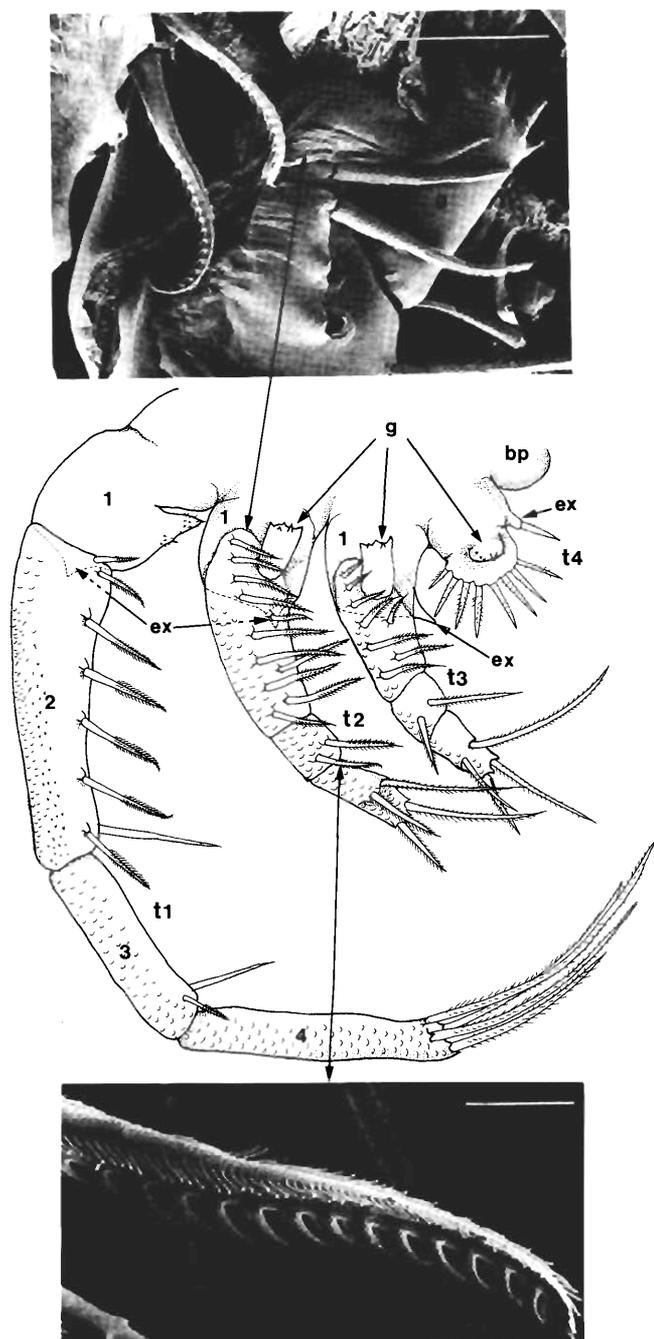


Fig. 13. The thoracopods, medial (inner) view, SEM insets show (top; scale bar = 100 μm) line of articulation between segments 1 and 2 of thoracopod 2, with gnathobasic process clearly arising from, and articulating with, segment 2, and (bottom; scale bar 20 μm) details of heavily spinulose spine-like seta always found as one of a pair of setae on segment 3 of thoracopods 2 and 3, and found also on segment 1 of thoracopod 1.

setae, to the more typical-looking exopod on the following (fourth) leg, and establishing the exopodal nature and derivation of these spines.

Fourth thoracopod. The fourth leg (Figs 12, 13, 14E, 18A–D) differs significantly from thoracopods 2 and 3. It is much smaller, and is composed of a single, inflated segment, although weak infoldings of cuticle suggest possible former segment boundaries. Distally it is armed with a circling of 7 or 8 heavy spine-like setae, each of which is slightly curved inward distally and armed with smaller spinules and setules. The armature on these setae

is slightly variable; some bear only scattered small spinules whereas others have well defined rows of equal-sized setules (Figs 14E, 18A, B). Two additional spine-like setae occur on the more external part of the distal border, outside the primary circling of spines. All of the spine-like setae are buttressed on the outer side of the socket by an extension of cuticle (Fig. 18A, B), allowing them to move only in an upward (i.e. toward the ‘food groove’ area) and inward plane.

On the posterior border of this leg, more or less in the same horizontal plane as the primary circling of spine-like setae, there is a single seta on a short, cylindrical, peduncle-like extension of the cuticle (Figs 13, 14E, 18A, 18D). This seta is not as robust as the more distal spine-like setae. The location of this seta-bearing peduncle, and therefore its similarity to the more spine-like process coming off the first segment of preceding limbs, especially leg 3, leads us to suggest that it is the remnant of the exopod.

The medial face bears a heavily armored and horizontally directed process (Figs 13, 14E, 18B, C), much as do thoracopods 2 and 3. However, here this process does not articulate with the appendage and is therefore immovable with respect to it—somewhat different from what is seen in legs 2 and 3. This process bears 4 or 5 denticles on the biting (distal) tip, the posteriormost of which is conical and the largest (Fig. 18B, C).

In preserved specimens, and we believe in life, the entire appendage is basally rotated so that the posterior seta-bearing tubercle (the exopod) is directed almost medially, toward the bulbous process (see below). As a result, the medial toothed gnathobasic process and all the spine-like setae are directed more anteriorly than medially, almost at 90° to the medial gnathobasic process of the third leg, with the two fourth legs together forming a posterior termination of the grasping basket formed by the legs (Figs 2, 12, 18A, B).

The external face of thoracopod 4 bears cuticular scales, but these are reduced and more widely scattered (Fig. 18B) than in legs 1 to 3.

There is no external basal spine on leg 4, but we believe that this spine, present on the anterior thoracopods, is represented by the cuticular peduncle on the postero-external face of this leg that bears a single seta.

Bulbous process. Posterior to the fourth leg in both males and females is a large, unsegmented bulbous process devoid of spines and setae (Figs 12, 13, 18A, C), a possible vestige of a former fifth thoracic appendage. Its function is unknown.

‘Abdomen’ and caudal process. A short region covered by thin, soft cuticle, and lying between the bulbous process and the currently functional article of the caudal process, has traditionally been termed the abdomen or metasome. The growth zone, where new somites are formed, occurs here (Fig. 1). The most distinctive feature of species of the Cercopagididae is the extremely long caudal process, sometimes referred to (incorrectly) as a caudal appendage. This feature has been well described for both *Bythotrephes* and *Cercopagis*, and is a key shared character in the separation of these genera from other onychopods

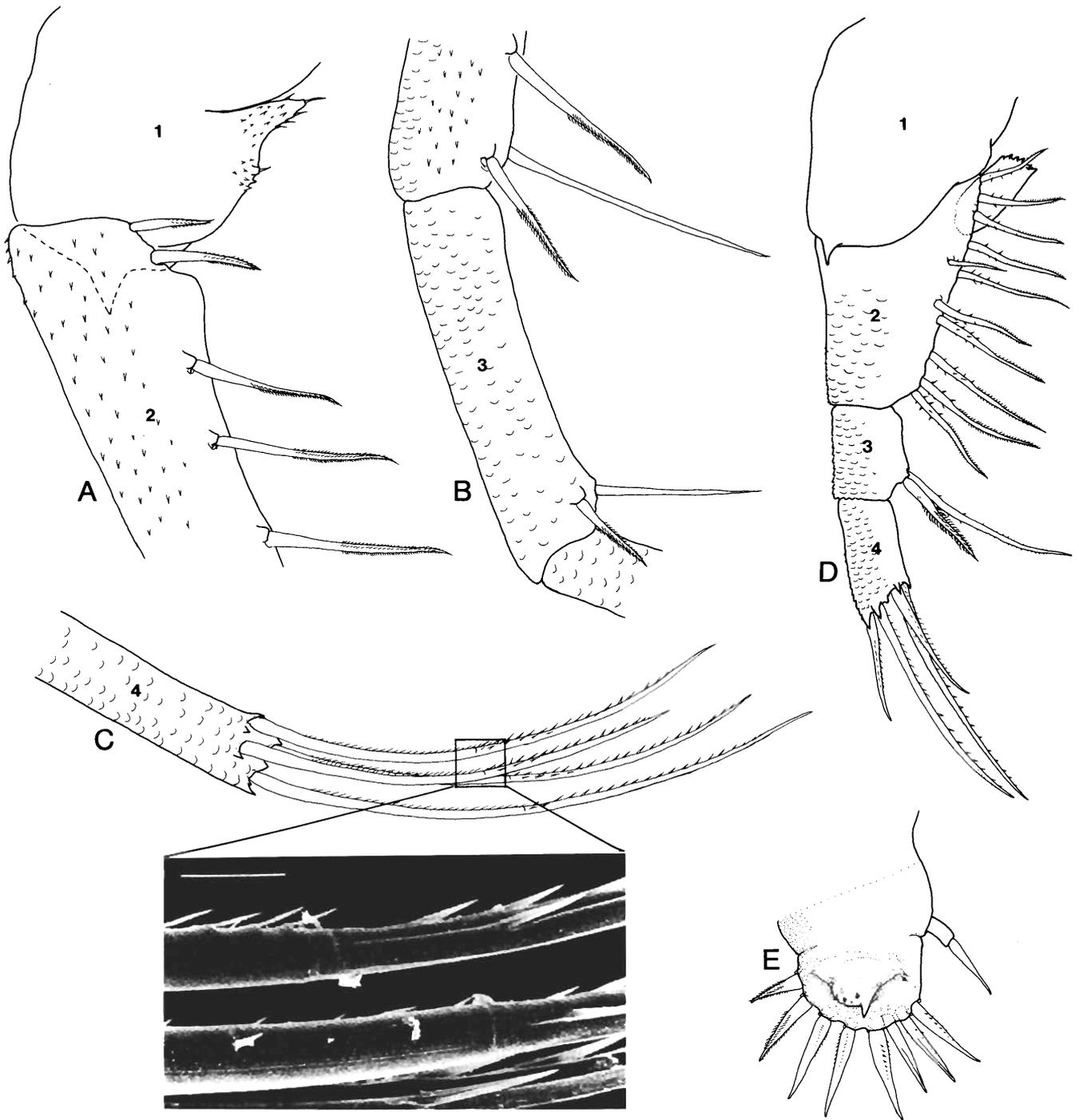


Fig. 14.—A. Thoracopod 1, segment 1 (with gnathobasic process directed toward right of figure) and part of segment 2.—B. Thoracopod 1, distal part of segment 2, and segment 3. Note pair of dissimilar spine-like setae at distal end of segments 2 and 3.—C. Thoracopod 1, segment 4, tip showing origination of four long spine-like setae and their morphology on either side of midlength annulus (S.E.M. inset).—D. Right thoracopod 2, viewed from anterior (looking backward at side of limb).—E. Thoracopod 4, from medial (inner) view. Scale bar $20\ \mu\text{m}$ for S.E.M. inset; others not drawn to scale.

(e.g., Mordukhai-Boltovskoi 1968; Mordukhai-Boltovskoi and Rivier 1987). In adults, the caudal process may exceed the length of the combined head and 'thorax' by a factor of 4 or 5 (e.g., Figs 1, 23). In adult *Bythotrephes*, the caudal process consists of three articles (although sexually mature individuals with 2 and 4 articles are known; e.g., see Fig. 1 and Yurista 1992), each bearing a pair of ventrally directed stout spines that flare outward from the midline and are located at the leading (anterior) edge of each article. These spines have received a variety of names over the years, such as Analtornene (anal denticles) (Müller 1867), Aftersta-

cheln (anal spines) (Lilljeborg, 1901), Furkakrallen (groove claws) (Flössner 1972), caudal claws (e.g., Mordukhai-Boltovskoi 1965) or barbs (e.g., Barnhisel 1991a, b). We refer to them as paired articular spines (Figs 1, 19A, 20A, B). As the animal grows, articles are added (via retention of shed cuticle) from a growth zone (Fig. 1) at the posterior terminus of the short 'abdomen' with the interesting result that sequential articles push earlier (older) articles in a posterior direction (see Discussion). Thus, the terminal article on an adult *Bythotrephes* is the oldest, and is therefore properly referred to as article 1, with more proximal articles numbered 2 and 3

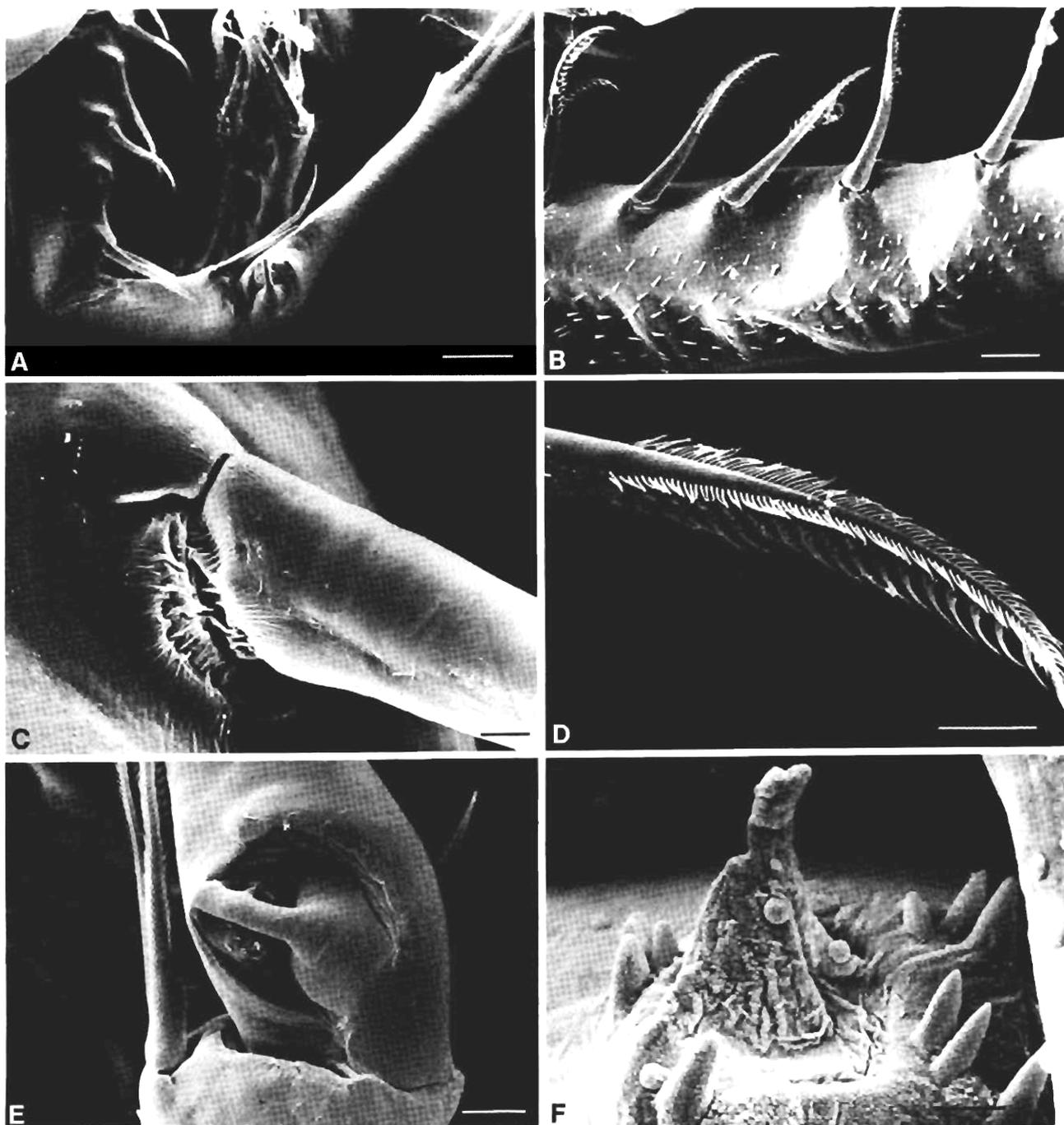


Fig. 15.—A. Inner view of segments 2, 3, and 4 of first thoracopod showing setation of all segments and clasping hook at base of segment 4.—B. Segment 2 showing line of heavy and spinulose spine-like setae along medial border.—C. Proximal region of one of large spine-like setae shown in B; note buttressing cuticular extension (toward top of figure) preventing movement in this direction.—D. Distal half of same setal type shown in B and C, also from segment 2.—E. The hook/recetacle complex at base of segment 4 (males only). Note sharp bend and twin teeth.—F. Circlelet of small teeth opposing movable hook shown in E. Scale bars: A 100 μm ; B 50 μm ; C 5 μm ; D 20 μm ; E 25 μm ; F 2.5 μm .

(e.g., see Fig. 1, where only article 2 is labeled). Tips of these articular spines may be acute or blunt, and occasionally are slightly curved anteriorly (e.g., see Ischreyt 1934: 193, figs 6, 7). The orientation of the articles of the caudal process is evidently not crucial to survival, as several authors have recorded a slight or even dramatic turning of one article. Ischreyt (1934, fig. 2) figured a third stage specimen with the first (caudal-most) article turned at approximately right angles to the shaft of the caudal process, while Lilljeborg (1901: plate 84, fig. 1) and Nilsson (1979: 136, fig. 10) illustrated a caudal process in which the terminal article is completely upside down. This orientation necessitates that the spines of the bend or kink

in the caudal process (see below) are also turned 180° from the 'typical' orientation, so that the larger field of spines is now on the ventral side of the shaft. Even more dramatic evidence of the ability to survive without the caudal process was given by Barnhisel (1991a, b), who successfully removed it (in order to assess its significance in deterring fish predation) and found that its absence did not adversely affect either survival or swimming ability. In specimens examined by us, all paired ventral spines were oriented in the 'typical' direction, i.e. with tips of the spines pointed antero-ventrally.

Each article functions for a time as the 'abdomen', that is, with the functional anus opening ventrally between the

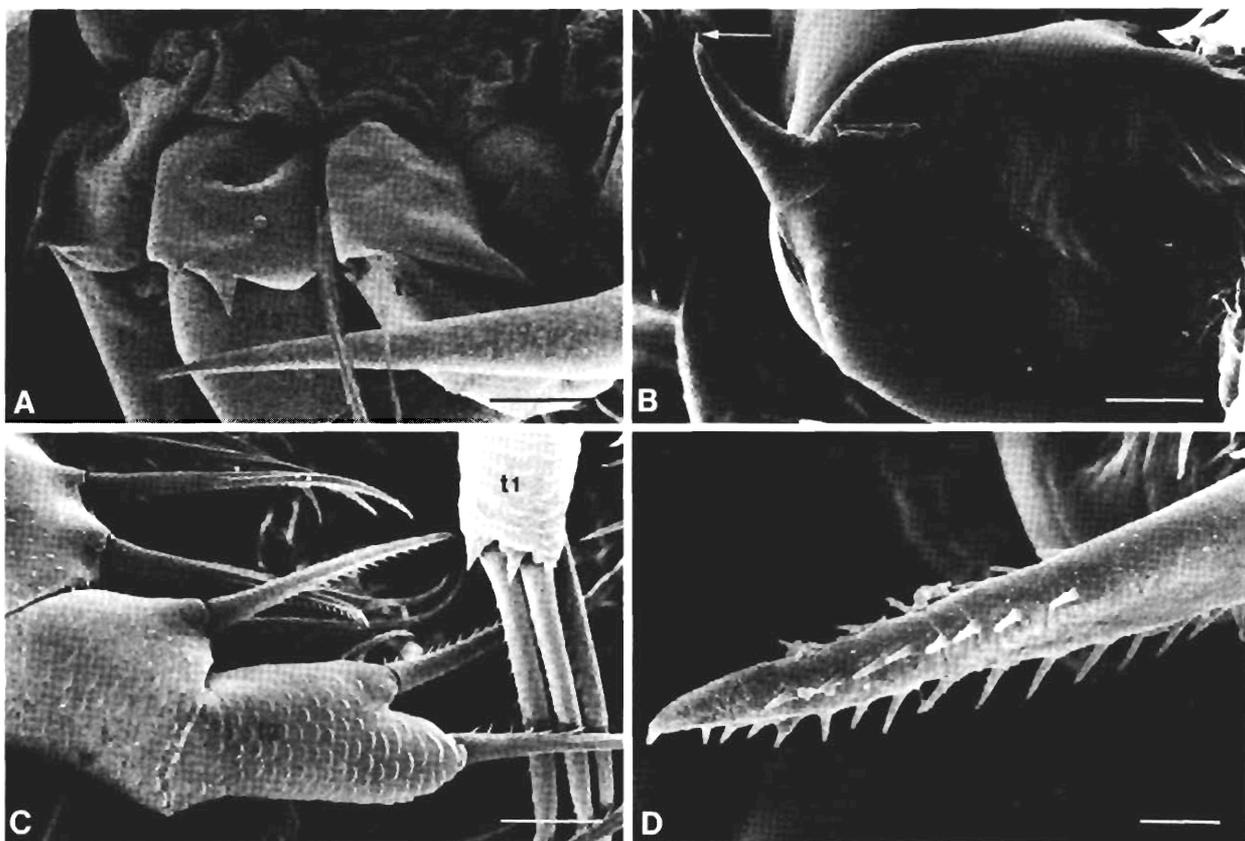


Fig. 16.—A. Outer view of spine-like exopods of thoracopods 1–3. Exopod of t4 also visible (although not spine-like).—B. Exopod of thoracopod two. Note small seta at apex (white arrow).—C. Tips of thoracopods 1 and 2. Note scales on segments of both thoracopods and nature of setae.—D. Distal part of lightly armoured spine-like seta at tip of thoracopod 2. Scale bars: A 100 μm ; B 50 μm ; C 50 μm ; D 5 μm .

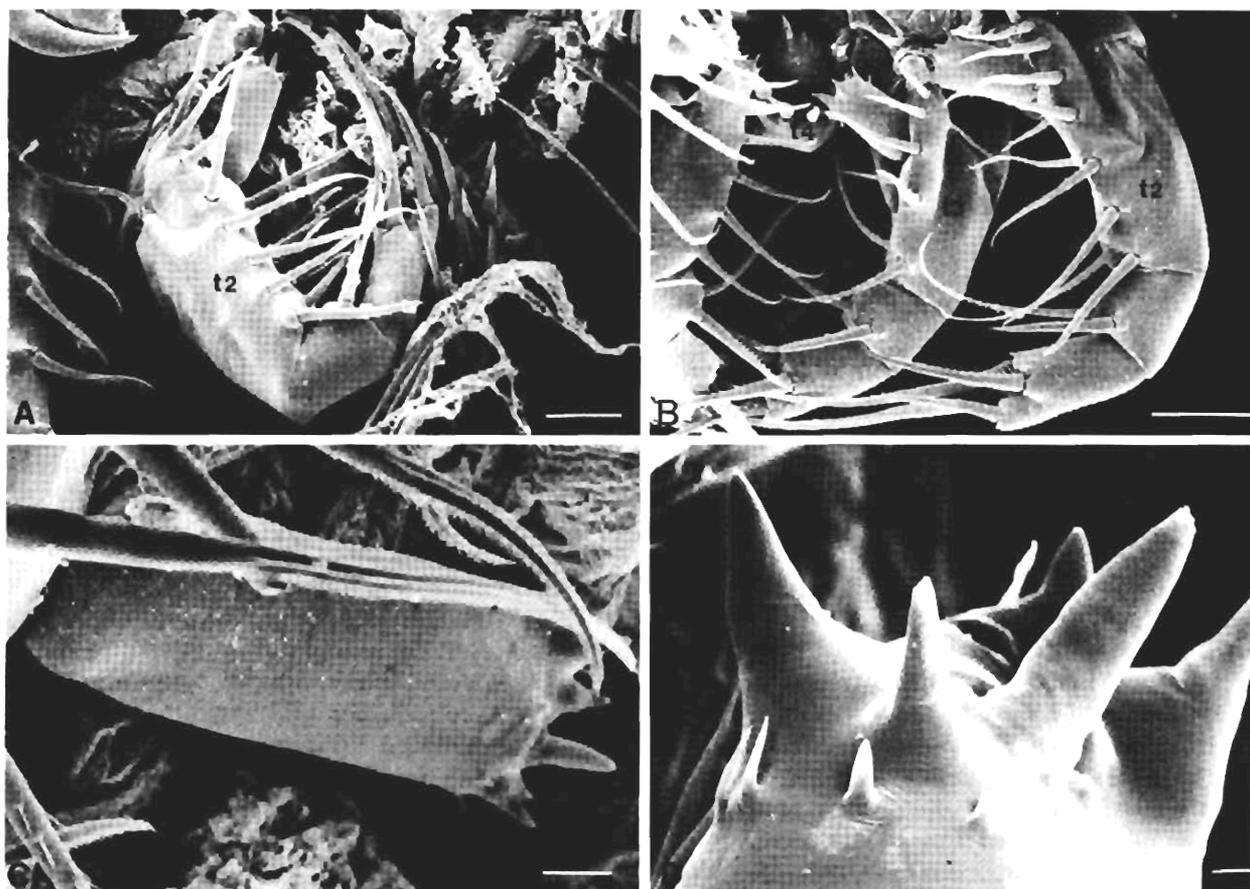


Fig. 17.—A. Inner surface of thoracopod two; first thoracopod visible to left, and labrum visible at upper left.—B. Inner surface of thoracopods 2–4.—C. Gnathobasic process (proximal endite) of thoracopod 2.—D. Tip of gnathobasic process showing stout teeth. Scale bars: A 100 μm ; B 100 μm ; C 20 μm ; D 5 μm .

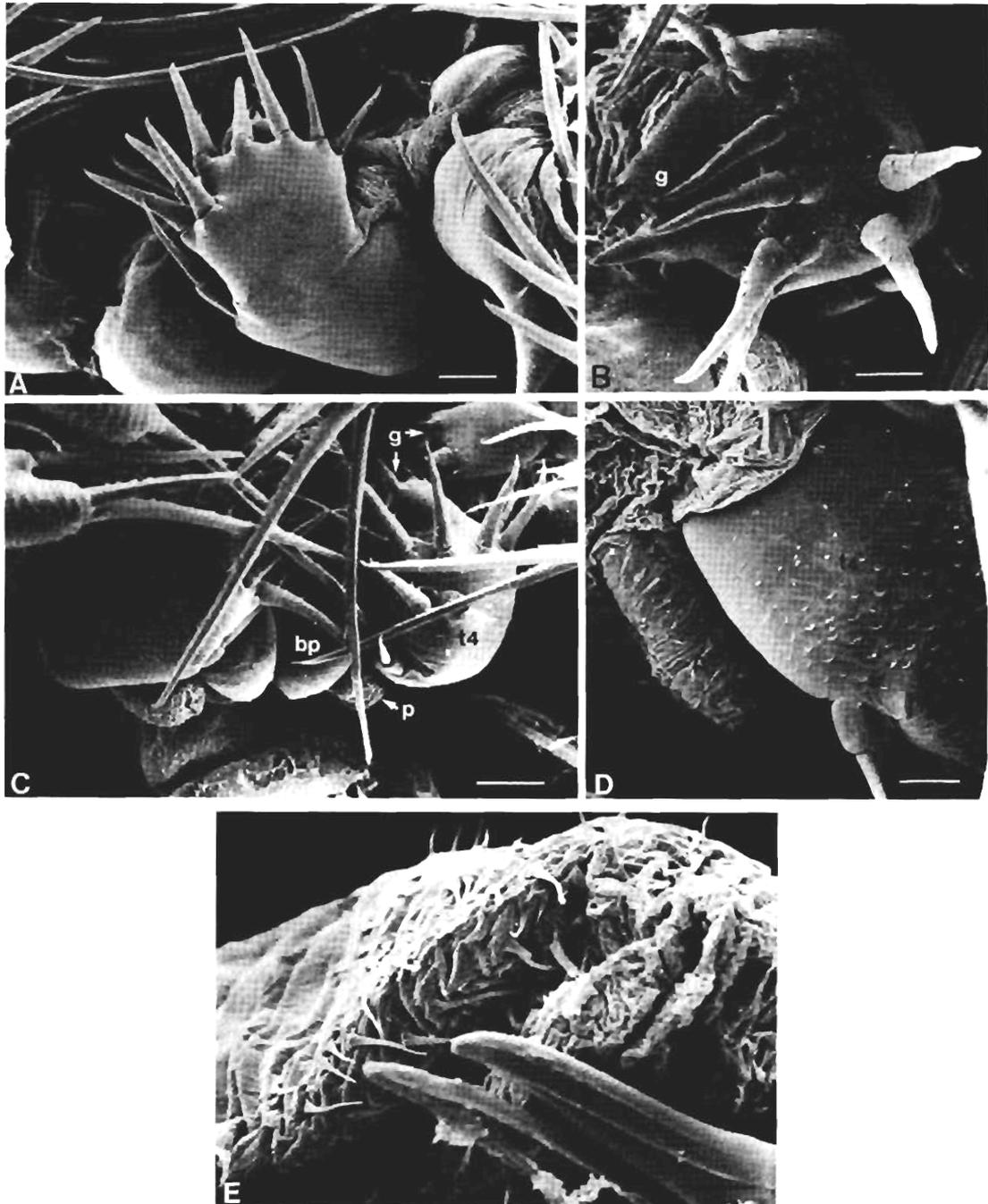


Fig. 18.—A. Outer view of thoracopod four showing distal spine-like setae. Note single seta on a peduncle-like extension (exopod) near posterior border of the leg.—B. Ventral view of thoracopod four showing immovable, heavily armored, gnathobasic process (g) and two outer spines.—C. Posterior region, ventral view. Note gnathobasic process of thoracopods 3 and 4 oriented at approximately 90°.—D. External lateral view of posterior region of thoracopod four (with short cylindrical exopod at bottom of figure) and penis.—E. Opening to penis (indicated by black arrow). Scale bars: A 50 μm ; B 25 μm ; C 50 μm ; D 25 μm ; E 10 μm .

paired articular spines (Figs 2, 3, 19A). As additional articles are created, the former anal opening is moved backward along with the corresponding shed cuticle forming the older caudal article. This anal opening is present in each article, although it is functional only in the currently-antiermost article (Figs 2, 3, 19A). By breaking the region of overlap of the articles, we find that the mode of attachment is a fusion of old and new cuticle (Fig. 20D–F), much as is seen in other instances of retained moults, such as the concentric growth lines on the valves of spinicaudate conchostracans.

The shaft of the caudal process is covered with minute, flattened, spine-like scales, each pointing posteriorly

(Figs 19A, D, 20). These are most obvious on the oldest (first and most posterior) article, and diminish somewhat as one proceeds along the branches of the paired articular spines and toward the far posterior region of the shaft, which terminates in a blunt point.

In mature adults, the first (posteriormost) article bears a conspicuous bend or kink at approximately one third of the distance from the leading edge of the article to the tip of the shaft (Figs 1, 19B, 23). This bend has been the subject of some controversy, and has been used to argue for recognition and distinctness of the two species of *Bythotrephes*, as it is absent in the *B. longimanus* 'form' (see Discussion). In all specimens examined by us, the

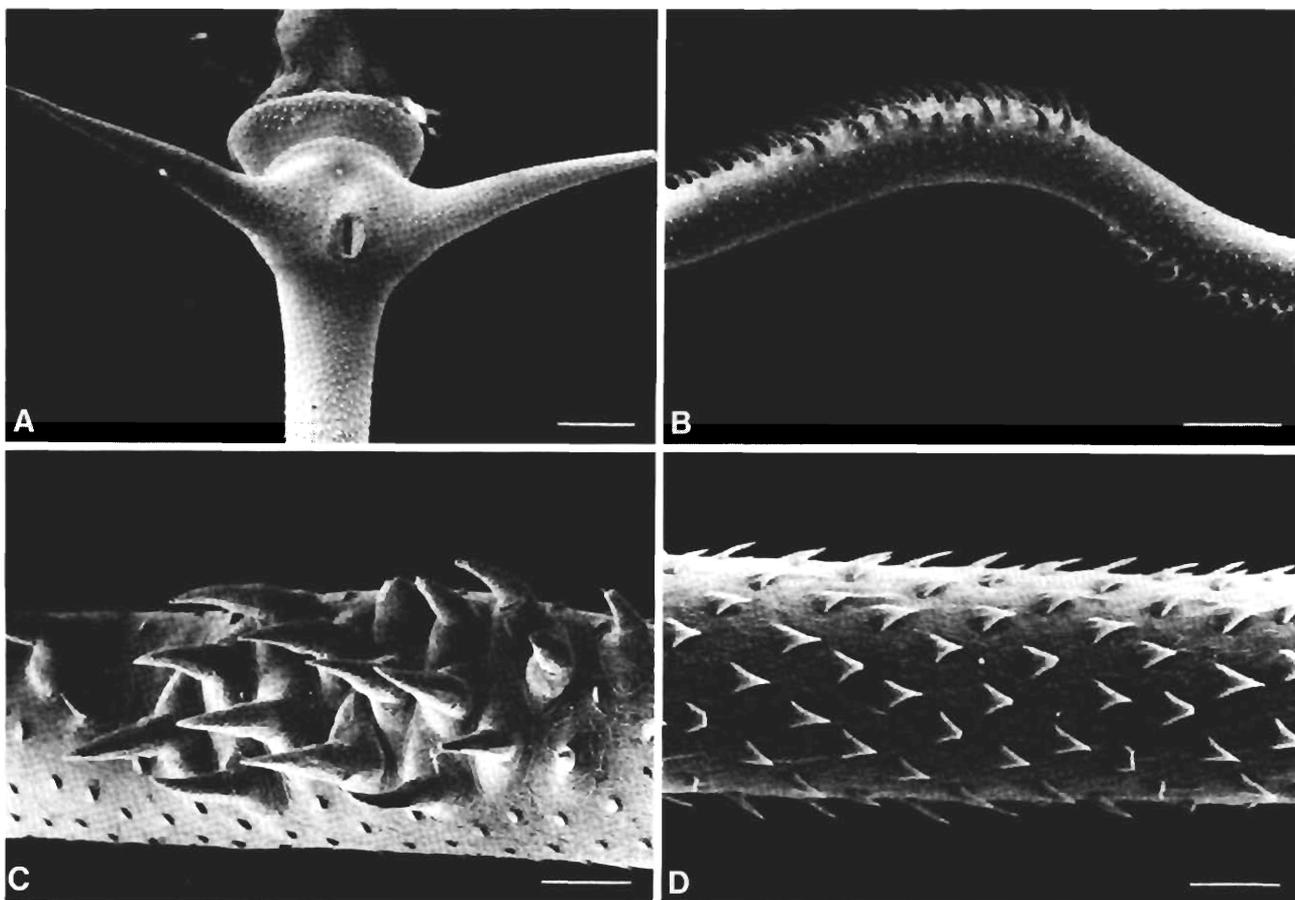


Fig. 19.—A. Ventral view of paired articular spines on article three of caudal process (youngest and functional article, immediately posterior to growth zone of 'abdomen'). Note anal opening centered between spines. Anterior is toward top of photograph.—B. Caudal bend in article one with small spines directed anteriorly.—C. Spines on ventral field (posterior field in B) of the bend.—D. Minute spines on shaft of caudal process. Anterior is to the left for Fig. B–D. Scale bars: A 100 μm ; B 100 μm ; C 25 μm ; D 25 μm .

bend bears two fields of sharp, anteriorly directed spines. The dorsal field of spines is the larger of the two, consisting of as many as 34 (Fig. 19B) spines; the ventral field (Fig. 19B, C) contains perhaps 15–20 spines in adults. Detailed examination of these spines (Fig. 19C) shows that each arises from a basal swelling of the cuticle, does not articulate with the shaft, is acutely tipped, and is sharply bent in an anterior direction. The function of these fields of spines is unknown.

Sexual dimorphism

Sexual dimorphism is evident in the relative size of the animals (females are consistently larger than males), female brood pouch, penis, and male first thoracic leg, which bears a hook/receptacle complex for grasping the female during mating.

Most obvious of these differences, apart from size, is the female brood pouch. If containing embryos (e.g., Fig. 3), its large size immediately sets females apart from males. It is extremely flexible, and enlarges to accommodate the growing embryos before finally rupturing to release them (e.g., see Yurista 1992). We consistently found a convexly folded layer of tissue on the anterior and anteroventral side within the brood pouch, which Rossi (1980) and others (see Martin 1992) have referred to as the Nährboden. Males, however, also bear a dorsal remnant of the carapace valves (the secondary shield of

Walossek 1993), and the difference between this 'brood pouch' in males and in females that are currently without embryos is not always immediately evident.

A less obvious difference between the sexes is the armature of the first thoracopod. In males, the proximal end of the fourth segment, which is slightly swollen, bears on its medial surface a movable, pronged hook (Fig. 15A, E), whose two prongs extend at approximately a right angle to the shaft and are equal in length (Fig. 15E). This hook closes against and into an opposing circlet of small teeth, which appear to encircle an area where the cuticle is softer than that of the surrounding leg (Fig. 15F). The far terminus of this circlet of small spines is occupied by a single larger spine that rises to meet the prongs of the descending hook. This circular area is found posterior to, and slightly distal to, the point of origin of the hook, such that the hook bends inward at 90° to make contact with the receptacle complex.

The penis of the male is immediately behind the bulbous process (Fig. 18C). Its cuticle is evidently not very rigid, as it invariably displays shrinkage and some distortion upon HMDS and critical point drying for S.E.M. (Fig. 18D). It appears to be a rather soft, tubular structure covered distally with minute setae (Fig. 18C–E); Mordukhai-Boltovskoi (1967: 114) used this feature as a distinction between *Bythotrephes* and *Cercopagis*, in which the penes were described as being 'cylindrical and smooth'.

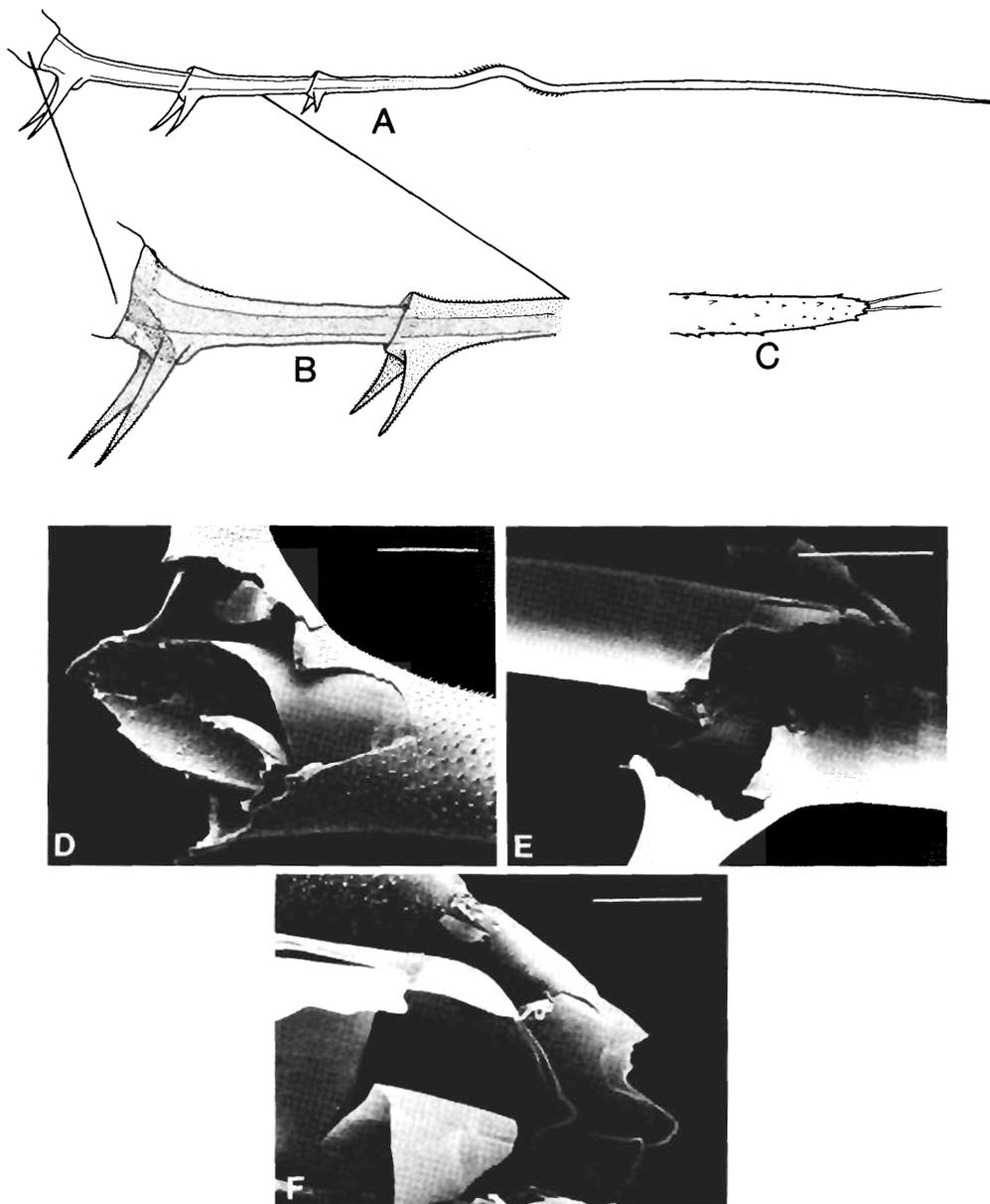


Fig. 20.—A. Caudal process in typical adult bearing 3 articles.—B. Enlargement of third and part of second article, showing intestine terminating at anus on youngest article (article 3 in this animal) and with some internal tissue visible extending into more posterior articles.—C. Terminus of caudal process in neonate, showing pair of caudal setae believed homologous and synapomorphic in all non-anostracan branchiopods (traced from photograph supplied by D. R. Barnhisel).—D. Dissected region of overlap of articles, showing older spinose cuticle to right with smoother cuticle of newer article beneath it.—E. Region of overlap broken open to show fusion of cuticle.—F. Higher magnification of region in E (directly beneath center of scale bar) where cuticle of older (top) and newer (below) articles are rather smoothly fused. Scale bars: D 100 μm ; E 200 μm ; F 50 μm .

Discussion

Number of species in Bythotrephes Leydig

At least two morphologically distinct forms of *Bythotrephes* are recognizable, one with a distinct and spinose bend or 'kink' in the long caudal process (described in this paper), and one without it, the caudal process being more or less straight. The form with a straight caudal process was described first, under the name *Bythotrephes longimanus*, by Leydig (1860). In erecting a second species of the genus, from Sweden, Schoedler (1863) described a number of differences between the new species, which he named *cederströmii* (now *cederstroemi*), and Leydig's *B. longimanus*. These differences included the smaller size of *B. cederstroemi* and the number of setae on the branches of the second antenna. Unfortunately,

Schoedler made his comparison using the illustrations of Leydig (1860), which, probably because they were based on macerated specimens from fish stomachs, are apparently incorrect concerning the second antenna (see earlier comments under the heading *Antenna*). All 'species' of *Bythotrephes* have 8 setae on the exopod and 7 setae on the endopod. This has been illustrated accurately by nearly all subsequent workers, including Lilljeborg (1901), and was used as a key character (along with the degree of eye pigmentation) separating *Bythotrephes* from *Cercopagis* (which have 7 + 7 setae) by Mordukhai-Boltovskoi and Rivier 1987. Because Leydig (1860: pl. 10) indicated only 7 setae on both branches of the antenna of *B. longimanus*, Schoedler thought that this was a difference between that species and his new species, *B. cederstroemi*. It is possible that Leydig's figure is of an unusual variant that did in fact have only 7 setae on the

antennal exopod, but there are other serious discrepancies between his figures and all subsequent treatments of *Bythotrephes*. The number of articles in the first thoracopod is wrong (the terminal article is incorrectly divided into two segments), the placement of the gnathobasic process (proximal endite) on the second and third thoracopods is incorrect (and they are illustrated as being fused to the leg), and the paired articular spines of the caudal process are illustrated as though they arise from a single, common shaft. We therefore suspect that Leydig's illustration of the second antenna also was flawed, invalidating this part of Schoedler's distinction between the two species. Schoedler (1863) did not mention the bend in the caudal process as a distinguishing factor (this he described later, in 1877), although this feature has been used more than any other in separating the *longimanus* and *cederstroemi* 'forms' (e.g., Lilljeborg 1901; Benisch 1930; Herbst 1962; Scourfield and Harding 1966). Lilljeborg (1901), in addition to recognizing *B. cederstroemi* as a valid species, also recognized several varieties of *B. longimanus*—*longimanus* s. str., *arcticus*, and *brevimanus*—although these forms today are considered conspecific with *B. longimanus* (see Mordukhai-Boltovskoi and Rivier 1987). Similarly, the varieties treated by Lilljeborg (1901) as forms of *B. cederstroemi*—*cederstroemi* s. str., *robustus*, and *conectens*—are today considered within the known morphological range of *B. cederstroemi*, as is an earlier variety recognized by Lilljeborg (*B. borealis*).

Evidence for the existence of two species is not, however, restricted to the caudal process, which has previously been shown to be morphologically rather plastic in cercopagidids (see section on Abdomen and Caudal Process). Several workers, including Pejler (1975) and Nilsson (1974, 1979; p. 137 and graph), have argued for recognition of two distinct species based on biometric evidence (mostly overall length measurements), although Pejler had earlier (1965) believed that only one species existed. For the population in Lake Vänern, Sweden, Nilsson (1979) reported a modal size of 9.4–10.2 mm for *B. cederstroemi*, as compared to only 2.2–2.4 mm for *B. longimanus* (despite Schoedler's statement that the *cederstroemi* form is the smaller). There are other differences based on the only previously published S.E.M. work of which we are aware. Mordukhai-Boltovskoi and Rivier (1987: fig. 3) published S.E.M. photographs of the mandible of *B. longimanus*. These differ from our description of the *B. cederstroemi* mandible in that the anterior mandibular process (mp, Fig. 9A) is smaller, the number of spines is fewer, and the degree of serration and curvature of these spines is less. However, it is possible that differences between their figures and ours are due only to ontogenetic differences; a study of morphological change throughout development might resolve this issue.

On the other hand, several lines of evidence point to recognition of a single, variable species, as was thought to be the case by Šrámek-Hušek (1962) and Flössner (1972), among others. For example, Zozulya and Mordukhai-Boltovskoi (1977) investigated populations of *Bythotrephes* collected from 1972 to 1975 in the Rybinsk Reservoir (Russia) from May to October each year, and concluded that the forms were cyclomorphic variants of

one species (see also Mordukhai-Boltovskoi and Rivier 1987). Observed changes occurred in the 'degree that the kink of the caudal appendage is expressed, but also in its length, the dimensions of the caudal claws, their arrangement, the space between the pairs of claws, and the length of the body'. 'Spring generations' live at temperatures below 15–16°C, possess a comparatively short caudal appendage (2–2.8 times longer than the body), lack the caudal bend, and have short caudal claws directed posteriorly. These authors further speculated that 'such an appendage is obviously most suitable for its basic function, as [a] stabilizer during forward motion'. In the warm summer months (temperatures commonly above 16°C), the caudal bend and its clusters of spines appear in at least some individuals, the length of the caudal process increases (averaging 3.1-times the body length), and the paired articular spines are directed forward. Because this new shape would not serve the function of a stabilizer well, Zozulya and Mordukhai-Boltovskoi (1977) speculated that the new dimensions might function as an aid to flotation. Similarly, Evans (1988) reported that in a North American introduced population the caudal process was relatively straight in immature specimens and became progressively more kinked in older animals, with a concurrent increase in the size of the ventrolateral paired articular spines, indicating that the two forms are only separated ontogenetically. The bend was more strongly developed in autumn (October) than in summer (July) *B. cederstroemi* populations (Evans 1988). Scourfield and Harding (1966) stated that the 2 species have similar body lengths 'of approximately 2–3 mm' without the caudal process (quote from Evans 1988: 236) (in contrast to the later statements of Nilsson and Pejler; see above), although they nevertheless recognized them as distinct species based on morphology.

Perhaps the most convincing evidence in favour of a single variable species is the work of Yurista (1992). He demonstrated that, at least in North American populations, presence of the caudal bend, and even differences in the number of instars before primiparity is reached, depends upon whether the animal develops from resting (gametogenic) eggs or parthenogenetically in the female brood pouch. The caudal process of gametogenically produced animals lacked the caudal bend, and differed in other ways not described in detail by Yurista. These individuals possessed 4 pairs of articular spines or barbs as adults rather than three (Yurista 1992). Electrophoresis (Berg and Garton in press) of specimens of North American and European *B. cederstroemi* and European *B. longimanus* also supports recognition of one morphologically variable species.

Comparative morphology of onychopods

Comparisons with other onychopods lead to the almost certain conclusion that *Bythotrephes*, and the closely related *Cercopagis* (together comprising the Cercopagididae), are derived compared to polyphemids and podonids, a conclusion reached by most previous workers as well (see next section). In the Polyphemidae, the legs become progressively smaller from anterior to posterior, but they are more or less of the same general shape. This

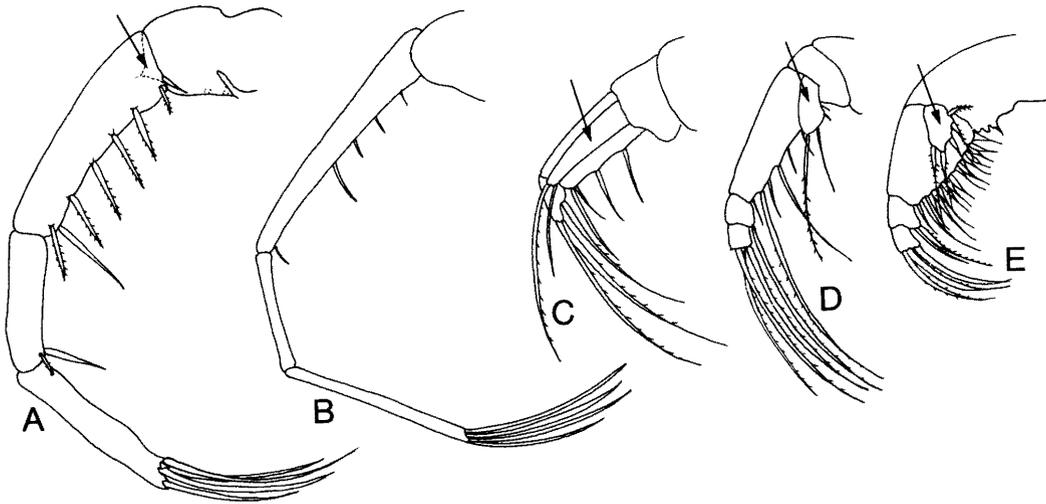


Fig. 21.—Comparison of the first thoracopod among several genera, representing the families Cercopagididae (A, B), Podonidae (C, D), and Polyphemidae (E), of the Onychopoda.—A. *Bythotrephes*.—B. *Cercopagis* (from Mordukhai-Boltovskoi 1968).—C. *Evadne* (from Mordukhai-Boltovskoi 1968).—D. *Podon* (from Mordukhai-Boltovskoi 1968).—E. *Polyphemus* (from Lilljeborg 1901). Arrow indicates exopod. Not drawn to scale.

is also true of the Podonidae (Figs 21, 22). In contrast, cercopagidids have a first thoracopod grossly different in size and shape from legs 2 and 3. Additionally, polyphemids possess a well developed, easily identifiable and setose exopod on the basal-most segment of all thoracopods (although more difficult to identify on thoracopod 4 than on more anterior limbs). This exopod is also identifiable in the podonids, but here it is narrow (although it may be longer, e.g. see Fig. 21C) and bears fewer setae. Reduction of the exopod in cercopagidids is extreme (assuming we are correct in calling this triangular process the exopod). In fact, were it not for the location of the 'exopodal spine' and the fact that it bears a single seta on its tip in *Bythotrephes*, it would be difficult to argue for recognition of any exopod in *Bythotrephes* or *Cercopagis*. Number of setae on the thoracopod segments appears to be similar among the three families, again with the exception of the exopod, although we have not confirmed using S.E.M. the illustrations reproduced here as Figs 21 and 22 (with the exception of *Bythotrephes*). Relative lengths of each segment are also similar; the penultimate is always the shortest, followed closely by the ultimate (distal-most), with the longest segment being the second, which bears the gnathobasic process in thoracopods 2 and 3 (see below). There appears to be a general evolutionary trend from a laterally compressed limb, as seen in the Ctenopoda and the non-cladoceran branchiopods, and as is more or less seen in *Polyphemus*, toward the more tubular stenopodous limbs of the cercopagidids (Figs 21, 22).

The exact location of the gnathobasic process (proximal endite) on each thoracopod is of interest for several reasons. First, as is evident in Fig. 22, most previous workers have illustrated this process ambiguously, showing it arising from somewhere between segments one and two, or, in the case of Leydig (1860), clearly but erroneously stemming from segment one. The difficulty in determining its origin is caused by the fact that segment two extends further proximally on its inner side than on its outer, giving the impression that this process might arise from segment one. Our study has shown rather clearly that it arises from segment two in *Bythotrephes* (Figs 12,

13), and we suspect that this is the case in other onychopods. Second, this finding indicates that the gnathobasic process on legs 2 and 3 cannot be homologous with the process seen on leg 1, which clearly arises from the first segment. This is not overly surprising, as the process on leg 1 differs greatly from what is seen on legs 2, 3, and even 4 in *Bythotrephes*. Such a process is not known on the first thoracopod of *Cercopagis* (Fig. 21B), and needs better documenting in other genera before further conclusions can be reached. In *Bythotrephes*, the gnathobasic process in thoracopod 4 is very similar to what is seen in legs 2 and 3, with two exceptions: it is fused to the cuticle of the leg, and the fusion (compression) of segments in this appendage makes it impossible to determine the original segment from which it arose. Based purely on gross morphology, we are of the opinion that it is homologous with the process in legs 2 and 3, but that it has become modified as the appendage has undergone severe reduction and compression of segments (or, alternatively, the limb never reached the level of development of the anterior thoracopods).

If we are correct in attributing this gnathobasic process to the second segment, then there is an immediate and phylogenetically important question that must be addressed: can this be homologous to the proximal endite that characterizes other branchiopods (e.g., see Calman 1909: 51, Walossek 1993) but that always arises as part of the basal segment? We know of no other case among crustaceans where such an 'endite' arises from a more distal segment of the thoracopod, rather than from the typical, proximal location.

The caudal process differs greatly among the three onychopod families, although it is not difficult to envisage the derivation of the elongate condition in cercopagidids from what is seen in polyphemids and podonids. The latter families have a caudal region much more reminiscent of the other, non-predatory, 'cladocerans' (the Anomopoda and Ctenopoda), with caudal forks and paired setae evident. Indeed, we propose (see next section) that the possession of paired caudal setae is a shared derived feature of at least the non-anostracan branchiopods.

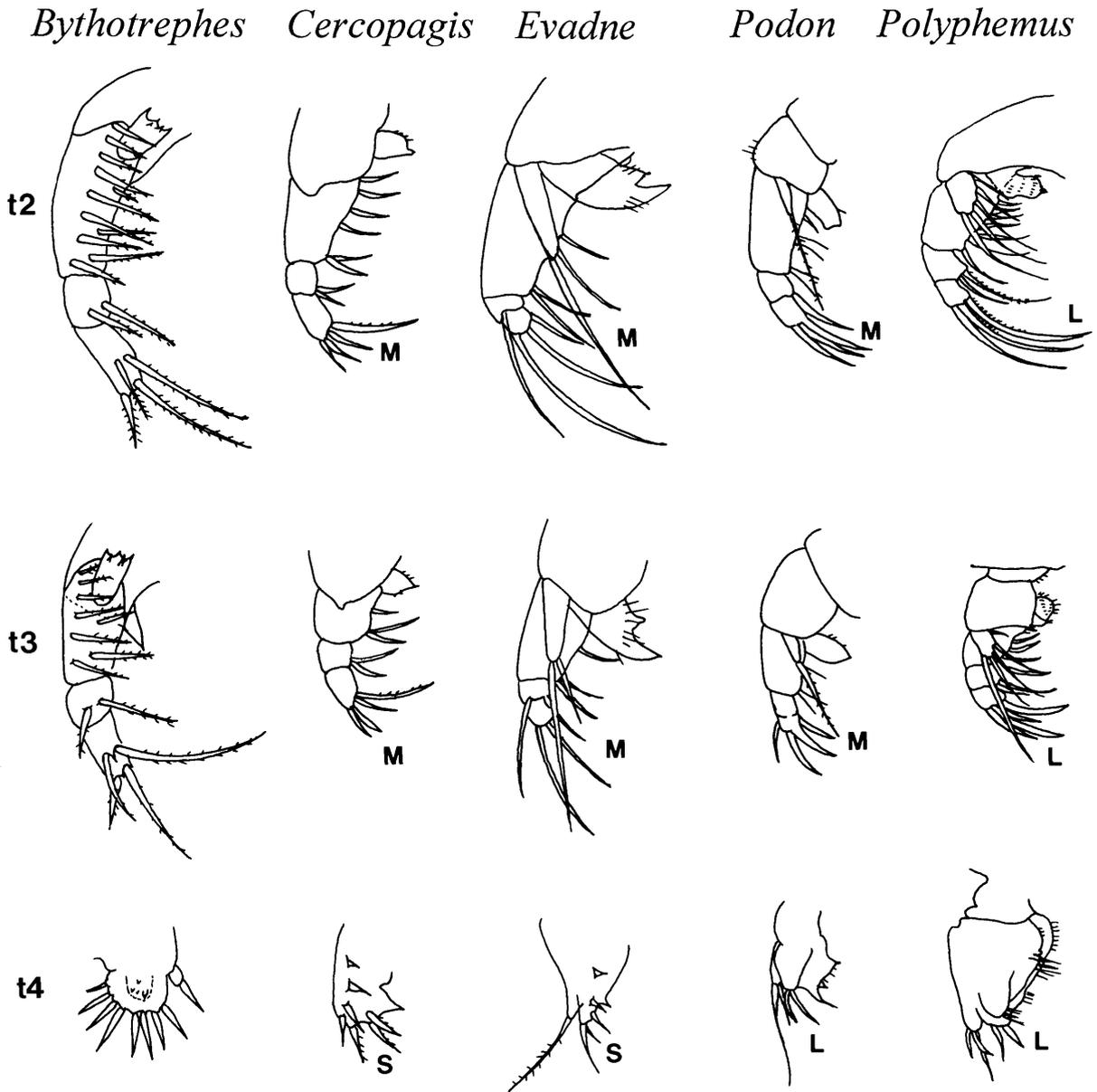


Fig. 22.—Comparison of thoracopods 2–4 in the three onychopod families. L, from Lilljeborg 1901; M, from Mordukhai-Boltovskoi 1968; S, from Sars 1897. Orientation is not the same for each illustration. Not drawn to scale.

Although absent in adult cercopagidids, the posterior paired setae seen in the Polyphemidae and Podonidae are still exhibited in developing cercopagidids (see Mordukhai-Boltovskoi and Rivier 1987, and Fig. 20C), demonstrating, in our opinion, the homology of the caudal region among these families.

It is clear from examination of the caudal process that in at least some branchiopod crustaceans, growth—in this case defined simply as an increase in length—is not always achieved solely by the addition of additional somites anterior to the pre-telsonic growth zone. In *Bythotrephes*, size increase is achieved also by retention of the shed cuticle of the previous instar. Marking the articles of the caudal appendage in *Bythotrephes* by clipping off the ventral paired spines facilitates following the caudal process through an ontogenetic sequence, where it is easy to see that newer articles are added anterior to earlier (shed, older) ones (D. R. Barnhisel, personal communication). Thus, the posterior-most article, the one bearing the bend in adults, is the oldest component of the caudal process.

Although this size increase in *Bythotrephes* does not constitute traditional crustacean growth, but instead is simply an increase in size caused by retention of shed cuticle, there is still a question as to how and why the caudal articles are retained. Dissection of caudal articles shows a rather smooth fusion of cuticle from the anterior ('current') article, bearing the functional anus, to the immediately posterior retained article (Fig. 20D–F), and there appears to be some tissue (although not musculature) extending the entire length of the caudal process. In this regard, *Bythotrephes* differs from the traditionally accepted pattern of crustacean growth. However, it is not unique in doing so. For example, Ferrari (1993) has documented that in some copepods, serially homologous legs can have articles that are older in posterior legs than in anterior ones, contradicting the long-held 'anterior-is-older' view.

Finally, we emphasize that our study was based on relatively few specimens from only two North American populations. Some of the characters discussed here may

differ in European populations. A detailed comparison of several populations is needed to determine the extent of morphological variability.

Onychopod phylogeny

In a beautifully detailed account of an Upper Cambrian fossil crustacean (*Rehbachella kinnekullensis*) with branchiopod (anostracan) affinities, Walossek (1993) reviewed the various characters that characterize the Branchiopoda. He concluded that the branchiopods are monophyletic and consist of two distinct lineages. Additionally, he described in detail some of the characters shared by at least the more primitive members of the group. Because his concern at that time was with the origin of the branchiopods, the recognition of their major clades, and the systematic position of the Upper Cambrian *Rehbachella*, for the purposes of the present paper many of his characters are not directly applicable, because the onychopods—which some workers have doubted even as to their inclusion in the Branchiopoda—have apparently lost or modified many of these presumably symplesiomorphic features. One obvious example is the primitive branchiopod post-naupliar feeding apparatus, a suite of related characters separating Branchiopoda from all other crustaceans (see Walossek 1993: 69–70). This feeding complex—which in its primitive condition involved, among other features, a deep thoracic sternal food groove and filtratory lobate endites along an elongate thoracopodal basipod—would of course serve no purpose in a predator such as *Bythotrephes*.

One possible synapomorphy of the branchiopods that to our knowledge has not been addressed in earlier literature (or rather, has been described but not as a shared derived character) is the presence of paired terminal or 'post-abdominal' setae at some point during development (see also Linder, 1945). These setae are known in the Notostraca and the closely related extinct Kazacharthra, both orders formerly comprising the Conchostraca, and in all four orders of former 'cladocerans'. Fryer (1987b: 371, his Table 2) cautioned that these setae may be innervated from a different somite in the laevicaudatans (e.g., *Lynceus*) from what is seen in the spinicaudatans, indicating non-homology, but we are not aware of a study that demonstrates this condition and feel that the paired setae are a feature shared by all non-anostracan branchiopods at some developmental stage (but see Fryer 1987a for a dissenting viewpoint). Even in the cercopagidids, in which the caudal process terminates in a single spine-like tip, these paired setae can be seen in earlier stages of development (e.g., see Muller 1867, pl. 5 fig. 17; Lilljeborg 1901, pl. 80 fig. 10; Sars, 1993, pl. 106–108). Mordukhai-Boltovskoi and Rivier (1987: fig. 7) illustrated these setae quite clearly in a developing *Bythotrephes*, and it is evident in neonates from the North American samples as well (Fig. 20C, from a photograph supplied by D. Rae Barnhisel). Thus, despite their many morphological peculiarities, it is clear that onychopods are indeed members of the Branchiopoda. In fairness, we note also that paired terminal setae sometimes appear in other crustacean larvae and adults, although not anterior to, and distinct from, the caudal furcae or claws such as in branchiopods.

We are unsure as to this condition (the paired caudal setae) in the Anostraca. Fryer (1987b) listed among the defining characters of anostracans a pair of setae on the dorsal region of each body somite. However, this might be a different situation from the paired caudal setae that appear anterior to, and distinct from, the caudal furca in, for example, the Ctenopoda. These paired setae were not seen in the detailed examination by Walossek (1993) of an Upper Cambrian branchiopod with anostracan affinities, and neither is this condition evident in any studies of anostracan larval development seen by us (e.g. Schrehardt 1987). It is possible that these setae have been subsequently lost in the anostracan lineage sometime after establishment of the Branchiopoda; however, if true, this must have been quite early to explain their absence in the Upper Cambrian *Rehbachella* and in naupliar larvae of extant anostracans. It is more likely that possession of these setae is a synapomorphy only for the non-anostracan branchiopods. If so, then this would further support the recognition of a monophyletic notostracan–conchostracan–cladoceran clade as recognized by Walossek (1993) (his Phyllopoda, although we disagree with that choice of name for the taxon; see Martin and Christiansen in press; see also Fryer's 1987b arguments against Schram's 1986 use of the term Phyllopoda).

In the most recently proposed classification of the 'Cladocera', Fryer (1987b) (see also Fryer 1987a) discussed many of the deep-seated morphological differences that separate the four groups that have traditionally been included in this taxon. The four groups were described by Fryer (especially 1987a) as being so distinct from one another that each was deserving of ordinal status, and it was further implied that derivation of any one group from any other was difficult to envisage. Doubt was also expressed by Fryer as to the possibility of deriving the Cladocera as a whole from the 'Conchostraca' (which encompasses two rather different assemblages of branchiopods), at least in the vague form that the theory has been presented in the past.

We are in agreement with Fryer's (1987a, b) assessment of the many marked morphological differences separating the four groups traditionally called the Cladocera. We also agree with his plea that any hypothesis involving derivation of cladocerans from conchostracans should state, more precisely than has been done previously, which taxa and characters are involved, and we agree that it would be difficult to argue for derivation of any extant cladoceran group from any other. However, we are less certain that these trenchant differences necessarily argue against monophyly, rather than simply highlighting the great age and morphological diversity of the branchiopods. Faced with the absence of a more likely evolutionary scenario, we postulate a phylogeny (Fig. 23) that suggests, instead, cladoceran monophyly. Moreover, we have decided to take up, again, the rather old hypothesis that some conchostracan groups—represented here by the monotypic spinicaudatan family Cyclestheriidae—may have given rise to at least some, more primitive, groups of cladocerans. Thus, we are attempting to clarify what Fryer (1987a) rightfully termed 'vaguely stated' forms of the conchostracan–cladoceran theory.

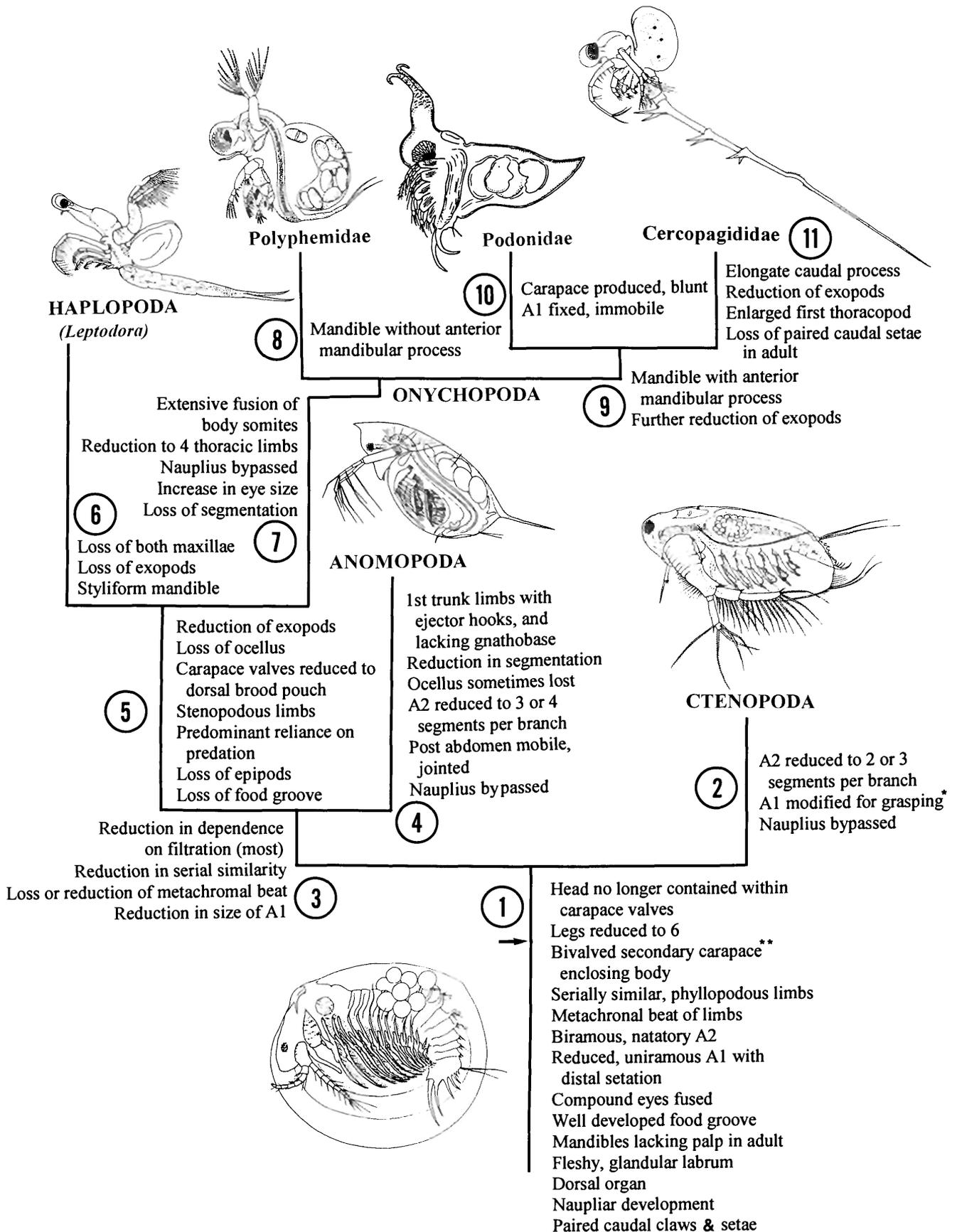


Fig. 23.—One hypothesis of cladoceran phylogeny, assuming cladoceran monophyly and assuming that cladocerans arose from some cyclestheriid-like conchostracan ancestor, both of which are subject to question. Characters above the arrow (reduction in leg number, reduction of carapace valves) are changes that would have had to have occurred prior to the first branch shown (i.e. were not present in the hypothesized cyclestheriid ancestor). See text, and also Fryer 1987a for arguments against such an origin. Circled numbers refer to character sets (changes at each node) discussed in text. Figures are from Belk 1982 (Polyphemidae), Martin 1992 (Cercopagididae and *Leptodora*), Fryer 1991 (Anomopoda), Sars 1901 (Ctenopoda), Mordukhai-Boltovskoi and Rivier 1987 (Podonidae), or are original (*Cyclestheria hislopi*, bottom of figure, from specimens collected in November 1990 from the Batok Nature Reserve, Singapore). Animals not drawn to scale. *In males only. **A secondary carapace is an outgrowth of cuticle that forms secondary to formation of the naupliar shield and subsequently overgrows it (see Walossek 1993).

According to our proposed scheme—Fig. 23, which represents, at best, a working hypothesis—such an origin could have led to the following modifications in each group. A cyclestheriid-like ancestor would possess the following ground pattern characters (among others):

1. Bivalved secondary shield (carapace) enclosing head and body.
2. Serially similar phyllopodous limbs.
3. Metachronal beating of the limbs.
4. A biramous natatory second antenna.
5. A short uniramous first antenna with distal setation.
6. Fused compound eyes.
7. A well-developed food groove.
8. Mandibles lacking a palp.
9. A fleshy, glandular labrum that produces entangling secretions.
10. A dorsal organ.
11. Naupliar development.

Many of the above features are shared by most branchiopods (2–5, 7, 8, 10), and some with other clam shrimps (1), whereas others (6, 9) are shared by cyclestheriids and at least some cladocerans. For our hypothetical ancestor, we have used a *Cyclestheria*-like conchostracan with naupliar development. *Cyclestheria hislopi*, sole member of the family Cyclestheriidae, has two modes of development, one involving eggs that hatch as a nauplius and one involving direct development. The presence of naupliar development in haplopods prevents our postulating the common loss of this feature before that node is reached.

The above conditions seem, to us, not terribly different from what is seen in extant Ctenopoda, and indeed ctenopods bear a striking resemblance to *Cyclestheria* (note especially the form of the caudal region and the tubular first antenna with distal setation). Modification of the cyclestheriid body plan to conform to a 'ground pattern' from which the Cladocera might have arisen would involve primarily the reduction of the carapace valves to the point that they no longer encompass the head, and reduction of the number of trunk limbs to 6, with the 6th being always reduced (character set 1, Fig. 23). Further specialization within the ctenopod lineage resulted in reduction of the rami of the second antenna to 2 or 3 segments (*Holopedium* has a secondarily uniramous second antenna; Fryer 1987b) and modification of the male first antenna as a grasping structure used in mating (character set 2). Additionally, the nauplius larval stage has been lost (bypassed in development).

Derivation of the anomopods, a highly specialized group, is more difficult to envisage, either from a ctenopod-like ancestor or independently from our hypothesized cyclestheriid-like ancestor. In our hypothesis, ctenopods form the sister group to the anomopods + haplopods + onychopods, with the anomopods appearing more basally on the latter branch, and forming the sister group to the haplopod + onychopod clade. The anomopods, although undoubtedly highly derived, nevertheless share certain features with ctenopods and with cyclestheriid conchostracans, such as the deep and narrow food groove, presence of osmoregulatory epipods (see Martin 1992 for discussion of epipod function), and form of the caudal claws and paired setae. The many specializations exhibited by anomopods set them off from other branchiopods, as Fryer correctly noted, but do not, in our estimation, eradicate the fact that there are also some shared features that could be dismissed as cases of convergence only with some difficulty. Fryer (1987a: 21) dis-

cusses some of the shared attributes of anomopods and ctenopods.

To reach the anomopod + haplopod + onychopod branch from the hypothesized cyclestheriid-like ancestor, the lineage must undergo the following changes (character set 3): Reduction in dependence on filtration (although the tremendously diverse Anomopoda also includes some of the most perfect filterers). Serial similarity of the trunk limbs has been lost, as has the metachronal beating of these limbs (although some daphniids have a modified form of this rhythm; see Fryer, 1987a). The first antenna is further reduced.

Anomopods additionally possess a suite of unique derived features (character set 4), which in our scheme would have arisen subsequent to the derivation of anomopod stock from the ancient lineage. These include the possession of unique ejector hooks on the first trunk limbs (which also lack the food-forwarding gnathobase or proximal endite). Segmentation has become even further obscured than in the ctenopods (where some segmentation is visible in the caudal region, possibly reminiscent of a cyclestheriid-like ancestor). The ocellus, present in cyclestheriids and ctenopods (the 'naupliar eye'), is occasionally lost, although Fryer (1987b) feels that its loss is 'clearly secondary' in these taxa. The second antenna is reduced from the cyclestheriid condition, having only 3 or 4 segments per ramus (but not as reduced as in ctenopods, which have only 2 or 3 segments; this is one of several reasons we chose not to suggest anomopods as arising from the ctenopod line). The 'postabdomen' (tail) is mobile, equipped with an elaborate joint and capable of great degrees of flexing and pushing against the substrate (although not practiced by all anomopods, and although some flexion is possible in a few ctenopods). The nauplius larval stage is lost, and some anomopods have lost the 6th pair of thoracopods. Additionally, there are peculiarities in the anomopod reproductive and digestive systems (see Fryer 1987a, b), which, although of great interest to functional morphology and evolution within the Anomopoda, serve only to highlight the distinctness of the anomopods rather than shedding light on phylogeny, and are not discussed further here.

Beyond the branching point of the anomopods, the lineage leading to the predatory cladocerans (character set 5) would, according to our scheme, lead to a further reduction of the carapace valves to the point that they serve as little more than a dorsal brood pouch in females. This presents some serious difficulties, primarily in that the brood pouch of the haplopods does not appear to arise from the same somite as does that of the onychopods (see below and Fryer, 1987a). The limbs have lost all similarity to any phyllopodous structure (although some serial similarity is evident) and are instead stenopodous (although perhaps this could be argued in the case of the polyphemids). The plesiomorphic mode of filter feeding (cyclestheriids, ctenopods, some anomopods) and scraping/grasping/sweeping (some anomopods) has been replaced by predation as the primary mode of food acquisition. As a consequence, the rolling and grinding mandible has been replaced, although whether this happened once or independently in haplopods and onychopods is debatable. The epipods have been completely lost. The exo-

pods have been reduced, although they are at least recognizable in most onychopods. The food groove has also been lost (although we seem to have detected at least a remnant of it in the onychopods; see discussion of food groove). Finally, the ocellus (naupliar eye) apparently has been lost (at least, we did not detect one), which is also the case, independently, in some anomopods (see Fryer 1987a).

Among the predatory cladocerans, the haplopods (*Leptodora*) are unique in several respects (character set 6). Both maxillae have been lost, as have the exopods of the thoracic limbs. The mandible is styliform and obviously adapted for biting. Other unique adaptations emphasize the unusual nature of these animals (e.g., Rossi (1980) discusses several unique components of the haplopod reproductive system) but do not add appreciably to an understanding of relatedness to other groups.

The pathway leading to the Onychopoda, in our hypothesis, involves even more fusion of body somites (some weak segmentation is evident in *Leptodora*, although not in any anomopod), a reduction in the number of trunk limbs to no more than 4 (if we do not consider the bulbous process of *Bythotrephes* and/or the penis to be a reduced appendage), and a dramatic increase in the size of the compound eye relative to the body size (character set 7). The naupliar stage has again been bypassed during development. (This last character cannot be placed further down the tree, as a naupliar stage occurs in *Leptodora* hatched from resting eggs; thus loss of the nauplius has occurred independently in ctenopods, anomopods, onychopods, and in gametogenically developing haplopods.)

Within the Onychopoda, the polyphemids are distinct from the other two families in that the mandible does not have an anterior masticatory mandibular process (character 8), a character that, along with further reduction of the thoracopodal exopods, unites in our scheme the podonids and cercopagidids (character set 9), despite the many obvious morphological differences between these families. It might also be argued that the limbs of the polyphemids display more serial similarity than do those of podonids or cercopagidids, although this difference could be contested. All of these character states in polyphemids are symplesiomorphs. Alternatively, complete loss of exopods could be argued to separate the cercopagidids from a polyphemid + podonid clade. Additionally, Mordukhai-Boltovskoi (1968) felt that polyphemids and podonids share a true 'shell' as compared to the weak and membranous brood pouch of the cercopagidids, so clearly there is room for questioning our uniting the podonids and cercopagidids as the sister group of the polyphemids, vs uniting the podonids and polyphemids. Podonids are unique in possessing a greatly elongate and often sharply attenuating carapace and immovable first antenna (apparently, although we have not confirmed this) (character set 10). Finally, cercopagidids are unique in their possession of a tremendously elongate caudal process (formed by retention of shed cuticle), virtual loss of thoracopodal exopods (although still identifiable as such at least in *Bythotrephes*), possession of a first thoracopod that differs dramatically in shape and size from the other thoracopods, and in the loss of the paired caudal setae in

adults (character set 11). Of the two cercopagidid genera, there is little doubt that *Cercopagis* is the more derived, given the often bizarre size and form of its caudal process, 'more delicate constitution' (Mordukhai-Boltovskoi 1965: 213), somewhat smaller eye (compared to *Bythotrephes*), larger thoracopod 1 relative to body size (Mordukhai-Boltovskoi and Rivier, 1987), and reduced size of the caudal articles and their paired spines (Mordukhai-Boltovskoi, 1965, 1968).

There are many obvious problems with this hypothetical phylogeny. One such is the independent loss of the naupliar larval stage in several different lineages (note even that in one of the developmental modes of the hypothesized ancestor, *Cyclestheria*, the naupliar stage is bypassed; this is unique among conchostracans). However, loss of larval stages is a very common theme throughout the Crustacea. A more serious problem is that, according to Fryer (1987b), the origin of the antennary muscles differs in laevicaudate and spinicaudate 'conchostracans'. The significance of this fact to the present discussion is that the laevicaudate condition—that is, with muscles that serve the antenna arising from both sides of the body wall—is what is seen in the cladoceran groups, whereas we are proposing a spinicaudate (not laevicaudate) origin for the Cladocera. Another serious drawback is that reduction of the carapace—indeed, the origin of a brood pouch from a particular somite and the question of whether it ever *was* a bivalved carapace—is poorly understood in the haplopods, where the 'carapace' appears to have arisen from more posterior regions than is the case in the onychopods (evident even in Fig. 23, taken from Martin 1992). Yet another problem is that character set 3 includes some ambiguous steps: if filtration is reduced here, is it then regained secondarily, and even perfected, in some filtering Anomopoda? This seems unlikely. The same problem is true for the character 'reduction of metachronal beat': is this rhythm present in some anomopods because of convergence (which is what we have suggested for independent reduction in number of thoracopods to fewer than 6), or is it indicative of phyletic history? If the latter is true, then this character should be placed within set 5 leading to the haplopod + onychopod lineage, as its loss in some anomopods would then be secondary. The status of the food groove needs further documentation in polyphemids and podonids before we can assess the merits of this feature as a systematic character for relationships within the Onychopoda. Our feeling is that even if what we have detected is a remnant of this feature, it certainly is not functional, at least not at the level of the food groove in ctenopods and anomopods, so this problem is not of concern when postulating relationships among the orders. We urge the interested reader to consult Fryer (1987a, b) for additional arguments concerning convergence, homoplasy, and independent origin of many of these characters.

Although this study has shed some light on morphology in one genus of the Onychopoda, it is apparent that we still have much to learn about the constituent taxa, including *Bythotrephes*, before any more comprehensive attempts at phylogeny of the 'cladoceran' taxa are possible. We hope that this study might serve as a catalyst for

additional investigations into these fascinating crustaceans.

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