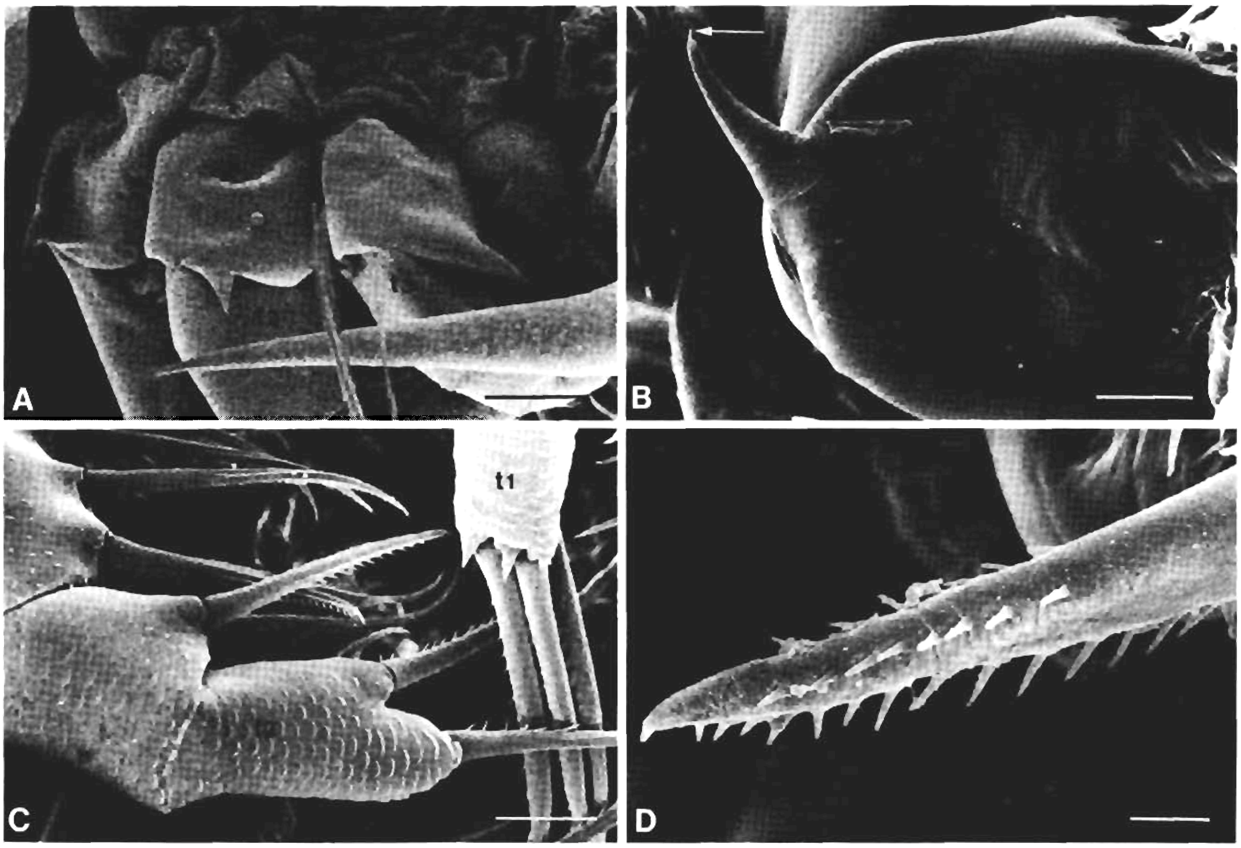
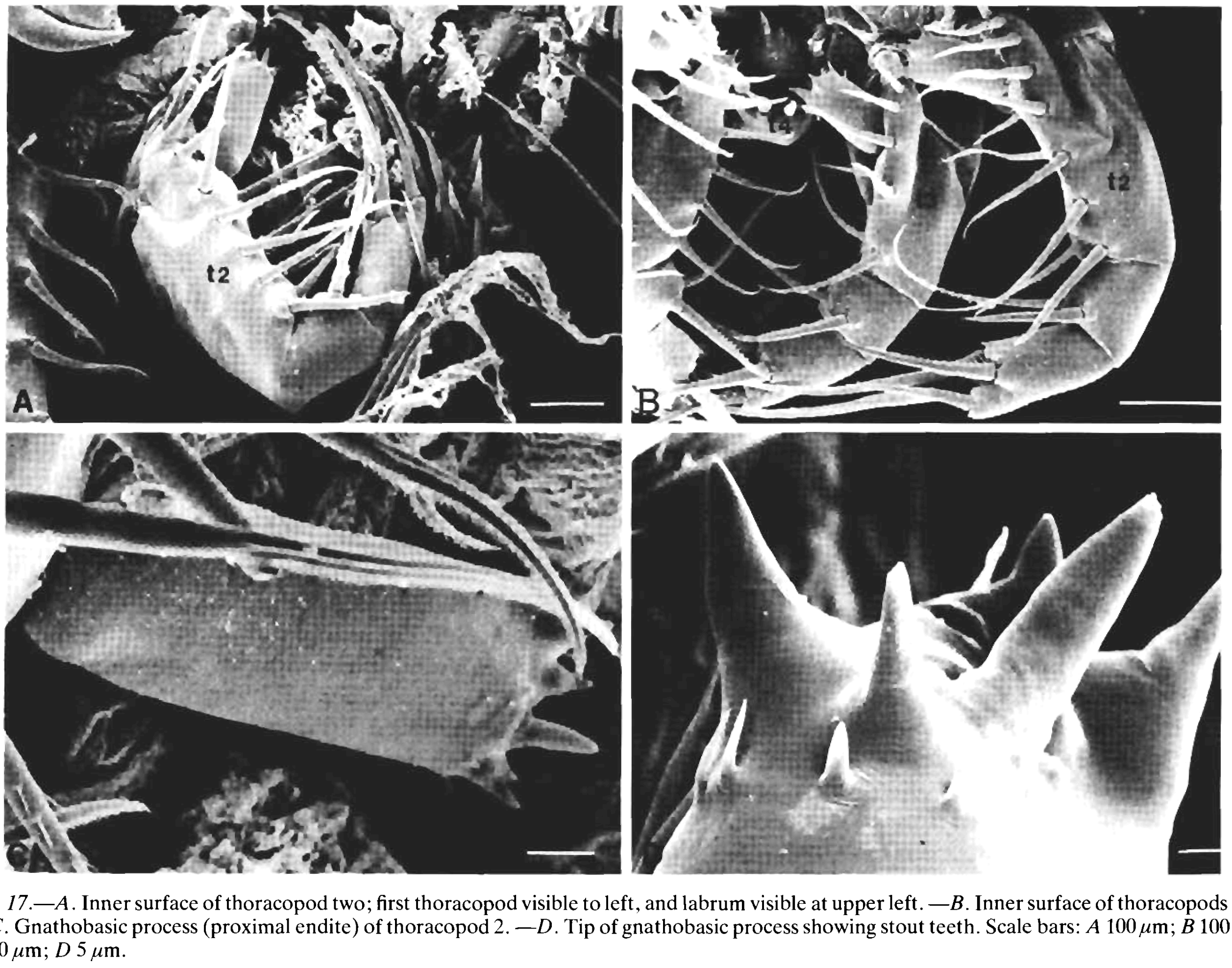


ig. 16.—*A*. Outer view of spine-like exopods of thoracopods 1–3. Exopod of t4 also visible (although not spine-like).—*B*. Exopod of thoracopod wo. Note small seta at apex (white arrow).—*C*. Tips of thoracopods 1 and 2. Note scales on segments of both thoracopods and nature of setae.—). Distal part 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.



ig. 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; 20 μm; *D* 5 μm.

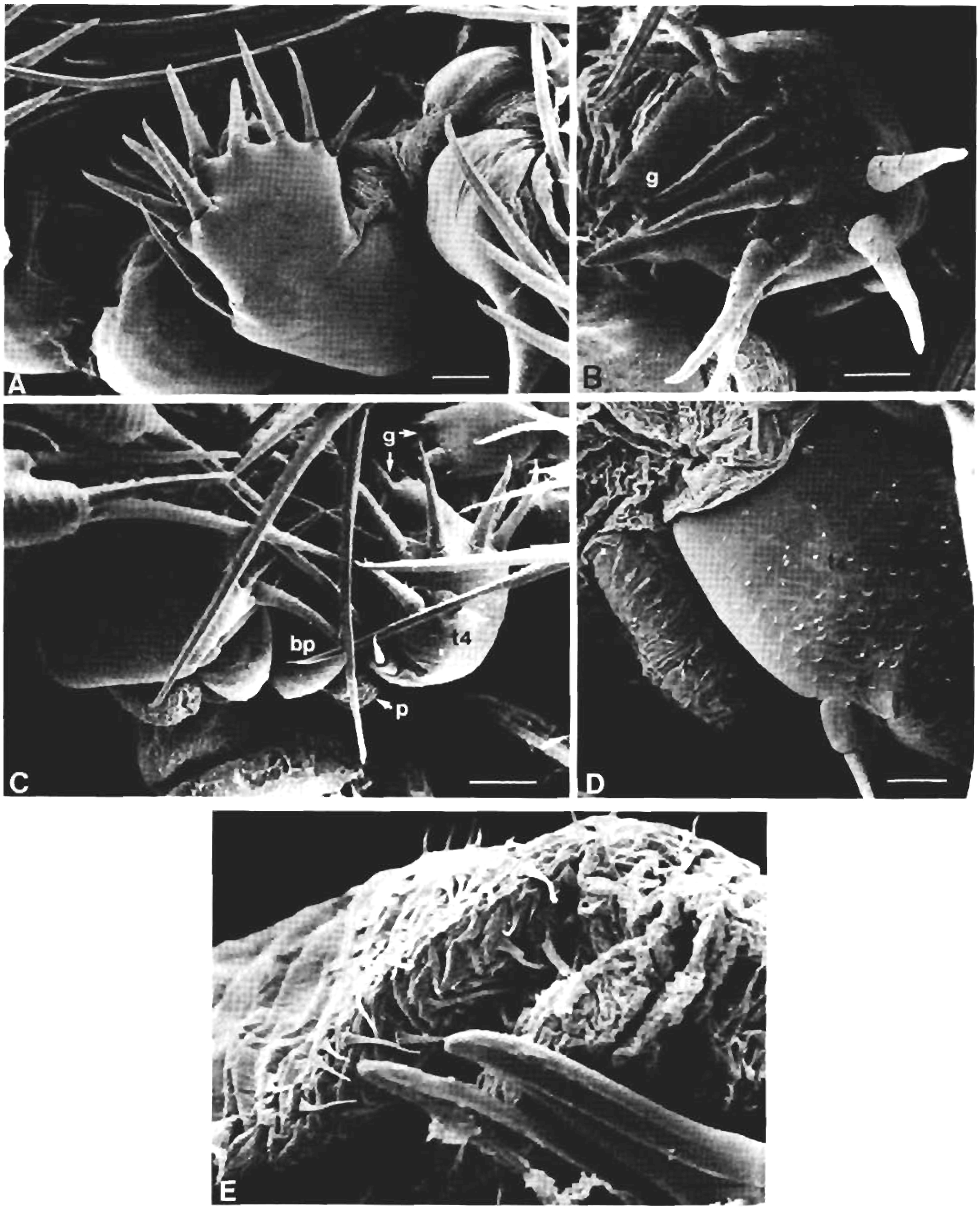


Fig. 18.—*A*. Outer view of thoracopod four showing distal spine-like setae. Note single seta on a peduncle-like extension (exopod) near posterior border of the leg.—*B*. Ventral view of thoracopod four showing immovable, heavily armored, gnathobasic process (g) and two outer spines.—*C*. Posterior region, 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-anteriormost 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

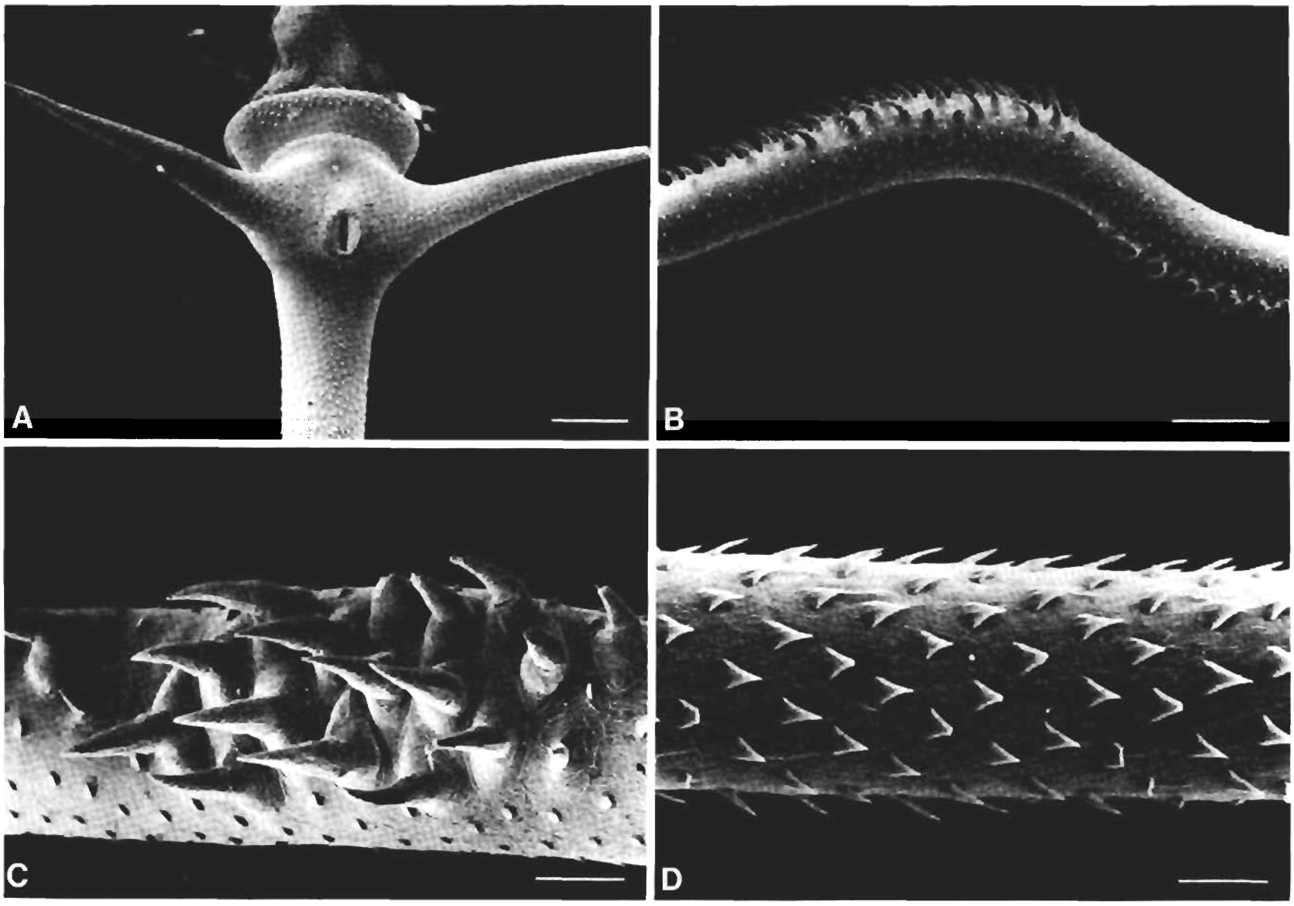


Fig. 19.—*A*. Ventral view of paired articular spines on article three of caudal process (youngest and functional article, immediately posterior to growth zone of 'abdomen'. Note anal opening centered between spines. Anterior is toward top of photograph.—*B*. Caudal bend in article one with small spines 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'.

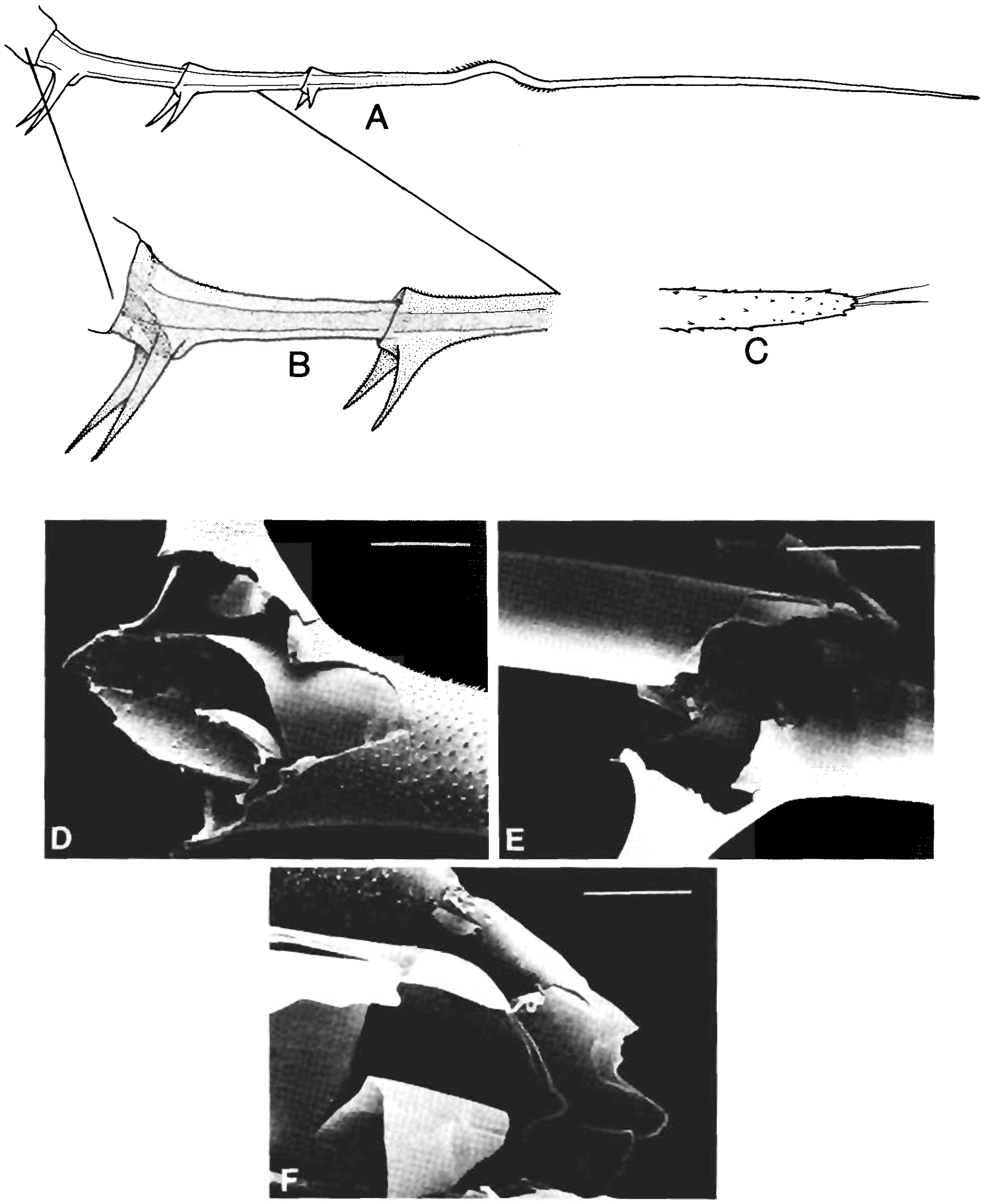


Fig. 20.—A. Caudal process in typical adult bearing 3 articles.—*B.* Enlargement of third and part of second article, showing intestine terminating at anus on youngest article (article 3 in this animal) and with some internal tissue visible extending into more posterior articles.—*C.* Terminus of caudal 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, Zozula 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 primaparity 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

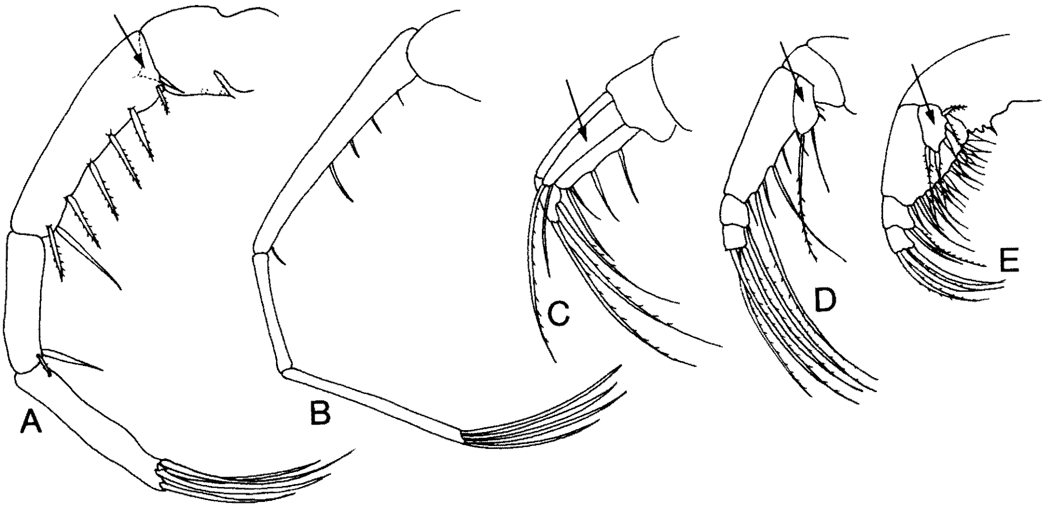


Fig. 21.—Comparison of the first thoracopod among several genera, representing the families Cercopagididae (*A*, *B*), Podonidae (*C*, *D*), and Polyphemidae (*E*), of the Onychopoda.—*A*. *Bythotrephes*.—*B*. *Cercopagis* (from Mordukhai-Boltovskoi 1968).—*C*. *Evadne* (from Mordukhai-Boltovskoi 1968).—*D*. *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 (distalmost), 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 is 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.

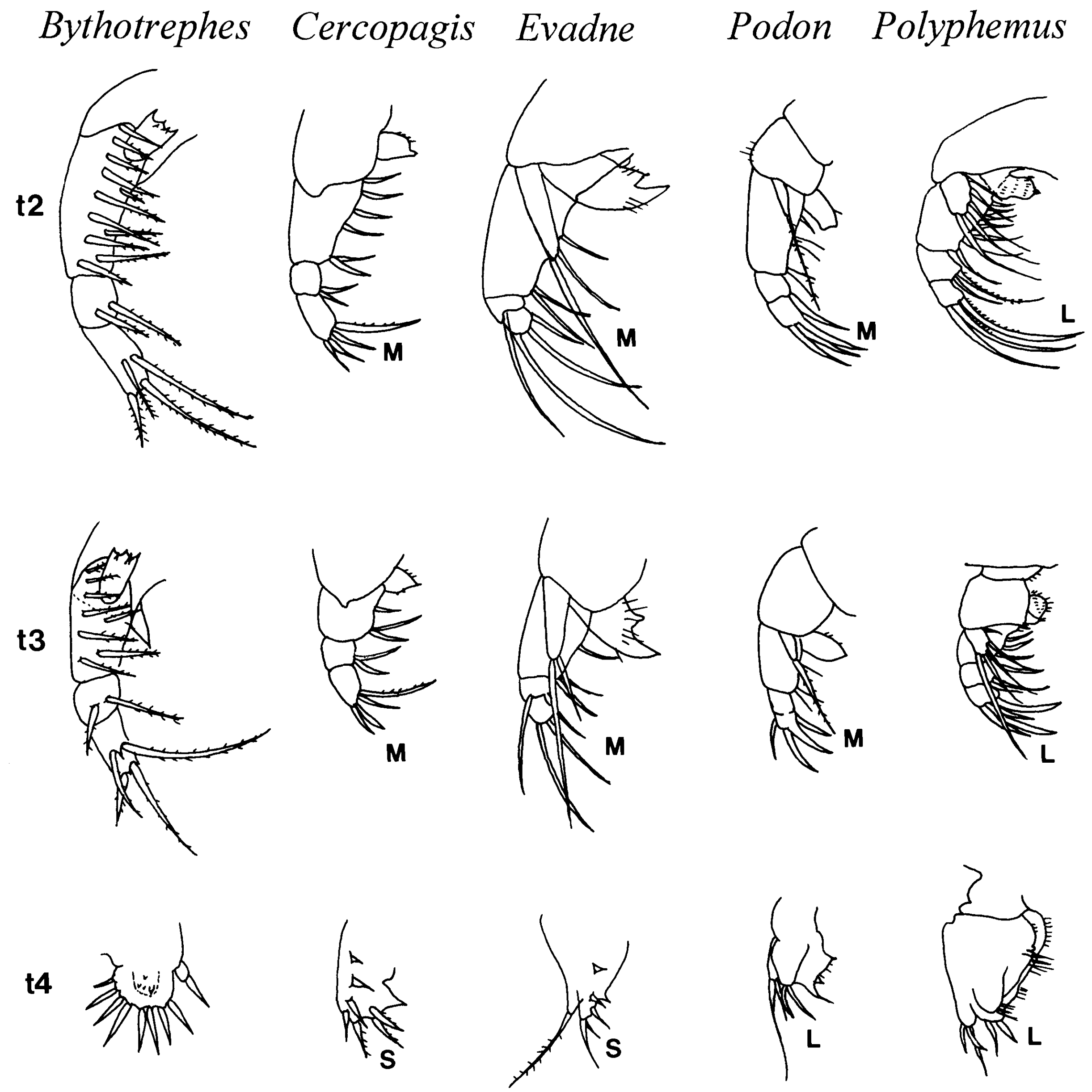


Fig. 22.—Comparison of thoracopods 2–4 in the three onychopod families. L, from Lilljeborg 1901; M, from Mordukhai-Boltovskoi 1968; S, from Sars 1897. Orientation is not the same for each illustration. Not drawn to scale.

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 (*Rehbachiella 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 *Rehbachiella*, 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 *Rehbachiella* 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 Walsossek (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.

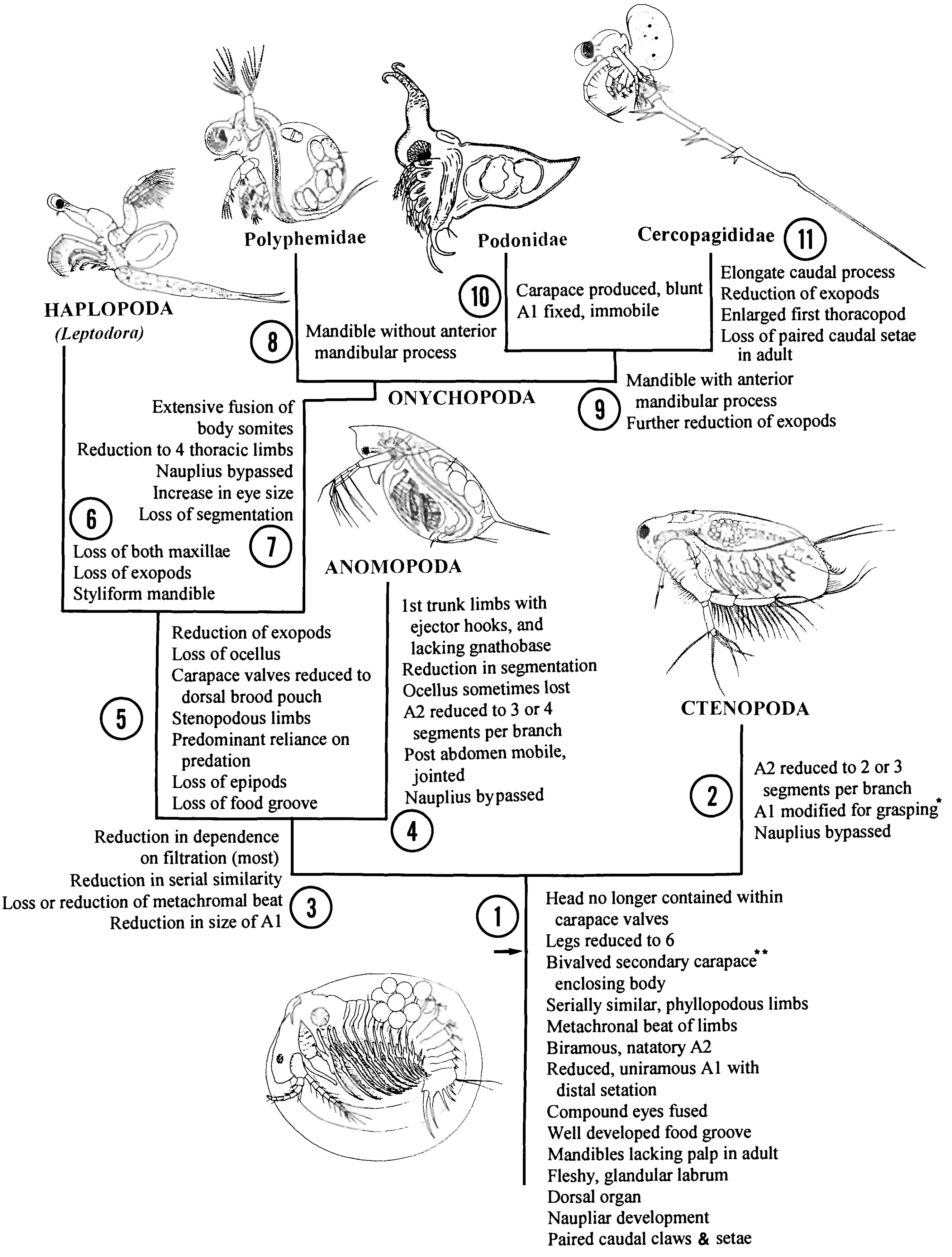


Fig. 23.—One hypothesis of cladoceran phylogeny, assuming cladoceran monophyly and assuming that cladocerans arose from some cyclestheriid-like conchostracan ancestor, both of which are subject to question. Characters above the arrow (reduction in leg number, reduction of carapace valves) are changes 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) discusses 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 187a, 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 exopods 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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