



External morphology of the male of *Cyclestheria hislopi* (Baird, 1859) (Crustacea, Branchiopoda, Spinicaudata), with a comparison of male claspers among the Conchostraca and Cladocera and its bearing on phylogeny of the 'bivalved' Branchiopoda

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The adult male of *Cyclestheria hislopi*, sole member of the spinicaudate conchostracan clam shrimp family Cyclestheriidae and a species of potential phylogenetic importance, is described for the first time. Several previously unknown features are revealed. Among these are (1) the morphology of the dorsal organ, which is roughly similar in shape to the supposedly homologous structure in other clam shrimps but bears a relatively large, centrally located pore unique to the species; (2) an anterior cuticular pore presumably leading to the 'internal' space surrounding the compound eyes, and thereby homologous to the same pore in other clam shrimps and in the Notostraca; (3) the spination and setation of the antennae and thoracopods, and (4) the mature male first thoracopods (claspers). The male claspers are paired and essentially equal in size and shape on right and left sides of the body. The second pair of thoracopods are not modified as claspers, a situation different from all other spinicaudate families but shared (plesiomorphic we propose) with the laevicaudatans and most cladocerans. The claspers bear a field of special spine-like setae on the extremity of the 'palm'; this setal type, previously unrecognized, is unique to *Cyclestheria*. The palm of the clasper also bears two palps (one very small), as in other conchostracan species (both laevicaudatans and spinicaudatans). The movable finger of the clasper, modified from the thoracopod endopod, bears a row of long setae along its outer extremity, also unique. *Cyclestheria* exhibits a mixture of characters, some unique and others typical of the Spinicaudata (Conchostraca). Cladoceran clasper types are briefly reviewed, as are the claspers in the Spinicaudata and Laevicaudata (Conchostraca). Morphology of the clasper of *Cyclestheria* shows typical spinicaudate characters. It is suggested that claspers on the first thoracopods may be a synapomorphy for the Conchostraca and the Cladocera. The possible role of *Cyclestheria* or a *Cyclestheria*-like ancestor in cladoceran phylogeny is briefly discussed in light of recent suggestions (Martin and Cash-Clark, 1995) of cladoceran monophyly and possible ancestral relationships with this genus. Some possibilities concerning the phylogenetic position of *Cyclestheria* — either as a sister group to the rest of the Spinicaudata or as a sister group to the Cladocera — are discussed. © 1997 The Norwegian Academy of Science and Letters

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Introduction

General

The spinicaudatan conchostracan *Cyclestheria hislopi* was described in 1859 by Baird, who based his description on specimens collected in India and named the species for its collector, the Rev. S. Hislop. Baird (1859) originally placed it in the genus *Estheria*, and it was not until 1887 that Sars recognized that its many distinctive features warranted the erection of a separate genus. Indeed, Sars

also suggested that it differed sufficiently from all described conchostracans to justify the establishment of a new family, the Cyclestheriidae, which remains to this day monotypic. Although another genus and species belonging to the family have been described subsequently from China (*Paracyclstheria sinensis*; see Shen and Dai, 1987), the description is lacking in detail and may represent young stages of *C. hislopi*; its validity is in need of verification.

Since the original description of *Cyclestheria hislopi*, the species has been shown to be widespread and has been reported from additional sites in India and Asia (Nair,



Fig. 1. Geographic distribution of *Cyclestheria hislopi* and *Paracyclestheria sinensis*. *C. hislopi* is widespread and has a circumtropical distribution but males are reported from four different sites only; two in America and two in Australia. The presented distribution is mostly based on available information in literature and the species is probably much wider distributed than the map indicates. See 'Introduction' and 'Results' for more details. * (Uncertain status, see text).

1968; Nayar and Nair, 1968; Paul and Nayar, 1977; Battish, 1981) as well as from the tropics or subtropics of most continents. Records exist from Australia (Sars, 1887, based on reared specimens from Australian mud samples; Timms, 1979, 1986), Africa (Barnard, 1929; Green, 1962; Egborge and Ozoro, 1989), Central and South America (Dodds, 1926, as *Gatuna spinifera*; Halloy, 1981; Roessler and Sanchez, 1986; Roessler, 1995a–c) and North America (Sissom, 1975, 1980). In some regions in Colombia and India it is reported to be the most common conchostracan and sometimes occurs in abundance (Roessler, 1995b; Paul and Nayar, 1977). (Fig. 1; see also the synonymy in the Results Section).

Natural history

Most of what is known of the natural history of *C. hislopi* comes from Sars (1887) and the recent work of E. Roessler (e.g. Roessler and Sanchez, 1986; Roessler, 1995a, b), both of whom had the opportunity to study living animals. Sars (1887), who cultured *C. hislopi* from Australian mud samples, observed that it reproduces parthenogenetically, with a change to sexual reproduction and the appearance of males when physical conditions become less favourable. He did not observe mating (which has to date not been observed) and was unable to tell how the fertilized eggs were deposited. However, the presence of empty carapaces with the upper part being rather dark and opaque reminded him of the ephippia of some cladocerans. Roessler and Sanchez (1986) and Roessler (1995b) confirmed the presence of cyclic parthenogenesis in Colombian populations (both in the field and in culture) and described the ephippium as well as certain features of

the male. The ephippium consists of the slightly modified carapace for egg protection, and its deposition necessitates the death of the female (Roessler, 1995b). This is in contrast to the cladocerans of the order Anomopoda, where only a larger or smaller part of the carapace is shed, and where the death of the female is not necessary when the ephippium is deposited. The presence of an ephippium is now considered a well established part of the life cycle of *Cyclestheria*. Furthermore, Roessler and Sanchez (1986) and Roessler (1995b) distinguish between the parthenogenetic female and the sexual female, the latter forming the ephippium, which remains when the female dies. The ephippium contains up to nine fertilized eggs, which are larger than parthenogenetic eggs (Roessler, 1995b). Although the function is undoubtedly the same, the homology of the *Cyclestheria* ephippium to that of some cladoceran families is possible but not yet documented. Another characteristic aspect in the life cycle is direct-developing eggs that are brooded by the female and released as juveniles with the adult number of limbs. In Colombian populations both the parthenogenetic eggs and the resting eggs undergo direct development (Roessler, 1995b), while meta-nauplii have been reported hatching from resting eggs in Cuba (Botnariuc and Viña Bayés, 1977). Sassaman (1995) has hypothesised that the retention of direct-developing eggs in the brood chamber in *Cyclestheria* evolved after the development of parthenogenesis. This is in contrast to the cladocerans, where the retention of the direct-developing eggs has been hypothesised to have arisen *first*, followed by the development of parthenogenesis (Hebert, 1987).

The natural habitat of *Cyclestheria* differs from that of all other conchostracans. It occurs sometimes in ephemeral ponds, but also in permanent bodies of water (whereas

other conchostracan families do not), and is almost always associated with a thick algal mat (e.g. Sissom, 1980) or other aquatic vegetation, especially *Hydrilla* (Paul and Nayar, 1977, in India, and Timms, 1979, in Australia) and less frequently *Eichornia* (e.g. Egborge and Ozoro, 1989, in Africa). Roessler (1995a, b) has reviewed its natural history based on Colombian populations.

Males of *Cyclestheria* have long been considered extremely rare, and seem to have been reported only from 4 sites (see Fig. 1): one young specimen from a cultured collection from Australian mud samples (Sars, 1887), one specimen found among hundreds of Australian field-collected individuals by Daday (1926), a few specimens from a population (probably introduced) in Texas, North America (Sissom, 1980), and in abundance from Colombian localities collected in the beginning of the dry season (December and January) (Roessler and Sanchez, 1986; Roessler, 1995b: Figs 2e, 4a–d). In addition, males have been inferred to be present in Cuba based on apparent clasper damage on the carapace of females (Botnariuc and Viña Bayés, 1977). Sissom reported a female/male ratio of 4:1. We examined his collections but found only a few males left. The female/male ratio in Colombian dry season

populations was up to 5:1 and differed among populations (Roessler and Sanchez, 1986; Roessler, 1995b). Evidence from Colombia, where males were largely present only for a short time of the year, suggests that they could occur in larger numbers elsewhere at appropriate times, but extensive collecting over much of the year in India failed to locate any males (e.g. see Nair, 1968; Paul and Nayar, 1977). Sassaman (1995) has recently presented a model where the lack of males in populations in Asia and Africa is explained as the lack of a mutation, which — from unisexuality (parthenogenesis) — restores a modified sexuality where males are expressed in a condition-dependent manner. In America and Australia this mutation — according to the model of Sassaman (1995) — has occurred, and males are therefore present.

Morphology

Because of some morphological features that appear to be shared with (or are at least similar to those of) some cladocerans, *Cyclestheria* has at times been proposed as something of a 'missing link' between the bivalved

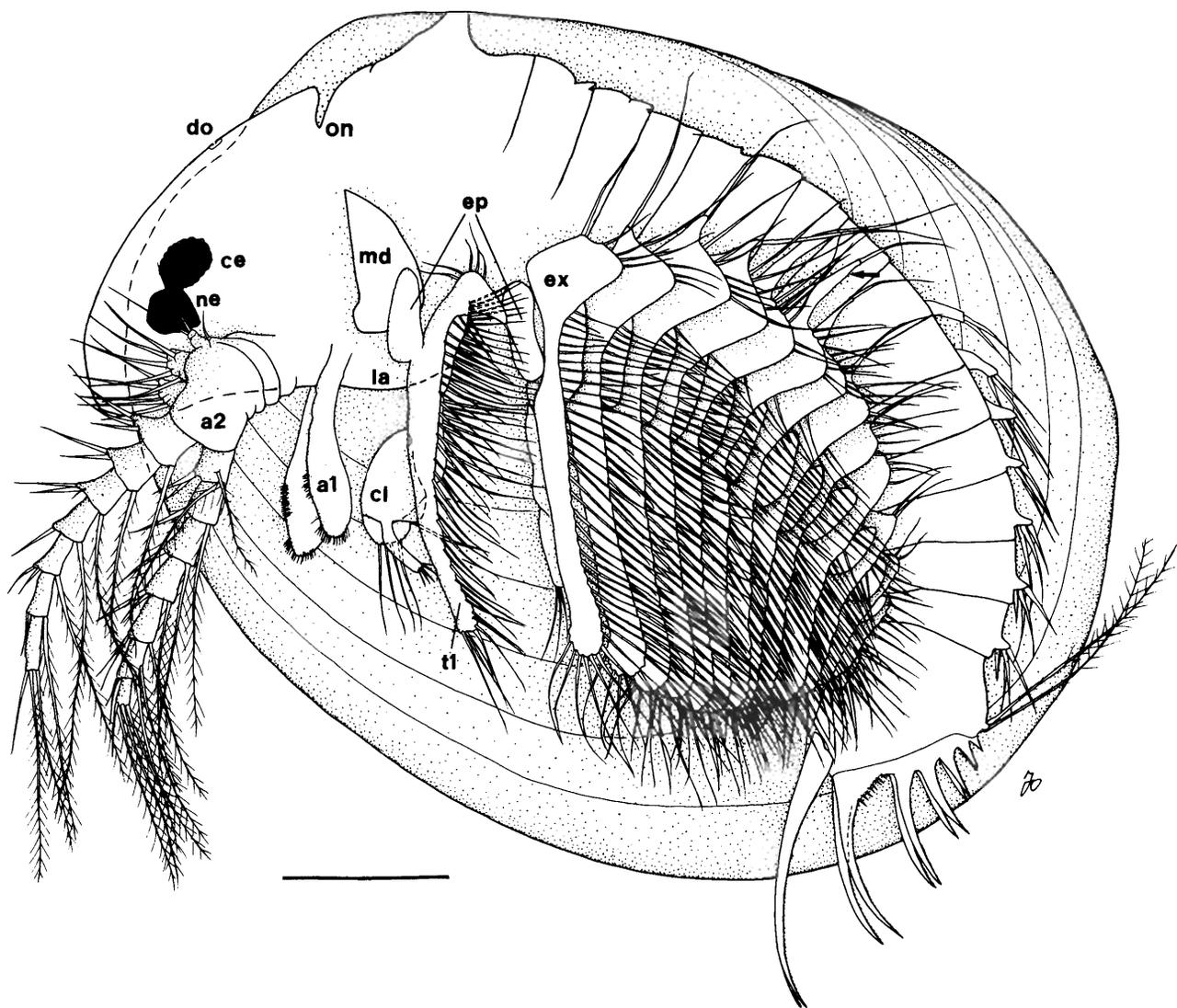


Fig. 2. *Cyclestheria hislopi* mature male, from Colombia (see text). Lateral view, left carapace valve removed. Black arrow indicates a dorsal protusion of the exopod. Scale bar: 250 μ m.

branchiopod crustacean groups formerly known as the Conchostraca and Cladocera (see Fryer, 1987a, b for arguments concerning the validity of those taxa). This long standing idea was repeated by Tasch (1963) and Schminke (1981) and reviewed most recently by Martin and Cash-Clark (1995), who proposed that the Cladocera might be a monophyletic group whose ancestor could be a *Cyclestheria hislopi*-like species, despite earlier and differing views on this subject (e.g. Fryer, 1987a, b). Whether *Cyclestheria hislopi* is the sistergroup to the Cladocera, and the consequent paraphyly of the Conchostraca, were not discussed in that paper, nor was the fact that the fossil record of ephippium-bearing cladocerans (in the Anomopoda) has been extended to the Lower Cretaceous and perhaps earlier (Fryer, 1991), whereas *Cyclestheria* is believed (at least by Tasch, 1963) to have had a post-Cretaceous origin. *Cyclestheria*-like fossils are, however, mentioned from the Permian (*Cyclestherioides lenticularis*, see Raymond, 1946). A number of potential synapomorphies, some morphological and some of an ecological nature, of *Cyclestheria hislopi* and the Cladocera are responsible for the hypothesis of their relatedness. They include the presence in both groups of (1) direct development, which is not seen in any other conchostracan family other than the Cyclestheriidae (although this has certainly arisen independently in a variety of other crustacean groups, and although at least one cladoceran (*Leptodora kindti*) has retained naupliar development of the resting eggs), (2) fused compound eyes (although in other groups of clam shrimps the eyes are not so separated as some texts indicate), (3) an antennule with sensillae restricted primarily to the tip (as opposed to sensillae appearing along the entire length of the antennule), (4) the presence of an ephippium (discussed previously), and (5) parthenogenesis as part of the life cycle. Because of the pivotal role that *Cyclestheria hislopi* might play in our understanding of conchostracan-cladoceran relationships, and because in the Conchostraca so many characters traditionally considered to be of phylogenetic importance are those of the male, it is somewhat surprising that prior to the present paper the external morphology of the mature adult male was undescribed.

A young male was described and illustrated from specimens raised from Australian mud by Sars (1887). However, that single male was removed from the dorsal brood chamber of a female and was not fully developed (based primarily on findings in the present paper). Several of the characters considered today to be of potential phylogenetic significance were not described, or were described incompletely by modern standards. Below we provide a description of selected morphological details of the adult male.

Materials and methods

Illustrations of males are from collections made in small ponds in Valley Magdalena, close to Bogotá, Colombia, by J. O. in October 1994 and by E. W. R. over the last 15 years. We also examined material from Australia, Nicaragua, North America (USNM 171402, the specimens reported by Sissom, 1980), India, and Singapore. Only the Colombian and North American collections contained males. Three SEM figures (Fig. 4a-c) are based on a male from the North American population. Specimens were prepared for SEM by briefly sonicating while still in 70%

ethanol, dehydrating in a graded ethanol series to 100% EtOH, and air drying from HMDS (hexamethyldisilazane; see Nation, 1983) prior to mounting on stubs and viewing with a Cambridge Stereoscan 360 at 10 KV. Illustrations (SEM photographs, Figs 11, 12) and drawings (Fig. 14) of other conchostracans included for comparative purposes were taken from the literature (e.g. Martin and Belk, 1988; Martin, 1989a) or from SEM negatives in the personal collection of J. W. M. Illustrations of different cladoceran male claspers were redrawn after Lilljeborg (1900) and Sars (1993) (Fig. 13). Specimens of the genus *Cyzicus* (Spinicaudata, family Cyzicidae) used for Fig. 12a, b were taken from an uncatalogued collection in the Natural History Museum of Los Angeles County, for which collection data are: #996, July 14, 1955, large shallow roadside pond, 7 mi. east of Ozona, Crockett County, Texas; coll. W. G. Moore. Terminology is in general in accordance with Walossek (1993). Concerning thoracopods, the term 'protopod' is used for the whole limb corm, and 'basipod' is used for the limb corm excluding the proximal endite. The endite number '6' has in some cases been retained for ease of comparison with older literature, although there is little doubt that this 'endite' is actually the true endopod (see Walossek 1993).

Abbreviations used in figures

a1	first antenna (antennule)
a2	second antenna
ar	anterior ramus of a2
ce	compound eye
do	dorsal organ
en	endopod
ep	epipod
ex	exopod
f	fornix
hp	hepatopancreas
la	labrum
md	mandible
ne	naupliar eye
on	occipital notch
p	palp
pe	proximal endite (= first endite)
pr	posterior ramus of a2
rs	rostral spine
s1	setal type 1 (endites)
s2	setal type 2 (endites)
s3	setal type 3 (endites)
sf	setal field

Results

Cyclestheria hislopi (Baird, 1859)

Estheria hislopi Baird, 1859: 232, pl. 63, fig. 1 (description, India); Grube, 1865: 203 (taxonomy); Daday, 1905: 231 (Paraguay).

Limnadia hislopi (Baird). Brady, 1886: 294 (*E. hislopi* transferred to *Limnadia*, Sri Lanka).

Cyclestheria hislopi (Baird). Sars, 1887: 223, pls. 1-8 (description, morphology, natural history, Australia); Stuhlmann, 1888: 1253 (mention of a '*Limnadia*' that can be only *C. hislopi*, Zanzibar); Weltner, 1898: 199 (short review of *C. hislopi*); Thiele, 1900: 563 (Africa); Sayce, 1903: 256 (catalogue of Australian Phyllopoda); Gurney, 1906 (India); Daday, 1910: 158 (Africa); Daday, 1913: 3 (Africa); Barnard, 1924: 223 (Namibia); Daday, 1926: 579, fig. 146 (taxonomy, report on one male, Australia); Barnard, 1929: 249 (distribution, Africa); Lutz, 1929: 3 (natural history, Brasil); Brehm, 1939: 111 (natural history); Linder, 1945: 1 (phylogeny, discussion); Raymond, 1946: 215 (palaeontology); Brehm, 1948: 95 (distribution, Cuba); Margalef, 1949: 41 (phylogeny); Fryer, 1957: 238 (Malawi, Tanzania); Mendes and Fernando, 1962 (Sri Lanka); Green, 1962: 415 (natural history, Nigeria); Tasch, 1963: 145 (phylogeny, palaeontology); Nair, 1968: 96 (natural history, India); Nayar and Nair, 1968: 221 (natural history, distribution, India); Michael, 1968: 37 (ecology, India); Petr, 1968: 469 (natural history, Ghana); Straskraba, 1969 (Cuba); Camacho, 1974 (palaeontology); Botnariuc and Viña Bayés, 1977: (Cuba); Fernando, 1974 (Sri Lanka); Bidwell and Clarke, 1977 (Nigeria); Paul and Nayar, 1977: 173 (natural history); Sissom, 1975; 1980: 175 (distribution, North America); Junk, 1977: 229 (natural history, Thailand); Timms, 1979: 57; 1986: 302, fig. 1 (natural history, distribution, Australia); Halloy, 1981: 5 (distribution, Argentina); Battish, 1981: 181 (distribution, India); Schminke, 1981: 629

(phylogeny); Timms, 1986: 302 (distribution, Australia); Roessler and Sanchez, 1986: 679 (natural history, Colombia); Hare and Carter, 1987 (Nigeria); Camacho Camacho Reyes, 1988 [unpublished]: 4 (histology, reproductive biology, Colombia); Egborge and Ozoro, 1989: 137 (natural history, distribution, Nigeria); Martin, 1989b: 123 (feeding morphology); Martin, 1992: 34 (microscopic anatomy); Realpe Rebolledo, 1993 [unpublished]: 104 (neurology, histology, anatomy, Colombia); Roessler, 1995a: 125 (natural history, Colombia); 1995b: 113 (ecology, life cycle, reproduction, males, Colombia); 1995c: 253 (morphotaxonomy, Colombia); Sassaman, 1995: 45 (life cycle, phylogeny); Martin and Cash-Clark, 1995: 85, fig. 23 (phylogeny).

Cyclestheria sarsiana Thiele, 1907: 288 (synonymised with *C. hislopi* by Lutz, 1929).

Eulimnadia victorae Brady, 1913: (synonymised with *C. hislopi* by Barnard, 1929 Zimbabwe).

Gatuna spinifera Dodds, 1926: 14, figs 2 and 3 (development, natural history, Panama).

Paracyclstheria sinensis Shen and Dai, 1987: 353 (description, female with only 12 pairs of thoracopods and without growth lines on shields) [questionable taxon; probably juvenile of *C. hislopi*].

In addition to these records, mentioned in the literature, *C. hislopi* has been reported from Nicaragua, near the city of Granada, Rio los Cocos, a tiny feed stream into Lago Cocibolca (Lago de Nicaragua) (personal communication, Al López, S.J.), and from Africa (Zambia, L. Bangweulu; Uganda, L. Victoria) (personal communication, Geoffrey Fryer).

Geographical distribution

Cyclestheria hislopi is a pantropical species (Fig. 1), found between approximately 30° N and 35° S latitude. Males have been reliably reported from only 4 sites, three of which (Texas, Australia (2)) are at the northern and southern extremes of the range, whereas the fourth (Colombia) is in the centre. It is possible that one of the extreme northern records (Texas) is a case of accidental introduction via cattle (see Sissom, 1980).

Description of the male

General shape and size

The carapace valves (= secondary shield; see Walossek, 1993, 1995 for definition of this term) of the males in side view are of the same almost rounded shape as in the female, being nearly as high as long. The secondary shield is not markedly globular (as is the case for the laevicaudatan Conchostraca) but is more laterally compressed, in keeping with females of the species and with other spinicaudate conchostracans. Shield lengths of the males examined by us ranged from 1.2 mm to 1.7 mm. The following description of morphological features is based only on morphologically fully developed males, bearing from 5 to 7 growth lines on the external shield surface.

Head and head appendages

Head. In side view the head is roughly triangular with a blunt tip; the dorsal surface is convex, the ventral side concave. It bears dorsally a keel like structure, the rostral carina (Figs 2, 3a, d). This allows for moving of the protopodal stiff setae on the second antennae; it is seen also in the family Limnadiidae. The blunt tip of the head is minutely serrated, with a row of teeth that increase in size towards the distal extremity (Fig. 5c). Dorsally in the head

is an incision which in earlier literature is termed the occipital notch (Fig. 2). A large slightly swollen oval field is set off from the rest of the cuticle extending from the occipital notch to the rostrum (the margin of the field are indicated by 4 white arrows in Fig. 4a). From the occipital notch, proceeding anteriorly along the rostral carina, there is, at approximately 1/5 the distance toward the tip, a slight lateral swelling of the carina that bears the oval or rectangular 'dorsal organ' (Figs 2, 4a, c, d). Inside the organ is a large central pore (Fig. 4c, d); in one specimen the pore appeared as two openings in contact with each other (Fig. 4d). This organ is almost certainly homologous to the so-called 'dorsal organ' (neck organ, nuchal organ) known in other conchostracan species and in other branchiopod groups (e.g. see Martin and Belk, 1988; Martin and Laverack, 1992; Martin, 1992; Olesen, In Press). More distally along the rostral carina (small black arrow, Fig. 4a) is another pore located in an area of little or no swelling (Fig. 4b). This pore has not been previously described for *Cyclestheria*, although its presence has been noted (see especially Egborge and Ozoro, 1989: Figs 7–12). It is most likely homologous with an opening in the same place in other conchostracan species (e.g. Martin *et al.*, 1986; Martin and Belk, 1988) and perhaps also with the pore seen in some notostracans (e.g. see Martin, 1992: fig. 124 F, G). If so, it leads to a space over the compound eyes (as suggested also by the illustrations in Egborge and Ozoro, 1989: fig. 12) and perhaps indicates the area of subsidence of these organs within the cuticle during ontogeny (Martin, 1992).

Antennule. The antennule is shorter and more dilated at the tip than in the female (e.g., see Fig. 16a). The sensillae are not restricted to the tip (which seems to be the case in the female) but are also, at least in some specimens, found along the anterior/medial side of this appendage (Figs 2, 5e–g). Up to 40 sensillae are present on a single antennule and some possibly carry more than this, as there appears to be variation in number even from side to side in a single individual. The cuticular walls of the sensillae, and the surrounding cuticle of the antennule, appear to be thin, and display shrinkage and distortion upon drying.

Antenna. The antenna has a superficially segmented protopod and two 7-segmented rami. Two main types of setae are present: long, plumose, natatory setae and shorter, stiff, curved setae (Figs 2, 3a, d, 5a–d). The natatory setae are found on the posterior side of each ramus and on the tip of the distal segment. The posterior ramus has eight such, one on each of segments 2–6, and three on the distal segment. The anterior ramus has the same setation except for the distal segment, which has only 2 natatory setae. The stiff, curved setae, which are smooth basally but may bear minute spinules on the distal half, are found all along the length of the antennae, but are most pronounced in the proximal region of the protopod and first few segments of the anterior ramus, where several rows of setae together constitute a cluster pointing in an anterior, anterolateral, or even anteromedial direction, fitting neatly into the space on either side of the distal part of the rostral carina (Fig. 3d). The stiff setae in this cluster arise from lobe-like protuberances of the antennal cuticle

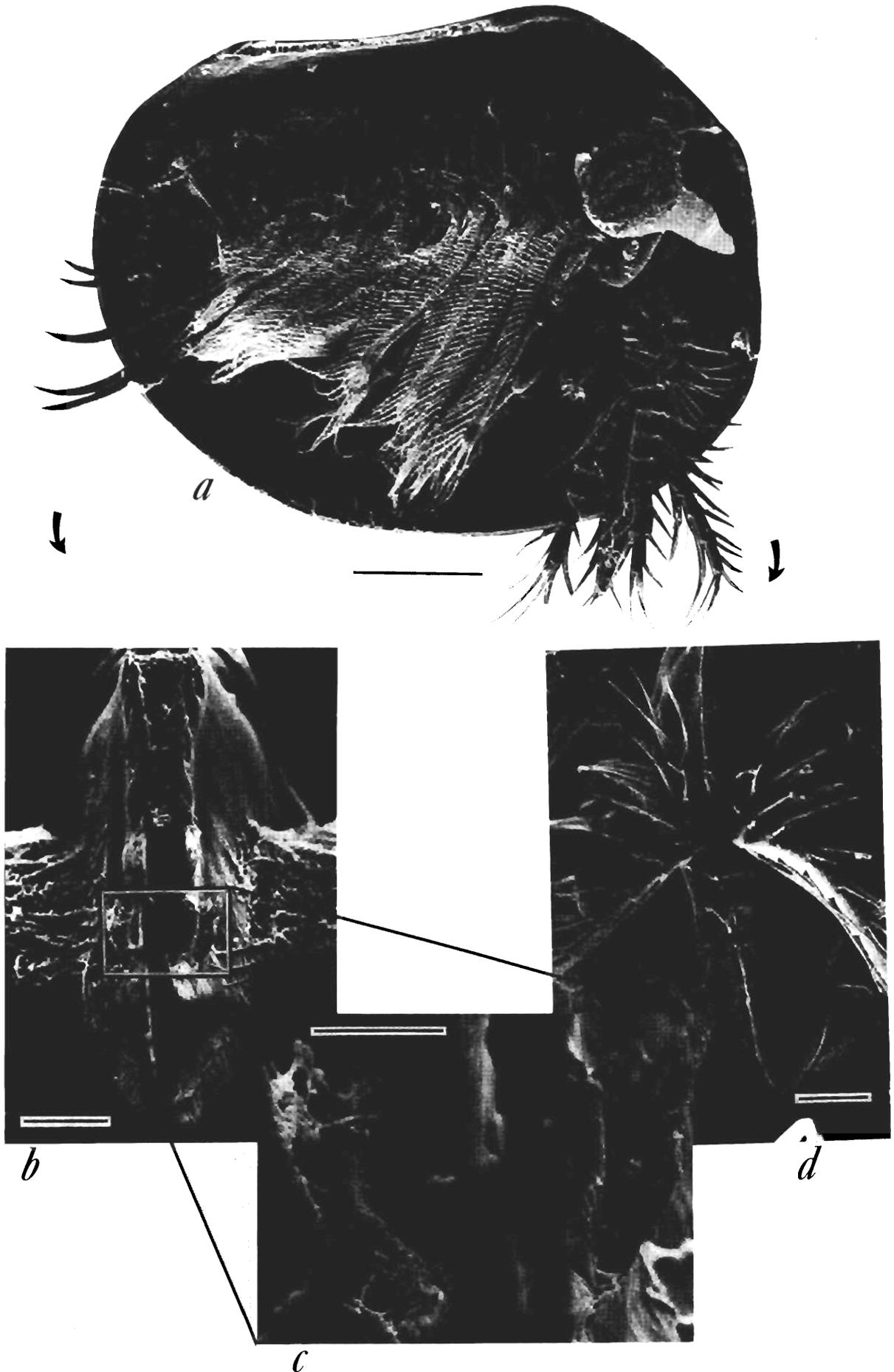


Fig. 3. *Cyclestheria hislopi* mature male, SEM of right side of body (with right carapace valve removed) and selected aspects of the anterior and posterior regions. a, lateral view, whole animal. b, posterior region with laterally-directed spine rows magnified higher in c. d, anterior view, showing rostral carina and spine-like setae of protopod of second antenna. Scale bars: a. 250 μm ; b. 50 μm ; c. 20 μm ; d. 100 μm .

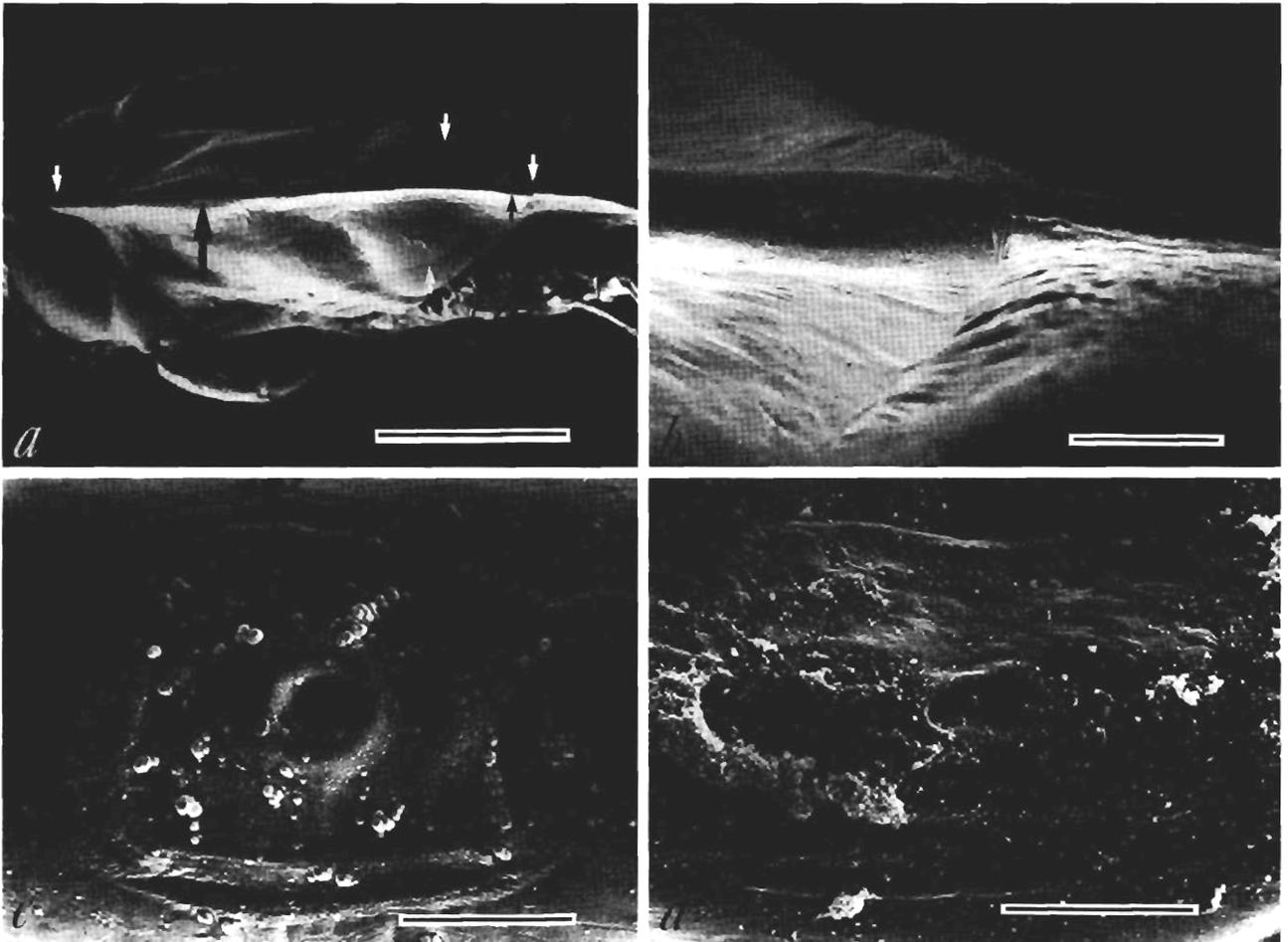


Fig. 4. *Cyclestheria hislopi* features of the head region. a, entire head of male from Texas population. Large black arrow indicates dorsal organ, smaller black arrow at right indicates more distal pore probably opening into a space surrounding compound eye. Small white arrows indicate extension of a large slightly swelled oval field set off from the rest of the cuticula. b, higher magnification of pore indicated by small black arrow in a. c, dorsal organ, male from Texas population. d, dorsal organ, male from Colombia, with 'double' central pores. Scale bars: a. 200 μm ; b. 20 μm ; c. 10 μm ; d. 10 μm .

(Fig. 5a–d). This trend is continued distally, with the lobes from which each seta arises becoming less pronounced toward the tip of the ramus. Three lobes are present at the protopod, the most proximal with 2 stiff setae, the middle with 5–6, and the most distal with 5. The five most proximal segments of the anterior ramus are produced into lobes on the anterior distal corner of each segment. The lobe of the first (proximal) segment bears 3 stiff setae; that of the next three either 1 or 2 setae. The posterior ramus also bears stiff setae, but these do not originate from a cuticular peduncle. Additionally, there are scattered stiff setae found on both rami, usually 2 per segment.

Mouthparts. These were not examined in our study of males. For the female these have been described briefly by Martin (1989b) and by Sars (1887).

Thoracopods

General. All males examined had 15 pairs of thoracopods which is the number mentioned by Roessler and Sanchez (1986) and Roessler (1995b) (females have 16, though 18 pairs were reported by Battish, 1981). Except for the first pair, which is modified for clasping during mating, the thoracopods show much serial similarity. From anterior to

more posterior limbs, there is a gradual reduction in overall size (Fig. 6). All thoracopods possess an elongate exopod and an oval or slightly triangular and unarmed balloon-like epipod. All thoracopods bear a proximal endite (or gnathobase) that differs structurally and functionally from the more distal endites, of which there are in a typical thoracopod of *Cyclestheria*, always four. The distal-most 'endite' ('endite 6') is actually not an endite at all, but is rather the reduced 'true' endopod of the limb, as is seen by the clear suture line separating this part of the limb from the protopod in other conchostracans (see Walossek, 1993: figs 46, 47 and 48, also for other branchiopods). Some authors (e.g. Martin and Belk, 1988 in discussing laevicaudatans) have numbered the endites from 1 through 6 (with the endopod numbered as 'endite 6'). In this paper we have numbered the endites from 1 to 5, proximal to distal and because many authors have referred to the endopod as 'endite 6', we retain this designation in our figures for ease of comparison and therefore use the terms 'endopod' and 'endite 6' interchangeably.

Thoracopod 1 (clasping leg). This consists basically of the same components as described above, but there has been much modification of the distal endites and the endopod. The proximal endite shows a characteristic row of relatively stiff, curved setae. Functionally anterior to this

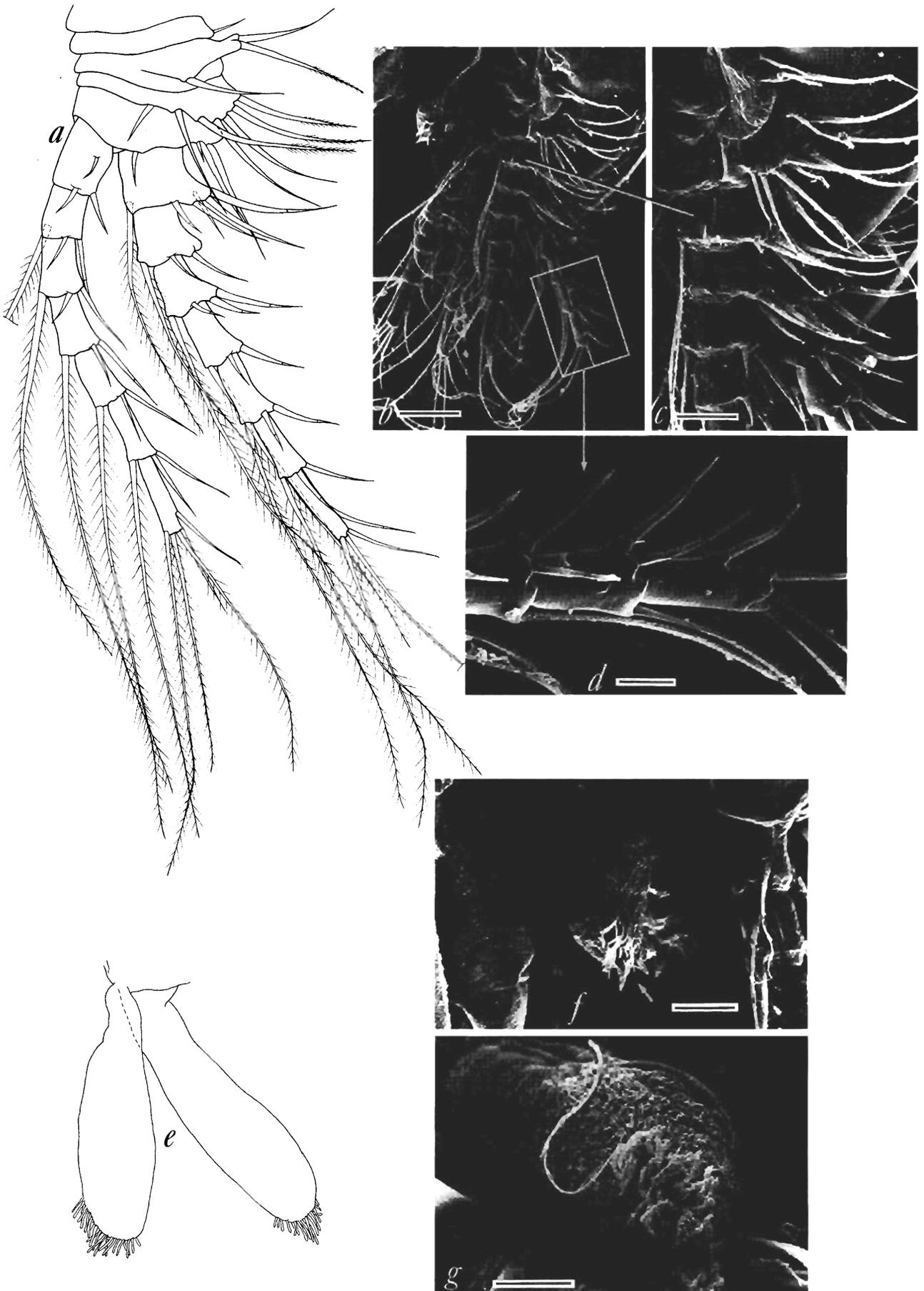


Fig. 5. *Cyclestheria hislopi* antennae and antennules of the male. a, entire second antenna, right side, with anterior ramus at right. b, SEM of second antenna (with antennule visible at upper left) partially obscuring rostrum (r), orientation same as for a. c, higher magnification of anterior ramus of second antenna, showing heavy spines arising from cuticular protuberances. Arrow connecting b and c indicates same segment for comparison. d, higher magnification of region delimited by white box in b, showing distal anterodorsal spines and ventral plumose setae. e, antennules. f, SEM of distal part of antennule; note sensillae at tip and shrinkage of cuticle caused by drying process. g, end-on view of distal part of antennule and its sensillae. Scale bars: b. 100 μm ; c. 50 μm ; d. 25 μm ; f. 25 μm ; g. 25 μm .

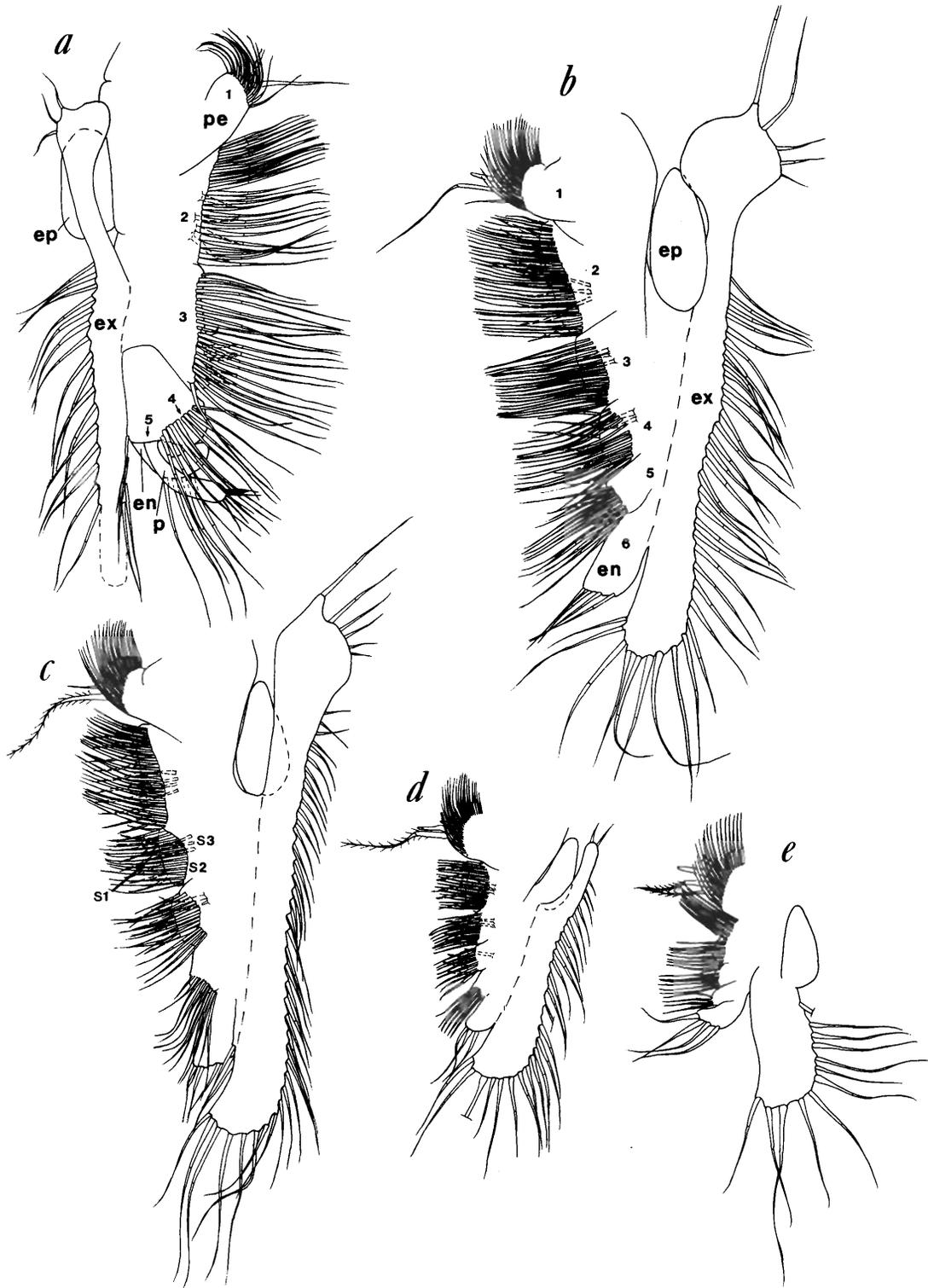


Fig. 6. *Cyclestheria hislopi* thoracopods of male, posterior views. a, left thoracopod 1 (male clasper). b, right thoracopod 5. c, right thoracopod 10. d, right thoracopod 12. e, right thoracopod 13. Arabic numbers refer to endites, except number '6' which is the endopod. Not to scale.

row are two small non-curved setae and one longer seta (Fig. 6a). Because the proximal endite is similar to that of the remaining thoracopods, it is described in greater detail in the next section. Of the more distal endites, numbers 2 and 3 are elongate, and seem to correspond with the same structures seen in the remaining (non-clasping) thoracopods (see below). These endites are almost equal in size. Both have posterior rows of setae that arise more or less along the border of the endites, the second endite with slightly fewer setae than the third. On the anterior side of

both endites are small groups of shorter and stiffer setae; the second endite has 4 of these and the third has 7.

Endites 4 and 5 and the endopod ('endite 6') have been modified into a clasping structure (see Fig. 14h–j), composed of the movable finger (endopod), the opposing 'palm' or 'hand' (endite 4 + 5) of the clasper, and 2 palps (a larger and a smaller, the latter of which was so small that it could not be drawn on Fig. 6). The posterior face of the 'palm' also bears a row of setae, fewer than on endites 2 and 3, and set at a distance from the border. We do not

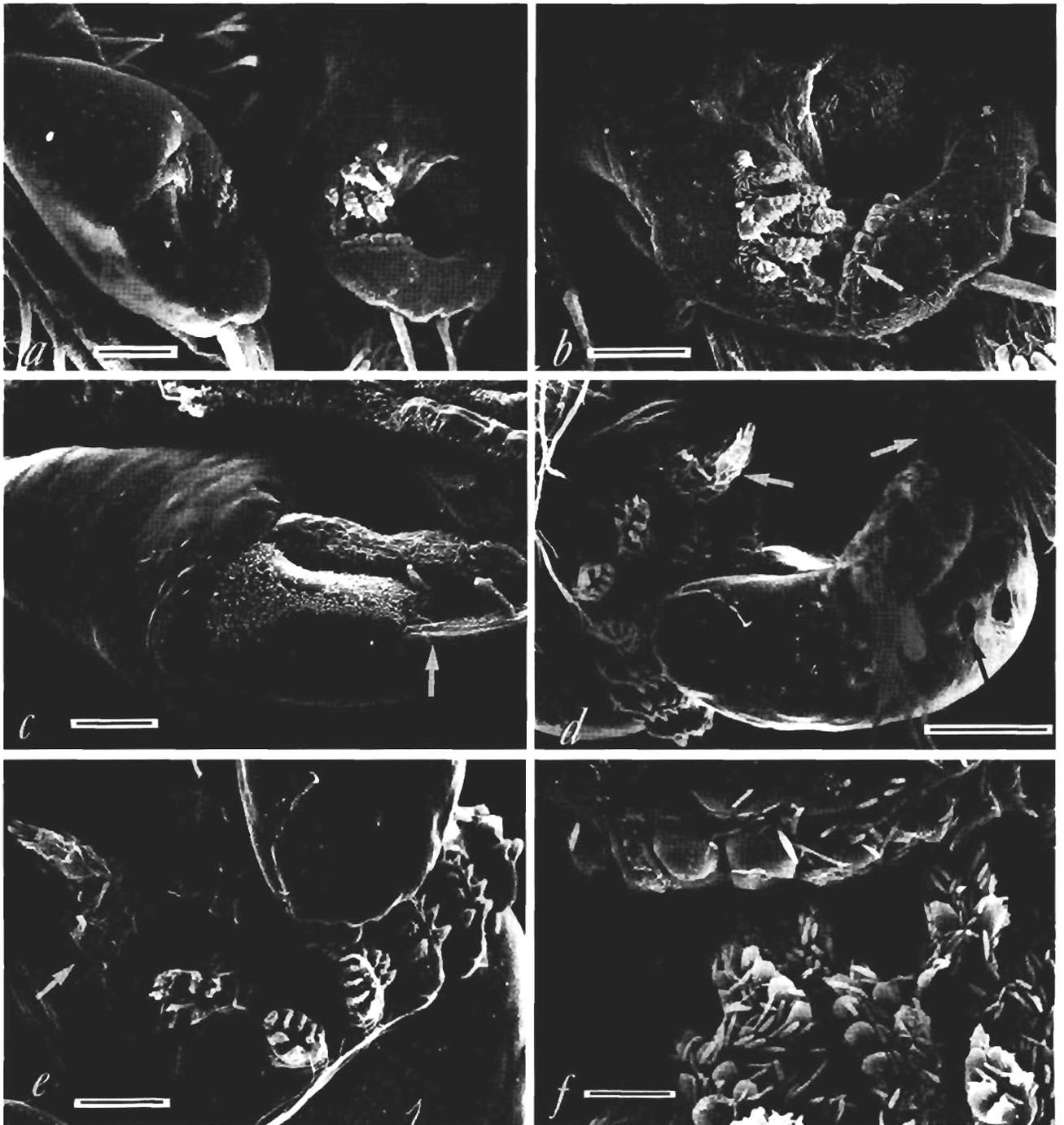


Fig. 7. *Cyclestheria hislopi* claspers of mature male. a, anterior view of right (at left of photograph) and left claspers. Note row of long setae on outer edge of movable finger (endopod [en]) and absence of palps, which in this view are obscured by clasper finger and hand. b, higher magnification of left clasper seen in a. Arrow indicates unique spine-like seta in field at tip of hand. c, base of movable finger with main palp visible just above it. Arrow indicates first of series of long setae of movable finger. d, tip of movable finger, field of spine-like setae of palm (hand), and both palps, smaller of which indicated by arrow at left of photograph. e, higher magnification of unique spine-like setae and smaller palp (white arrow). f, flattened teeth at distal tip of movable finger and spine-like setae of hand, against which they close. Elongate rods are bacterial fouling. Scale bars: a. 25 μm ; b. 20 μm ; c. 25 μm ; d. 20 μm ; e. 10 μm ; f. 5 μm .

know whether this row corresponds to the setae row on endite 4 or on endite 5, or perhaps to both. On the part of the 'palm' that opposes the tip of the movable finger there is a field of about 10 specialized spine-like setae (Fig. 7a, b, d–f). These are all curved in the same direction — towards the base of the movable finger — and are equipped with 7–8 scale-like outgrowths directed toward the tip of the movable finger. The 'palm' also bears the two palps, one of which is large and arises near the base of the movable

finger, the other small and directly behind and slightly lateral to the field of spine-like setae (Figs 7d, e, 14j). Both palps displayed much shrinkage during the drying process, which indicates that they are made of a thin cuticle (Fig. 7d, e). Both are attached to the 'palm' at what is the functionally posterior side of the movable finger, such that they are not visible in anterior view (e.g. Fig. 7a, b). The larger palp bears at its tip a group of smooth setae (Fig. 7d); resolution did not allow us to make detailed

observations of the tip of the smaller palp, but it may bear setae or a pore (suggested in Fig. 7d, e).

The movable finger, which is the modified endopod ('endite 6'), is long and curved, and on its tip it bears flat, teeth-like setae that lack the scale-like outgrowths seen on the opposing field of setae of the 'palm'. On the 'dorsal' side (functionally ventral) of the movable finger are 3–5 long setae (Fig. 7a–c); some of these were broken off during sonication and their sockets can be seen clearly in Fig. 7d (black arrow).

The exopod of the first thoracopod illustrated in Fig. 6a is broken at the distal end. Its length is shown by the dashed line. The proximal part of the exopod is extended as a free and slightly dilated lobe, where only 3 setae are present. The more distal part of the exopod bears numerous large setae, larger than those of the endites although not so closely placed. The epipod is oval and sac-like.

Thoracopods 2 to 15. The remaining (non-clasping) thoracopods are described together because they show much serial similarity. However, there are some differences, most obviously in size. The description of the various setal types below is based mostly on those on the anterior side of thoracopods 2 and 3, since these limbs were subjected to the most study under SEM (Fig. 8).

The same components are found in all the post-clasper legs (at least until thoracopod 13, as thoracopods 14 and 15 were not dissected). These components are the proximal endite (or gnathobase), endites 2–5, endopod ('endite 6'), exopod, and epipod.

Proximal endite. Submarginally there is a characteristic row of curved setae (pointing towards the food groove) (Fig. 8a–c, i), 23–24 per endite, the number slightly decreasing on the more posterior thoracopods. These are densely plumose, with overlapping setules forming a tight grid (Fig. 8c), and are of a stiffer type than the setae on the other endites (see below). Marginally on the proximal endite of thoracopods 2 and 3 (and most likely on other thoracopods also) there is five setae of different types (Fig. 6b, 8b–d, i), which are marked with the letters 'a–e' on Fig. 8 with setae 'a' most proximal. Seta 'a' has a stout and curved proximal half, with a sparse row of setules on one side, and a thin and soft distal half. Seta 'b' is stout and straight with no setules. Seta 'c' is slightly curved, basally stout, and bears strong double serrations along most of its length (Fig. 8d, top of photograph and Fig. 8i). Seta 'd' is the longest seta on the proximal endite (seen also on Fig. 6) and is straight, basally stout, and bears a dense row of long setules. It continues distally into a thinner and softer part also with setules (Fig. 8d, i, white arrow). Seta 'e' resembles seta 'd' but with no thin and soft distal part (Fig. 8d, i). The entire anterior side of the basal part of the proximal endite is covered by a dense pile of setules (Fig. 8b, i). From the border of the basal part of the proximal endite projects a short, pointed cuticular outgrowth (Fig. 8d, where it is almost covered by debris; Fig. 8i, black arrow).

Endites 2–5, and endopod ('endite 6'). In general, for all endites on the post-clasper thoracopods, the number of setae on each endite decreases in a proximal to distal

direction. Endites 2, 3 and 4 are similar in shape, have setae in three different rows, and differ only in the size of the endite and in the number of setae. In accordance with this, Walossek (1993) mentions three rows of setae on the endites of the Upper Cambrian branchiopod fossil *Rehbachella*. The three rows in *Cyclestheria* are: (s1) a sparse row of relatively long setae at the border of the endite, (s2) a dense row of long setae situated at a distance from the border at the posterior side of the leg — probably the filtratory set (Fig. 8f), and (s3) a small group (2 or 3) of short, stiff, distally serrated setae located a little further from the border and on the anterior side of the leg (Fig. 8e) (the setae types are marked on Figs 6c, 8e, f). There are also several rows of minute hair-like setae scattered on the anterior face of the limb (e.g. Fig. 8a, e, g). Endite 5 is somewhat different and lacks the group of stiff, distally serrate setae.

The endopod has only a row of setae on the distal border (Figs 6, 8a, h). This pattern is repeated for thoracopods 2 to 12, the only difference being that the number of setae per endite decreases posteriorly (Fig. 6b–e). The number of setae on thoracopod 13 is few in comparison to more anterior appendages (Fig. 6e), and the same is true for thoracopods 14 and 15 although these were not removed and examined. On the clasper leg, setae row (s1) is missing.

Exopod and epipod. The laterally directed exopod is the only part of the limb seen in a typical sideview (e.g. Figs 2, 3a). It is composed of one more or less rectangular part distally (Figs 6, 8), which is directed ventrally in life, and one more or less characteristically quadratic and slightly inflated part located proximally and extending dorsally beyond and over the inflated epipod, and also covering parts of the trunk (Figs 2, 3a, 6, 9e, f). The two parts are connected by a straight part of the exopod, which always bears evenly spaced, long, annulate, plumose setae (Figs 2, 3a, 6, 9a–e). The outer margin of the exopod is curved posteriorly, such that the entire limb is strongly concave with the concavity facing backward (thought to be a characteristic of all branchiopods primitively and apomorphic to this group; see Walossek, 1993). The setae of the rectangular distal part of the exopod are of the same type, and also originate on the outer edge of the limb. These overlap slightly those of the following thoracopod, and their setules form a dense screen (Figs 2, 3a, 9c, d). There are no great differences between the rectangular parts of the different exopods except in size and number of setae, both of which decrease posteriorly. The quadratic dilated part, on the other hand, displays some differences. For example, after approximately thoracopod 10, it loses its dilated, quadratic shape and becomes a short, simple, non-dilated rounded lobe (Fig. 6d). The typical setation on this quadratic lobe is a posterior row of from 3–7 small posteriorly directed setae, and one anterior larger seta, directed more or less dorsally and arising from a slight triangularly-shaped protrusion. This is particularly noticeable on thoracopods 3–9 (Figs 2, 6, 9e, f). In some cases (thoracopods 6 and 7) this pointed part is extremely long (Fig. 2, black arrow). In thoracopods 1–3 and 11–15 the large seta arising from a triangular protrusion is missing (Figs 2, 6), only the shorter posteriorly-directed setae remaining. An elongated sac-like epipod, more or less

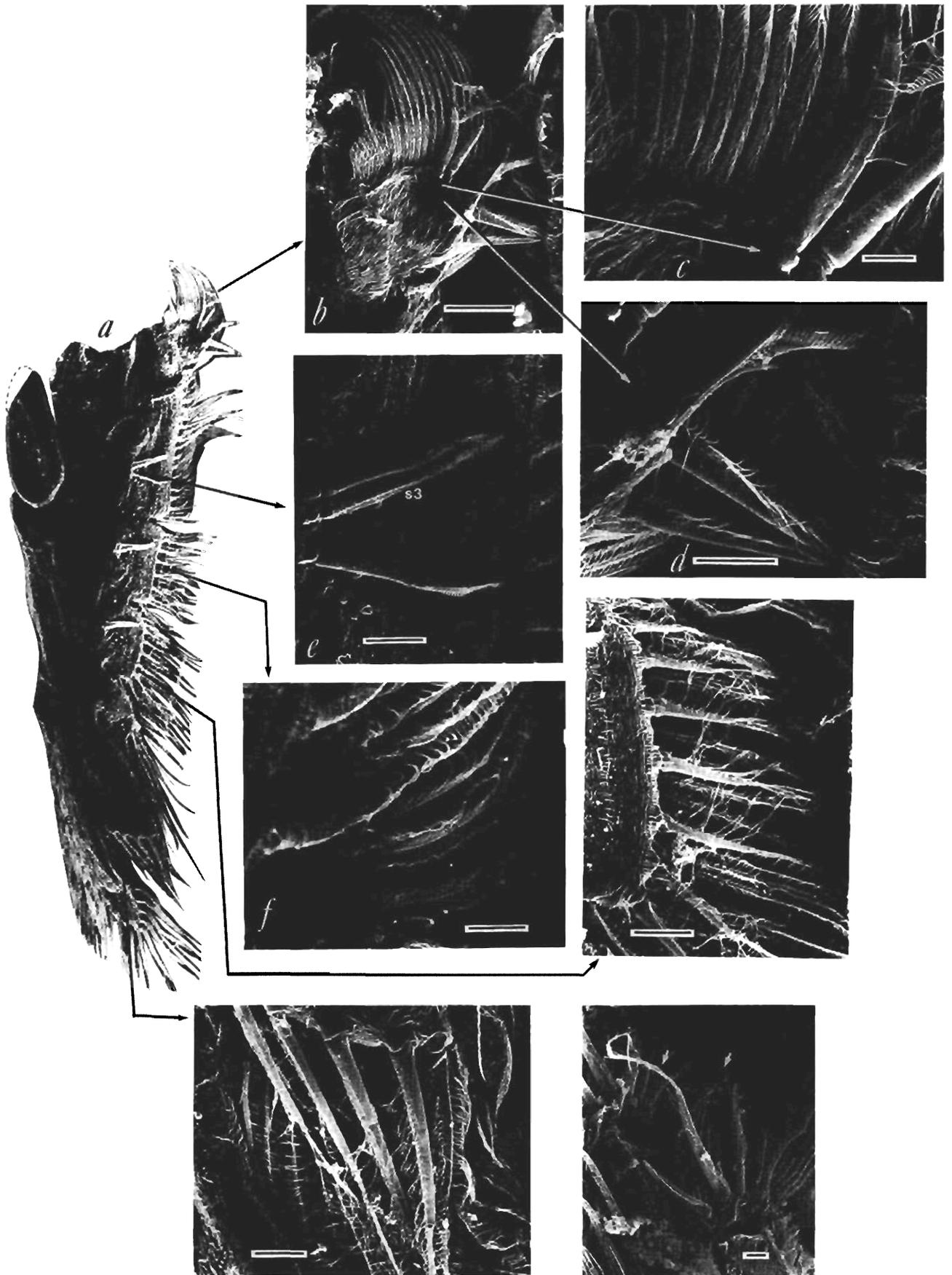


Fig. 8. *Cyclestheria hislopi* typical thoracopod in anterior view (a–h right thoracopod 3, i left thoracopod 2). a, SEM of entire appendage, with proximal end uppermost. b, higher magnification of proximal endite showing setal types and their location. Different setae indicated by letters (a–e) and explained in text. c, higher magnification of seta indicated by arrow in b. d, cluster of setae and small cuticular spine (partly obscured by debris) on anterior lobe of proximal endite. e, group of small, distally serrate setae of endites 2–4. f, long plumose setae typical of densely spaced row arising from posterior surface of limb. g, more sparsely setulose setae typical of limb border. h, tip of endopod and its setae. i, proximal endite from another individual. Setae types (a–e) explained in text. Arabic numbers indicate endites. Scale bars: a. 100 μm ; b. 25 μm ; c. 5 μm ; d. 10 μm ; e. 10 μm ; f. 5 μm ; g. 10 μm ; h. 10 μm ; i. 10 μm .

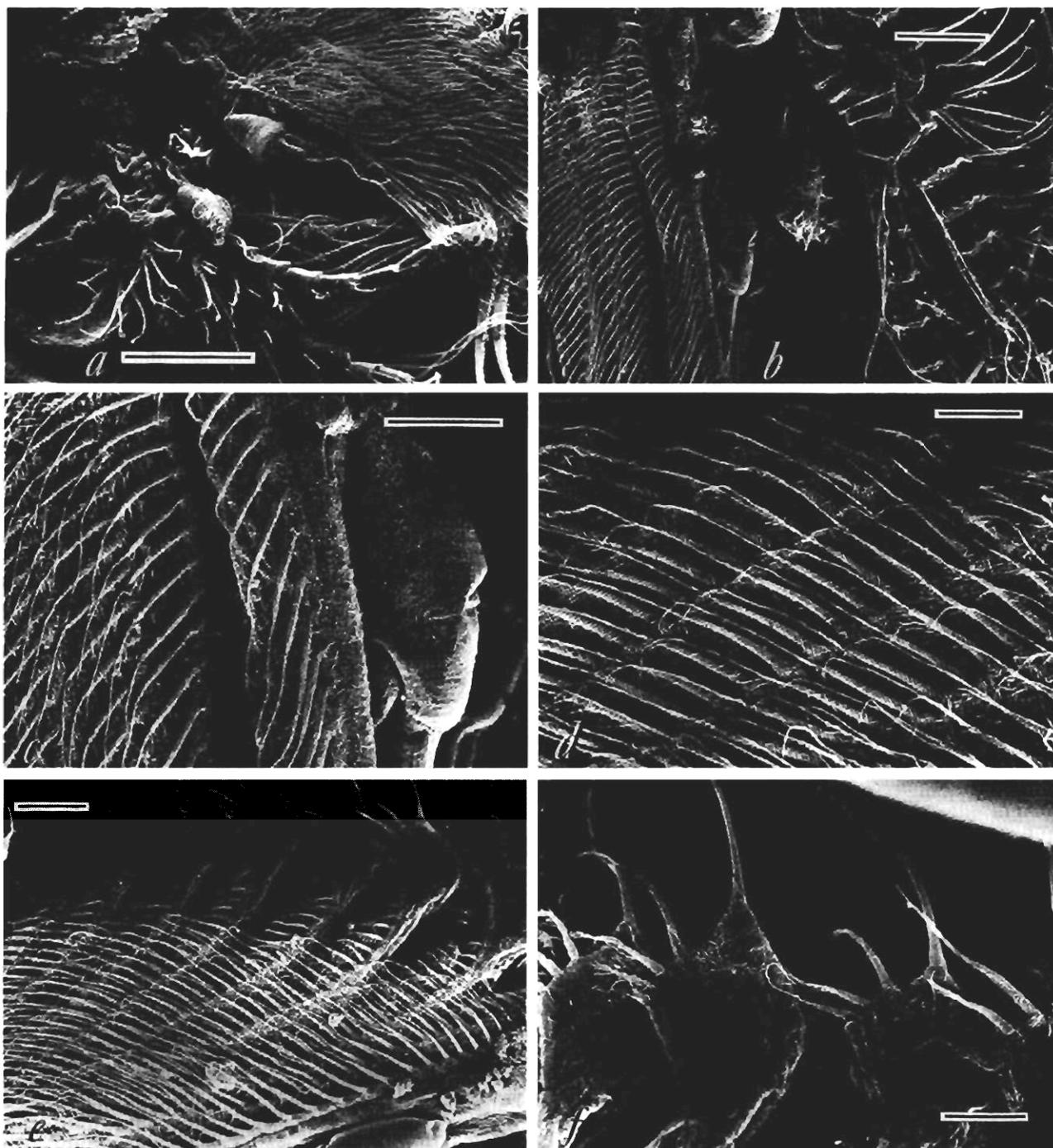


Fig. 9. *Cyclestheria hislopi* male thoracopods. a, ventrolateral view of anterior region, showing rostrum (r), antennules, antennae, clasper, and outer edge of exopod of first several thoracopods. b, antennae, antennules, clasper, and thoracopods 2 and 3; note apparent similarity in exopod of claspers and non-clasping thoracopods. c, higher magnification of b. d, overlapping margins of exopods of several more posterior thoracopods. Note dense grid formed by overlapping setules. e, upper (proximal) part of approximately 8 thoracopods in outer view, with more or less quadrately lobed exopod visible at top of photograph. f, higher magnification of three quadrately lobed exopods and their setae. Note single dorsally-directed seta arising from triangular protrusion of lobe. Scale bars: a. 200 μm ; b. 100 μm ; c. 50 μm ; d. 25 μm ; e. 50 μm ; f. 25 μm .

similar to that described above for the clasper, is present at least on the first 14 thoracopods.

Dorsal side of trunk and caudal region

As does the female, the male bears on the dorsal side of each of the most posterior trunk segments a cuticular folding, bearing a group of setae (2–5) directed in a posterior direction (Figs 2, 10c, d) These setae are stout,

and bear spinulations on the distal two thirds of their length. The middle and anterior trunk segments bear only a small cuticular lobe, in some cases with a short seta (Figs 2, 3a). Posterior to the last of these clusters of setae, and arising from the upper part of the base of the telson (sometimes called the 'post abdomen'), is a pair of telsonal filaments or 'post abdominal setae', probably homologous with corresponding setae found in all other conchostracans, notostracans and cladocerans (except *Leptodora kindti*) and presumably a synapomorphy to

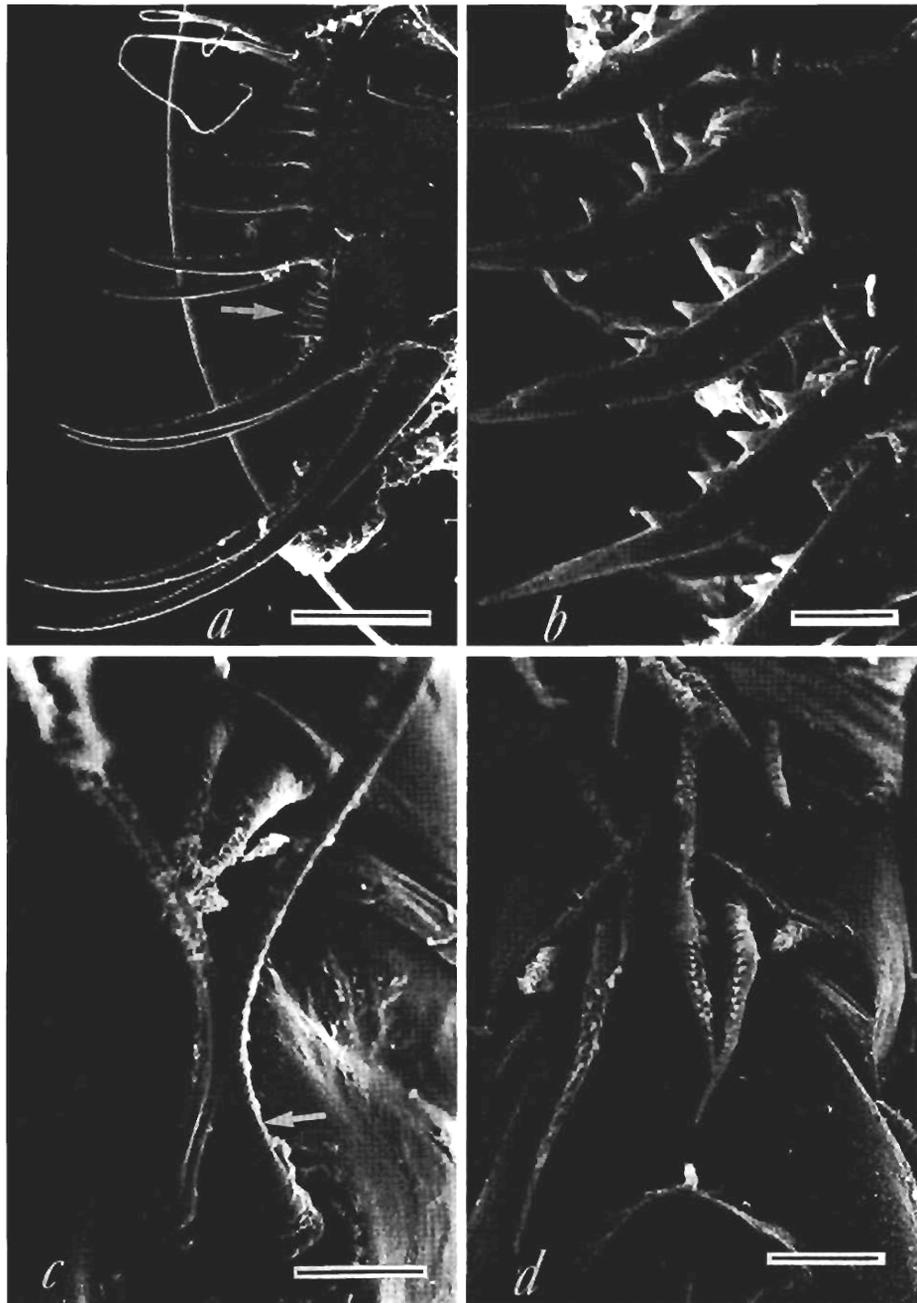


Fig. 10. *Cyclestheria hislopi* caudal region and dorsal view of posterior trunk somites. a, lateral view of telson and furca, right valve (shield) removed. b, higher magnification of laterally directed spines indicated by white arrow in a (see also Fig. 2a–c). c, base of telsonal filaments (or 'post abdominal setae') (white arrow), surrounding cuticle, and most posterior of dorsal somite setal armatures. d, slightly more anterior view (base of three setae at bottom of figure is same field of setae seen at top of c), showing stout, serrate setae at infolded region along midline of trunk somites. Scale bars: a. 100 μm ; b. 5 μm ; c. 20 μm ; d. 20 μm .

these taxa (see Martin, 1992 for terminology). Each originates on a small tubercle, inserted in a membranous plate surrounded by small scale-like denticles (Figs 2, 10c). These long, slender setae are minutely plumose on at least their distal half. Further back along the telson there are seven (fewer if the male is less developed) pairs of large spines, which become larger and more curved the more posteriorly they are situated. On the dorsal side of all spines are rows of small scales directed more or less medially (Fig. 10a), and not always visible in lateral view. Between the penultimate pair (the 5th in Fig. 10a, counting proximal to distal), and the ultimate (6th) pair, are two rows of small spines (one on each side of the

telson) with usually 6 spines directed laterally, in a different plane from the paired curved spines of the telson described above (Figs 2, 3b, c, 10a (arrow), b). The angle of orientation of this row is at approximately 45° away from the dorso-ventral axis (recognisable only in caudal view; Fig. 3b, c). *Cyclestheria* can swing the abdomen between the thoracopods, so these rows of spines possibly have cleaning functions.

The terminal spines (furcal claw) articulate with the telson just below and slightly anterior to the point of origin of the last (6th) pair of telson spines. The furcae are long, gently curved upwards, and bear minute denticles along their entire length (Figs 3a, b, 10a).

Discussion

Comparison with previous descriptions

The only other description of the external morphology of a male *Cyclestheria hislopi* is that of Sars (1887) of a male taken from a female brood chamber. The only details shown are the right first thoracopod and its clasper, so there is little with which to compare our description. However, where comparison is possible, only minor differences are present, a testimony to Sars' accuracy. These slight differences include the number of setae and the relative size of the proximal part of the exopods, and the relative size of the dorsal organ, which is slightly larger in Sars' figure as a result of that specimen's stage of development. Because we used fully developed individuals (5–7 growth lines), the few differences between these and Sars' description suggest that the male is already mature when it leaves the brood chamber. Roessler and Sanchez (1986) and Roessler (1995b) found that males in the brood chamber have fully developed spermatozoa in the testes.

Antennule and dorsal organ

The antennule of *Cyclestheria* is strikingly different from that of the other conchostracans and shows some similarity to the cladoceran antennule. Except for *Cyclestheria*, conchostracans can be divided into two groups with distinctly different and very characteristic antennule morphology. In the Laevicaudata, the antennule in both sexes is short, more or less pear-shaped, and composed of two segments (Fig. 16e). Aesthetasc setae (sensillae) are found on the tip, but also extend around the sides of the limb on anterior and posterior faces. In the Spinicaudata (except for *Cyclestheria*), the antennule is rather long and subdivided into smaller sensillae-bearing lobes (Fig. 16b–d). In contrast, *Cyclestheria* in most cases bears sensillae only at the tip of the antennule (e.g. Figure 16a) (except for some male specimens, see Figs 2, 5f, g), which is a feature usually found in the Cladocera.

Concerning the dorsal organ (Fig. 4), there is little to add other than that it is unique among conchostracans in its large central opening and lacks the external pits or bumps seen in the Laevicaudata. We do not know what significance to attribute to the fact that some individuals (Fig. 4d) have a 'double' pore at the centre of the organ.

The male clasping organs in the Conchostraca and Cladocera (= Diplostraca)

General. All males of Cladocera or Conchostraca (which together, because both groups have a bivalved carapace [= secondary shield of Walossek, 1993] have been termed the Diplostraca, or at times the Onychura, although higher level arrangements are still the subject of some controversy; Fryer, 1987b; Martin, 1992) have either the first or the first two pairs, of thoracopods modified for claspers to hold the female during mating. In some treatments of the group this is used as a synapomorphy for the Cladocera and Conchostraca (e.g. Wingstrand,

1978), although homologies of structures of the claspers are far from resolved. In the following discussion we compare claspers among the Conchostraca and the non-predatory Cladocera (i.e., excluding the clearly derived groups Haplopoda and Onychopoda), with special attention to the clasper of *Cyclestheria hislopi*, and use this comparison to point out possible synapomorphies in clasper morphology in these groups. Comparisons at an ultrastructural level are difficult because of the paucity of SEM studies of cladoceran claspers (with a few exceptions, such as Frey's, 1991 work on Australian and New Zealand chydorids and in some specialized taxa, e.g. Martin and Cash-Clark, 1995 for the cercopagidids) and because of the great variation in this group.

Cladoceran clasper morphology. We find it likely that at least the 'movable finger' (if at all movable in all taxa) is homologous between the Conchostraca and the Cladocera. The argument for this is that we find it difficult and unnecessarily complicated to imagine an evolutionary process of replacing the clasper part capable of moving with another leg part. This argument rests, naturally, on the assumption that the claspers in the groups are homologous, rather than developed in parallel. However, we see no reason to assume parallel development. We therefore consider as homologous the movable finger of cladoceran and conchostracan claspers, and consider both to be modifications of the original limb endopod.

A striking similarity in the movable finger morphology of *Cyclestheria hislopi* (Figs 6, 14i, j) and a cladoceran species *Simocephalus congener* (order Anomopoda) (Fig. 13b) is interesting to observe. These are, to our knowledge, the only species known to have setae on the outer margin of the movable finger. The interpretation of this similarity is uncertain, but the setae could be homologous and retained as plesiomorphies in the two species. Setae on the outer margin of the movable finger would then appear as either apomorphic to the Diplostraca, and be a part of the ancestral clasper morphology, or appear apomorphic to *Cyclestheria* and the Cladocera (if *Cyclestheria* is sister group to the Cladocera, see Fig. 15b). This information is not included in Fig. 15. Furthermore, we would like to point out the possible homology between some of the conchostracan palps and some of the palp-like structures in a number of cladoceran species (see Fig. 13). Of cladocerans, the Ctenopoda is the group having clasper legs most similar to *Cyclestheria*, but this similarity is also shared more or less with the rest of the Conchostraca. In general appearance the clasper legs of, for instance, *Sida crystallina* (Fig. 13a) are similar to the Conchostraca in the presence of a proximal endite (or gnathobase), well developed exopod, and dense setation along the sides of the exopod and endopod. An obvious difference is the lack of the two palps in the Ctenopoda.

Despite the great variation in clasper morphology in the rest of the Cladocera, some groupings, which may correspond to pre-existing tentative ideas of phylogeny, are possible. For instance, in both *Daphnia*, *Ceriodaphnia* (Fig. 13c, d), and *Megafenestra* (Dumont and Pensaert, 1983) there is a lobe with a long curved seta anterior to the claw, and a lobe with two shorter setae at the median side

of the claw. At first sight the pattern for *Bosmina* looks similar, but the two lobes are arranged oppositely, and the homologies are therefore uncertain (Fig. 13f). Another even more obvious grouping concerns the claspers of the Chydoridae. All illustrations of claspers of species belonging to this group (e.g. Frey, 1991) show characteristic rows of setae along the anterior side of the clasper leg (seen also in the female). Furthermore, claws of the species of Chydoridae (e.g. Figure 13e), excluding *Eurycerus*, seem to be of a characteristic curved shape and are more heavily chitinized than is typical for claws of other cladocerans (according to drawings by Sars, 1993; see also Frey, 1991). This would support widespread belief that *Eurycerus* is the sistergroup to the rest of the Chydoridae (e.g. Smirnov, 1971). Also in *Saycia*, another presumed early offshoot of the Chydoridae, the male claw is less curved than is typical for chydorids (Frey, 1971).

We have found no clasper characters of *Cyclestheria* convincingly shared with the non-predatory Cladocera (Anomopoda + Ctenopoda; see Fryer, 1987b for use of taxon names). The hypothesis of *Cyclestheria* as the sister species to the Cladocera is therefore not further supported on the basis of clasper morphology.

Clasper morphology and derivation in the Spinicaudata and the Laevicaudata. All known conchostracan (Spinicaudata + Laevicaudata; see Linder, 1945; Fryer, 1987b) claspers share some obvious similarities, such as an enlarged 'hand' or 'palm', a movable finger, and two palps, one small and one large, coming off the posterior side of the clasper palm. However, there is no universal agreement on the common origin of these structures, and significant differences in clasper morphology and derivation in the two groups of conchostracans, i.e. what are now known as the orders Spinicaudata and Laevicaudata, were suggested by Botnariuc (1947) and repeated by Fryer (1987b). By examination of ontogenetic changes in the clasper of two spinicaudate and one laevicaudate species, Botnariuc (1947) pointed out that, of the different parts of the clasper, only the 'movable finger' (the true endopod, often referred to as 'endite 6'; see Fig. 14) seems to be homologous between the two groups. The two small palps of the clasper and the 'apical club' (Fryer's term for the enlarged endite that forms the palm that opposes the movable finger) are derived from the endites in different ways in the two groups (see below).

The clasper of the Laevicaudata. In the Laevicaudata, only the first thoracopods of the laevicaudatan male are modified as claspers. However, in some lynceids the second thoracopods are also modified, to various degrees, although never as claspers (Martin and Belk, 1988). The claspers of lynceids differ from those of *Cyclestheria* in that they are strongly dimorphic in all species described to date, with the right clasper usually the larger (Martin and Belk, 1988). Another difference is that the lynceid clasper is greatly inflated, and much larger relative to the size of the limb and to the size of the animal, than is that of *Cyclestheria* or any of the Spinicaudata. The clasper finger never bears modified spines on its distal border, and closes against a circlet of more or less 'normal' stout setae on the clasper hand (as opposed to the modified

spine-like setae described for other spinicaudatans below). Occasionally some of the stout setae in this circlet are short and may be modified with ridges or other cuticular elaborations, but they are never of the type seen in the spinicaudatans. There are always two palps on the functionally posterior side of the clasper, and the most distal of these (that is, the one closest to the base of the movable finger) is always the longest; in this way they are similar to spinicaudatans (Fig. 11a, b; see also Martin and Belk, 1988). The basic thoracopod bears a proximal endite, 4 additional endites, and an endopod ('endite 6' of Martin and Belk, 1988 Fig. 3a) (Fig. 14a). The endopod is easily recognized by its rather clear demarcation from the rest of the limb. The male clasper has the same number of components as a basic thoracopod, and it is easy to see that the hand or palm of the clasper must be derived from endite 3 (also according to Botnariuc, 1947; see also Fryer, 1987b; Martin and Belk, 1988: 457, Fig. 3) (Fig. 14a, b). Therefore, in the Laevicaudata, endites 4 and 5 are apparently transformed into palps themselves which was shown by the ontogenetic study of Botnariuc (1947), and which can also be seen by comparing descriptions of thoracopods and claspers in this group (Fig. 14a–c, see also Sars, 1896: pl. 20, figs 1, 2, 7 and 9; Martin *et al.*, 1986: fig. 3; Martin and Belk, 1988: fig. 3). The resulting clasper (Fig. 14c) has an inflated hand or palm (derived from endite 3), a small palp (shaded black) that is probably derived from endite 4, a larger palp probably derived from endite 5, and the movable finger, derived from the endopod ('endite 6').

The clasper of the Spinicaudata. In all spinicaudatan genera, except *Cyclestheria*, the second pair of thoracopods as well as the first are modified for claspers. This seems most likely to be the apomorphic state, as all possible closely related outgroups (Ctenopoda, Laevicaudata) have only the first pair modified. Thus, the character 'two pairs of claspers' could be treated as a potential synapomorphy for the members of Spinicaudata except for *Cyclestheria*. Additionally, several spinicaudatan families have unique clasper components, such as the unusual and poorly understood sucker-like, dorso-distal projection on the movable finger in all known species of the Limnadiidae, and perhaps also the multi-segmented palp of the male thoracopods and claspers in some limnadiids and leptestheriids.

The spinicaudatan clasper is at first glance amazingly similar (e.g. Figure 14e, g, i, j) to that of the laevicaudates. There is a large hand or palm, one small palp (shaded black in Fig. 14 for ease of comparison), one larger palp, and the movable finger (the endopod or 'endite 6'). However, whereas in the laevicaudates the resulting limb (Fig. 14b) has a single endite (endite 2) between hand and proximal endite, in the spinicaudates the clasper has normally more endites between the proximal endite and the hand (Fig. 14i) (see later). Some previous authors have assumed that the larger of the two palps in the spinicaudatan clasper is derived from the 5th endite. Thus, in Roessler, 1989 description of the male clasper of *Eulimnadia colombiensis* (repeated here as Fig. 14d, e), the larger 2-segmented palp of the clasper is assumed to have been a modified endite 5 (Roessler, 1989: fig. 6). The smaller palp is not labelled in



Fig. 11. Selected conchostracan claspers. a and b, the laevicaudatan *Lynceus gracilicornis*. a, posterior view showing both palps and movable finger. b, end-on view of movable finger and opposing setae, with larger palp visible at top of photograph. c, the two left-side claspers of a limnadiid (*Limnadia* sp.). d, limnadiid clasper with long, 2-segmented palp clearly visible behind movable finger. e, close up view of tip of movable finger of a limnadiid, showing unique suckerlike process (at bottom left) and opposing teeth on movable finger and palm. Scale not recorded.

that figure, and we are left not knowing whence it arose. If, in all spinicaudatan taxa, this is the case, then the larger palp would always be a modified endite 5, and the smaller palp (shaded black in Fig. 14) is a new structure, unique to the clasper.

In the following we propose another possibility. In some spinicaudatans, the basic non-clasping thoracopod bears a

'palp' on one of the endites. Examples are known for all families (excluding the Cyclestheriidae). As one example, Nourisson and Thiery, 1988 figures of the leptestheriid *Eoleptestheria ticinensis* are repeated here as Fig. 14f, g. This palp (indicated by hatched lines in Fig. 14f) bears distal setae of a presumed sensory nature, and it seems likely that it is this pre-existing palp, rather than one of the



Fig. 2. Claspers of the conchostracan families Cyzicidae and Leptestheriidae. a, anterior region of *Cyzicus* sp. from Arizona, with two left claspers (thoracopods 1 and 2) visible. b, higher magnification of clasper of *Cyzicus* sp. from California. Note main palp is 2-segmented, although first segment is small. c and d, the male clasper of the Leptestheriidae. Scale bars: a, not available; b, 500 μm ; c, 500 μm ; d, 200 μm .

...es, that is preserved as the palp on the clasper (Fig. 14f). Indeed, in some species the thoracopodal palp is 2-segmented, and extremely similar to the clasper palp; Botnariuc (1947) showed that this palp (his 'palpe endopoditale' though there appears to be some confusion in his terminology) does in fact become the larger male clasper palp over the course of development in several spinicaudate species. In the Limnadiidae the palp of the thoracopod may be extremely long and multi-segmented (e.g. Roessler, 1991: Fig. 5, for *Limnadia orinoquiensis*). Botnariuc (1947) illustrates this clearly in a cyzicid, where he refers to the thoracopodal palp as the 'tactile process' (Botnariuc, 1947: fig 19). Because of the mentioned similarities of the thoracopodal palp and the long clasper palp they are assumed by us to be homologous, and since thoracopodal palps always originate from endite 5 (e.g. Olesen, 1991: Fig. 14f), we conclude that endite 5 must constitute at least part of the 'palm' of the clasper. This is in accordance with Botnariuc (1947) who showed that in the development of the claspers in a species of *Cyzicus* the long palp ('palpe endopoditale') moves backward (away from the proximal side) together with endite 5. At the same time he showed that endite 4 chitinises heavily and ends up constituting the 'apical club' (his 'massue endopoditale')

which is the part of the 'palm' that opposes the tip of the movable finger. From this, the small palp originates ('palpe enditale'). We therefore conclude that the 'palm' of the clasper consists of endites 4 and 5 together with the remaining part of the basipod (endites are only lobes of the basipod). At least this derivation is true for the species investigated by Botnariuc (1947), but we find it likely that it is a general pattern within the spinicaudates. Some species of spinicaudates have fewer than 2 endites between the proximal endite and the clasper which we believe is due to loss or fusions.

Weak corroboration of the more significant difference in origin between laevicaudate and spinicaudate claspers might be seen in the structure of the palps in these two groups. At least in our SEM examinations of different species, the palps of the Spinicaudata seem always to consist of softer cuticle than do those of the Laevicaudata, based solely on the amount of shrinkage and distortion observed during drying. If the palps in the two groups do indeed have different origins, as discussed above and indicated by Botnariuc's study, then clearly the presence of two palps on the clasper can not be used as a synapomorphy for the two conchostracan orders. However, it may still be the case that the differences between the

claspers of the same order. We find the presence of thoracopods can ord

The clasper phylogeny of the spinicaudate claspers is the same as in Botnariuc's hand of Fig. 14 with the from laevicaudate cladoceran endites have these non-C and C exhibit the spinicaudate presence such setal 4 or the p inter apor is no *Cycl* first iden bear thor not the show mor of c I par ont ma biv bein

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claspers in the two orders are independent modifications of the same clasper in a common ancestor, which means that the clasper itself would be homologous in the two orders. We find that possibility likely and therefore propose the presence of one pair of claspers on the first pair of thoracopods as a synapomorphy for the two conchostracan orders and the Cladocera (see below).

The clasper of Cyclestheria hislopi and its bearing on phylogeny. The clasper of *Cyclestheria* (Fig. 14i, j) is clearly of the spinicaudate type, and we find it most likely that the clasper should be derived from a normal thoracopod in the same way as in other spinicaudates (see above and Botnariuc, 1947). Between the proximal endite and the hand of the clasper are two endites (numbered 2 and 3 in Fig. 14i). The hand we derive from endites 4 and 5 together with the remaining basipodal part; the movable finger from the endopod (as in all conchostracans, both laevicaudates and spinicaudates and perhaps also the cladocerans, see above); the palps are 'true' palps on the endites (as in other spinicaudates). *Cyclestheria* does not have true palps on the basic thoracopods, so presence of these palps could be used to argue for an alliance of the non-*Cyclestheria* families (Limnadiidae, Leptestheriidae, and Cyzicidae). However, not all species of those families exhibit this character either. Another difference between the claspers of *Cyclestheria* and the three other spinicaudate families is that *Cyclestheria*, in general, has preserved more of the setation of the 'normal' thoracopod, such as long setae on the movable finger (endopod) and a setal row on the 'hand', which originates from either endite 4 or 5 (or both) of the normal thoracopod. It is likely that the preservation of these setae on the clasper should be interpreted as the primitive condition and their loss as an apomorphy for the three other spinicaudate families. This is not included in Fig. 15. In all spinicaudatans except *Cyclestheria*, in which only the first pair is so modified, the first two pairs of thoracopods are modified into nearly identical claspers. In the Laevicaudata only the first pair bears claspers though in a few species the second thoracopod is modified into structures that are at present not understood (Martin and Belk, 1988). Comparison with the presumably closest related outgroup, the Cladocera, shows that one pair of thoracopods modified as claspers is more likely plesiomorphic, compared to having two pairs of claspers modified.

Ideally, to establish firmly the homology of different leg parts between clasper legs and non-clasper legs, the ontogeny of the male should be followed. We lacked the material to do this; indeed it has not been done for most bivalved branchiopods, the study of Botnariuc (1947) being, to our knowledge, the sole exception.

The phylogenetic position of Cyclestheria and phylogeny of the Diplostraca

Position of Cyclestheria hislopi. Despite the fact that similarities between *Cyclestheria* and cladocerans have been mentioned many times (e.g. Sars, 1887; Linder, 1945; Tasch, 1963; Schminke, 1981; Martin and Cash-Clark, 1995), nobody has previously discussed the consequences

for conchostracan phylogeny in strict phylogenetic terms. Below we compare two cladograms; one with *Cyclestheria* as sister group to the rest of the Spinicaudata (Fig. 15a) and one with *Cyclestheria* as sister group to the Cladocera (Fig. 15b). The latter leaves the Conchostraca paraphyletic. The main difference is that in Fig. 15a the similarities between *Cyclestheria* and the Cladocera ('fused eyes' (9), 'direct development' (10), and 'ephippium'(11)) have developed convergently, while in Fig. 15b they represent synapomorphies. In addition 'growth lines on shield' (6) appear as an apomorphy for a monophyletic Spinicaudata in Fig. 15a but as an apomorphy for the Diplostraca in Fig. 15b (excluding the Laevicaudata if placed in position 'a') and lost in the Cladocera. We hesitate to choose between these cladograms but, if Sassaman (1995) is right and 'direct development' in *Cyclestheria* evolved from parthenogenetic ancestors, instead of the opposite — parthenogenetic reproduction developed from direct developing ancestor — as has been suggested for the Cladocera (Hebert, 1987), then it certainly indicates that direct development (as a potential synapomorphy for *Cyclestheria* and the Cladocera) should be treated with caution. It should also be noted that direct development has certainly appeared several times in other groups within the Crustacea. Also the 'fused eyes' may not be so convincing since among conchostracans it is very common to have the complex eyes close together (e.g. see Martin and Belk, 1988). Furthermore, if the 'ephippium' is viewed as an apomorphy of *Cyclestheria* and the Cladocera (Fig. 15b) it must be considered secondarily lost in the cladoceran groups Ctenopoda, Onychopoda and Haplopoda, as these have no ephippium. Two similarities between *Cyclestheria* and the Cladocera are not included in Fig. 15. One is 'sensillae of antennule restricted to the tip' which is considered as plesiomorphic to the Diplostraca, as it is found in the Anostraca and in typical branchiopod nauplii. Another is 'parthenogenetic reproduction', which has most likely appeared at least 4 times independently within the Conchostraca (Sassaman, 1995). On the other hand — despite the general similarity between *Cyclestheria* and the rest of the spinicaudates — the possible sister group relation between these can only be based on few apomorphies (see Fig. 15a)

Monophyly of the Diplostraca and the Cladocera. Three groups are considered by us to be monophyletic with a high level of certainty. These are the Diplostraca/Onychura (Conchostraca + Cladocera), the Cladocera, and the 'true' spinicaudates (Spinicaudata excluding *Cyclestheria*). The monophyly of the Diplostraca has been supported by Walossek (1993, 1995) by the recognition of the bivalved shield as a unique novelty to this group (termed 'secondary shield'). We share the belief that the Diplostraca is monophyletic, supported (together with the 'secondary shield', Walossek, 1993) by 'claspers on the first pair of thoracopods' (see above). In addition we propose 'eggs (embryos) attached to dorsal prolongation of exopod' (3) as an apomorphy for the Diplostraca. Actually, this condition is only present in the two conchostracan orders, but we believe that the cladoceran ancestor may have had the eggs attached to the exopod, since this is an obvious intermediate step in getting the eggs

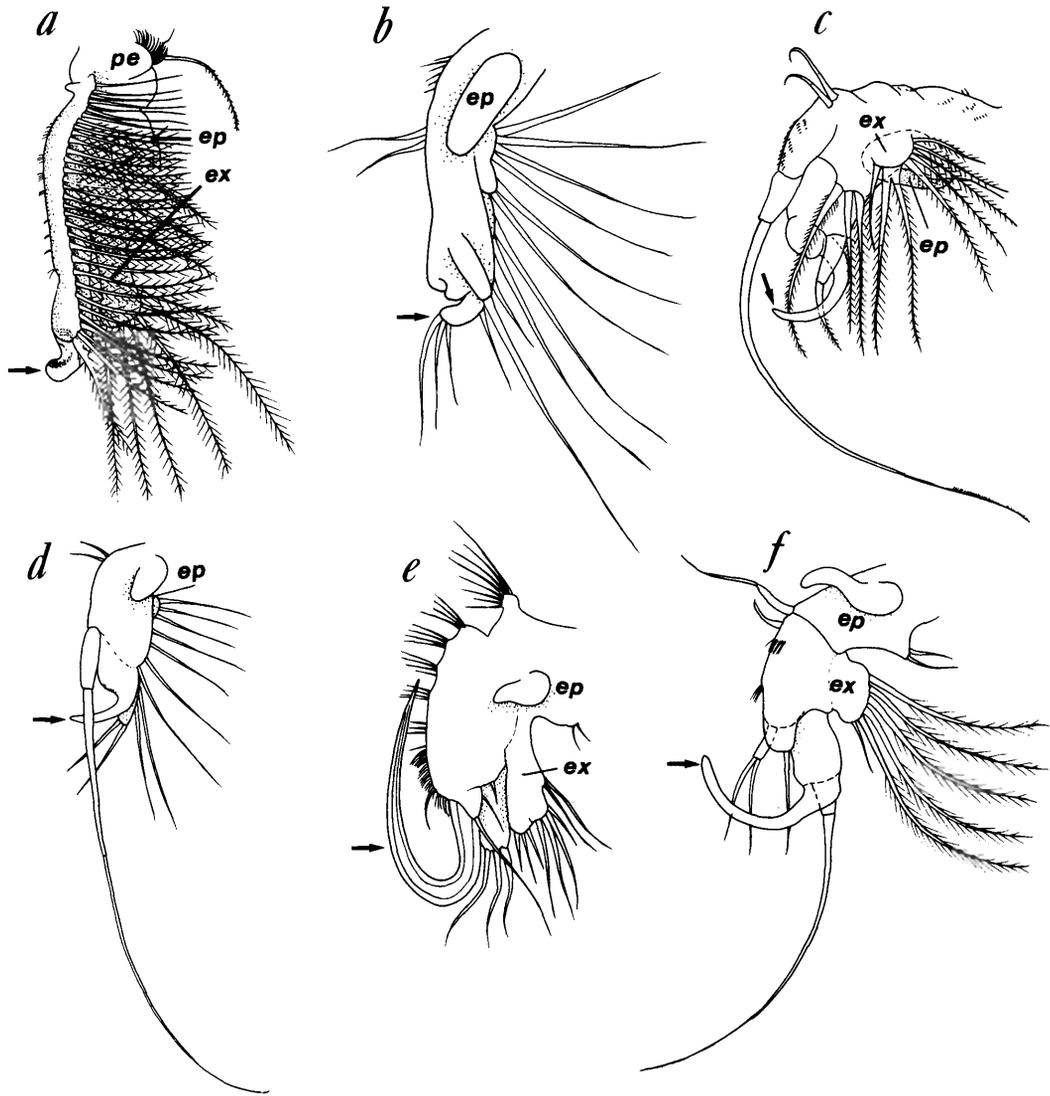


Fig. 13. Selected cladoceran claspers of the Ctenopoda (a) and Anomopoda (b–f). a, *Sida crystallina*. — b, *Simocephalus congener*. — c, *Daphnia magna*. — d, *Ceriodaphnia reticulata*. — e, *Alona quadrangularis*. — f, *Bosmina obtusirostris*. All are lateral views. The clasper claw/movable finger (most likely the endopod) is indicated by arrows. a, c seen from 'inside'. b, d–f seen from 'outside'. a, c redrawn after Lilljeborg (1900). b, d–f redrawn after Sars (1993). Not to scale.

placed dorsally as in the Cladocera. We suggest that placement of the eggs has developed from a lateral exopod attachment, apomorphic to the Notostraca (eggs encapsulated in exopod), Conchostraca, and Cladocera (often together termed Phyllopoada), to a dorsal exopod attachment, apomorphic to the Conchostraca and Cladocera (Diplostraca), and finally the dorsally placed eggs have lost the exopod connection, apomorphic to the Cladocera and connected to a possible shift in position of the gonopore from ventral to lateral/dorsal (this position of the gonopore in the Cladocera is mentioned by Calman, 1909 and Schram, 1986). The monophyly of the Diplostraca might also be supported by the 'backwardly curved furcal claws' (4), a condition found in all spinicaudates, ctenopods, anomopods, in most onychopods (except *Polyphemus* and modified in others) and with a different morphology in *Leptodora* (Haplopoda). If the cladogram with *Cyclestheria* as sister group to the Cladocera is chosen (Fig. 15b), then the Diplostraca (excluding the Laevicaudata if placed in position 'a') is supported by 'growth lines on shield' (6)

since this character then must be interpreted as a plesiomorphy to the Spinicaudata appearing already at the diplostracan level. Growth lines must then be assumed lost in the Cladocera ('re-appear' in two cladoceran genera, *Ilyocryptus* and *Monospilus*) and in the Laevicaudata (except if placed in position 'a'). If the cladogram with *Cyclestheria* as sister group to the rest of the Spinicaudata is chosen (Fig. 15a), then the growth lines would be an apomorphy for the Spinicaudata. It is, however, important to note some plasticity in this character as Linder (1945) refers to a then undescribed laevicaudatan with growth lines.

Below we give a short comment on the possible morphology of the ancestral diplostracan clasper. We find it fairly established that only the so-called movable finger (the endopod) is homologous among the diplostracan taxa and that the two palps and the 'palm' in the two conchostracan orders are non-homologous structures (see above; Botnariuc, 1947; Fryer, 1987b). It therefore seems likely that the clasper in the recent groups has been modified from an ancestral clasper with only the endopod

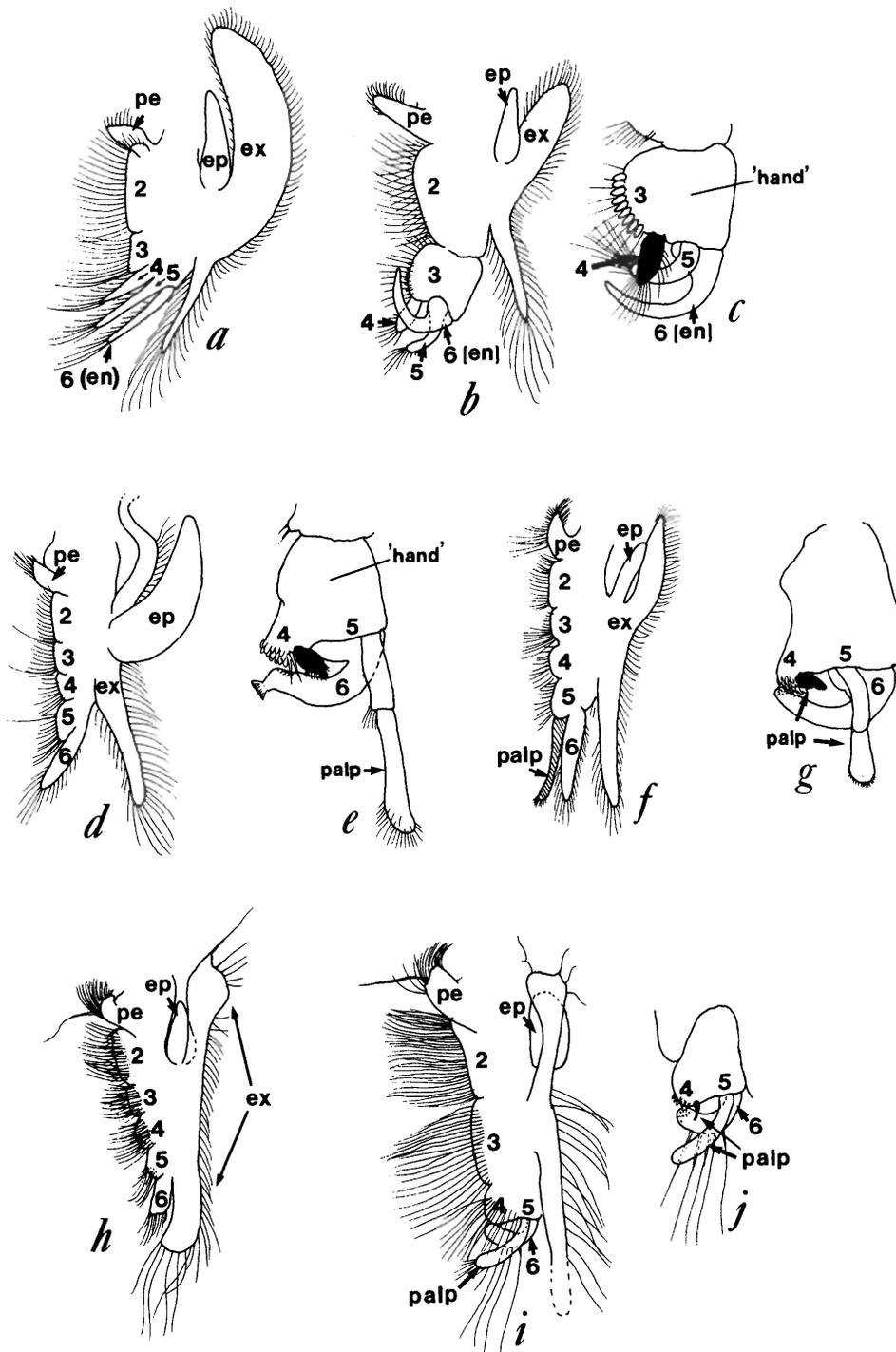


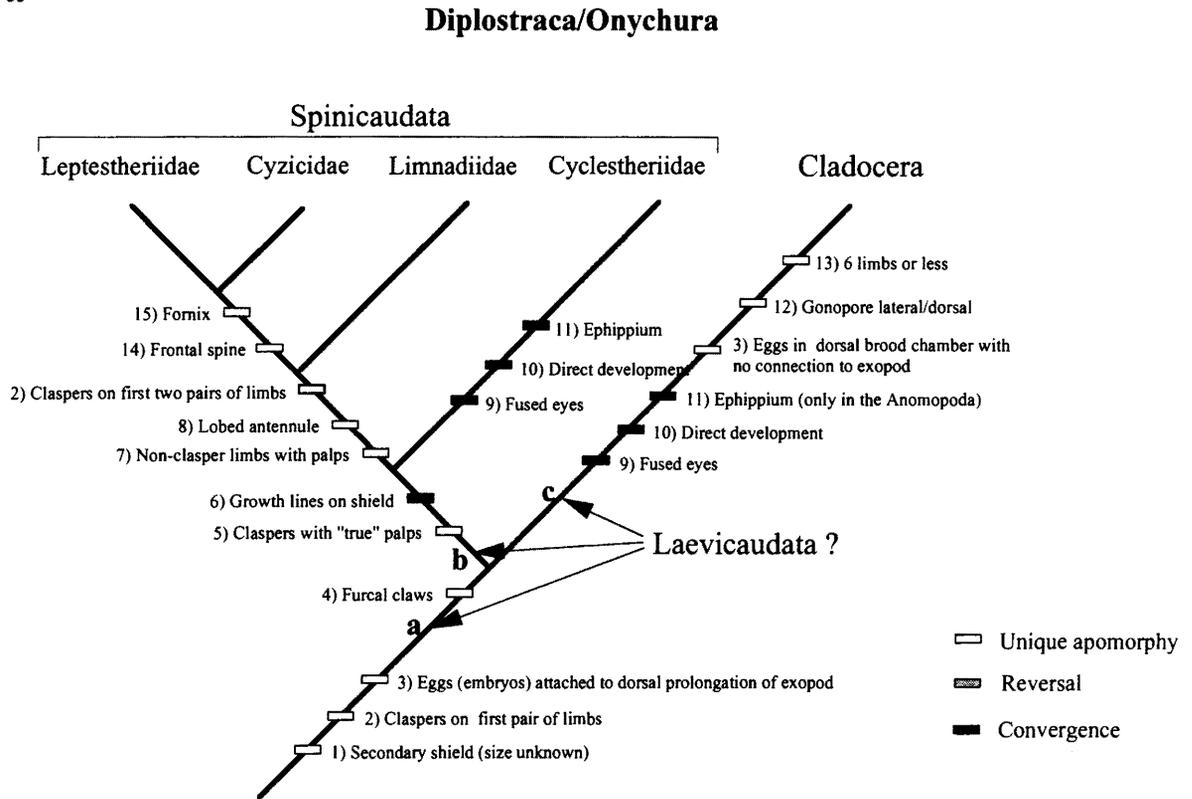
Fig. 14. Comparison of thoracopod types among the 'conchostracan' groups Laevicaudata (a–c) and Spinicaudata (d–j) and the suggested pathways of modification of thoracopodal components into male claspers. a–c, *Lynceus brachyurus* (Laevicaudata) (after Sars, 1896). a, thoracopod 3 of female. b, thoracopod 1 (clasper) of male. c, enlarged view of clasper components. d–e, thoracopod 10 of female (d) and clasper of male (e) of *Euleptestheria colombiensis* (Spinicaudata) (after Roessler, 1989). f–g, thoracopod 2 of female (f) and clasper of male (g) of *Eoleptestheria ticinensis* (Spinicaudata) (after Nourisson and Thiery 1988). h–j, thoracopod 10 of female (h) and clasper (i, j) of *Cyclestheria hislopi* (Spinicaudata) (this study). Arabic numbers refer to endites; note that 'endite 6' is the 'true' endopod but has lost demarcation from (i.e. has fused with) the protopod in some taxa. The enditic numbers on the clasper hand are placed close to the margin to show the parts of the 'hand' that presumably correspond to the endites of a 'normal' thoracopod. Smaller palps on all claspers are coloured black for ease of visualization, but are not meant to be homologous. Shaded appendage on f is a palp of the thoracopod, possibly homologous with the 2-segmented palp in g. The position of the 'hand' ('palm') has been indicated in c and e for laevicaudates and spinicaudates respectively. This structure is the part of the claspers that opposes the movable finger (endopod) in both conchostracan groups. In the Laevicaudata it consists of endite 3 and the corresponding basipodal part (endites are basipodal lobes, see Walossek 1993); in the Spinicaudata it consists of endite 4 and 5 and the corresponding basipodal parts. The 'hand' is therefore not homologous between the two groups (see text and Botnariuc 1947). All drawings modified from originals by turning so that orientation is the same. Not to scale.

modified as a clasping structure (no palps and no fusion of the endites to a 'palm'), actually very much like what is seen in the ctenopod cladocerans (see Fig. 13a, *Sida crystallina*). This morphology (without palps) in the Ctenopoda is therefore possibly retained from the

common diplostracan ancestor and with palps developed independently in the two conchostracan taxa (Fig. 15a).

We find that the 'true' spinicaudates (Spinicaudata excluding *Cyclestheria*), regardless of the position of *Cyclestheria*, are strongly supported by 'two pairs of

a



b

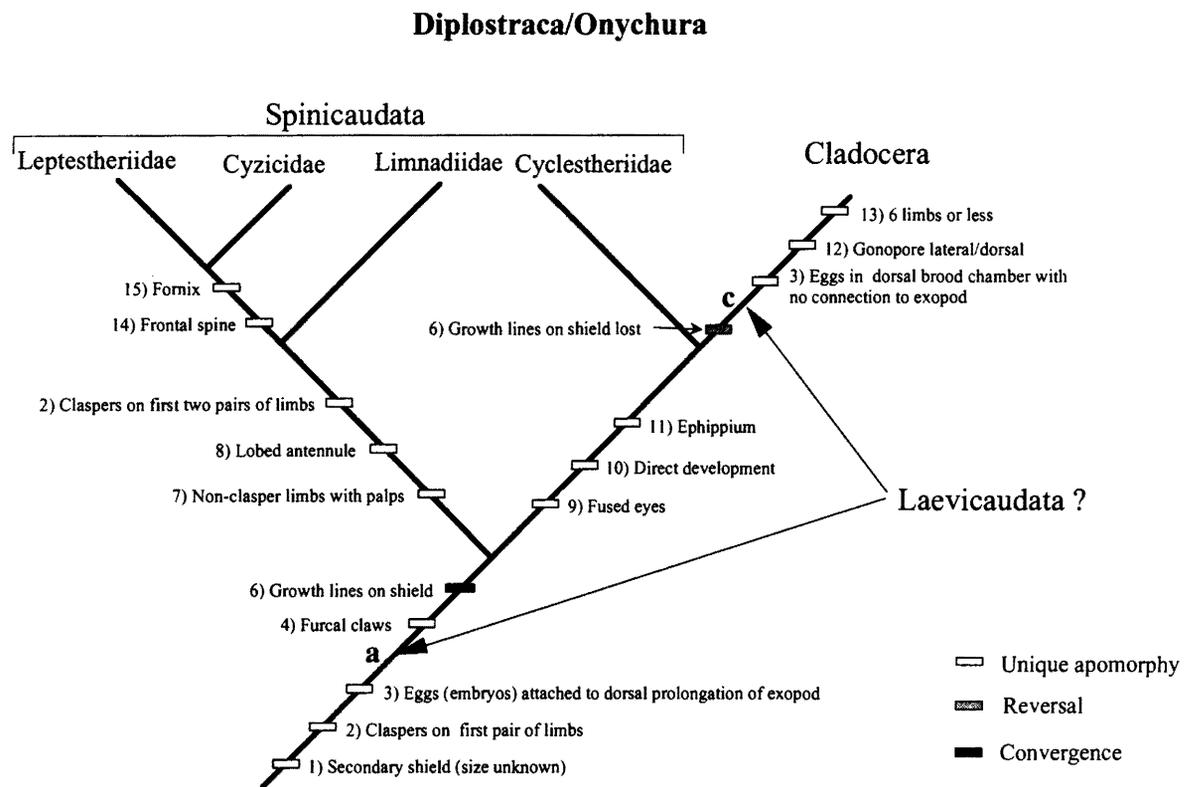


Fig. 15. Two different possible phylogenetic positions of *Cyclestheria*. It is proposed that the Diplostraca (Cladocera and Conchostraca), the Cladocera, and the Spinicaudata (excluding *Cyclestheria*) are monophyletic, regardless of the status of the Conchostraca and the position of *Cyclestheria*. See text for details. a, *Cyclestheria* as sister group to the rest of the Spinicaudata. b, *Cyclestheria* as sister group to the Cladocera which leaves the Conchostraca paraphyletic. Different possible positions of the Laevicaudata are indicated and discussed in the text.

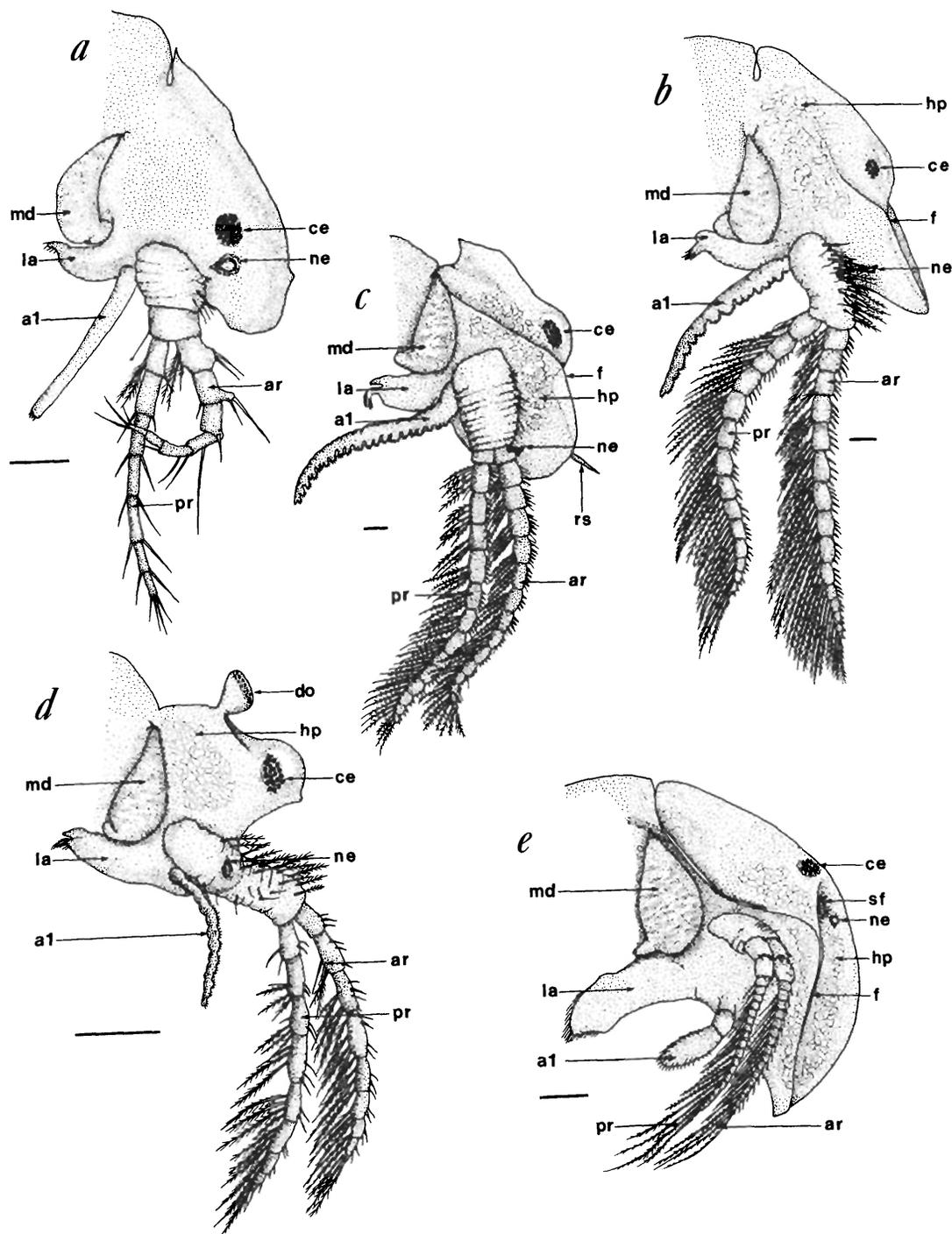


Fig. 16. Lateral view of head region of members of the 5 conchostracan families. a, *Cyclestheria hislopi*, female, from Paraguay (family Cyclestheriidae). b, *Canestheriella setosa*, male, from Arizona (family Cyzicidae). c, *Leptestheria compleximanus*, female, from Arizona (family Leptestheriidae). d, *Limnadia lenticularis*, female, from Florida (family Limnadiidae). e, *Lynceus gracilicornis*, male, from Florida (Laevicaudata, family Lynceidae). Scale bar = 0.25 mm.

claspers' (2), by a 'lobed antennule with sensillae along the sides' (8) — instead of an antennule with sensillae confined to the tip, which we see as a plesiomorphy found in anostracans and typical branchiopod nauplii — and by the presence of 'palps on the non-clasping legs' (7), which must be assumed lost in a couple of spinicaudates.

Also, in accordance with Martin and Cash-Clark (1995), we find that there is support for the Cladocera as a monophyletic group (see Fryer, 1987a, b on the same subject). As supporting characters we use 'reduction to six pairs of legs' (13), as did Martin and Cash-Clark (1995). In

addition we propose the 'laterally/dorsally placed gonopores' (12) (see above) and 'eggs in dorsal brood chamber with no connection to the exopods' (3) (see above) as apomorphies for the Cladocera. Other apomorphies (fused eyes, direct development, ephippium) depend on the position of *Cyclestheria* (see Fig. 15 and above). The reduction of the carapace (secondary shield) to enclose the trunk of the animal only — instead of the whole animal as in the Conchostraca — is probably also an apomorphy for the Cladocera. The status of this character depends on the ancestral diplostracan condition. If the ancestral diplos-

tracan had the whole body (including the head) enveloped by the shield then the reduction of the shield (to not enclose the head) should be treated as an apomorphy for the Cladocera. If the opposite is true — the ancestral diplostracan shield did not cover the head also — then the enlargement of the shield (to enclose the head also) should be treated as a potential apomorphy for the Conchostraca. It is important to note that only one of these interpretations is possible at the same time.

The position of the Laevicaudata. The phylogenetic position of the Laevicaudata has long been a puzzling question. We believe that it belongs to the monophyletic group the Diplostraca, since it possesses both secondary shield and claspers. Beyond that, a large number of possibilities exist. No convincing apomorphies that unite the Laevicaudata with the Spinicaudata (position 'b' in Fig. 15a) could be located. The same way of carrying the eggs in the two groups can be interpreted as a plesiomorphy for the Conchostraca (see above). A shield that comprises the whole body (including the head) is most likely also a conchostracan plesiomorphy being ancestral to the Diplostraca, the reduction (to not enclose the head) being apomorphic to the Cladocera (as already suggested by Martin and Cash-Clark, 1995). Therefore, the Conchostraca might be a monophylum, but we see no convincing evidence pointing in that direction (see Fryer, 1987b on the same subject). There are two other possibilities: the Laevicaudata as sister group to the rest of the Diplostraca (position 'a' in Fig. 15) or as sister group to the Cladocera (position 'c' in Fig. 15). The Laevicaudata as sister group to the rest of the Diplostraca would to a certain degree be supported by a number of similarities between the Laevicaudata and the Notostraca. The latter is probably the sister group to the Diplostraca [often together termed the Phyllopoda, based on a number of synapomorphies which includes 'nauplius eye composed of 4 ocelli', internalisation of the compound eyes', 'a pair of 'post abdominal' setae' (see Linder, 1945 and Martin and Cash-Clark, 1995) and 'egg bearing exopod' (see above); see also Walossek, 1993 Walossek, 1995]. The similarities could therefore be interpreted as the plesiomorphic condition preserved in the Notostraca and in the Laevicaudata and lost in the remaining diplostracans. These similarities, mentioned by Linder (1945), include mandibles with similar triturating surfaces and some vague similarity of the trunk legs (some endites prolonged) (see Martin and Belk, 1988 on the same subject). Another possible position of the Laevicaudata would be as sister group to the Cladocera. This may be supported by a similarity in the arrangement of the antennary muscles. According to Fryer (1987b) and repeated by Martin and Cash-Clark (1995) all the antennary extrinsic muscles originate in the same side of body as the appendage they serve in the Spinicaudata, whereas in the Laevicaudata and in the cladoceran orders some of them originate in the opposite side.

Relationships among the Spinicaudata. Ignoring, for a moment, the position of the Laevicaudata and Cyclestheriidae, the relationships among the three 'true' spinicaudate families are easier to postulate. The families

Cyzicidae and Leptestheriidae are much more similar to one another than either is to the Limnadiidae. Shared characters include a unique frontal spine, found only in adults of the Leptestheriidae but present in juveniles of at least some cyzicids (Fig. 15, character 14). Additionally supporting the grouping of these two families is the presence and shape of the fornix, a supportive ridge of cuticle on either side of the head (Fig. 16b, c) (Fig. 15, character 15). The Laevicaudata also have a fornix (Fig. 16e) but the homology to that of the spinicaudates is uncertain. Indeed, if the frontal spine is removed, it becomes much more difficult to separate leptestheriids from cyzicids, so similar are they in other ways. The limnadiids possess no such spine, and bear no fornix, instead possessing a thin blade-like head, that displays similarities to that of *Cyclestheria*. The phylogenetic arrangement is depicted in Fig. 15.

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