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External morphology and phylogenetic significance of the dorsal/neck organ in the Conchostraca and the head pores of the cladoceran family Chydoridae (Crustacea, Branchiopoda)

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Abstract

On basis of a SEM study the homology between the neck/dorsal organ of the Conchostraca and the head pores of the cladoceran family Chydoridae is established. Species of *Lynceus* (Conchostraca) and *Eurycercus* (Chydoridae) show a characteristical similar arrangement of four elevated areas within a circular/oval organ. Presence of two lateral pores may be an apomorphy for the Chydoridae lost in the Chydorinae and in some other genera. Some species of the Chydoridae (*Rhynchotalona falcta* and *Tretocephala ambigua*) display what can be interpreted as intermediate stages between the circular/oval organs in *Eurycerus* and more aberrant neck organ structures in the remaining Chydoridae. A characteristic neck organ morphology – two widely separated median pores with two smaller pores in between and without lateral pores – is considered as a synapomorphy for the Chydorinae. In contrast, no component of the neck organ morphology could be given synapomorphic status for all the species of the Aloninae. A number of potential apomorphies, related to the neck organ, seem to place subgroups of the Aloninae closer to the Chydorinae than to the rest of the subfamily. These apomorphies include, among others, 'elongation of the neck organ' after *Eurycercus* has been branched off and subdivision of the neck organ into discrete pores after *Rhynchotalona* and *Tretocephala* has been branched off. If this interpretation is correct it will leave the Aloninae paraphyletic with respect to the Chydorinae.

Introduction

External cuticular structures in the neck region, termed 'dorsal organ', 'neck organ', 'nuchal organ' or 'head pores', (in this study called 'neck organ') have been described for various species of the Branchiopoda and for the Crustacea in general (see Martin and Laverack, 1992; Walossek, 1993 for revies of the crustacean 'dorsal organ' and Martin, 1992 for a review of the branchiopod 'dorsal organ'). The internal anatomy and function has only been examined in a few cases and is mostly involved in ion transport. For the Branchiopoda, salt excretion has been suggested in larval *Artemia* (Conte et al., 1972), in marine cladoceran species of the order Onychopoda (Dejdar, 1931; Meurice & Goffinet, 1983; Potts & Durning, 1980; Aladin, 1991) and in species of the Conchostraca (Rieder, 1984). In each of the eight recent orders that now constitute the Branchiopoda (after Fryer, 1987) is found at least one species (often most or all species) with a variation of these structures in the adult. The external morphology in many taxa is so similar that it is quite convincing when Walossek (1993), despite some obvious variation, consider the structures as homologous between the different main groups of Branchiopoda.

However, the homology with structures found in some cladoceran taxa – especially those of the family Chydoridae – has, because of very aberrant neck organs and because of lack of SEM investigations, hitherto remained uncertain. SEM photographs of cladoceran and conchostracan neck organs available in the literature make the homology of neck organs between the Conchostraca and some non chydorid cladoceran taxa quite likely. Most studied cladocerans (except for the family Chydoridae) show the typical arrangement of a more or less circular cuticular area surrounded by an elevated rim which is also seen in some species of the Conchostraca and Anostraca (Martin & Belk, 1988; Martin & Laverack, 1992; Martin, 1992; Walossek, 1993). This neck organ morphology exists in all species of the cladoceran order Onychopoda (shown for *Podon leucarti*, by Aladin, 1991; for *Podon intermedius*, by Meurice & Goffinet, 1983). Furthermore, it is documented for the Macrothricidae (Anomopoda), where a large number of species are known to have a neck organ (Dumont and Van de Velde, 1976; Smirnov, 1992). Finally, this morphology is documented for the Daphniidae (order Anomopoda) for the whole genus *Megafenestra* (by Dumont & Pensaert, 1983), for a few species of *Ceriodaphnia* (Berner, 1987) and with a deviating morphology for one species in the genus *Simocephalus* (Meyer-Rochow, 1979). In the Daphniidae neck organs are, except for these few examples, known from developing specimens only (Halcrow, 1982; Aladin, 1991, for *Daphnia magna*). In the last two orders of the Cladocera (Haplopoda and Ctenopoda) a neck organ is described in TEM for *Leptodora kindti* (Haplopoda) by Halcrow (1985) and for *Sida crystallina* (Ctenopoda) by Günzl (1978, 1980), but not shown in SEM.

Sida crystallina is the only species of Ctenopoda known to have a neck organ and is, among cladocerans, the most well documented example of a neck organ modified into an attaching device. The attachment organ is split into three parts, one large horseshoe shaped area on the head shield and two smaller lateral areas anterior on the secondary shield (= carapace) (Günzl, 1978, 1980). The homology with the neck organ of other branchiopods is not obvious from adult specimens but is apparent when juveniles are examined (unpublished). The attachment organs of juvenile specimens of *Sida* show, at this stage, a close resemblance to the neck organ of other adult cladocerans. Another seemingly well documented example of attachment by a neck organ is seen in a species of *Simocephalus* as a supplement to the normal antennal way of attachment (Meyer-Rochow, 1979).

The most deviating neck organ morphology among cladocerans (apart from *Sida crystallina*) are found in the family Chydoridae (order Anomopoda), where the structures have been described as different types of head pores. The systematic significance of these pores was first established by Frey (1959, 1962) who later used their presence to support the Chydoridae and also used their arrangement – together with other characters like mandible articulation type and limb setation – to recognise four subfamilies within the family, the Aloninae, Chydorinae, Eurycercinae and Sayciinae (Frey, 1967) (see comments to this in discussion). Since then drawings of head pores have been commonly shown in taxonomical literature but only a few SEM studies have been performed (e.g. Dumont & Van De Velde, 1976; Masson & Amoros, 1992). The function of the head pores has never been examined.

The present work is a comparative SEM study on the external morphology of the head pores of the cladoceran family, *Chydordiae*. The purpose is first to establish an eventual homology between these head pores and the neck/dorsal organ found in the same place – the posterior part of the head shield – in other branchiopods. Furthermore, I attempt, by use of SEM, to provide new characters associated with the head pores to add information in solving the intrinsic phylogeny of the Chydoridae. To do this the neck organ of 30 chydorid and 8 non chydorid branchiopod species has been examined.

Materials and methods

The material were partly collected by the author and partly obtained from the Zoological Museum, University of Copenhagen (Table 1). The material from the Zoological Museum has in most cases been collected and identified by Dr U. Røen. Specimens were fixed in 70% ethanol (in a few cases in formaldehyde), dehydrated through acetone, critical point dried in CO_2, mounted, coated by gold and examined through a JEOL JSM-840 scanning electron microscope (SEM) at 15 kV.

Results

Anostraca

Siphonophanes grubei (Figure 2A), *Tanymastix stagnalis* (Figure 2B)

The neck organ in *Siphonophanes grubei* is large and rounded. The surface of the organ is heavily wrinkled, probably an artefact due to the critical point drying. The wrinkled surface is subdivided into smaller units which may correspond to the underlying cells. The organ is surrounded by a slightly elevated rim.

The neck organ of *Tanymastix stagnalis* is large and with a more angled outline than in *Siphonophanes*

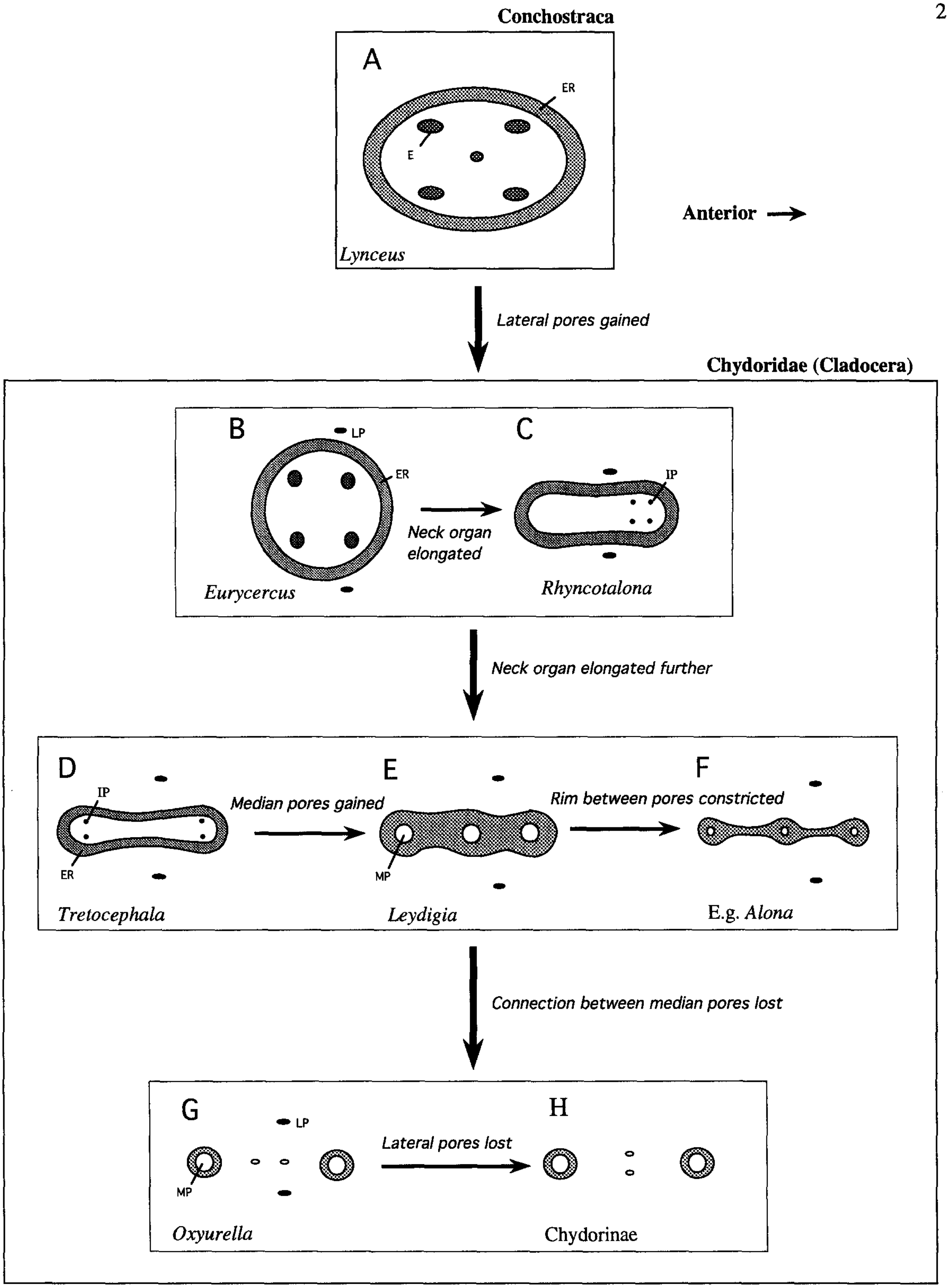

Figure 1. Schematic representations of eight types of neck organs of the Conchostraca (A) and the cladoceran family Chydoridae (B: Eurycercinae, C–G: Aloninae, H: Chydorinae). The arrows indicate a likely route for the transformation of the neck organ morphology. The specific character change are stated for each transformation. The different colours (black, dark grey, light grey, white) refer to presumed homologous parts of the neck organs between the different species. A. *Lynceus brachyurus*; B. *Eurycercus glacialis, E. lamellatus*; C. *Rhynchotalona falcata*; D. *Tretocephala ambigua*; E. *Leydigia acanthocercoides*; F. *Graptoleberis testudinaria, Alonopsis elongata, Acroperus harpae*, the two species of Camptocercus and most species of *Alona*; G. *Oxyurella tenuicaudis*; H. *Pseudochydorus globosus, Peracantha truncata* and most species of *Chydorus, Pleuroxus* and *Alonella*. Figure not drawn to scale. Abbreviations: E = elevated area; ER = elevated rim; IP = inner pore; LT = lateral pore; MP = median pore.

Table 1. Species represented in this study

Species	Locality and date
Acroperus harpae Baird, 1835	Disko, Greenland, 1992*
Alona affinis (Leydig, 1860)	Bornholm, Denmark, 1986
Alona costata Sars, 1862	Bornholm, Denmark, 1985
Alona guttata Sars, 1862	Hede Sø near Flyndersø, Denmark, 1980
Alona quadrangularis (O.F. Müller, 1785)	Tange Sø, Denmark, 1960
Alona rectangula Sars, 1862	Mors, Denmark, 1988
Alona rustica Scott, 1895	Flyndersø, Denmark, 1965
Alonella excisa Sars, 1862	Laesø, Denmark, 1987
Alonella exigua (Lilljeborg, 1853)	Bornholm, Denmark, 1985
Alonella nana (Baird, 1843)	Northern Jutland, Denmark, 1988
Alonopsis elongata Sars, 1862	Slåen Sø, Denmark, 1951
Camptocercus lilljeborgi Schoedler, 1862	Huul Sø, Denmark
Camptocercus rectirostris Schoedler, 1862	Løvenborg, Denmark
Chydorus ovalis Kurz, 1874	Greenland, 1970
Chydorus sphaericus (O.F. Müller, 1785)	Als, Denmark, 1988
Cyclestheria hislopi Baird, 1859	Colombia, 1994*
Eurycercus glacialis Lilljeborg, 1887	Søndre Strømfjord, Greenland, 1992*
Eurycercus lamellatus (O.F. Müller, 1785)	Søndre Felding, Denmark, 1988
Graptoleberis testudinaria (Fischer, 1848)	Dyrehaven, Denmark, 1993*
Ilyocryptus sordidus (Liévin, 1848)	Thy, Denmark, 1988
Lathonura rectirostris (O.F. Müller, 1785)	Almindingen, Bornholm, 1986
Leydigia acanthocercoides (Fischer, 1854)	Dyrehaven, Denmark, 1865
Lynceus brachyurus O.F. Müller, 1776	Dyrehaven, Denmark, 1994*
Lynceus pachydactylus	South Africa, 1929
Macrothrix hirsuticornis Norman et Brady, 1867	Thule Tørvemose, Greenland, 1960
Monospilus dispar Sars, 1862	Kalgård Sø, Denmark, 1951
Oxyurella tenuicaudis (Sars, 1862)	Langeland, Denmark, 1988
Peracantha truncata (O.F. Müller, 1785)	Krejbjerg, Denmark, 1988
Pleuroxus aduncus (Jurine, 1820)	Northern Jutland, Denmark, 1987
Pleuroxus laevis Sars, 1862	Brabrand Sø, Denmark, 1964
Pleuroxus trigonellus (O.F. Müller, 1785)	Tåstrup Sø, Denmark, 1965
Pleuroxus uncinatus Baird, 1850	Northern Jutland, Denmark, 1988
Pseudochydorus globosus (Baird, 1843)	Kobberdam, Hellebaek, Denmark, 1964
Rhynchotalona falcata Sars, 1862	Hostrup Sø, Denmark, 1988
Siphonophanes grubei (Dybowski, 1860)	Dyrehaven, Denmark, 1993*
Streblocerus serricaudatus (Fischer, 1849)	Bornholm, Denmark, 1984
Tanymastix stagnalis (Linnaeus, 1758)	Öland, Sweden, 1982
Tretocephala ambigua (Lilljeborg, 1900)	Lolland, Denmark, 1988

* Collected by the author

grubei. The organ is characteristically subdivided into small porous units which may correspond to underlying cells.

Conchostraca

Lynceus brachyurus (Figures 1A, 2C), *Lynceus pachydactylus* (Figure 2D), *Cyclestheria hislopi* (Figure 2E)

The neck organ of *Lynceus brachyurus* is oval of shape surrounded by an elevated rim. One small elevation surrounded by four larger elevations is found in the middle of the organ.

The neck organ of *Lynceus pachydactylus* is egg shaped surrounded by a less conspicuous rim than in *Lynceus brachyurus*. Small pits can be seen scattered all over the organ. No elevations are found. The neck

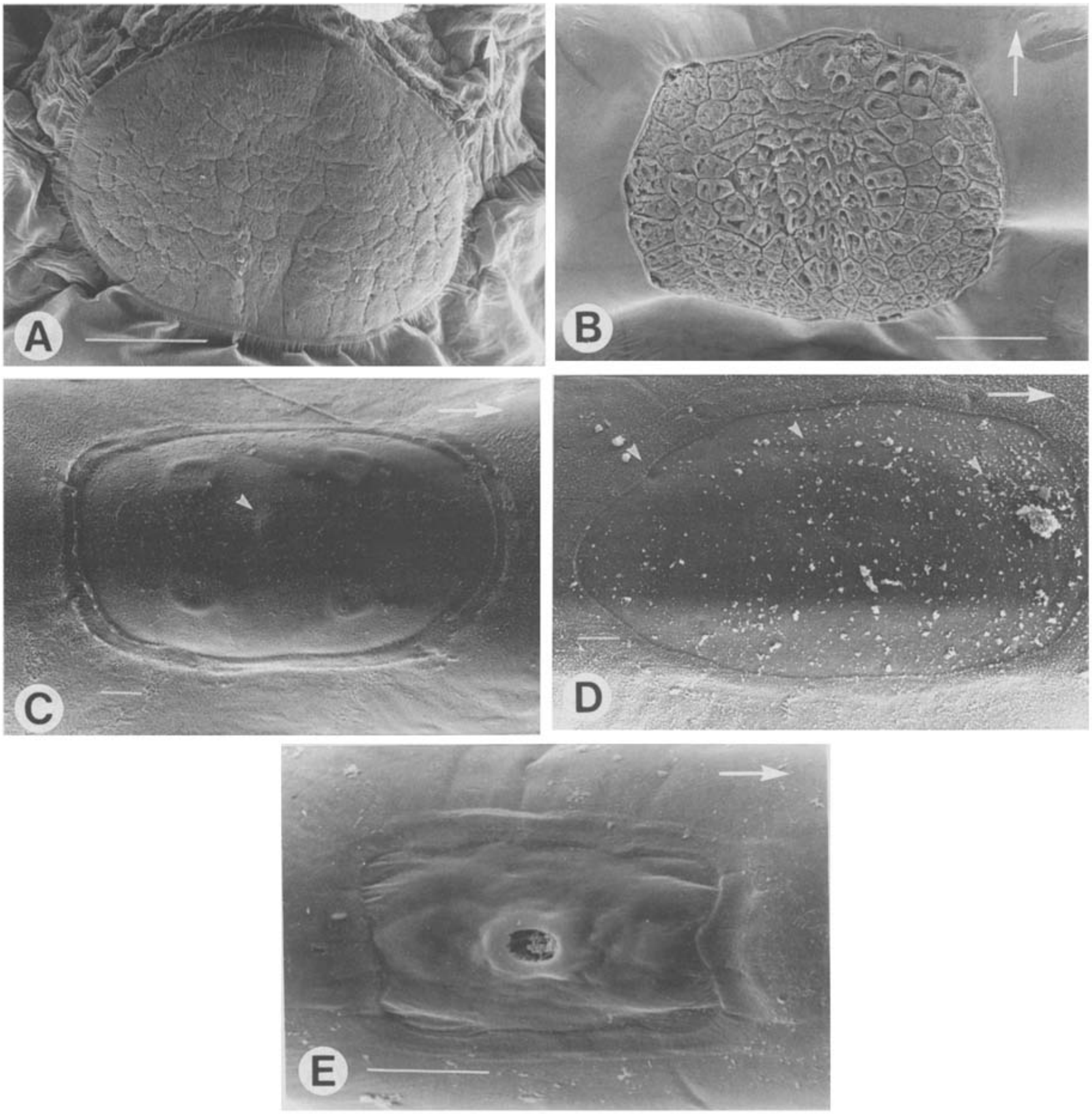

Figure 2. SEM photographs of neck organs in the Anostraca (A–B) and the Conchostraca (C–E). A. *Siphonophanes grubei*; B. *Tanymastix stagnalis*; C. *Lynceus brachyurus*; D. *Lynceus pachydactylus*; E. *Cyclestheria hislopi*. The arrows indicate anterior direction. Scale bars: A–B 100 μm; C–E 10 μm.

organ of *Cyclestheria hislopi* is more or less rectangular of shape with a characteristical large pore in the middle.

Cladocera

Fam. Macrothricidae

Macrothrix laticornis (Figure 3A), *Lathonura rec-*

tirostris (Figure 3B), *Ilyocryptus sordidus* (Figure 3C) and *Streblocerus serricaudatus* (Figure 3D)

Both the organ of *Macrothrix laticornis* and *Lathonura rectirostris* resemble the neck organs of the Anostraca and the Conchostraca in having an oval to circular shape delimited by a slightly elevated rim. The area within this rim is wrinkled in *Macrothrix laticornis* but smooth in *Lathonura rectirostris. Ilyocryptus sordidus* has a furrow at the normal place for a neck organ (posterior part of the head shield). This may/may not have something do with a neck organ.

Streblocerus serricaudatus has an organ with a small pore in the middle. The homology with a neck organ is uncertain.

Fam. Chydoridae

Within the Chydoridae I recognise following types of neck organ morphology.

Type A (Figure 1B), *Eurycercus glacialis* (Figure 4A), *Eurycercus lamellatus* (Figure 4B)

The neck organ consists of a circular/oval cuticular area with four elevated areas *(E. glacialis)* or just marked fields *(E. lamellatus)*, surrounded by an elevated cuticular border. Both species with lateral pores. In *E. glacialis* the lateral pores are placed in a wrinkled area surrounding the elevated rim. In *E. lamellatus* there is no wrinkled area and the lateral pores are placed in a greater distance from the elevated rim.

Type B (Figure 1C,D), *Rhynchotalona falcata* (Figure 4C), *Tretocephala ambigua* (Figure 4D)

The neck organs in both species consist of an elongated keyhole-shaped cuticular area (elongation most pronounced in *Tretocephala ambigua*), surrounded by an elevated cuticular rim. In *Rhynchotalona falcata* four small depressions/pores are seen in the anterior end of the organ. The poration in the posterior end is unclear because of debris. In *Tretocephala ambigua* a pair of small depressions is seen in both the anterior and the posterior end of the organ. The depressions in *Tretocephala ambigua* and at least some of the depressions in *Rhynchotalona falcata* are assumed to be homologous with the elevated areas in *Lynceus brachyurus* and in the *Eurycercus* species. Both species with lateral pores.

Type C (Figure 1E,F), *Alona guttata* (Figure 5A), *A. costata* (Figure 5B), *A. rectangula* (Figure 5C), *A. rustica* (Figure 5E), *A. quandragularis* (Figure 5F), *A. affinis* (Figure 5G), *Leydigia acanthocercoides* (Figure 4E), *Graptoleberis testudinaria* (Figure 4F), *Acroperus harpae* (Figure 6A), *Camptocercus rectirostris* (Figure 6B), *C. lilljeborgi* (Figure 6C), *Alonopsis elongata* (Figure 6D)

With one exception (*Alona affinis*, Figure 5D) all the mentioned species share a characteristic component of their neck organ morphology, namely three median pores in a row on a slightly elevated rim in anterior/posterior direction.

In two genera, *Acroperus* and *Camptocercus* (Figure 6A–C), the examined species have their median pores situated on a elevated keel of the head shield. In general the median pores found in the species of *Camptocercus* are more oval of shape than in *Acroperus*. Lateral pores are according to Frey (1959) present, but were only detected in a few cases.

Alonopsis elongata (Figure 6D) shows the typical arrangement of three median pores on an elevated rim. The size of the median pores are relatively small, compared to those of most other species. On the constricted parts of the rim between the median pores, two very small pores can be seen. The distance between the middle and anterior median pores are larger than between the posterior and the middle median pores. No lateral pores are seen, but are, according to Frey (1959), present very close to the lateral margins of the head shield.

In *Leydigia acanthocercoides* (Figure 4E) the three pores are located on a elevated rim which is constricted mostly between the middle and the anterior median pores. The lateral pores are situated relatively close to the median pores a little anteriorly to the middle median pore.

In *Graptoleberis testudinaria* (Figure 4F) the rim between the median pores are very constricted with a larger distance between the middle and the anterior median pores than between the middle and the posterior median pores. The lateral pores are extremely large and situated a little anterior to the middle median pore.

The morphology of the neck organ in *Alona* is in general varied but the morphology is very similar within a group of three species, *A. rectangula, A. guttata* and *A. costata* (Figure 5A–C). They all have a simple lateral pore arrangement with the lateral pores situated a little anterior to the middle of the median pores, or

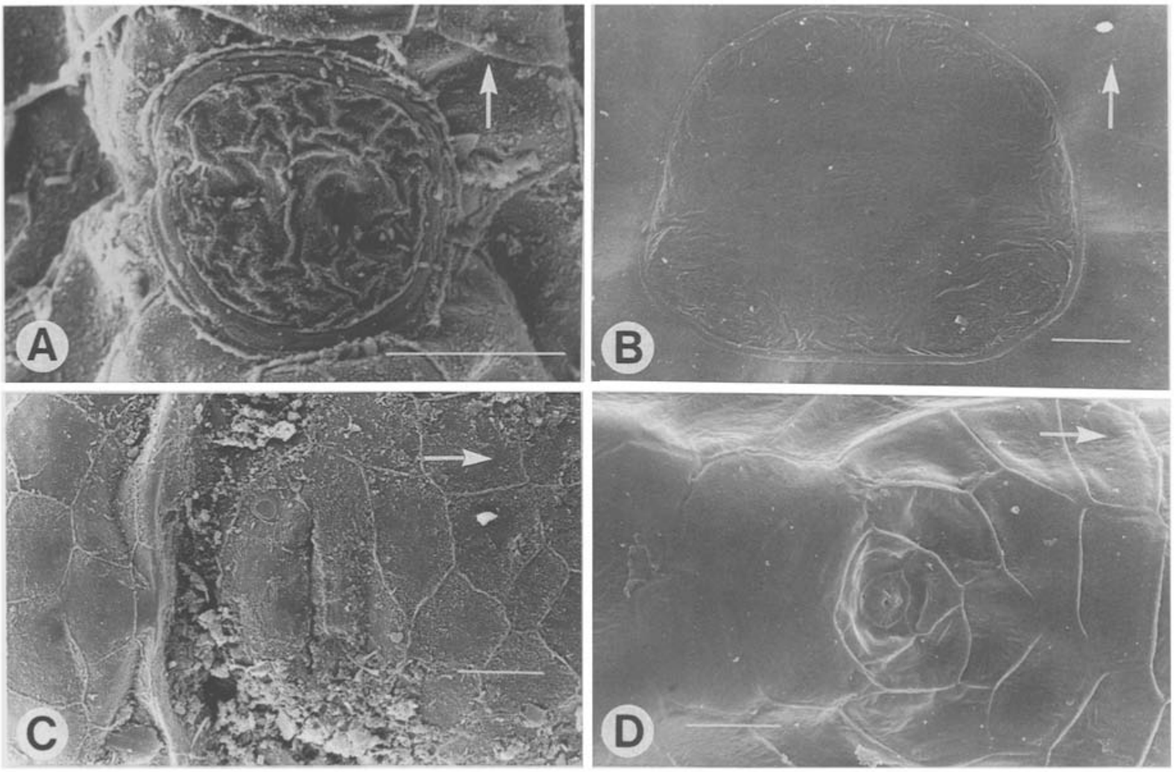

Figure 3. SEM photographs of neck organs in the cladoceran family Macrothricidae. A. *Macrothrix laticornis*; B. *Lathonura rectirostris*; C. *Ilyocryptus sordidus*; D. *Streblocerus serricaudatus*. The arrow indicate anterior direction. Scale bars: 10 μm.

at about the same level as the middle pore *(Alona guttata)*. The middle median pore is in all three species smaller than the two other median pores and lies about midway between the anterior and posterior pores.

Alona affinis (Figure 5D) has two instead of three median pores connected by a narrow rim. The lateral pores are located anterior to the two median pores. Shallow groves exist between the lateral pores and the median pores.

Also in *A. quadrangularis* (Figure 5F) – with the typical arrangement of three median pores – a shallow grove is seen between the lateral pores and the median pores.

In *Alona rustica* (Figure 5E) the lateral pores are large cuticular slits situated obliquely relatively to the median pores, pointing towards the middle median pore. The median pore arrangement is very similar to *Leydigia acanthocercoides* (Figure 4E). The rim between the middle and the anterior pore is, as in *L. acanthocercoides*, narrower than the rim between the posterior and the middle median pore. The distance between the middle and the anterior median pores is bigger in *A. rustica* than in *L. acanthocercoides*. The size of the median pores are, in contrast to other species of *Alona*, at about equal size (as in *L. acanthocercoides* and many others).

Type D (Figure 1H), *Pseudochydorus globosus* (Figure 7A), *Chydorus spaericus* (Figure 7B), *C. ovalis* (Figure 7C), *Peracantha truncata* (Figure 7D), *P. laevicaudatus* (Figure 7E), *P. trigonellus* (Figure 7F), *P. uncinatus* (Figure 7G), *P. aduncus* (Figure 7H), *Alonella nana* (Figure 8A), *A. excisa* (Figure 8B), *A. exigua* (Figure 8C,D)

All the species in this group display variation over the same pattern. Two relatively big median pores with two smaller median pores in between. The two small pores in the middle can be oriented at a right angle relative to

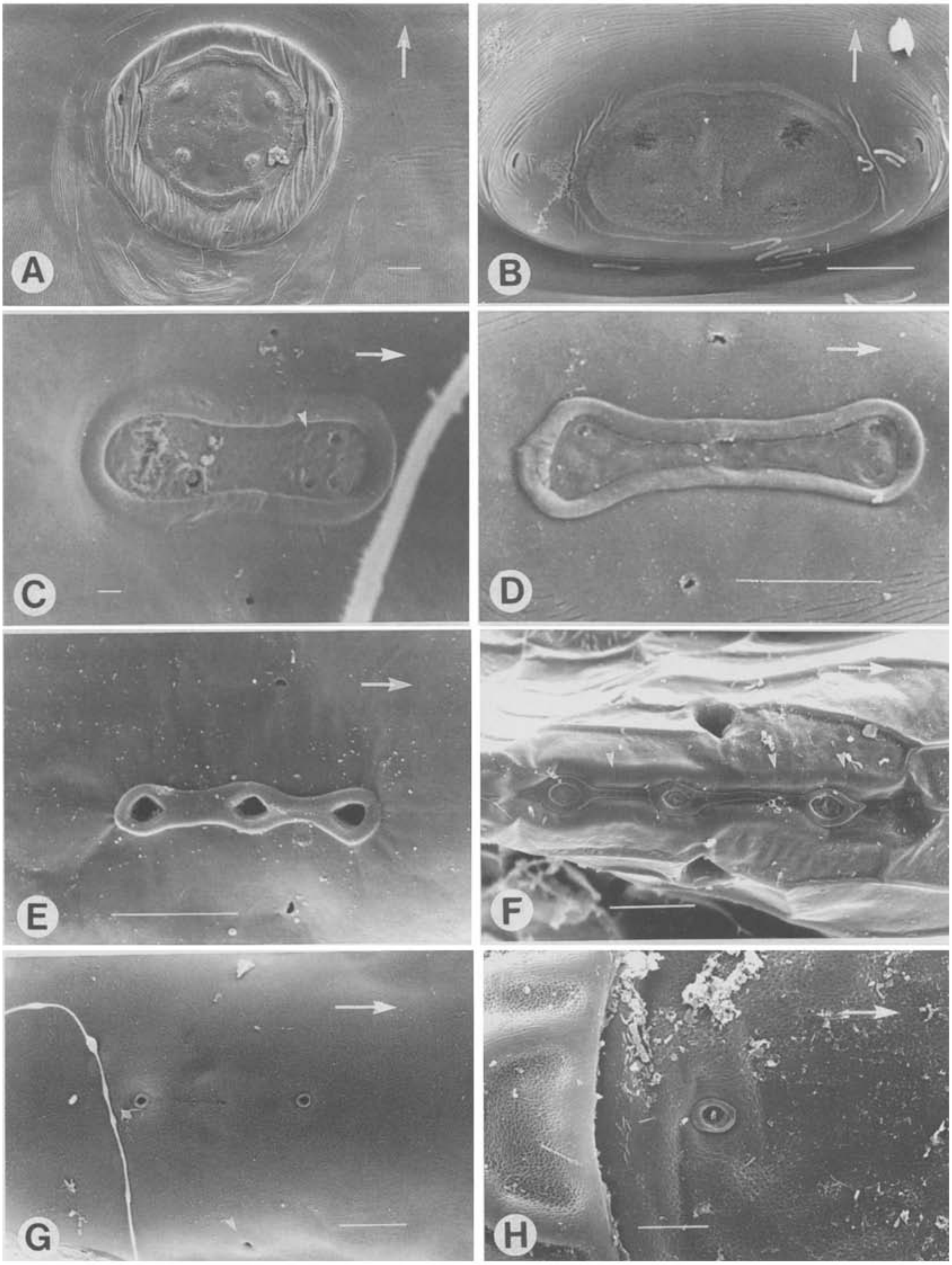

Figure 4. SEM photographs of neck organs in the cladoceran family Chydoridae. A. *Eurycercus glacialis*; B. *Eurycercus lamellatus*; C. *Rhynchotalona falcata*; D. *Tretocephala ambigua*; E. *Leydigia acanthocercoides*; F. *Graptoleberis testudinaria*; G. *Oxyurella tenuicaudis*; H. *Monospilus dispar*. The arrows indicate anterior direction. Scale bars: A–B 10 μm; C 1 μm; D–H 10 μm.

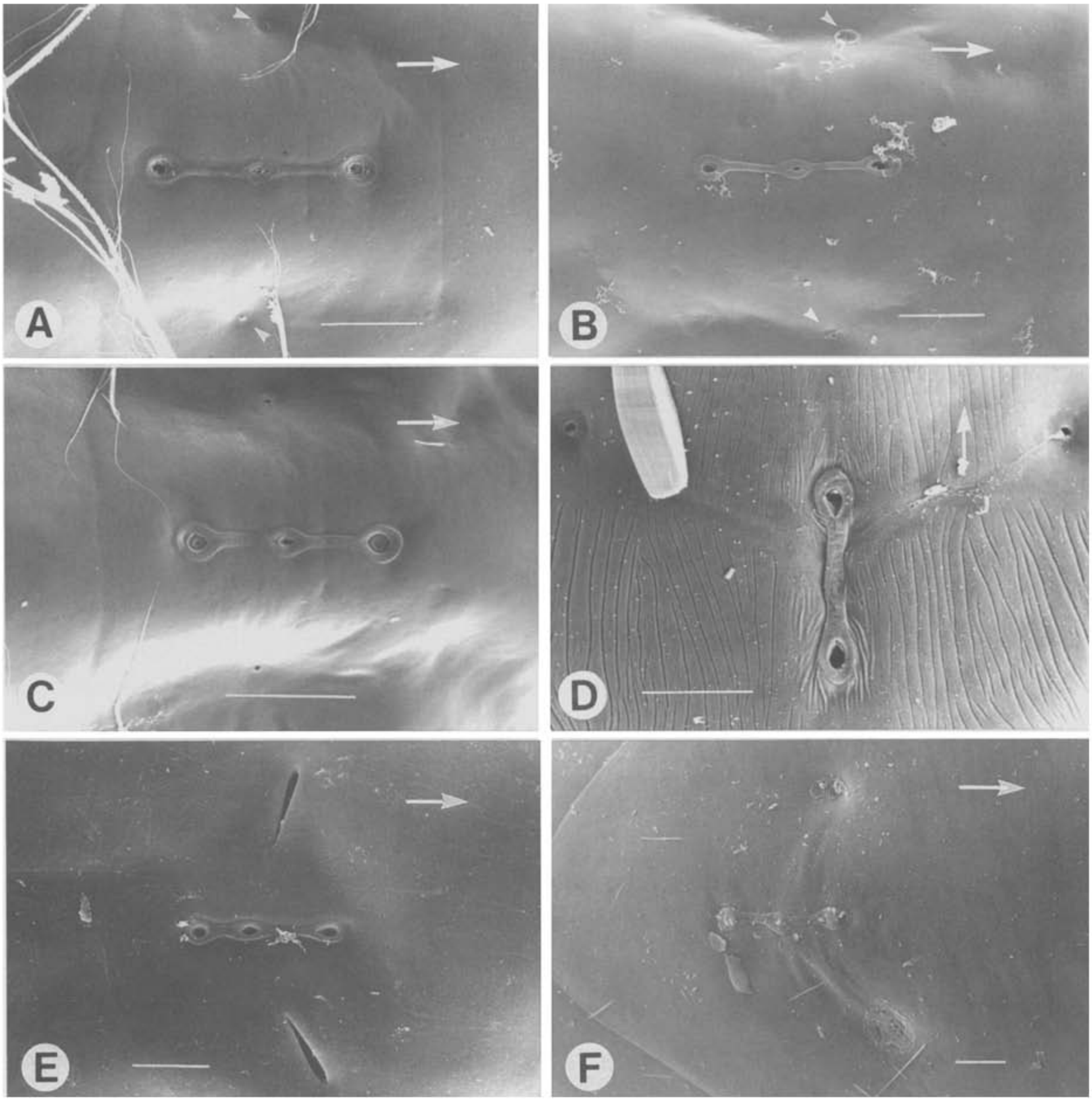

Figure 5. SEM photographs of neck organs in the cladoceran family Chydoridae. A. *Alona gutatta*; B. *Alona costata*; C. *Alona rectangula*; D. *Alona affinis*; E. *Alona rustica*; F. *Alona quadrangularis*. The arrows indicate anterior direction. Scale bars: 10 μm.

the two bigger pores (*Chydorus sphaericus*, Figure 7B, and to a certain extent in *Pseudochydorus globosus*, Figure 7A) or be oriented in different oblique directions as in all other species in this group. The angle of these small median pores is not always species specific since two different specimens of *Alonella exigua* have the pores oriented in different angles (Figure 8C,D). In all examined species of *Alonella* (Figure 8) the area surrounding the pores is elevated to different degree, especially in *Alonella exigua* (Figure 8C,D) which resemble the situation in for example *Alona*. In *Alona excisa* (Figure 8B) and in *Pleuroxus uncinatus* (Figure 7G)

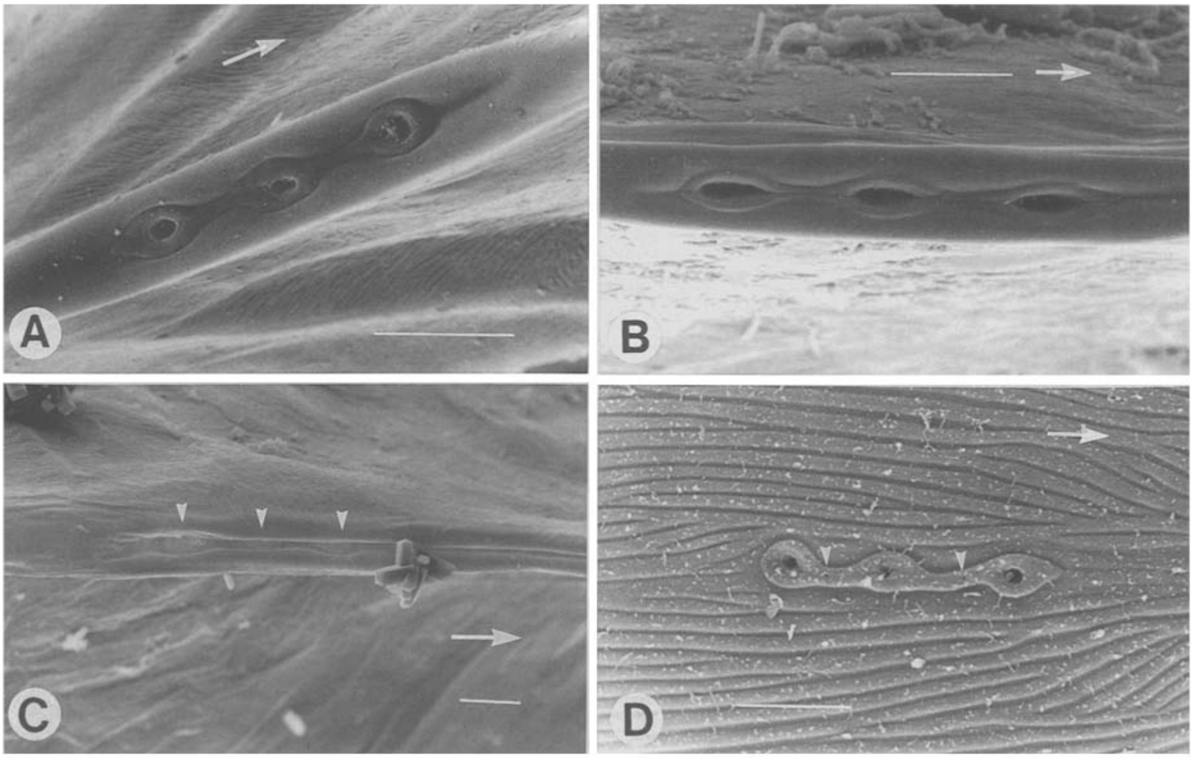

Figure 6. SEM photographs of neck organs in the cladoceran family Chydoridae. A. *Acroperus harpae*; B. *Camptocercus rectirostris*; C. *Camptocercus lilljeborgi*; D. *Alonopsis elongata*. The arrows indicate anterior direction. Scale bars: 10 μm.

only one large pore is present. The smaller pores are present as usual. Anterior to these in *Alonella excisa*, a wrinkled part of the cuticula is enclosed by a circular rim. For the same species, Frey (1959, 1962) has described a neck organ with the poration typical for the subfamily (see Figure 1H) and since only one specimen has been examined in this work, the deviating poration may be an anormal exception. In all examined species of *Chydorus, Pleuroxus* and in the single species of *Peracantha* and *Pseudochydorus* no elevated cuticular areas were seen surrounding the pores.

E. *Oxyurella tenuicaudis* (Figure 1G, 4G) and *Monospilus dispar* (Figure 4H)

These two species do not fit into any of the above mentioned groups. *Oxyurella tenuicaudis* has lateral pores as well as median pores. Two bigger median pores are present, and, between these, two smaller pores arranged on the same line as the two larger pores.

Monospilus dispar has only one medially placed pore.

Discussion

The homology of conchostracan neck/dorsal organ and the chydorid head pores

This study clearly establishes the homology between the neck organ of the Conchostraca and the head pores of the cladoceran family Chydoridae. The evidence comes from the two *Eurycercus* species that display both typical conchostracan characters (four elevated areas surrounded by a cuticular rim) and typical Chydoridae characters (lateral pores) (Figure 1). The resemblance of the *Eurycercus* neck organ to the neck organ of some conchostracans is probably of plesiomorphic nature since similar structures (the four elevated areas or pores) have been reported in other crus-

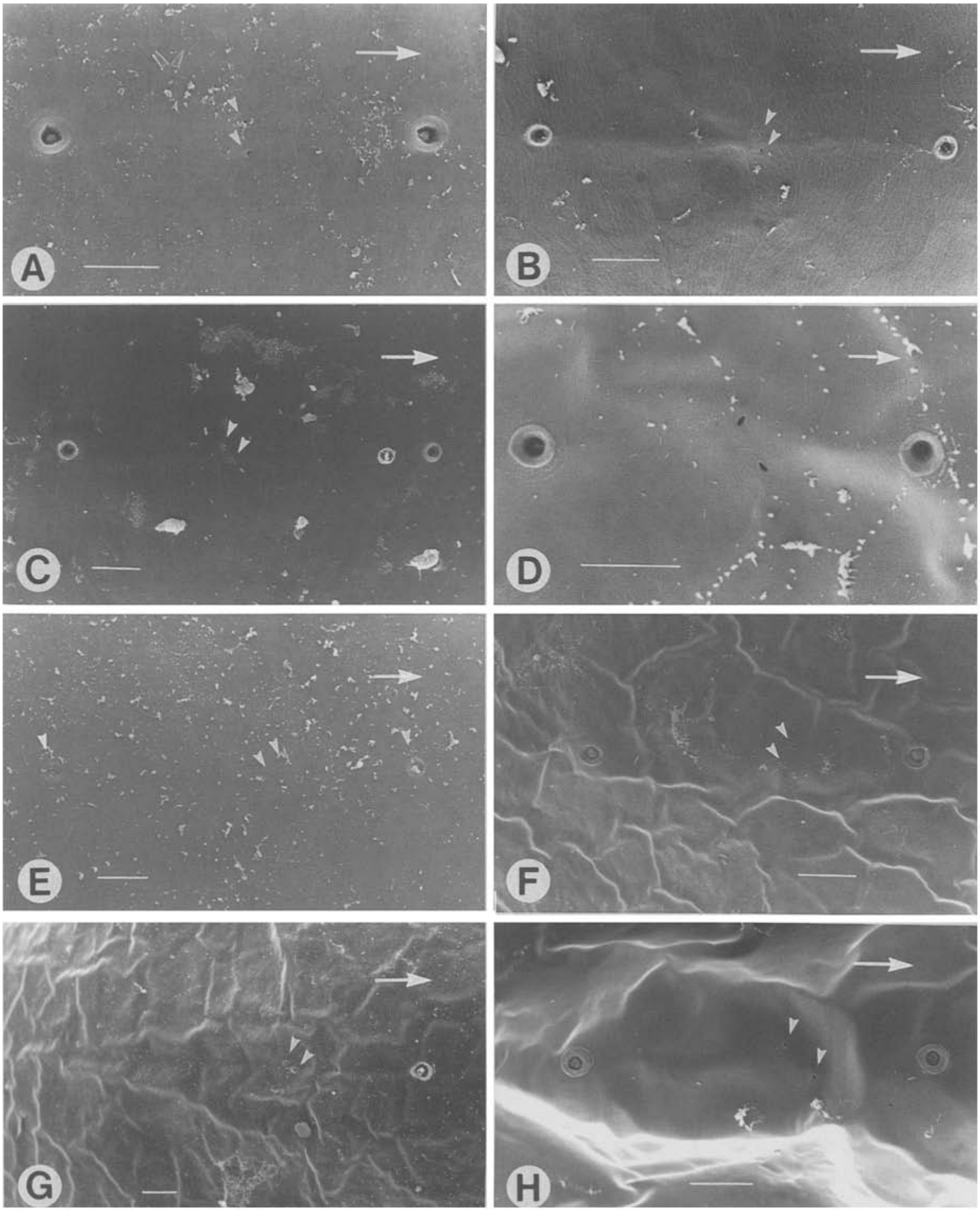

Figure 7. SEM photographs of neck organs in the cladoceran family Chydoridae. A. *Pseudochydorus globosus*; B. *Chydorus sphaericus*; C. *Chydorus ovalis*; D. *Peracantha truncata*; E. *Pleuroxus laevicaudatus*; F. *Pleuroxus trigonellus*; G. *Pleuroxus uncinatus*; H. *Pleuroxus aduncus*. The arrows indicate anterior direction. Scale bars: 10 μm.

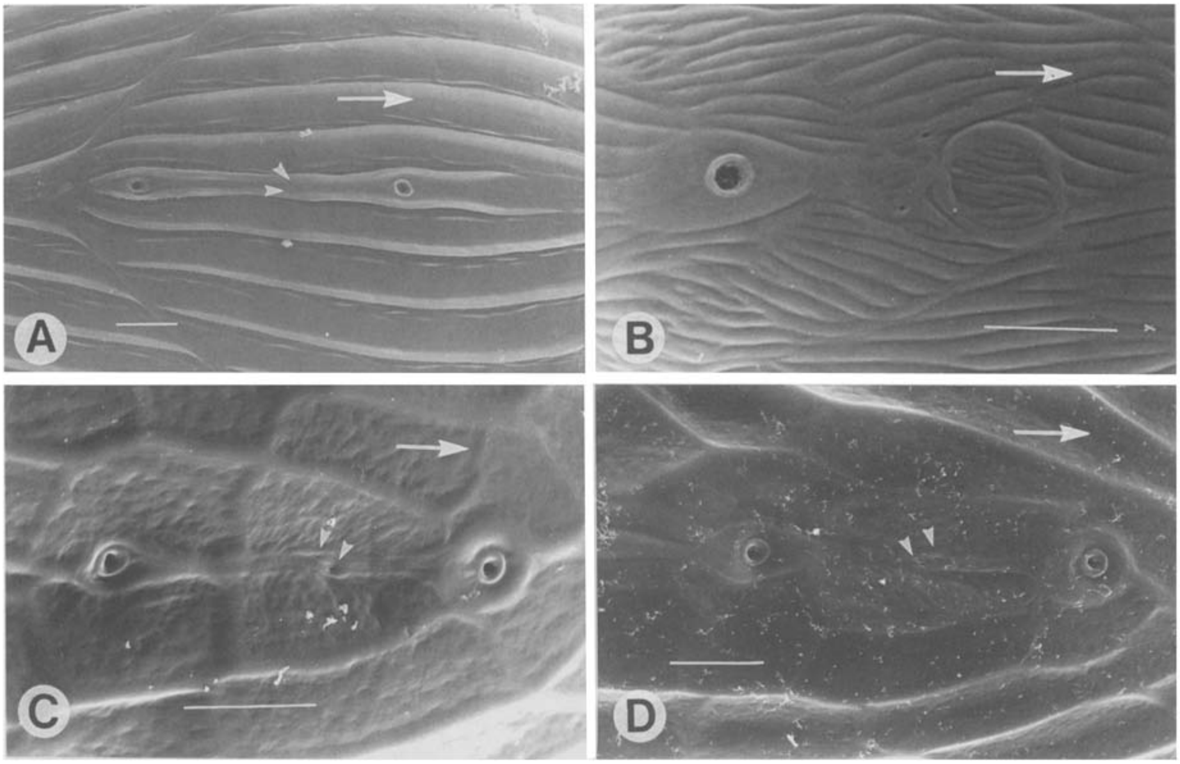

Figure 8. SEM photographs of neck organs in the cladoceran family Chydoridae. A. *Alonella nana*; B. *Alonella excisa*; C. *Alonella exigua*; D. *Alonella exigua*. The arrows indicate anterior direction. Scale bars: 10 μm.

taceans (zoea larva of *Sesarma* (Decapoda, Brachyura) and species of Syncarida, Martin and Laverack, 1992). Similar pore patterns have also been described from the upper cambrian fossils, *Rehbachiella* (Walossek, 1993) and *Bredocaris* (Müller & Walossek, 1988). Two chydorid species, *Rhynchotalona falcata* and *Tretocephala ambigua* display neck organs that might be interpreted as intermediate stages between the rounded *Eurycercus* type and the more elongated *Alona* type (Figure 1). Both species even show four pores within the cuticular rim, in *Tretocephala ambigua* two at each end of the organ and in *Rhynchotalona falcata* four at the same end. These are assumed to be homologous to the elevated areas seen in some conchostracan species and in the *Eurycercus* species.

The similarity in neck organ morphology between some conchostracans and some chydorids makes it difficult to use the neck organ morphology as a characteristic of the Chydoridae the way Frey (1959) suggests (head pores present in the Chydoridae vs. not present outside the Chydoridae). At least, it should be specified precisely what component of the neck organ that could be considered as a possible apomorphy of the Chydoridae. Such a character could be the presence of lateral pores which in the present investigation are found in all chydorid species except in those of Chydorinae and in *Monospilus dispar*. In this explanation, *Monospilus dispar* and the Chydorinae must have lost the lateral pores secondarily, or, in the Chydorinae, the lateral pores could have evolved into the two smaller median pores characteristic of this group. Lateral pores are found in *Eurycercus* and since this genus, perhaps together with *Saycia*, quite likely are early off splits within the Chydoridae, it follows that the presence of lateral pores must be plesiomorphies within the Chydoridae. This position of *Eurycercus* and *Saycia* is based on the fact that the remaining chydorids all have two subitan eggs in their brood chamber whereas the two mentioned genera have many. A neck organ with lateral pores has also been documented in a species of *Simocephalus* (Daphniidae) (Meyer-Rochow, 1979) but the external morphology is somewhat different and the similarity is therefore, for the moment, considered to be convergence. If later examination (e.g. sectioning) shows that these lateral pores must be interpreted as homologous then the lateral pores could be seen as a synapomorphy for Chydoridae and Daphniidae (+ Moinidae), since lateral pores are absent in the Macrothricidae. Marginal pores have been described from the conchostracan (Laevicaudata) *Lynceus gracilicornis* (Walossek, 1993) but they appear not to be widespread within the genus as two species of *Lynceus* examined in this paper appear to lack them. They may therefore not be part of the ground pattern of the Laevicaudata.

The neck organ and the phylogeny of the Chydoridae

Comparing the neck organ of the two largest subfamilies of the Chydoridae, Chydorinae and Aloninae (leaving out the Eurycercinae and Saycinae which only contain few species), reveals that the morphology of the neck organ is most constant within the Chydorinae. Almost all examined species of this subfamily have a characteristical neck organ design, two bigger pores with two smaller pores in between and without lateral pores. This could well be considered as an apomorphy for the Chydorinae.

In contrast to this, the Aloninae has a much more varied neck organ morphology and it seems difficult to find synapomorphies, related to the neck organ, for this group. The majority of species have three pores on a row, and this may turn out to be an apomorphy for at least a part of the Aloninae. A neck organ with this morphology is in the present investigation found in *Graptoleberis testudinaria, Leydigia acanthocercoides, Alonopsis elongata*, in all species of *Acroperus* and *Camptocercus* and in most species of *Alona*. Two pores in a row is seen in some *Alona* species and in *Biarpetura*.

Some species *(Graptoleberis testudinaria* and *Alona rustica)* show a special morphology of their lateral pores, as opposed to more simple pores, but these are autapomorphies and therefore not useful in phylogenetic speculations. More useful is the neck organ morphology in *Acroperus* and *Camptocercus* where it is placed on a characteristic dorsal keel. The presence of this keel, mentioned by Fryer (1968), should be regarded as a synapormorphy for these two genera. *Monospilus dispar* only has a single pore which is shared with for example *Rak* and *Monope* (examined in light microscopy by Smirnov & Timms, 1983) or *Euryalona* (Frey, 1967). However, I hesitate making any phylogenetic conclusions on that basis alone since a single pore stage can quite likely be obtained many ways and because only SEM examination can show the exact nature of the pores. They could for instance have a morphology like the *Eurycercus* species which can by no arguments be united with *Monospilus* despite they both appear as single pores in light microscopy. *Monospilus diporus*, an Australian species, display an arrangement of two interconnected pores (light microscopy based drawing, Smirnov & Timms, 1983) which most likely are the plesiomorphic type within *Monospilus* since this type is found also outside the genus (e.g. in *Biarpertura*).

In *Oxyurella tenuicaudis* the neck organ both display some unique components and some similarities to other species. A feature shared with the rest of the species in Aloninae (except *Monospilus*) and with the species of *Eurycercus*, is the presence of two lateral pores. However, as mentioned earlier this is probably a plesiomorphic character within the Chydoridae and therefore not an indication of relationship. The presence of two lateral pores only tells that this species at least does not belong within the Chydorinae since the loss of the lateral pores, as mentioned above, was considered as a synapomorphy to the species of this group.

Concluding remarks

Most of this discussion is summarised in Figure 1 which presents what appear to be the most simple transformation series of the morphology of the neck organ. The most important neck organ apomorphies are as follows. Presence of lateral pores (the Chydoridae); lateral pores secondarily lost (Chydorinae and in some single genera like *Monospilus*); elongation of the neck organ in anterior/posterior direction after *Eurycecus* has branched off; subdivision of the neck organ into discrete pores (Aloninae and Chydorinae, only excluding *Rhynchotalona* and *Tretocephala*); arrangement of two large median pores with two small median pores between and without lateral pores (Chydorinae). Whether the loss of cuticular connection between the median pores – seen in both the Chydorinae and in *Oxyurella* – is a synapomorphy for these two groups is uncertain.

If the presented picture will be accepted then it seems likely that the Aloninae is no monophylum. It is certainly impossible to mention a neck organ component that include all genera in the Aloninae and not found outside this group, e.g. the lateral pores is a plesiomorphy also found in *Eurycercus*. Another character – the 'mandibles articulated on a apodeme' versus 'articulated without apodeme' – is also problematic since the type found in Aloninae – 'articulated without apodeme' (see Frey, 1967 and Fryer, 1968) – is also found in the *Eurycercus* and is therefore plesiomorphic. Left is only some constancy in the number of exopodal setae (Smirnov, 1966) which is not so convincing when viewed alone. It is therefore likely that the Aloninae is paraphyletic since some of the genera within the Aloninae seem closer related to the Chydorinae than to the rest of the Aloninae (based on the above mentioned head pore characters).

I predict that similar studies on the neck organ of the Anostraca, Notostraca and Conchostraca would most likely be useful in phylogenetic speculations also in these groups. Some examples of neck organs in these groups have been shown (Figure 2), but due to the small material examined, no conclusions can be made.

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