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# Phylogeny of Branchiopoda (Crustacea) – Character Evolution and Contribution of Uniquely Preserved Fossils

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## > Abstract

Phylogeny of Branchiopoda (Crustacea) has received intensive attention the last decade and a widely accepted full resolution of the relationships between the major branchiopod taxa is close. Various well-preserved fossil branchiopods (e.g., *Castracollis*, *Lepidocaris*, Kazacharthra, *Leptodorosida*) combine characters from major recent taxa and are therefore necessary for a full understanding of branchiopod phylogeny and evolution. Here is presented a morphology-based phylogenetic analysis of Branchiopoda, which combines recent taxa with the most well-preserved and informative fossils. The analysis results in support of the following clades: Branchiopoda, Sarsostraca (= Anostraca + *Lepidocaris*), Phyllopoda, Calmanostraca (= Kazacharthra + Notostraca), an unnamed clade consisting of *Castracollis* and Calmanostraca, Diplostraca, an unnamed clade consisting of Spinicaudata and Cladoceromorpha, Spinicaudata, Cladoceromorpha, Cladocera, and Gymnomera. The character support for all clades is presented, which provides a basis for a discussion of aspects of branchiopod evolution.

## > Key words

Anostraca, Notostraca, Conchostraca, Laevicaudata, Spinicaudata, Cyclestherida, Cladocera, systematics, classification, larva, development.

## 1. Introduction

Branchiopoda is a relatively small taxon of mainly freshwater Crustacea with many ancient-looking members, such as Anostraca (fairy shrimps) and Notostraca (tadpole shrimps), but also with highly modified taxa among the Cladocera (water fleas) such as the predatory *Leptodora* or the parasitic *Anchistropus* (on *Hydra*) (e.g, Martin 1992; Dumont & Negrea 2002). About 1200 species are described but more than twice as many have been estimated to exist (Adamowicz & Purvis 2005). About half of the known species are cladocerans, where also the largest diversity in morphology and lifestyles are found. All non-cladocerans (fairy shrimps, tadpole shrimps, clam shrimps) are commonly termed 'large branchiopods', despite the group being clearly paraphyletic. However, the term is useful because 'large branchiopods' share a number of characteristics such as their generally larger size compared to cladocerans, many serially similar phyllopodous trunk limbs, and their preference for temporary wetlands or salt lakes. Much of the basis for the current understanding of branchiopod systematics was provided by G.O. Sars. For the 'large branchiopods' he introduced the well-known names Anostraca, Notostraca, and 'Conchostraca' (now recognised as paraphyletic) (Sars 1867). He also organised the more diverse Cladocera into four taxa, Ctenopoda, Anomopoda, Onychopoda, and Haplopoda (Sars 1865), the monophyly of which is still accepted by most authors. Linder (1945) was the first to notice that Conchostraca were actually composed of two groups of quite different clam shrimps which he named Spinicaudata and Laevicaudata, and the distinct nature of these two taxa was later supported by Fryer (1987). Still later it was realised that also Spinicaudata sensu Linder (1945) is paraphyletic, since the former spinicaudatan, *Cyclestheria hislopi*, is sister group to Cladocera (Martin & Cash-Clark 1995; Olesen et al. 1996; Olesen 1998). Hence, the well-known term 'Conchostraca' should be abandoned, but 'clam shrimps' can be used when referring to Laevicaudata, Spinicaudata, and

Cyclestherida collectively, which, after all, are quite similar (plesiomorphic). Another important step in the exploration of branchiopod phylogeny was the work of Preuss (1951, 1957), who recognised a taxon composed of all Branchiopoda except Anostraca. He named it Phyllopoda and based it on a number of convincing similarities, some of which are included as characters in this work. More problematically, Preuss (1951, 1957) did not recognise the close relationship between Anostraca and Phyllopoda (see Olesen 2007).

In branchiopod phylogenetics there has been a fruitful meeting between the morphological and molecular contribution. A number of the morphology-based hypotheses have been confirmed by molecular data, such as the monophyly of Branchiopoda, Phyllopoda, Cladocera, Gymnomera, and the sister group relationship between Cladocera and *Cyclestheria* (Taylor et al. 1999; Spears & Abele 2000; Braband et al. 2002; Swain & Taylor 2003; Stenderup et al. 2006; deWard et al. 2006; Sun et al. 2006; Richter et al. 2007). In other respects molecular and morphological data conflict. Diplostraca, for example, is supported by morphological data but not by molecular data, which rather suggests a paraphyletic Diplostraca with Notostraca as ingroup (Stenderup et al. 2006). In other respects neither molecular data nor morphology yet provides clear results, which, e.g., is the case for the position of Laevicaudata and the intrinsic phylogeny of Cladocera.

The fossil record adds significant information to the understanding of branchiopod evolution. A number of uniquely preserved branchiopod fossils have a morphology combining that of various Recent taxa. A classical example is *Lepidocaris rhyniensis* Scourfield, 1926, an anostracan-like branchiopod described more than 80 years ago, but more have subsequently been described (see section 2.). Since some of these fossils close morphological gaps between well-known branchiopod taxa such as Anostraca, Notostraca, and Diplostraca, their inclusion in phylogenetic analyses is of tremendous importance. The recently described Rhynie Chert branchiopod, *Castracollis wilsonae* Fayers & Trewin, 2003, is such a chimera because it combines notostracan and diplostracan morphology. It is clear that *Castracollis* cannot be sister group to Notostraca and Diplostraca at the same time, so some of the characters are symplesiomorphies, which can only be sorted out in the context of a cladistic analysis.

If fossils are to be included in phylogenetic analyses, morphology needs to be included in the dataset. For Branchiopoda there have only been few attempts to transfer morphological knowledge into characters useful for more formalised phylogenetic analyses. The first was Olesen (1998, 2000) followed by Negrea et al. (1999). The most recent and comprehensive attempt was that of Richter et al. (2007). As a part of a work combining morphological and molecular data, Richter et al. (2007) provided a morphological dataset which was a much updated and supplemented version of Olesen (1998, 2000). Much new larval and anatomical information was included. Since the focus was a large-scaled analysis of the systematics of Branchiopoda, no attempt was made to map the morphological information on any tree, and no fossils were included.

The purpose of the present paper is two-fold. Firstly, to include some of the well-preserved branchiopod fossils now available in a phylogenetic analysis on a more formal basis, since it is clear that they in some cases represent unique, early 'experiments' in branchiopod evolution. Another purpose is to present and discuss the character support for various clades within Branchiopoda, and thereby get one step closer towards an understanding of branchiopod evolution.

## 2. Short introduction to the fossils included in the phylogenetic analysis

Only six species of fossil branchiopods have been included in this work. Two criteria for the inclusion of fossils have been used: (1) Their state of preservation, which is important for an informative comparison with Recent branchiopods. (2) Their position outside the classical Recent branchiopod taxa ('crown groups'), which means that they provide new characters, or character combinations, not present in these classical taxa. Many fossils have therefore been excluded from the analysis, for example the large fossil record of spinicaudatan-like fossils since for most taxa of these only the carapace valves are known (e.g., Raymond 1946; Jones & Chen 2000; Olempska 2004; Stigall & Hartman 2008).

The following fossil taxa have been included:

- ***Lepidocaris rhyniensis*** Scourfield, 1926 (Lipostraca) (Fig. 1B) is a 3-mm-sized anostracan-like branchiopod from Rhynie chert, an early Devonian Lagerstätte from Aberdeenshire, Scotland, which in Devonian times consisted of flatlands and short-lived shallow pools of freshwater. The fossils are preserved in 3D in chert, which is a result of silica replacement of organic material (Trewin 1994). Already Scourfield (1926) noticed that *Lepidocaris* exhibits a very curious combination of branchiopod characters, some shared with branchiopods in general, some shared specifically with Anostraca, and also some special features only seen in *Lepidocaris*. He wisely decided to erect a separate order for it, Lipostraca, and mentioned that it showed 'closer approach' to the Anostraca than to the other branchiopod orders. Later, uniquely preserved larvae of *Lepidocaris* were described with head appendages (mandible and antenna 2) being very similar to those of larvae of Recent Anostraca (Scourfield 1940). Since then *Lepidocaris* has most often been mentioned as related to anostracans (stem-lineage anostracan) among branchiopods (e.g., Walossek 1993), but as pointed out by Schram & Koenemann (2001) and later discussed by Olesen (2004), another possibility is to treat it as a stem-lineage branchiopod. Certainly, the morphology of the larval antenna 2 and mandible as well as the reduced second maxilla places it as a member of the Branchiopoda (Olesen 2007).

- ***Rehbachiella kinnekullensis*** Müller, 1983 (Fig. 1A) is a minute branchiopod-like crustacean from the 'Orsten', a Cambrian Lagerstätte from Sweden. The largest stage known is 1.8 mm and probably at least 30 stages starting with an ortho-nauplius are present. The very detailed fossilisation in 3D is a result of phosphatic displacement of organic material (Maas et al. 2006). Walossek (1993) recognised the branchiopod affinity of *Rehbachiella* based mainly on the presence of what appeared to be a branchiopod-like food groove and a branchiopod-like type of filtration system, and placed it more specifically on the anostracan stem lineage. Olesen (2004, 2007) later identified a number of branchiopod synapomorphies not present in *Rehbachiella*, and therefore placed it one step further down on the branchiopod stem lineage. The phylogenetic position of *Rehbachiella* is still under debate (Schram & Koenemann 1998; Wills et al. 1998; Walossek & Müller 1998), but the affinity to branchiopods seems as the most convincing suggestion. In this treatment *Rehbachiella* is used as an obvious outgroup to the (crown group) Branchiopoda, so the question of the phylogenetic position of *Rehbachiella* has not been treated directly.
- ***Castracollis wilsonae*** Fayers & Trewin, 2003 (Fig. 1C) is another millimetre-sized Devonian branchiopod from the Rhynie Chert (see above), and was the first unequivocal crustacean from this fauna since the description of *Lepidocaris* in 1926. The preservation is of the typical Rhynie Chert type (see above), so many details are available. Fayers & Trewin (2003) preferred to place *Castracollis* close to the Notostraca, which was followed by Olesen (2007). As mentioned by Fayers & Trewin (2003) *Castracollis* is definitely a branchiopod, and arguments for its position within Phyllopoda sensu Preuss (1951) are also present. However, whether *Castracollis* is a branch of the notostracan lineage or of the diplostracan lineage is uncertain, since it shares characters with both lineages. For example, the specific morphology of the multi-segmented abdomen appears similar to that of the Notostraca, while the possession of long biramous second antennae with symmetrical rami is similar to the Diplostraca.
- ***Almatium gusevi*** (Chernyshev, 1940) belongs to Kazacharthra (Fig. 1D), which is a group of now extinct Jurassic/Triassic branchiopod crustaceans with a distribution limited to Kazakhstan, Mongolia, and certain parts of China (McKenzie & Chen 1999). Some 25 species and nine genera have been described of Kazacharthra, but the most common and well-known species is *Almatium gusevi*, which is therefore included in this analysis. Kazacharthra are considered close to Notostraca due to many general similarities in tail region, limb morphology, and carapace morphology (Tasch 1969; McKenzie et al. 1991; Walossek 1993; McKenzie & Chen 1999). The most comprehensive work is that of McKenzie & Chen (1999), which shows that the similarities to recent branchiopods in general and to Notostraca in particular go very far. Many similarities between Notostraca and Kazacharthra are included for the first time in a formalised cladistic analysis by the present work.
- ***Limnestheria ardra*** Wright, 1920 (Fig. 1E) is one of the few fossil spinicaudatans with other details preserved than the bivalved carapace (Orr & Briggs 1999). *L. ardra* is from the Castlecomer fauna, a Carboniferous Lagerstätte from south-eastern Ireland, which is particular rich in 'conchostracan' (spinicaudatan) branchiopods. There is a large literature dealing with fossilised spinicaudatan carapaces (e.g., Raymond 1946), but the fossilisation of the Castlecomer fauna allows for the reconstruction of other aspects of the external morphology such as the caudal region, male claspers, and the second antennae, which is crucial for more precise considerations of the phylogenetic position of spinicaudatan fossils. Another spinicaudatan fossil with preserved soft parts is *Euestheria luanpingensis* Shen & Niu, 1990, found in high numbers in the middle Jurassic Jiulongshan formation in China (e.g., Zhang et al. 1990). This species has not been included in the present analysis. Zhang et al. (1990) summarised that about 15 species of clam shrimps with preserved soft parts have been recorded worldwide, two of which probably are laevicaudatans, eight are spinicaudatans with preserved cephalons and telsons, while the remaining are just isolated parts such as eggs or digestive tubes. Considering the uncertain phylogenetic position of Laevicaudata within Branchiopoda, the rare fossils of Laevicaudata are of special interest. The Chinese species, *Prolynceus beipiaoensis* Shen & Chen, 1986, from middle Jurassic is mentioned and depicted by Zhang et al. (1990). It lacks caudal furcae and the carapace has a rounded shape, so the suggested laevicaudatan affinity is convincing. Laevicaudata normally lack growth lines of the cara-

**Tab. 1.** Material used in the study.

| Species | Taxon | Figures | Collecting data |
|---|---|---|---|
| *Branchinella* sp. | Anostraca | 2A | The Paroo, a river wetland area in eastern Australia, 2/7-2001. Coll. Brian Timms and Jørgen Olesen |
| *Eubranchipus grubii* (Dybowski, 1860) | Anostraca | 6A, 9B, 11A, 12A–C | 'Dyrehaven' about 10 km north of Copenhagen, 2001. Coll. Ole Møller and Jørgen Olesen (see Møller et al. 2004) |
| *Branchinecta raptor* Rogers, Quinnney, Weaver, Olesen, 2005 | Anostraca | 8A,B, 9A | Idaho, USA, 2005 (see Rogers et al. 2006) |
| *Triops australiensis* (Spencer & Hall, 1895) | Notostraca | 2B, 11B | The Paroo, a river wetland area in eastern Australia, 2/7-2001. Coll. Brian Timms and Jørgen Olesen |
| *Cyclestheria hislopi* (Baird, 1859) | Cyclestherida | 3A, 6D, 7C, 8C, 11E, 13A–C | Colombia, 1994. Coll. Ewald Roessler and Jørgen Olesen (see Olesen et al. 1996; Olesen 1999) |
| *Caenestheria* sp. | Spinicaudata | 3B | Kings Rock, Western Australia, August 2005. Coll. Jørgen Olesen |
| *Caenestheria* sp. | Spinicaudata | 6B, 11D | Elachbutting Rock, August 2, 2003. Coll. Brian Timms |
| *Caenestheria* sp. | Spinicaudata | 10F | Frank Hahn Natural Park, August 19, 2005. Coll. Brian Timms |
| *Caenestheria mariae* Olesen & Timms, 2005 | Spinicaudata | 7A | Western Australia. See Olesen & Timms (2005) |
| *Caenestheriella* sp. | Spinicaudata | 10D,E | Elachbutting Rock, Western Australia, August 2, 2003. Coll. Brian Timms |
| *Eulimnadia braueriana* Ishikawa, 1895 | Spinicaudata | 12D–G | See Olesen & Grygier (2003) |
| *Lynceus tatei* (Brady, 1886) | Laevicaudata | 4 | The Paroo, a river wetland area in eastern Australia, 2/7-2001. Coll. Brian Timms and Jørgen Olesen |
| *Lynceus brachyurus* O.F. Müller, 1776 | Laevicaudata | 6C, 7B, 9C, 10A–C, 11C | 'Dyrehaven' 10 km north of Copenhagen, May 1994. Coll. Jørgen Olesen |
| *Leptodora kindtii* (Focke, 1844) | Cladocera, Haplopoda | 5A, 6F, 8D, 9D, 13D | Tegeler See, 1999. Coll. Stefan Richter and Jørgen Olesen |
| *Bythotrephes longimanus* Leydig, 1860 | Cladocera, Onychopoda | 5C, 9E | Tegeler See, 1999. Coll. Stefan Richter and Jørgen Olesen |
| *Sida crystallina* (O.F. Müller, 1776) | Cladocera, Ctenopoda | 6E | Europe |
| *Diaphanosoma brachyurum* (Liévin, 1848) | Cladocera, Ctenopoda | 13E | Europe |
| *Eurycercus lamellatus* (O.F. Müller, 1776) | Cladocera, Anomopoda | 11F | Europe |
| *Polyphemus pediculus* (Linnaeus, 1761) | Cladocera, Onychopoda | 5B, 7D | Europe |

pace, but *P. beipiaoensis* has a single, marginal growth line, and is in this respect similar to a single specimen of an undescribed Recent laevicaudatan species mentioned by Linder (1945). It is beyond the scope of this work to explore the relationships between fossil and Recent spinicaudatans/laevicaudatans in any detail. It has traditionally been difficult to combine fossil-based classifications, which is mostly based on characteristics of the carapace, with classifications based on Recent taxa, which is mostly based on limb details (e.g., Tasch 1956; Zhang et al. 1990).

- ***Leptodorosida zherikhini*** Kotov, 2007 (Fig. 1F) is a new cladoceran fossil species, which together with another species is placed in a new order, Cryptopoda, from the Ust'-Baley, a fossil lake area from the Jurassic. Traditionally only very few and rather weakly preserved fossils have been recognised as cladocerans, all anomopods or ctenopods (Smirnov 1971; Fryer 1991; Smirnov 1992; Kotov & Korovchinsky 2006), so the fossil record of Cladocera has until now contributed but little to our understanding of cladoceran evolution. The oldest cladoceran fossils have traditionally been from Cretaceous or Jurassic, but a potential benthic anomopod has been described from the Devonian Rhynie Chert hot spring complex (Anderson et al. 2004). The recently described *Leptodorosida zherikhini* of the new order Cryptopoda is the first that falls outside the existing four cladoceran orders. The fossilisation is not superb but enough is known to recognise that it combines characters from three of the existing four cladoceran orders. With Ctenopoda it shares the six pairs of serially similar filtering limbs. With Haplopoda (*Leptodora*) it shares four segments in the rami of the second antennae (maximum number for Cladocera). With (some) Anomopoda is shares the presence of what traditionally has been called a 'head shield', but which is actually rows of cuticular duplicatures (fornices). Hence, the two species referred to

Cryptopoda are clearly cladocerans, but since characters are shared with different cladoceran orders, the erection of a new order is the best solution. Cryptopoda, with its two species, yield an insight into cladoceran monophyly and early evolution (Kotov 2007), and its inclusion is therefore important in this analysis. Prochydoridae Smirnov, 1992, from the Jurassic-Cretaceous boundary in Mongolia, is another relatively recently described fossil taxon of cladocerans which provides important information on early cladoceran evolution. Kotov (2009) questions the affinity to Chydoridae (Anomopoda) of Prochydoridae suggested by Smirnov (1992) and Fryer (1995), but rather prefers it as a basal anomopod or even as as separate cladoceran branch. It was beyond the scope of the present work to include Prochydoridae in the analysis.

## 3. Material, methods, and results

The material used in this study is listed in Tab. 1. Scanning electron microscopy followed standard methodology as, for example, outlined in Olesen et al. (2003).

The branchiopod character list (section 4.) and matrix (Tab. 2) were modified from Olesen (1998) and Richter et al. (2007). The following modifications have taken place: (1) Characters relevant for determining the phylogenetic position of the included fossils have been added. (2) Species of several branchiopod subtaxa such as Anostraca, Spinicaudata, Notostraca, and Cladocera have been deleted since the intrinsic phylogeny of these taxa was beyond the scope of the present work. The deletion of several taxa has made some characters uninformative in the sense that they do not contribute to the phylogeny. However, for completeness they have been kept in the matrix.

The character matrix was constructed in NDE, a Nexus Data Editor program for Windows provided freely by Rod Page (University of Glasgow), modified slightly in Mesquite (Maddison & Maddison 2009), exported to TNT (Tree analysis using New Technology), subsidized by the Willi Hennig Society (Goloboff et al. 2008), where all tree searches and character analyses where performed. Traditional tree searches (1000 replications, 1000 trees saved for each replicate) resulted in three equally parsimonious trees. In order to discard nodes not supported by data the ‘collapse trees after search’ option was used in the search menu in TNT. The resulting three trees differed with respect to the resolution within Cladocera. The least resolved tree (identical to the strict consensus tree) was used as the tree on which character evolution was mapped and classificatory suggestions based. Character evolution was traced in TNT.

## 4. Character list

A complete list of characters is provided below. The character matrix (Tab. 2) is basically the same as used by Richter et al. (2007) (corresponding characters in Richter et al. 2007 mentioned in “[ ]” after each character), but with some characters added and some modified, mostly to accommodate the fossils included in this work. Comments are provided for the new characters or if significant changes have been made to the existing characters.

**1.** [1] ***Segmentation of trunk*: (0)** posterior segments without limbs (i.e., an abdomen is present); **(1)** all trunk segments with limbs (no abdomen present).

**2.** [2] ***Food groove*: (0)** present; **(1)** absent.

**3.** [3] ***Carapace*: (0)** present; **(1)** absent.

**4.** [4] ***Shape of carapace*: (0)** carapace as simple extension of naupliar shield; **(1)** carapace as a flattened dorsal shield; **(2)** carapace covers limbs and head; **(3)** carapace covers limbs but the head is free; **(4)** carapace as a dorsal brood pouch.

*An extra state has been added for* Rehbachiella *(state 0). Notostraca and Kazacharthra have been scored the same way (state 1).*

**5.** [5] ***Carapace growth lines*: (0)** absent; **(1)** present.

**6.** [6] ***Position of female genital opening*: (0)** into the ventral brood pouch; **(1)** dorsally within the carapace; **(2)** at the base of thoracic limbs; **(3)** to the base of flap-like lamellar extensions of the body wall.

**7.** [7] ***Position of male genital opening*: (0)** the sperm ducts open apically at the gonopods of the 12th/13th (or 20th) segment; **(1)** base of the 11th pair of limbs through a simple pore; **(2)** paired genital openings behind the sixth pairs of limbs; **(3)** between limb IV and the anus in a pair of penes; **(4)** fused genital ducts leading to the telson; **(5)** paired opening at the third abdominal segment; **(6)** at the base of the 8th thoracopods; **(7)** at the base of the 6th thoracopods.

**8.** [8] ***First antennae*: (0)** present; **(1)** largely absent, only sensilla present.

**9.** [9] ***First antennae*: (0)** without lobes; **(1)** lobate.

**10.** [10] ***First antennae sensilla*: (0)** sensilla not restricted to tip; **(1)** sensilla restricted to the tip.

**11.** [11] ***Second antennae in adults: rami*: (0)** rami of different length, endopod shortest; **(1)** rami of similar length (‘symmetrical’); **(2)** uniramous and unsegmented.

*A new state has been included to cover the similarity in second antennae morphology of Notostraca and Kazacharthra. In both taxa they are small, uniramious, and unsegmented. An example of notostracan second antennae morphology can be seen for* Lepidurus arcticus *in Sars (1896). The second antennae of* Almatium gusevi *(Kazacharthra) were first identified as small and biramous (McKenzie et al. 1991), but based on more abundant material, McKenzie and Chen (1999) identified them as "relatively small, uniramous, and unsegmented".*

**12.** [12] ***Second antennae in adults: number of segments in exopod*: (0)** more than seven segments; **(1)** seven segments; **(2)** five segments; **(3)** four segments; **(4)** three segments; **(5)** two segments.

*This character has been divided into more states to allow for a more refined coding of the number of antenna exopod segments.* Lepidocaris *is reported to have five segments (Scourfield 1926).* Castracollis *has an unspecified number between five and seven (Fayers & Trewin 2003).* Leptodorosida *(Cryptopoda) has four segments as both* Leptodora *(Haplopoda), Onychopoda, and most Anomopoda.*

**13.** [13] ***Second antennae in adults: number of segments in endopod*: (0)** more than seven segments; **(1)** seven segments; **(2)** five segments; **(3)** four segments; **(4)** three segments; **(5)** two segments.

*This character has been divided into more states to allow for a more refined coding of the number of antenna endopod segments.* Lepidocaris *has two (female) or three (male) segments.* Castracollis *has between five and seven segments.* Leptodorosida *(Cryptopoda) has four segments as* only Leptodora *(Haplopoda) within Cladocera.*

**14.** [14] ***Mandible gnathal edge*: (0)** with incisor and molar process; **(1)** ellipsoid with pores, not divided into distinct molar and incisor; **(2)** with separate teeth.

Almatium gusevi *(Kazacharthra) is reported by McKenzie et al. (1991) to have 6–7 strong, multicuspidate teeth at the gnathal edge, which is the same as described for species of Notostraca, and to some extent for Laevicaudata (but not multicuspidate) (Richter 2004), which are therefore scored the same way.*

**15.** [new] ***Mandible: row of teeth along edge of molar surface (left md)*: (0)** absent; **(1)** present.

*This new character deals with a specific similarity in the morphology of the mandible gnathal edge in* Lepidocaris *and Anostraca. In both* Lepidocaris *and* Branchinella lyrifera *(Anostraca) the gnathal edge of the left side mandible has a distinct row of teeth along the dorsal margin of the gnathal edge (see Scourfield 1926: 164; Richter 2004: 33).*

**16.** [new] ***Maxilla 1, degree of reduction*: (0)** with proximal endite and more distal parts; **(1)** only proximal endite retained or reduced further.

*A new character which deals with the for branchiopods typical reduction of maxilla 1. It is well-known that maxilla 1 in 'large' branchiopods and many cladocerans is reduced to a small, food handling setose process (see Cannon & Leak 1933), quite certainly corresponding serially to the proximal/first endite of more posterior limbs. This is also the case for* Lepidocaris, *but since males have a longer maxilla 1 (probably modified for clasping), this taxon has been scored as ambiguous. In some taxa within Cladocera (Haplopoda and Onychopoda) maxillae 1 are reduced even further, for example to a pair of lateral lobes of a 'lower lip' (Haplopoda) (e.g., Olesen et al. 2003, Korovchinsky & Boikova 2008).*

**17.** [new] ***Maxilla 2, degree of reduction*: (0)** with coxa and more distal segments; **(1)** only coxal segment retained or reduced further.

*A new character which deals with the reduction of maxilla 2 seen in all branchiopods.*

**18.** [16] ***Trunk limbs: number*: (0)** 11; **(1)** at least 35; **(2)** 10; **(3)** 12; **(4)** 18–32; **(5)** 15 or 16; **(6)** 6; **(7)** 5; **(8)** 4; **(9)** 14; **(10)** 9.

Lepidocaris *has 11 pairs of trunk limbs (not counting limb pairs 12 and 13 modified as a brood pouch).* Almatium gusevi *(Kazacharthra) also has 11 limb pairs.* Castracollis *is reported to have between 18 and 32 limb pairs divided in two distinct limb series (see character 19).* Leptodorosida *(Cryptopoda) has 6 pairs of limbs.*

**19.** [new] ***Trunk limbs: subdivision into series*: (0)** not divided in two series; **(1)** divided in two series (11 in anterior series).

*This is a new character dealing with a particular similarity between Notostraca and* Castracollis. *Both have a rather long series of trunk limbs which are divided into two series, in both cases with 11 in the anterior series (Fayers & Trewin 2003; Fryer 1988).* Almatium gusevi (Kazacharthra) *is by McKenzie & Chen (1999) mentioned to have 11 limb pairs, but a figure in the same work shows what seems to be a few gnathobase-like structures at the anterior abdominal segments, so* Almatium *may have small abdominal limbs as well, and the limbs series in Kazacharthra therefore subdivided in two series as in Notostraca and* Castracollis (confirmed by Tom Hegna, who has studied additional material of *A. gusevi*, pers. comm.). *This aspect of* Almatium gusevi *needs more exploration so the character is scored '?'.*

**20.** [new] ***Anterior trunk limbs: orientation*: (0)** not particularly laterally directed; **(1)** laterally directed.

*This is a new character dealing with the similarities in some parts of the feeding apparatus in Notostraca,* Almatium gusevi *(Kazacharthra), and* Castracollis. *It is well-known that Notostraca has a non-filtratory feeding strategy involving scavenging, deposit feeding, predation, etc. (Fryer 1988), a feeding style reflected in the laterally directed anterior trunk limbs exposing the median edges of the limbs directly to the food items. The same is seen in* Almatium gusevi *(Kazacharthra) (McKenzie & Chen 1999) and seemingly also in* Castracollis *(Fayers & Trewin 2003). In all three taxa the anterior part of the thorax is flattened, but since this probably is evolutionarily related to the laterally placed trunk limbs, it is not treated as a separate character. Other more specific similarities in limb morphology in Notostraca and Kazacharthra are treated as separate characters.*

**21.** [17] ***Trunk limbs: function*: (0)** swimming and feeding; **(1)** feeding only.

**22.** [18] ***Trunk limbs: shape*: (0)** phyllopodous limb corm with endites and a segmented or unsegmented endopod; **(1)** stenopodous with four/five segments (in main axis of limb if biramous).

**23.** [19] ***Trunk limbs: epipods*: (0)** present; **(1)** absent.

*An epipod seems to be absent in* Lepidocaris *(Scourfield 1926), and its presence in* Castracollis *has been reported as uncertain (Fayers & Trewin 2003).* Almatium gusevi *(Kazacharthra) has an epipod (McKenzie & Chen 1999), in contrast to earlier reports (Novojilov 1959; McKenzie* et al. *1991).*

**24.** [20] ***Trunk limbs: number of endites*: (0)** about eight; **(1)** six (at least during development); **(2)** five.

Rehbachiella *(outgroup) has the highest number of median endites on the trunk limbs (about eight). The remaining taxa have six endites or less.* Lepidocaris *has six as in Anostraca (see Møller* et al. *2004; Williams 2007).* Castracollis *has five endites as in Notostraca, Laevicaudata, Spinicaudata, and Cyclestherida. An entire trunk limb of Kazacharthra was reconstructed by Novojilov (1959), but the terminology was different from what is most often used for branchiopod limbs. McKenzie & Chen (1999) clarified that the trunk limbs of* Almatium gusevi *(Kazacharthra) are very similar to those of Notostraca (see characters 25 and 29), and they could account for the same number of endites having a very similar morphology as in Nostostraca. Hence, Kazacharthra has five endites with an unsegmented endopod distally.*

**25.** [21] ***Trunk limbs: shape and position of endites*: (0)** lobate, not elongate, placed along median edge; **(1)** endites 4–5 elongate, placed distally.

*The trunk limbs of* Almatium gusevi *(Kazacharthra) are very similar to approximately trunk limbs 2–4 in the limb series of Notostraca. Based on these similarities two characters are identified (chs. 25 and 29). One character concerns similarities in the shape and position of the endites. Notostraca and* Almatium gusevi *(Kazacharthra) have a very similar condensation of endites 4 and 5 distally at the trunk limbs close to the endopod. Furthermore, the endites are of the same length, are elongate in shape, and become narrower distally. Laevicaudata have been scored the same way since their endites 4 and 5 are also elongate and placed distally (but different from Notostraca and Kazacharthra).*

**26.** [22] ***Trunk limbs: endite palps*: (0)** without palps; **(1)** with palps.

*It is well-known that many spinicaudatans have a slender, sometimes two-segmented palp inserted at the fifth endites of the trunk limbs (e.g., Sars 1895, 1898). Such palps were not known from other branchiopods until the description of the Devonian* Castracollis wilsonae. *In* Castracollis *endites 2–5 are each equipped with a palp, smallest at endite 2, largest at endite 5 (termed 'spines' by Fayers & Trewin 2003, but 'palp' is a better term). The large palp at endite 5 is very similar to the single palp of endite 5 of spinicaudatans, and enditic palps are therefore scored present in both taxa.*

**27.** [23] ***Trunk limbs: segmentation of endopod*:** **(0)** more than one segment; **(1)** unsegmented.

Lepidocaris, Castracollis, *and* Almatium *clearly have an unsegmented endopod articulated to the stem of the limb.*

**28.** [new] ***Trunk limbs: dorsal lobe of exopods*: (0)** absent; **(1)** small; **(2)** long.

*This is a new character dealing with the presence of dorsal lobes of the exopods on most limbs in Laevicaudata, Spinicaudata, Cyclestherida (all clam shrimps), and some limbs of Notostraca. In clam shrimps this lobe is long, while it is short in Notostraca, which are therefore treated as separate character states.*

**29.** [new] ***Trunk limbs: subdivision in sclerotised portions, distal portion large with endites and endopod distally*: (0)** not present; **(1)** present.

*As mentioned in character 25 the trunk limbs in Kazacharthra are very similar to at least some of the* *trunk limbs in Notostraca. A new character deals with a specific similarity in the way the limb corm is subdivided in a pattern of sclerotised portions. The limb corms of the anterior trunk limbs of Notostraca (e.g., Sars 1896; Hansen 1925) consist of at least two major portions (plus a couple of smaller portions) with an articulation about where the epipod is attached. Based on McKenzie and Chen (1999) this is very similar to what is seen in* Almatium gusevi *(Kazacharthra).*

**30.** [24] ***1st thoracopod as clasper*: (0)** absent; **(1)** present.

**31.** [25] ***2nd thoracopod as clasper*: (0)** absent; **(1)** present.

**32.** [26] ***Claspers on trunk limbs 1 and 2, 'movable finger' (endopod)*: (0)** with scales or spines; **(1)** with sucker-like structure.

**33.** [27] ***Ejector hooks on trunk limb 1*: (0)** absent; **(1)** present.

**34.** [new] ***Abdomen: somites*: (0)** not many narrow somites with denticles; **(1)** many, narrow somites with serrate denticles along posterior margin.

*This is a new character dealing with a similarity in the morphology of the abdomen in Notostraca, Kazacharthra, and* Castracollis. *In these three taxa the abdomen consists of a high number of narrow somites with rows of serrate denticles along the posterior margin (Sars 1896; McKenzie et al. 1991; Fayers & Trewin 2003).*

**35.** [new] ***Tergopleural scales on the thoracopod-bearing segments*: (0)** absent; **(1)** present.

*This is a new character dealing with absence/presence of tergopleural scales. Such scales are among branchiopods present only in the two Devonian fossils* Lepidocaris *and* Castracollis *(Scourfield 1926; Fayers & Trewin 2003).*

**36.** [28] ***Telson: shape*: (0)** cylindrical; **(1)** laterally compressed.

*Character 28 in Richter et al. (2007) but Laevicaudata changed to '0' from '1' since the telson region is not characteristically laterally compressed as in Spinicaudata, Cyclestherida, and most Cladocera.*

**37.** [29] ***Telson: telsonal setae*: (0)** absent; **(1)** present.

*As mentioned in other papers (Richter et al. 2007; Olesen 2007) a pair of dorsal telsonal setae is present in all known species of Notostraca, Laevicaudata, Spinicaudata, Cyclestherida, and Cladocera, and is therefore a supporting character for Phyllopoda. Such setae are unknown from* Castracollis, *but seem to be present in* Almatium gusevi *(Kazacharthra), where a pair of structures called 'circular ducts' (McKenzie & Chen 1999) is found in a position very similar to the telsonal setae seen in Notostraca. Probably these structures in Kazacharthra are not 'ducts' but rather small depressions like in Notostraca. No such setae are described for Kazacharthra, but these may not have been preserved.*

**38.** [30] ***Telson: dorsal spines on arranged in two rows*: (0)** absent; **(1)** present.

*In Spinicaudata, Cyclestherida, Ctenopoda, and Anomopoda all dorsal spines on the telson are arranged in two rows. Such a pattern is also seen in* Castracollis *despite the telson region being much different from that of the other taxa.*

**39.** [31] ***Furca articulation*: (0)** present; **(1)** absent.

**40.** [32] ***Furca shape*: (0)** straight; **(1)** curved, claw-like.

**41.** [33] ***Neck organ*: (0)** present but not extended; **(1)** present and extended (pyriforme); **(2)** absent.

**42.** [34] ***Compound eyes: position*: (0)** externally; **(1)** internalized.

*The internalised compound eyes of many branchiopods (Notostraca plus Diplostraca) have been recognised as a synapomorphy of Phyllopoda. In* Lepidocaris *no external eyes are visible so we are left with speculation whether the compound eyes are internal. Uncertainty also applies to* Castracollis *since the fossils are badly preserved in this respect. In* Almatium gusevi *(Kazarchartha) is described a pair of ventral slit-shaped pores ventrally at the front of the head, which presumably leads to internalized compound eyes (McKenzie et al. 1991; McKenzie & Chen 1999).*

**43.** [35] ***Compound eyes: fusion of left and right ommatidial parts*: (0)** not fused; **(1)** fused only ventrally; **(2)** fused to a globular organ.

**44.** [36] ***Compound eyes: midline of ommatidia*: (0)** absent; **(1)** present.

**45.** [37] ***Compound eyes: fusion of left and right laminae*: (0)** absent; **(1)** present.

**46.** [38] ***Compound eyes: fusion of left and right medullae*: (0)** absent; **(1)** present.

**47.** [39] ***Compound eyes: ommatidial structure*: (0)** tetrapartite; **(1)** pentapartite.

**48.** [40] ***Nauplius eye: number of ocelli*: (0)** three; **(1)** four.

**49.** [41] ***Nauplius eye: shape*: (0)** globular; **(1)** triangular.

**50.** [42] ***Nauplius eye: position*****: (0)** close to compound eye; **(1)** displaced, space between nauplius and compound eyes filled by gut diverticles.

**51.** [43] ***Gut system: anterior diverticles*****: (0)** anterior diverticles extended; **(1)** anterior diverticles small; **(2)** anterior diverticles absent.

**52.** [44] ***Heart structure: number of pairs of ostia*****: (0)** 18; **(1)** 11; **(2)** 7; **(3)** 4; **(4)** 3; **(5)** 1.

**53.** [45] ***Oogenesis: groups of four cells, including oocyte and three nurse cells*****: (0)** absent; **(1)** present.

**54.** [46] ***Spermatozoa: size*****: (0)** small; **(1)** gigantic, with lateral vesicles; **(2)** gigantic, empty-looking vesicles.

**55.** [47] ***Spermatids: type of maturation*****: (0)** cystic type; **(1)** lumenal type; **(2)** vacuolar type.

**56.** [48] ***Protection of eggs/embryos*****: (0)** ventral brood pouch; **(1)** encapsulated between a sub-apical lobe and the exopod of the 11th pairs of limbs or just in 'modified exopods' (Kazacharthra); **(2)** carried between carapace and trunk.

Lepidocaris *has a ventral brood pouch as the one seen in Anostraca, apparently originating from the same somites (12th and 13th) (Olesen 2004).* Almatium gusevi *(Kazacharthra) has been reported to carry egg masses in modified exopods of the 11th limb pair (McKenzie & Chen 1999), which appears similar to what is seen in Notostraca (Sars 1896; Fryer 1988), even though there is conflicting information on exactly which parts of the limbs forms the egg chambers.*

**57.** [49] ***Protection of eggs/embryos*****: (0)** carried under the carapace, attached to or supported by dorsal parts of the exopod; **(1)** carried under the carapace but not attached to the limbs.

*This character splits up state 2 of character 56 in two separate states treating two different ways of carrying the egg masses between the carapace and the trunk in Laevicaudata, Spinicaudata, Cyclestherida, and Cladocera. Either the eggs/embryos are carried attached to (or supported by) dorsal prolongations of the trunk limbs exopod (state 0) as seen in Spinicaudata (eggs), Cyclestherida (embryos, see Figs. 3A, 13A), and Laevicaudata, or they are carried dorsally non-attached to the limbs as in Cladocera (embryos) (state (1)).*

**58.** [50] ***Alternation between parthenogenetic and sexual reproduction (heterogony)*****: (0)** absent; **(1)** present.

**59.** [51] ***Free living larvae hatching from resting eggs*****: (0)** present; **(1)** absent.

**60.** [52] ***Subitaneous eggs with direct development (embryonized larvae)*****: (0)** absent; **(1)** present.

**61.** [53] ***Resting eggs protected by carapace (ephippium)*****: (0)** absent; **(1)** present.

**62.** [new] ***First antennae in larvae or embryos: setation*****: (0)** setae/sensilla not confined to tip; **(1)** setae/sensillae confined to tip. *Character not included in Richter et al. (2007) but used by Olesen (2007).*

**63.** [56] ***First antennae in larvae: shape*****: (0)** elongate, tubular; **(1)** as small buds; **(2)** as horn-like structure.

**64.** [57] ***First antennae in embryos*****: (0)** remain separate; **(1)** basally close to each other in 'V'-shaped pattern.

**65.** [58] ***First antennae in naupliar larval stages: large seta*****: (0)** absent; **(1)** present.

**66.** [new] ***Second antennae in larvae: length of protopod*****: (0)** less than half total length of limb; **(1)** more than half total length of limb.

*Was mentioned as a characteristic feature of branchiopod larvae already by Sanders (1963), and later discussed by Olesen (2004, 2007).*

**67.** [new] ***Second antennae in larvae or embryonised larvae: masticatory process*****: (0)** present; **(1)** absent.

**68.** [new] ***Second antennae in larva: endopod setation*****: (0)** not distal setation only; **(1)** distal setation only.

*Character not included in Richter et al. (2007) but discussed by Olesen (2007).*

**69.** [55] ***Second antennae in larvae or embryonised larvae: morphology of masticatory process*****: (0)** cluster of about 5 spines; **(1)** divided in two branches after a few molts.

*Modified version of character 55 in Richter et al. (2007) and was discussed by Olesen (2004, 2007). All branchiopod larvae (except* Rehbachiella*) have a very similar masticatory process ('naupliar process') of the second antennae. In Anostraca, Notostraca, Spinicaudata, and Laevicaudata it starts as an unbranched pointed structure, which becomes branched after a few moults; in most taxa the posterior branch has a characteristic annulus basally (Olesen & Grygier 2003, 2004; Olesen 2005). Larvae of* Lepidocaris *have a very similar second antenna masticatory process (Scourfield 1940).*

**70.** [60] ***Second antennae in larvae or embryonised larvae: basipodite with small segment*****: (0)** absent; **(1)** present.

**Tab. 2.** Character matrix combining recent and fossil branchiopod taxa. Polymorphism entered as: A = 0/1; B = 1/2; C = 2/3; D = 3/4; E = 4/5; F = 6/7.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rehbachiella* | 0 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepidocaris* | 0 | ? | 1 | - | - | ? | ? | 0 | 0 | 1 | 0 | 2 | E | 1 | 1 | A | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Anostraca | 0 | 0 | 1 | - | - | 0 | 0 | 0 | 0 | 1 | - | - | - | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Notostraca | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 2 | - | - | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | - | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Almatium* | 0 | 0 | 0 | 1 | 0 | ? | ? | 0 | 0 | 1 | 2 | - | - | 2 | 0 | 1 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | - | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Castracollis* | 0 | 0 | 0 | ? | ? | ? | ? | 0 | ? | ? | 1 | B | B | 1 | 0 | 1 | ? | 4 | 1 | 1 | 0 | 0 | ? | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | - | 0 | 1 | 1 | 0 | ? | 1 | 0 | 0 |
| Laevicaudata | 1 | 0 | 0 | 2 | 0 | 3 | ? | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 1 | C | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | - | - |
| Spinicaudata | 1 | 0 | 0 | 2 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 4 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | A | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Limnestheria* | 1 | ? | 0 | 2 | 1 | ? | ? | 0 | ? | ? | 1 | ? | ? | 1 | ? | ? | ? | ? | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 1 | 1 | ? | ? | 0 | 0 | 1 | ? | 1 | 0 | 1 |
| *Cyclestheria* | 1 | 0 | 0 | 2 | 1 | 2 | ? | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 5 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Leptodora* | 0 | 1 | 0 | 4 | 0 | 1 | 5 | 0 | 0 | 1 | 1 | 3 | 3 | - | 0 | 1 | 1 | 6 | 0 | 0 | 1 | 1 | 1 | - | - | - | - | - | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | - |
| Onychopoda | A | 1 | 0 | 4 | 0 | 1 | 3 | A | 0 | 1 | 1 | 3 | 4 | - | 0 | 1 | 1 | 8 | 0 | 0 | 1 | 1 | 1 | - | - | - | - | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | - |
| Ctenopoda | 1 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | E | E | 1 | 0 | 1 | 1 | 6 | 0 | 0 | 1 | 0 | 0 | - | 0 | 0 | - | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| Anomopoda | 1 | 0 | 0 | 3 | A | 1 | 4 | 0 | 0 | 1 | 1 | D | 4 | 1 | 0 | 1 | 1 | F | 0 | 0 | 1 | 0 | 0 | - | 0 | 0 | - | 0 | 0 | - | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Leptodorosida* | 1 | ? | 0 | 3 | ? | ? | ? | ? | ? | ? | 1 | 3 | 3 | 1 | ? | ? | ? | 6 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | 0 | 1 | ? | ? | 0 | 1 |

| | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rehbachiella* | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepidocaris* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | - | ? | 0 | 0 | ? | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | ? | 0 | 2 | ? | 0 | 0 | 1 | 1 | 1 | 0 | - |
| Anostraca | ? | 0 | 0 | - | 0 | 0 | ? | 0 | 0 | - | 1 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | - |
| Notostraca | 0 | 1 | 0 | - | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | - | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | B | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Almatium* | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | - | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Castracollis* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Laevicaudata | 0 | 1 | 1 | - | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | - | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 2 | 1 | 1 |
| Spinicaudata | A | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 3 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | A | 1 | 1 |
| *Limnestheria* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Cyclestheria* | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | ? | 0 | 1 | 2 | 0 | 1 | A | 1 | 1 | 1 | 1 | 0 | 1 | 1 | A | 1 | - | ? | ? | ? | ? | ? | A | 1 | 1 | 2 | 1 | 1 |
| *Leptodora* | 0 | 1 | 2 | - | 1 | 1 | 1 | - | - | - | 2 | 5 | 1 | 0 | - | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | - | A | - | - | - | ? | 2 | 0 | 0 | A | ? | ? | - | 1 | 1 |
| Onychopoda | 0 | 1 | 2 | 1 | 1 | 1 | 1 | - | - | - | 1 | 5 | 1 | 1 | - | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | 1 | 1 |
| Ctenopoda | 2 | 1 | 2 | 1 | 1 | 1 | 1 | - | - | - | 2 | 5 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | 1 | 1 |
| Anomopoda | 0 | 1 | 2 | 0 | A | 0 | 1 | 1 | 0 | A | 1 | 5 | 1 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | 1 | 1 |
| *Leptodorosida* | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

**71.** [61] ***Second antennae in larvae or embryonised larvae: anterior branch of masticatory process*: (0)** with brush-like setae; **(1)** with single comb-row.

**72.** [62] ***Second antennae in larvae or embryonised larvae: number of segments of endopod*: (0)** not clearly divided into segments; **(1)** two clear segments; **(2)** three clear segments.

**73.** [63] ***Second antennae in larvae or embryonised larvae: number of setae on exopod*: (0)** many; **(1)** seven; **(2)** five.

**74.** [64] ***Second antennae in larvae: segmentation of exopod*: (0)** segments of same size or gradually getting smaller distally; **(1)** one or two small segments proximally, followed by larger segment, again followed by three setae-bearing segments.

**75.** [54] ***Mandibular palp in larvae or embryonised larvae*: (0)** present; **(1)** absent.

**76.** [new] ***Mandibles in larvae: segmentation of endopod*: (0)** three segments; **(1)** two segments.

*New character dealing with the segmentation of the mandibular endopod in larvae. This and the following character cover two aspects of the very similar larval mandibles in all branchiopod larvae with the exception of* Rehbachiella *(and the modified* Leptodora*) (see Olesen 2004, 2007).*

**77.** [new] ***Mandibles in larvae: exopod*: (0)** present; **(1)** absent.

*New character dealing with the absence/presence of the exopod in branchiopod larvae. In* Rehbachiella *the larval mandible has an exopod, but in all other branchiopod larvae it is lacking (unclear for larval* Leptodora*).*

**78.** [65] ***Mandibular palp: setation of endopod segment 1*: (0)** more than two setae; **(1)** two setae; **(2)** one seta.

*Two fossils with preserved larvae have been included:* Rehbachiella*, which has more than two setae on endopod segment 1 of the mandible, and* Lepidocaris*, which has two setae.*

**79.** [new] ***Trunk limbs development*: (0)** tip of early limb bud points ventrally; **(1)** tip of early limb bud points laterally.

*This character was not included in* Richter et al. *(2007) but has been discussed by* Olesen *(1999, 2004,* *2007). In all Recent branchiopods the trunk limbs start their development as large, elongate limb buds with the tips of the future endopods and exopods pointing laterally and the future endites facing the ventrally. During development the limbs 'bend' to a vertical orientation. In* Rehbachiella *and* Lepidocaris *in contrast, the trunk limbs start as bifid limb buds with tips of the future endopod and exopod pointing laterally already from the onset.*

**80.** [new] ***Carapace development*****: (0)** Develops as a simple posterior extension of the naupliar shield; **(1)** Early development of carapace behind the head, often as paired anlagen.

*This is a new character dealing with a specific similarity in the way the carapace develops in Notostraca and Diplostraca. The carapace starts its development behind the head and separate from it, often as paired anlagen. Sometimes the carapace later overgrows the head as in* Cyclestheria *(Olesen 1999). This is what Walossek (1993) termed a 'secondary shield'. See discussion in Richter et al. (2007: character 3).*

## 5. Discussion

### 5.1. Monophyly of Branchiopoda and phylogenetic position of the Devonian *Lepidocaris* and the Cambrian *Rehbachiella*

The monophyly of Branchiopoda has rarely been questioned in recent taxonomic literature and has been supported by several recent molecular works (e.g., Regier et al. 2005; Giribet et al. 2005). The morphological support is relatively strong (see Tab. 3 for clade apomorphies). One set of characters include similarities in the naupliar feeding apparatus of the larvae (characters 62, 66, 69, 76, 77; Fig. 12). For example, the second antennae and mandibles in the larvae of 'large branchiopods' such as anostracans, notostracans, spinicaudatans, and laevicaudatans, and also larvae of the Devonian fossil *Lepidocaris* share characteristics not found in the same way in larvae of other crustaceans (e.g., Olesen 2004, 2005, 2007; Olesen & Grygier 2003, 2004; Møller et al. 2003, 2004). Larvae have become embryonised in most cladocerans and in *Cyclestheria* (Fig. 13), and the feeding structures therefore reduced, but this has happened secondarily within Branchiopoda and does not affect the interpretation of certain larval characters as branchiopod synapomorphies. Another important branchiopod character is a special morphology of the trunk limbs. In all 'large branchiopods' these are composed of a large flattened corm with 5–6 median endites and a reduced, unsegmented endopod (characters 24, 27; Fig. 9A–C; Olesen 2007). The precise homologies of this type of limb with those of other crustaceans are still being debated (Ferrari & Grygier 2003; Olesen 2007; Pabst & Scholtz 2009), but this does not influence the status of at least the unsegmented endopod as a branchiopod synapomorphy. The optimisation of the number of endites is more uncertain, but it is suggested that the presence of six endites is a branchiopod synapomorphy.

Among the classical branchiopod characters is the reduced, gnathobasic nature of the first and second maxillae (e.g., Cannon & Leak 1933; Fig. 8A,C,D). The reduced second maxillae hold as a branchiopod synapormorphy (character 17), while the situation for the first maxillae is more uncertain. In the uniquely preserved Devonian *Lepidocaris*, which is here treated as sister group to the recent Anostraca and therefore an ingroup branchiopod, males have a pair of large clasper-like first maxillae. It is uncertain whether the large size of the male maxillae 1 in *Lepidocaris* is an ingroup branchiopod specialisation, or whether the large size has been retained from a pre-branchiopod condition. Since females of *Lepidocaris* have reduced maxillae 1, it is assumed that reduced maxillae 1 in at least females is a branchiopod synapomorphy. Yet another branchiopod synapomorphy is in the morphology of the gnathal edge of the adult mandible (character 14; Fig. 8A–C). Richter (2004) showed that the gnathal edge of the majority of branchiopods consists of a large, ellipsoid molar process with no incisor, and suggested this morphology to be a branchiopod synapormorphy.

Some characters which potentially are branchiopod synapomorphies are difficult to optimise on the tree with certainty due to much variation within Branchiopoda. This applies, for example, to the number of trunk limbs (character 18). I tentatively suggest that the original number for branchiopods were 11 (but equally parsimonious optimisations are possible). Such a number is present in both *Lepidocaris* and Anostraca, not counting the modified 12th and 13th limb pairs, which have given rise to the ventral brood pouch. The same number is found in *Almatium* (Kazacharthra) and in the anterior limbs series in both Notostraca and the possible stem-lineage notostracan *Castracollis* (both have an additional posterior limb series, see character 19). Returning to larval morphology, Sanders (1963) mentioned distally placed setae on the endopod of the antennae in branchiopods as being one of the characters separating branchiopod larvae from other crustacean larvae (character 68; Fig. 12A). However, this pattern is not shared by the larvae of *Lepidocaris*, which has setae along the side of the segmented antennal endopod. Hence, if *Lepidocaris*, because of

**Tab. 3.** List of synapomorphies for selected tree (Fig. 14).

| **Taxa** | **Synapomorphies** |
|---|---|
| Branchiopoda (s.str.) | 14 Mandible gnathal edge consists of large ellipsoid molar process<br>16 Maxilla 1 reduced to coxa only (in females only)<br>17 Maxilla 2 reduced to coxa only<br>18 11 pairs of trunk limbs<br>24 Six endites on trunk limbs<br>27 Trunk limbs with unsegmented endopod<br>62 Setae/sensilla of first antennae in larvae confined to tip<br>66 Second antennae protopod more than half total length of limb<br>69 Second antennae masticatory process divided in two branches after a few molts<br>76 Mandible in larvae composed four segments: coxa, basis and two endopod segments<br>77 Mandible in larvae lacking exopod |
| Anostraca + Lipostraca (= Sarsostraca) | 3 Carapace absent<br>15 Mandible (left) molar surface with row of teeth along edge<br>56 Ventral brood pouch |
| Phyllopoda | 11 Second antennae rami of same length (‘symmetrical’)<br>24 Trunk limbs with 5 endites<br>37 Pair of telsonal setae<br>42 Compound eyes internalized<br>48 Nauplius eye with four ocelli<br>53 Oogenesis: groups with four cells (oocyte and three nurse cells)<br>73 Second antennae in larvae with endopod divided in two clear segments<br>79 Trunk limbs with tips pointing laterally during early development<br>80 Early development of carapace behind the head and separate from it, often as paired anlagen (‘secondary shield’) |
| Notostraca + Kazacharthra | 4 Carapace as flattened dorsal shield<br>11 Second antennae uniramous and unsegmented<br>14 Mandible gnathal edge with row of large separate teeth<br>24 Anterior trunk limb endites 4 and 5 elongate<br>29 Trunk limbs subdivided in sclerotisized portions<br>56 Eggs/embryos on 11th pairs of limbs encapsulated between a sub-apical lobe (Notostraca) and exopod or ‘in exopod’ (Kazacharthra) |
| *Castracollis* + Notostraca + Kazacharthra | 19 Trunk limbs in two series (11 in anterior series)<br>20 Anterior trunk limbs directed laterally<br>34 Many narrow somites with serrate denticles along posterior margin |
| Diplostraca | 1 All trunk segments with limbs<br>4 Carapace covers limbs and head<br>28 Trunk limbs with long dorsal extension of exopod<br>30 First pair of trunk limbs as claspers<br>56 Eggs/embryos carried between carapace and trunk<br>57 Eggs/embryos supported by or attached to exopods<br>70 Second antennae in larvae with extra, small basipodal segment<br>71 Second antennae in larvae with setae on anterior branch of masticatory process arranged comb-like |
| Spinicaudata + Cladoceromorpha | 5 Carapace with growth lines<br>21 Trunk limbs used for feeding only (not locomotion)<br>36 Telson laterally compressed<br>38 Telson dorsally with spines arranged in two rows<br>40 Furcae curved and claw-like<br>43 Ommatidial part of compound eyes fused to a globular organ<br>47 Ommatidia of compound eyes pentapartite<br>52 Heart with four pairs of ostia<br>55 Spermatid maturation of luminal type<br>63 First antennae in larvae/embryos as small buds |
| Spinicaudata | 31 Second pair of trunk limbs as claspers<br>65 First antennae in larvae with characteristic large seta |
| Cyclestherida + Cladocera (= Cladoceromorpha) | 10 First antennae sensilla restricted to tip<br>58 Alternation between parthenogenetic and sexual reproduction (heterogony)<br>60 Subitaneous eggs with direct development |
| Cladocera | 4 Carapace covers limbs but head is free<br>6 Female genital system opens dorsally within carapace<br>12 Adult second antennae with four segments in exopods<br>13 Adult second antennae with four segments in endopods<br>18 Six pairs of trunk limbs<br>28 Dorsal extension of trunk limb exopods lost<br>52 Heart with one pair of ostia<br>57 Embryos under carapace with no connection to exopods |
| Onychopoda + Haplopoda (= Gymnomera) | 1 Posterior trunk segments without limbs (abdomen)<br>2 Food groove absent<br>4 Carapace as dorsal brood pouch<br>22 Trunk limbs stenopodous with four/five segments (in main axis if limb biramous)<br>23 Trunk limb epipod absent<br>36 Telson cylindrical in cross section<br>38 Telson without dorsal spine rows<br>39 Furcae not articulated to telson |

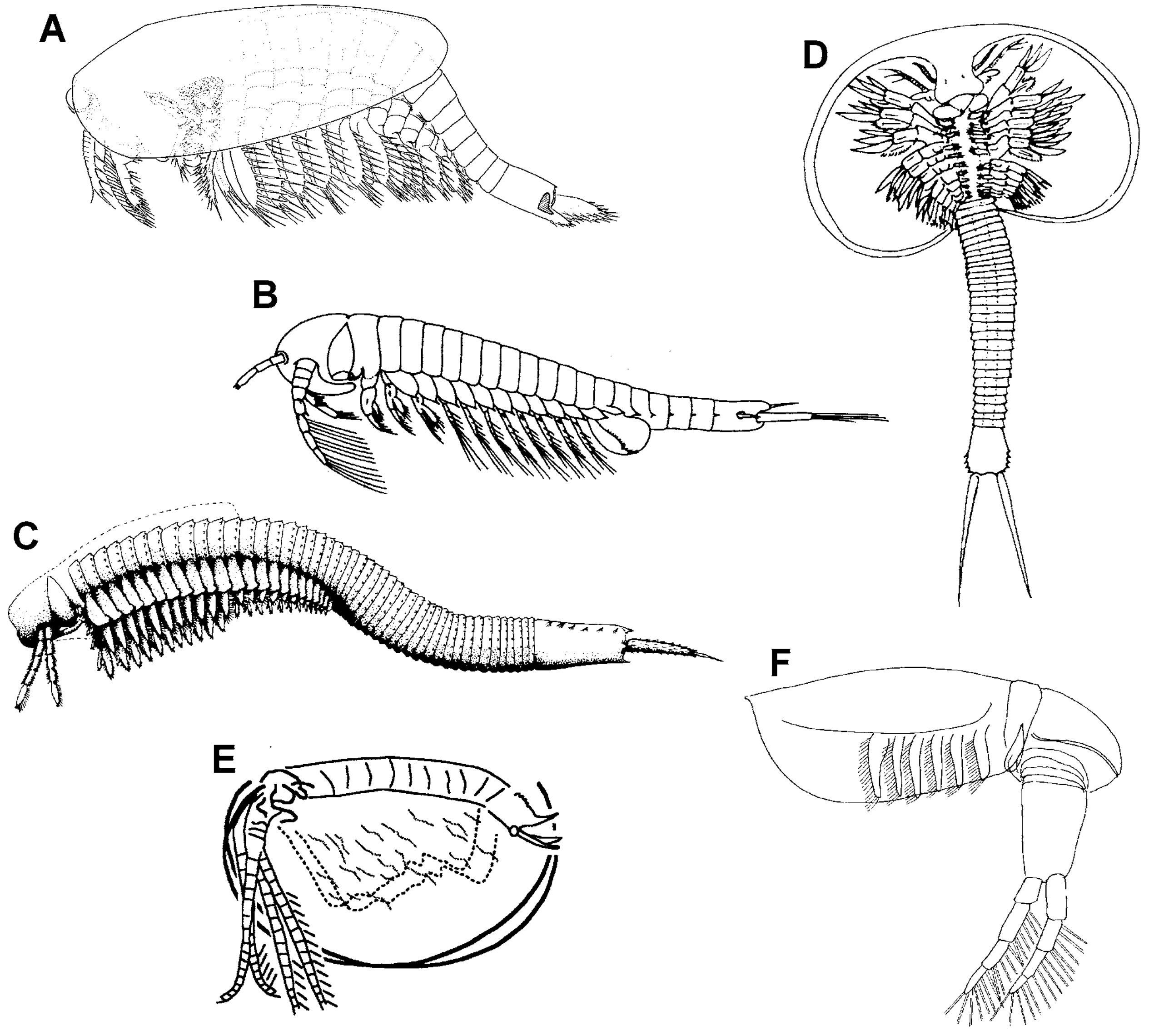


**Fig. 1.** Well-preserved branchiopod fossils included in the phylogenetic analysis. **A**: *Rehbachiella kinnekullensis* Müller, 1983, a Cambrian early branchiopod used as outgroup. From Walossek & Müller (1992). **B**: *Lepidocaris rhyniensis* Scourfield, 1926 (Lipostraca), a Devonian branchiopod with anostracan affinities. From Scourfield (1926). **C**: *Castracollis wilsonae* Fayers & Trewin, 2003, a Devonian branchiopod with affinities to Notostraca (or Diplostraca). From Fayers & Trewin (2003). **D**: *Almatium gusevi* (Chernyshev, 1940) (Kazacharthra), a Triassic branchiopod with affinities to Notostraca. From Walossek (1993), who based the reconstruction on McKenzie et al. (1991). In the meantime McKenzie & Chen (1999) have found that the second antennae are small and uniramous, and not asymmetrically biramous as in this reconstruction. **E**: *Limnestheria ardra* Wright, 1920, a Carboniferous Spinicaudata. The illustration is a schematic drawing from Orr & Briggs (1999). **F**: *Leptodorosida zherikhini* Kotov, 2007 (Cryptopoda), a Jurassic cladoceran with no unambiguous affinities to any of the other four cladoceran orders. From Kotov (2007).

other characters, is viewed as the sister group of the Recent Anostraca, then probably the distal condensation of setae at the antennal endopod is convergent in anostracan larvae and other Recent branchiopod larvae. Another potential branchiopod synapomorphy is the laterally pointing early limb buds seen in larvae and embryos of all Recent branchiopods (character 79; Olesen 2004, 2007) (Fig. 12A,C,F), but again here, if *Lepidocaris* is sister group to Anostraca, there is a character conflict. Scourfield (1940) showed clear illustrations of larvae of *Lepidocaris* with bifid limb buds (endopod/exopod) pointing ventrally, largely similar to the trunk limb development in *Rehbachiella* and a number of other Crustacea. Hence, the laterally directed limb buds seen in Recent Anostraca and Phyllopoda may be convergent.

The characters supporting *Lepidocaris* as sister group to Anostraca are: the shared possession of a ventral brood pouch associated apparently with trunk segments 12 and 13 in both taxa (*Lepidocaris* needs restudy with respect to somite numbers) (character 56), the absent carapace (character 3), but also what apparently is a specific similarity in the surface structure of the gnathal edge of the mandible (character 15 and Fig.

8D: row of small, distinct cusps). It should be noted, however, that the fact that the oldest known stage of *Rehbachiella* (outgroup) is premature, leaves som uncertainty with respect to precise optimisation of a character like 'brood pouch'. Conflicting with these characters are some characters which in some trees result in *Lepidocaris* as sister group to the remaining branchiopods, as suggested by Schram & Koenemann (2001). These characters are the reduced maxilla 1 in Recent branchiopods (not reduced in males of *Lepidocaris*) (character 16), the distal setation of the larval antennal endopod (also lateral setation in *Lepidocaris*) (character 68), and the laterally directed early limb buds (directed ventrally in *Lepidocaris*) (character 79).

Another well-preserved fossil with similarities to Branchiopoda is *Rehbachiella kinnekullensis* Müller, 1983, from the Swedish 'Orsten' fauna from the Cambrian (Fig. 1A). Walossek (1993) convincingly argued that *Rehbachiella* is a branchiopod and placed it in the anostracan stem lineage. However, *Rehbachiella* shares none of the branchiopod synapomorphies mentioned above, so it may be better placed in the branchiopod stem lineage, accepting the similarities between *Rehbachiella* and other branchiopods put forward by Walossek (1993) (food groove and complexity of filtratory apparatus). In the present work *Rehbachiella* has served as an ideal outgroup. With its many general similarities to other branchiopods, character homologies are mostly straightforward to establish. On an evolutionary scale it is quite simple to 'derive' the morphology of Branchiopoda from that of *Rehbachiella*, but this does not necessarily mean that they are sister groups. This should be tested in a larger-scaled morphological analysis including more crustacean or even arthropod taxa. Recent molecular works have suggested that the closest Recent relatives to branchiopods perhaps should be found among noncrustacean arthropods (Hexapoda; Regier et al. 2005; Glenner et al. 2007).

## 5.2. The Devonian *Castracollis wilsonae* belongs to Phyllopoda and is probably a stem-lineage Notostraca

Before considering the phylogenetic position of *Castracollis wilsonae*, it is useful to treat Phyllopoda, a high-level taxon including all branchiopods exept Anostraca and *Lepidocaris*. Phyllopoda has found strong support in the present phylogeny based on a number of clear-cut synapomorphies: a pair of telsonal setae (character 37; Fig. 3), internalised compound eyes (character 42), nauplius eye with four ocelli (character 48), and an oogenesis with characteristic groups of four cells (oocyte and three nurse cells; character 53). Another likely synapomorphy is the presence of only five median endites of the trunk limbs in contrast to six in Anostraca and *Lepidocaris* (character 24). The trunk limbs have five endites in all the 'large' branchiopods, including the fossil taxa Kazacharthra and *Castracollis*. Endites are reduced in number or entirely absent in Cladocera. It should be mentioned that since the outgroup, *Rehbachiella*, has another (larger) number of endites, it is equally parsimonious to treat the number of five endites as being present already at the Branchiopoda level, and the number of six endites being a synapomorphy for Anostraca and *Lepidocaris*. However, this character is preferredly optimised with the number of six endites being ancestral (and synapomorph) for Branchiopoda and the number five being a synapomorphy for Phyllopoda. Another likely synapomorphy of Phyllopoda is the presence of biramous swimming (second) antennae with symmetrical rami in adults (endopod and exopod similar) (character 11; Fig. 7). Such a morphology is very characteristic for all taxa of Diplostraca (including Cladocera), but is also present in the Devonian *Castracollis*. Since *Castracollis* is placed as a stem-lineage notostracan, it follows that a symmetrical biramous condition of the second antennae was present already in the ancestor of Phyllopoda, further modified in Notostraca and Kazacharthra (see below). The outgroup, *Rehbachiella*, has the for Crustacea typical second antennal arrangement of a long, annulated exopod and a smaller endopod with only a few segments. Since *Lepidocaris* – in this analysis placed as a stem-lineage anostracan – also has an asymmetrical condition of the antennal rami, but less distinct than in *Rehbachiella*, it follows that such were present in both the branchiopod and the anostracan ancestors, only later modified to a symmetrical condition in the phyllopod ancestor. Evidently, the phylogenetic positions of both *Lepidocaris* and *Castracollis* plays a major role for the precise optimisation of this character. If *Lepidocaris* is actually a stem-lineage branchiopod, the symmetrical biramous condition of the second antennae could be a branchiopod character, including also Anostraca which have strongly modified second antennae. Or if *Castracollis* rather is a stem-lineage diplostracan (for which arguments can be raised, see below), then the symmetrical biramous condition could be a later evolutionary phenomenon, common only to *Castracollis* and Diplostraca. However, based on the preferred phylogeny, a symmetrical, biramous condition of the second antennae maps as a synapomorphy of Phyllopoda. Some other synapomorphies of Phyllopoda are less clear-cut. For example, if *Lepidocaris* indeed is a stem-lineage anostracan, it follows that the laterally directed early limb buds seen in both anostracan larvae and all other Recent branchiopods have appeared convergently in Anostraca and Phyllopoda, since *Lepidocaris* has the ancestral condition with ventrally di-

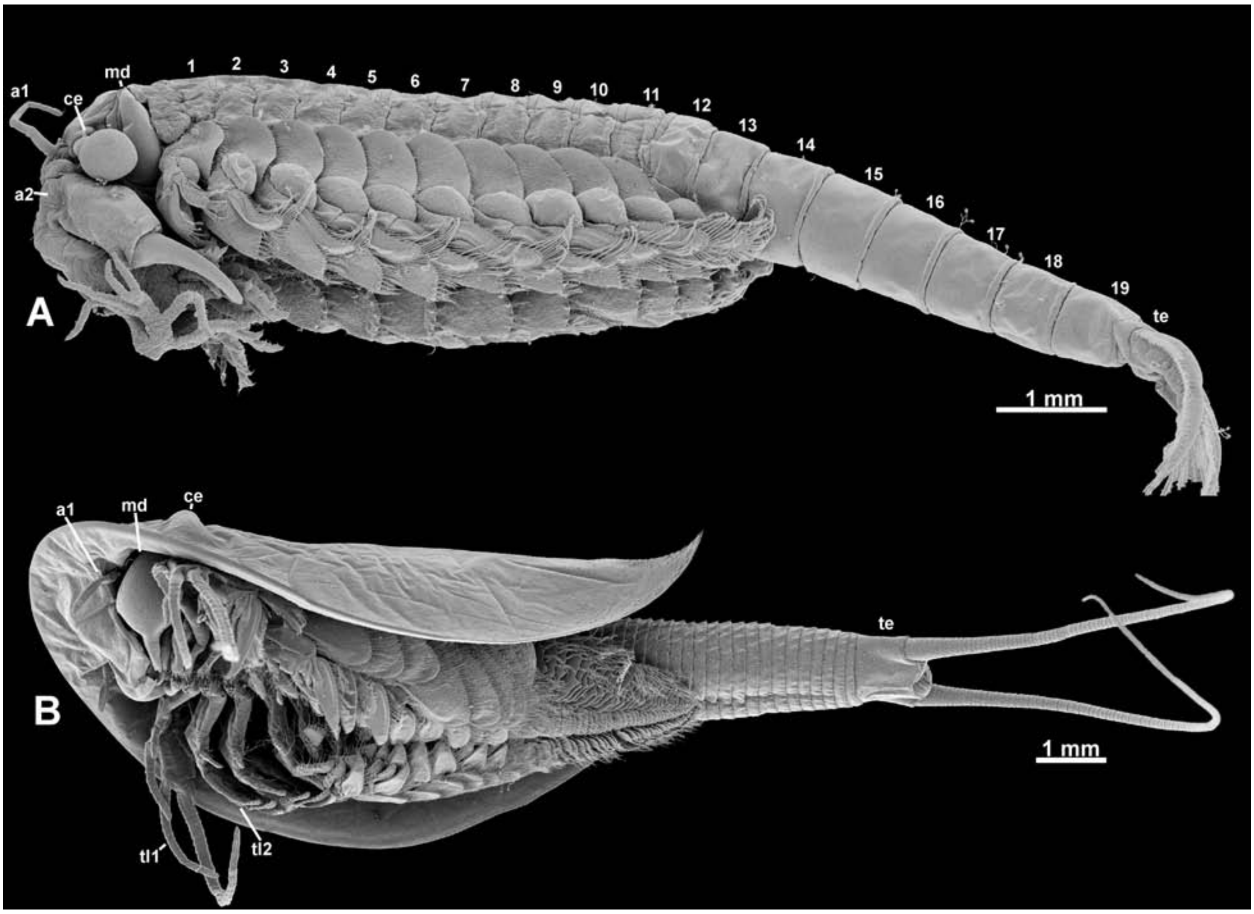


**Fig. 2.** Anostraca and Notostraca, overview illustrations. **A**: *Branchinella* sp. (Anostraca). **B**: *Triops australiensis* (Notostraca). Abbreviations: a1 = antenna 1; a2 = antenna 2; ce = compound eye; md = mandible; tl1–2 = trunk limbs 1–2; te = telson; arabic number 1–19 = somite number.

rected, bifid early limb buds as found in the outgroup *Rehbachiella* and in many other Crustacea. Another potential synapomorphy for Phyllopoda is the development of the carapace. Walossek (1993) suggested that a dorsal 'disconnection' between the head region and carapace anlage in the trunk region seen in various diplostracans (termed 'secondary shield') could qualify as a synapomorphy. As such a 'disconnection' certainly is present in many taxa, it has been included as a character here, but since it has been found that a similar condition is present during early development of *Triops cancriformis* (Notostraca; Møller et al. 2003), the character maps as a Phyllopoda synapomorphy. All in all, Phyllopoda is one of the morphologically best supported higher-level categories within the Branchiopoda.

The discovery of *Castracollis wilsoni* only a few years ago (Fayers & Trewin 2003) was of major importance for the understanding of early branchiopod evolution. Until then we had only *Lepidocaris rhyniensis* of likely anostracan affinity as an early experiment of the branchiopod design, but having now an entirely different variation represented by *Castracollis*, tells us that there probably has been many such early experiments. *Castracollis* is of exceptional interest because its morphology provides a link between the notostracan and diplostracan design. In some ways it looks like a notostracan, but in other ways it looks like a diplostracan. In all equally parsimonious trees in this analysis *Castracollis wilsonae* appears as a stem-lineage notostracan as sister group to Kazacharthra and Notostraca, which were collectively termed Calmanostraca by Tasch (1969). The monophyly of this clade (*Castracollis* plus Calmanostraca) is based on at least three synapomorphies. One synapomorphy is the subdivision of the trunk limbs into two series with 11 limb pairs in the anterior series (character 19), as seen in both *Castracollis* and Notostraca. Evidence for *Almatium gusevi* (Kazacharthra) is ambigous since in McKenzie & Chen (1999) the text mentions 11 trunk limbs but one figure (fig. 32.12) shows some additional gnathobase-like structures which possibly are small abdominal limbs, so the trunk limb series in *Almatium* may also have been subdivided in two series. Another synapormorphy for *Castracollis* and Calmanostraca is the laterally directed, non-filtratory anterior trunk limbs (character 20). This is well-known for Notostraca and is associated with the feeding mode (e.g.,

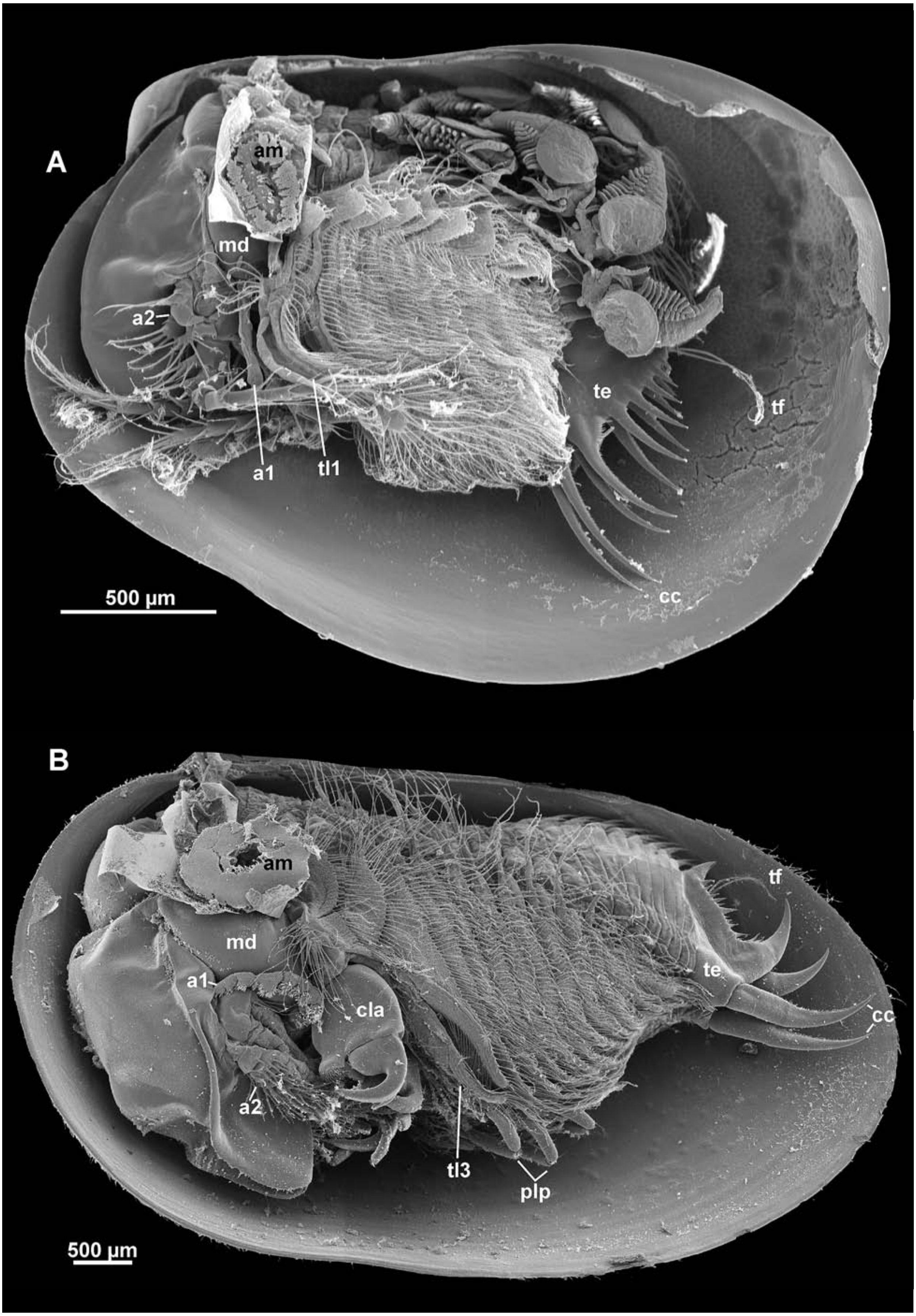


**Fig. 3.** Cyclestherida and Spinicaudata, overview illustrations. **A**: *Cyclestheria hislopi* (Cyclestherida), female. **B**: *Caenestheria* sp. (Spinicaudata, Cyzicidae), male. Abbreviations: a1 = antenna 1; a2 = antenna 2; am = adductor muscle; cc = caudal claw; cla = clasper; md = mandible; plp = palp of fifth endite; te = telson; tf = telson filament; tl1 = trunk limb 1; tl3 = trunk limb 3.

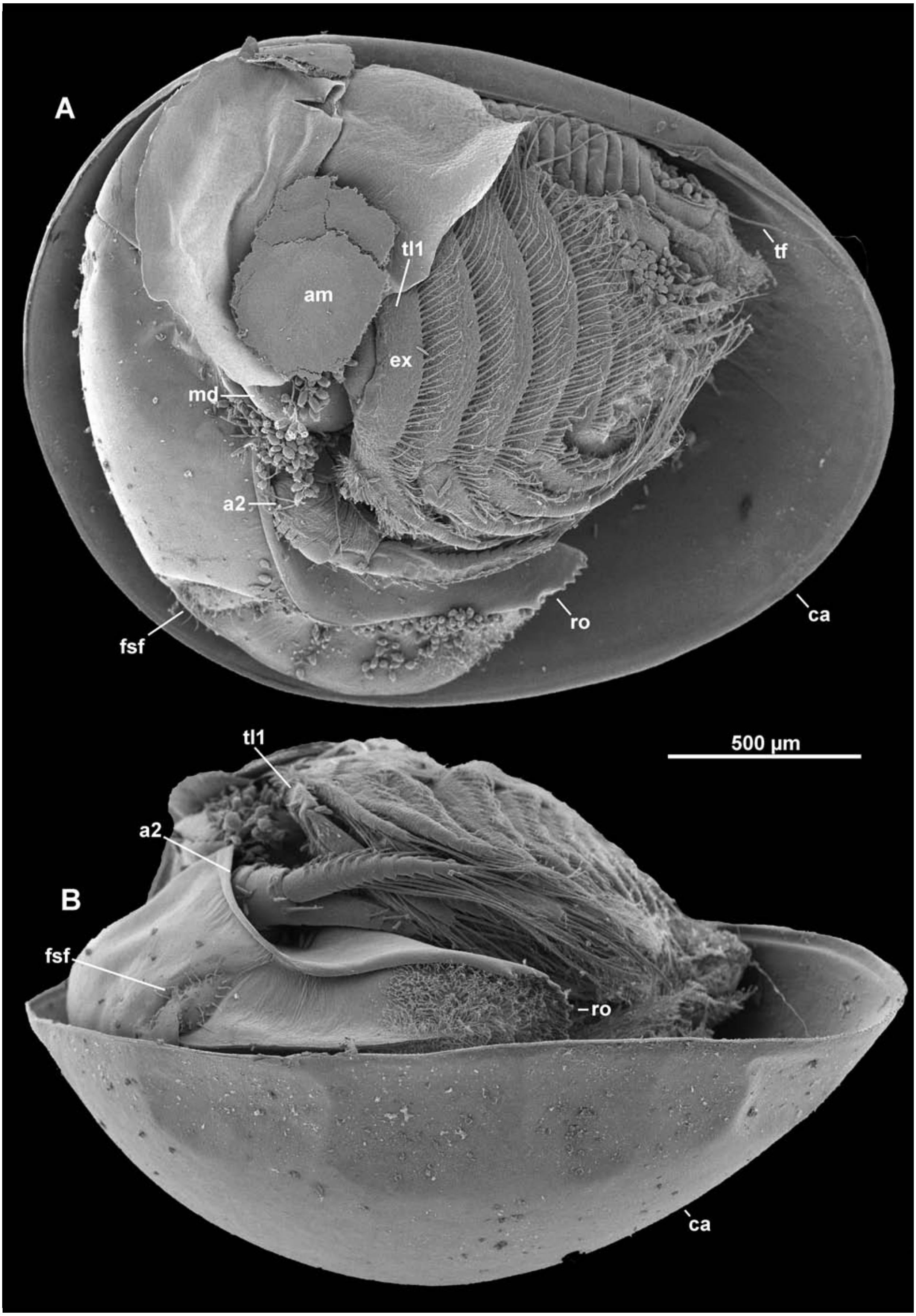


**Fig. 4.** Laevicaudata, overview illustrations. **A**: *Lynceus tatei*, female, lateral view. **B**: *Lynceus tatei*, female, frontal view. Abbreviations: a2 = antenna 2; am = adductor muscle; ca = carapace; ex = exopod; fsf = frontal sensory field; ro = rostrum; tf = telson filament; tl1 = trunk limb 1.

Fryer 1988; Walossek 1993). In *Almatium* (Kazacharthra) the trunk limbs are arranged in a way very similar to Notostraca, and something like it seems to be present in *Castracollis*. Yet another synapomorphy for this clade is the high number of narrow abdominal somites with serrate denticles along the posterior margin (character 34). In contrast to Fayers & Trewin (2003) and Olesen (2007), it is here preferred to restrict the term Calmanostraca to include only Kazacharthra and Notostraca as it was originally used by Tasch (1969). This favours nomenclatural stability since Calmanostraca in the original sense most certainly is monophyletic (see below), while there is still room for discussion of the phylogenetic position of *Castracollis*.

Conflicting with the notostracan affinity, a number of characters suggest *Castracollis* as sister group to Diplostraca. One character is the symmetrically biramous swimming antennae (character 11), which above were optimised as a Phyllopoda synapomorphy, since other characters link *Castracollis* to Notostraca and Kazacharthra. Another character shared with Diplostraca is the two rows of short spines on the telson in *Castracollis*, which can be argued to be homologous with the dorsal spine rows on the otherwise different telson of diplostracan taxa such as Spinicaudata, Cyclestherida, and some cladocerans (character 38; Fig. 11D–F). A third striking similarity between *Castracollis* and certain diplostracans are the sausage-like palps on the endites of the trunk limbs of *Castracollis*. These palps, which are on all endites, resemble strikingly the well-known palps of the fifth endite of certain spinicaudatan trunk limbs (character 26). On the presented phylogeny (Fig. 14) this character optimises as convergent, but this is not convincing. It is more likely to be a symplesiomorphy, but the details are yet uncertain. It should also be mentioned here that molecular data suggest a position of Notostraca, and thereby *Castracollis* and Kazacharthra, within Diplostraca (Stenderup et al. 2006). This may eventually bring the palp-bearing *Castracollis* and Spinicaudata ‘closer to each other’, and thereby make a homology between the trunk limb palps more parsimonious.

## 5.3. Kazacharthra – close relatives of Notostraca

The Kazacharthra has long been considered closely related to Notostraca (e.g., McKenzie et al. 1991; Walossek 1993; McKenzie & Chen 1999) and the taxa were united in Calmanostraca by Tasch (1969), but it has been difficult to scrutinise the detailed arguments in favour of this idea because of lack of detailed morphological information about the taxon Kazacharthra. However, in the last couple of decades one species has become known in considerable detail, and a meaningful comparison with Notostraca and other branchiopods can therefore be made. *Almatium gusevi* was redescribed by McKenzie et al. (1991), a description later corrected and supplemented by McKenzie & Chen (1999). First of all, based on this description, it is clear that *Almatium* is a branchiopod. It has typical branchiopod trunk limbs with a row of median endites (five) and an unsegmented endopod (characters 24, 27). Also the reduction of maxillae 1 and 2 to consist of gnathobases (or proximal endites) only, as well as the presence of a food groove document the branchiopod affinity of Kazacharthra. Within Branchiopoda several characters suggest a phyllopodan affinity of Kazacharthra. One is the presence of a pair of ‘circular ducts’ dorsally on the telson in both *Almatium gusevi* (see McKenzie & Chen 1999) and *Panacanthocaris* (see Novojilov 1959). As McKenzie & Chen (1999) remark for *Almatium gusevi*, they are probably homologous to similar structures in Notostraca. However, in Notostraca, these structures are actually not ‘ducts’ but rather a pair of telsonal setae, treated by several authors (e.g., Martin & Cash-Clark 1995; Olesen 2007; Richter et al. 2007) as homologous to a pair of telsonal setae (= post-abdominal setae) in Spinicaudata, Laevicaudata, Cyclestherida, and Cladocera, and therefore as a phyllopodan synapomorphy (character 37). Probably the paired dorsal ‘ducts’ on the telson of *Almatium* (Kazacharthra) are small depressions each with a seta as in Notostraca. Another Phyllopoda character is the internalised eyes connected to the environment via a duct (character 42). A pair of slits ventrally on the head of *Almatium gusevi* are presumed to be the external openings of a pair of internalised eyes (McKenzie & Chen 1999). Another character, here interpreted as a phyllopodan synapomorphy, is the presence of only five median endites at the trunk limbs (but equally parsimonious optimisations are available, character 24).

Within Phyllopoda, Kazacharthra convincingly finds its place as sister group to Notostraca (combined in Calmanostraca) based on a number of detailed synapomorphies. There has been some uncertainty regarding the precise morphology of trunk limbs of Kazacharthra, but for *Almatium gusevi* this appears largely clarified by McKenzie & Chen (1999), who recognised the trunk limbs as very similar to those of *Triops* (Notostraca). When comparing limbs of Notostraca and Kazacharthra one needs to consider that the trunk limbs in Notostraca have a different morphology along the limb series (e.g., Fryer 1988), while the 11 anterior limbs in Kazacharthra appear to have been uniform (McKenzie & Chen 1999). Kazachathran trunk limbs are most similar to the limbs of Notostraca immediately after the first pair of limbs. These notostracan limbs have slender endites and a slender endopod, which are articulated to the limb stem, and have

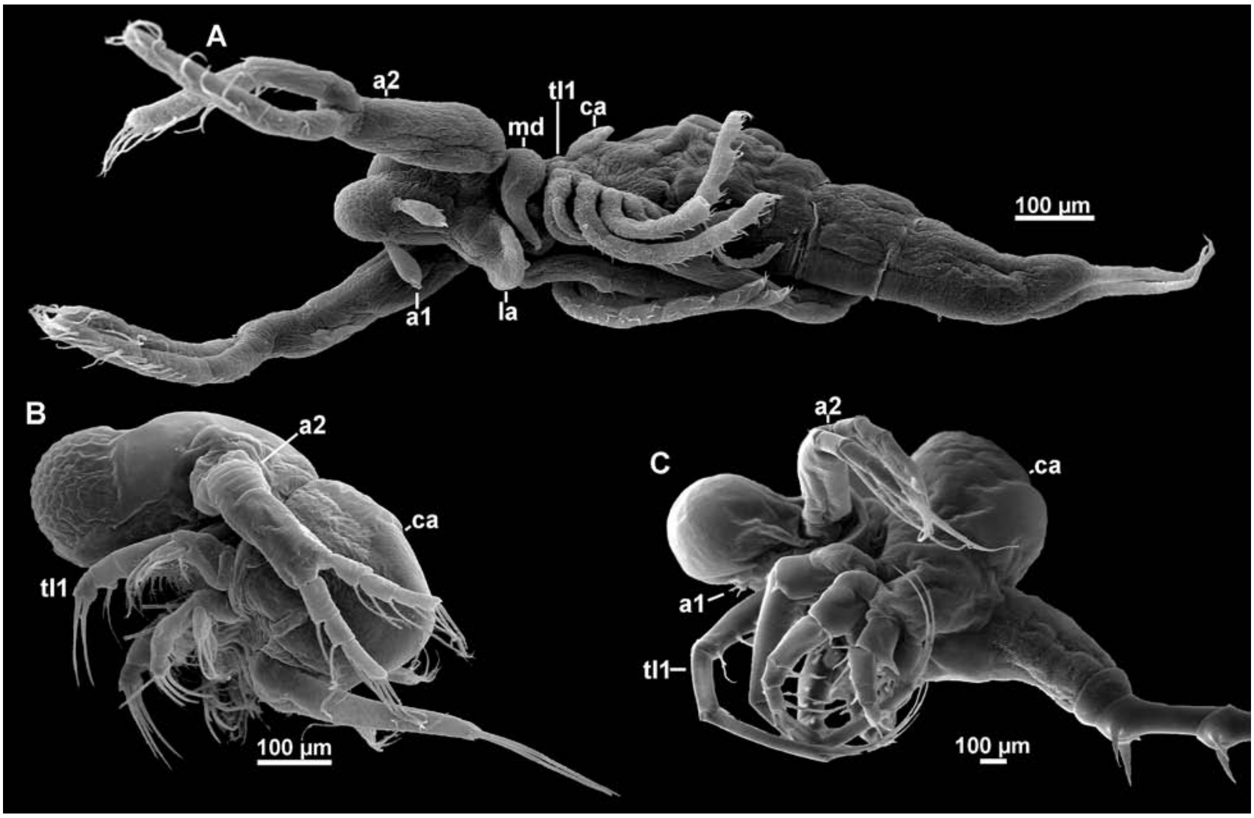


**Fig. 5.** Gymnomera (Haplopoda and Onychopoda), overview illustrations. **A**: *Leptodora kindtii* (Haplopoda). **B**: *Polyphemus pediculus* (Onychopoda). **C**: *Bythotrephes longimanus*. Abbreviations: a1 = antenna 1; a2 = antenna 2; ca = carapace; la = labrum; md = mandible; tl1 = trunk limb 1.

a general shape and size similar to the corresponding limb parts in Kazacharthra. In contrast, the first pair of trunk limbs in most Notostraca (except *Lepidurus batesoni*, see Longhurst 1955) has long, flagelliform endites, probably substituting the smaller antennae 1 and 2 as feelers, and a reduced endopod, in general being quite different from the following limbs and from the limbs of Kazacharthra. The similarities between notostracan and kazacharthran trunk limbs have been expressed in two characters (25 and 29), one dealing with the similar sclerotisation pattern of the limbs, and one dealing with the similar general morphology of the endites and the endopod. In *Lepidurus arcticus*, illustrated in detail by Sars (1896), the stem of the anterior trunk limbs is subdivided in at least two major parts. Hansen (1925) even illustrated the anterior trunk limbs of *Lepidurus* as being subdived in 4–5 more rigid portions. Based on Novojilov (1959), who illustrated a generalised trunk limb of Kazacharthra, and on McKenzie & Chen (1999), this appears very similar to Kazacharthra. While the precise sclerotisation pattern of the proximal part of the limb stem in Kazacharthra is uncertain in the reconstructions presented by Novojilov (1959) and McKenzie & Chen (1999), the distal part clearly consists of a rather long and distinct part carrying endites 4 and 5 and the endopod distally, exactly as in Notostraca (character 29). No such sclerotisation pattern is present in other branchiopods and it is therefore a new development within Branchiopoda, here interpreted as a synapomorphy for Kazacharthra and Notostraca. A related synapomophy is the elongate morphology of the endites and endopod (Character 25).

An additional distinct similarity between Kazacharthra and Notostraca is the morphology of the second antennae (character 11). A comparison with the outgroup (*Rehbachiella*) and other Crustacea (e.g., Cephalocarida) suggests that the adult branchiopod second antennae, used mainly for swimming, originally was composed of a stem divided in a coxa and basis with two rami: a long flagelliform, annulated exopod, and a shorter endopod. Several taxa have retained the second antennae as swimming appendages in adults, including *Lepidocaris*, which still has asymmetrical rami (exopod longer than endopod), and *Castracollis* and Diplostraca, where the two rami have attained an identical morphology ('symmetrical' rami, synapomorphy of Phyllopoda, see above). Anostracans are well-known to have modified second antennae in adults. Also Kazacharthra and Notostraca have modified second antennae, and apparently in a similar way (character 11). In Notostraca, for example *Lepidurus arcticus* (illustrated by Sars 1896), the second antennae are small and uniramous. This is also the case in *Almatium* (Kazacharthra), at least according to McKenzie & Chen (1999), who, based on better material, modified earlier statements concerning second antennae morphology by McKenzie et al. (1991). Another synapomorphy seems to be available in the mandible morphology. The gnathal edge of the mandible in Notostraca is composed of a row of large teeth (e.g., Richter 2004), which are very similar to those seen in *Almatium* (Kazacharthra), at least based on the description provided by McKenzie et al. (1991) (character 14). Also the flattened, dorsal carapace is a likely synapomorphy for Notostraca and Kazacharthra (character 4), but this is uncertain since the carapace structure in *Castracollis*, the closest relative to the Kazacharthra/Notostraca clade, is unknown (even uncertain whether a carapace was present in *Castracollis*). Yet another synapomorphy between Kazacharthra and Notostraca is a detailed similarity in the way the eggs are encapsulated in parts of the 11th pairs of trunk limbs. McKenzie & Chen (1999) reported for *Almatium* (Kazacharthra) that 'the 11th limbs bore the egg masses in modified exopods', but unfortunately provided no illustrations. This sounds very similar to the situation in Notostraca, where the eggs are born between a sub-apical lobe of the limbs and the exopods of the 11th limbs (Fryer 1988). All in all, the sister group relationship between Kazacharthra and Notostraca is very well-supported.

## 5.4. Monophyly of Diplostraca? Conflict between morphology and molecules

The monophyly of Diplostraca (Laevicaudata, Spinicaudata, Cyclestherida, Cladoceromorpha) is rather strongly supported morphologically but not molecularly (see below). The morphological support is mentioned and discussed here. None of the mentioned characters supporting Diplostraca show up unmodified in all taxa, but in that respect Diplostraca is not different from many other high-level taxa. Many characters must be assumed lost or modified in Cladocera.

One character is the presence of limbs on all trunk segments (character 1). Such morphology is present in Laevicaudata, Spinicaudata, and Cyclestherida, which is in contrast to the plesiomorphic possession of a limbless abdomen in *Rehbachiella*, the Anostraca-lineage, and the Notostraca-lineage. Cladocerans are much reduced in this body region, but at least in Haplopoda and some onychopods, a limbless abdomen has reappeared.

Another synapomorphy is the presence of a large, bivalved carapace, capable of covering the whole body (character 4; Figs. 3, 4), but again this has been further modified in Cladocera. An uncertainty concerns how early at in the tree such a morphology of the carapace evolved. In Anostraca and *Lepidocaris* a carapace is absent and its presence in *Castracollis* is uncertain. In Notostraca and Kazacharthra the carapace has more the shape of a flattened, dorsal shield (Figs. 1D, 2B). Despite the preferred optimisation of a large, bivalved carapace as a Diplostraca synapomorphy, such a condition could have been ancestral to the Notostraca-lineage as well. This possibility is suggested by the presence of paired carapace *anlagen* in early larvae of *Triops* (Møller et al. 2003), which are similar to early carapace *anlagen* in spinicaudatans, where the paired structure represents the future two valves of the juvenile/adult bivalved carapace, and possibly also by the division of the dorsal shield in Notostraca into a left and right side, separated by a distinct dorsal keel. A number of synapomorphies are related to the trunk limbs. One is the rather long dorsal lobes of the exopods as seen in Laevicaudata, Spinicaudata, and Cyclestherida (character 28; Figs. 3, 4). As a consequence of the preferred phylogeny (Fig. 14), the lobes must be assumed lost in Cladocera. Notostracan limbs have in some cases also a dorsal exopodal lobe, but much smaller. A rather clear-cut synapomorphy of Diplostraca is the fact that eggs/embryos are carried dorsally/laterally between the trunk and the carapace valves (character 56). A related synapomorphy is the presence of dorsal exopodal prolongations of some trunk limbs specialised for supporting the eggs/embryos in Laevicaudata, Spinicaudata, and Cyclestherida (character 57); but, again, as a consequence of the phylogeny, these connections must be assumed lost in Cladocera, where embryos are situated dorsally between the carapace valves unsupported by the limbs.

One of the classical supporting characters for Diplostraca is the modification of the first pair of trunk limbs in males for clasping or holding the female during mating (character 30; Fig. 10). This character was used as support for Diplostraca already by Wingstrand (1978) and has since been discussed by various authors (e.g., Fryer 1987; Olesen et al. 1996). The similarities between the claspers in Laevicaudata, Spinicaudata, and Cyclestherida (= clam shrimps) are at first glance profound. All consist of largely the same parts: a large, swollen 'hand' on which inserts a 'movable finger' and two palps. At least some of these similarities are good arguments for a common ancestry of the claspers in all clam shrimps, but arguments have been raised for a non-homology of at least the clasper palps (see discussion by Fryer 1987; Olesen et al. 1996; Richter et al. 2007). The various hooks in Cladocera on the first pair of trunk limbs are most likely modifications of the clasper morphology seen in clam shrimps, but since homologies are difficult to establish, they have been scored as inapplicable in the matrix. A couple of similarities in larval morphology, such as an extra small

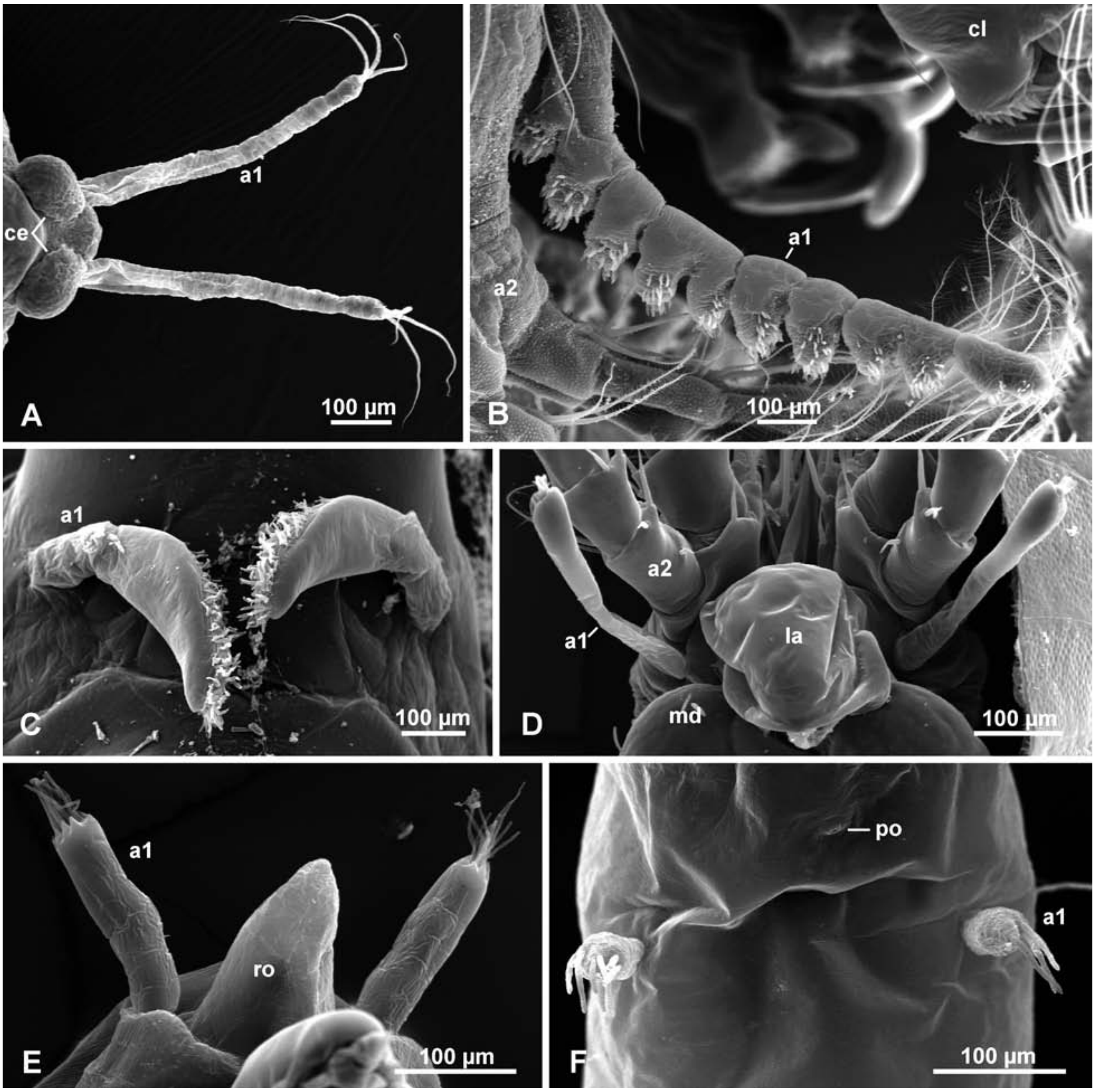


**Fig. 6.** Branchiopod first antennae (a1). **A**: *Eubranchipus grubii*, late juvenile, dorsal. **B**: *Caenestheria* sp. (Spinicaudata, Cyzicidae), left side a1. **C**: *Lynceus brachyurus* (Laevicaudata), ventral. **D**: *Cyclestheria hislopi* (Cyclestherida), ventral. **E**: *Sida crystallina* (Cladocera, Ctenopoda), ventral. **F**: *Leptodora kindtii* (Cladocera, Haplopoda). Abbreviations: a1 = antenna 1; a2 = antenna 2; ce = compound eye; cl = clasper of male; md = mandible; po = pore leading to compound eye; ro = rostrum.

basipodal segment of the second antennae (character 70), and a special, comb-like arrangement of the setae on the second antennae masticatory process (character 71) are present in Laevicaudata and Spinicaudata and therefore map as synapomorphies of Diplostraca.

Diplostraca is well-supported in the present analysis, similar to the result of a number of morphology-based works in the last years (Wingstrand 1978; Walossek 1993; Olesen 1998, 2000, 2002; Negrea et al. 1999; Richter et al. 2007). It is therefore surprising that Diplostraca finds virtually no molecular support but instead is paraphyletic with respect to Notostraca (see Stenderup et al. 2006; Richter et al. 2007). Mainly three positions of Notostraca have been suggested based on molecular data: (1) sister group to Laevicaudata; (2) sister group to Spinicaudata + Cyclestherida + Cladocera; (3) sister group to Cyclestherida + Cladocera. If any of these possibilities were to be preferred on morphological grounds, then probably (2) would be in least conflict with morphological data (Stenderup et al. 2006). If Notostraca eventually finds stronger support as an ingroup diplostracan, then the same phylogenetic position would apply also to its fossil stem-lineage relatives, Kazacharthra and *Castracollis*. Such a diplostracan ingroup position of Notostraca together with its fossil relatives would not necessarily change other parts of branchiopod phylogeny. It would merely mean that all the Diplostraca synapomorphies mentioned above would apply to the Phyllopoda ancestor as well, but were lost in the notostracan lineage. Another consequence would be that Diplostraca with its current content would be paraphyletic. One solution would be to redefine Diplostraca to include the notostracan lineage as well. Then this new Diplostraca would be synonymous with Phyllopoda, a term which would then be superfluous in branchiopod classification. This is sensible for two reasons: (1) the term Diplostraca has more descriptive value since the taxon ancestrally would have had a bivalved carapace. (2) Phyllopoda has a less descriptive value since many other crustacean taxa have phyllopodous limbs, and furthermore the term has been used for many other taxa (see Martin & Christiansen 1995).

## 5.5. Monophyly of Spinicaudata plus Cladoceromorpha and position of Laevicaudata

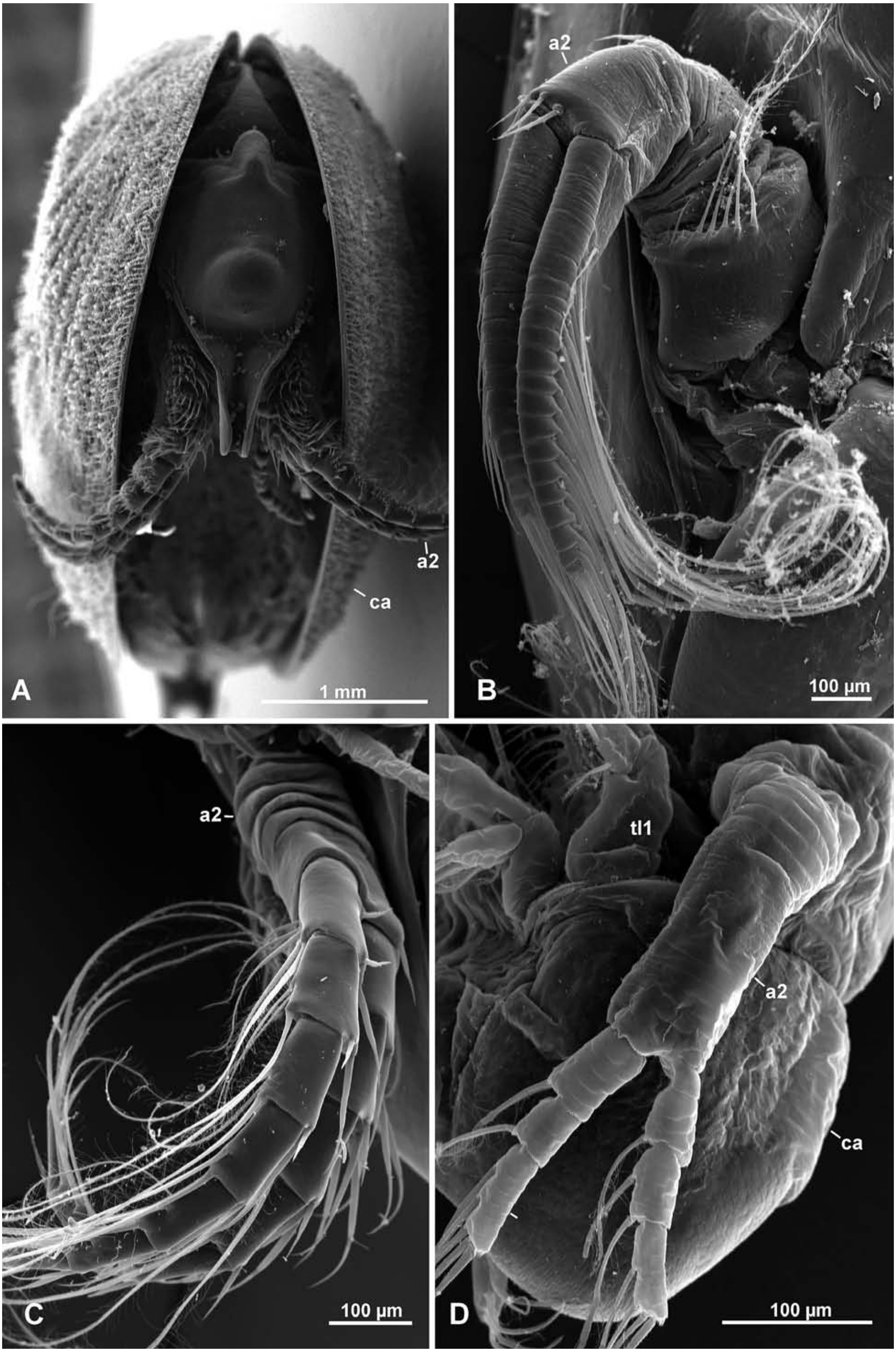
Another strongly supported group in branchiopod systematics is a yet unnamed clade consisting of Spinicaudata plus Cladoceromorpha. One synapomorphy is small, budlike first antennae in larvae or embryos (character 63). A couple of characters are related to the compound eyes. One is the fusion of the two compound eyes into one globular organ (Richter et al. 2007, character 43), which is not a synapomorphy for Cladocera and Cyclestherida as perceived previously (e.g., by Ax 1999, based on observations by Sars 1887). Another eye character is the unique pentapartite ommatidia of the compound eyes (character 47, Richter et al. 2007). A number of characters, which may not be entirely independent, relates to the telsonal region. In most Spinicaudata, Cyclestherida, and most cladocerans the telson has spines dorsally arranged in two rows (character 38), the caudal furcae are curved and claw-like (character 40), and the telson region is laterally compressed (character 36; Fig. 11D–F). A more general synapomorphy is related to the general function of the trunk limbs. In Anostraca, Notostraca, probably also in *Lepidocaris*, and to some extent in Laevicaudata (pers. obs., reported also by Sars 1896 and Fryer & Boxshall 2009), the trunk limbs have a double function as they are involved in feeding and locomotion at the same time. This is clearly ancestral for branchiopods and goes far back in crustacean/arthropod evolution (Walossek 1993). In Spinicaudata and Cladoceromorpha the locomotion is taken over entirely by the second antennae, while the trunk limbs are involved in filtration or other types of food intake only (character 21). As a consequence of the preferred phylogeny the growth lines on the carapace also maps as a synapomorphy at this level (character 5), which must then be assumed lost in Cladocera, probably more than once. It is uncertain whether the carapace growth lines in certain cladocerans such as *Monospilus* and certain *Ilyocryptus* species is a convergence or a plesiomorphy. Spinicaudata plus Cladoceromorpha is supported by some molecular works (e.g., Braband et al. 2002).

Laevicaudata, a taxon with many morphological peculiarities (Martin et al. 1986; Olesen 2005), has been difficult to place in a number of recent phylogenetic analyses. In this morphology-based analysis, Laevicaudata is placed as the first branch within Diplostraca as sister group to Spinicaudata plus Cladoceromorpha.

## 5.6. Monophyly of Cyclestherida plus Cladocera (= Cladoceromorpha)

One of the major surprises in branchiopod phylogenetics was the non-monophyly of the Spinicaudata *sensu* Linder (1945). Even though the peculiarities of *Cyclestheria hislopi* and some of its similarities to Cladocera were pointed out already by Sars (1887), the phylogenetic consequenses were not explored until late (Martin & Cash-Clark 1995; Olesen et al. 1996; Olesen 1998, 1999). As pointed out by Olesen et al. (1996) the similarities between Cyclestherida and Cladocera could be interpreted as synapomorphies suggesting a sister group relationship between these taxa, resulting in a paraphyletic Spinicaudata. This hypothesis has since been confirmed by nearly all molecular based phylogenetic analyses (Taylor et al. 1999; Spears & Abele 2000; Braband et al. 2002; Stenderup et al. 2006; deWard et al. 2006; Richter et al. 2007). The content of the Spinicaudata has since been redefined to exclude Cyclestherida (see Martin & Davis 2001; Olesen 2002, 2004) and the clade consisting of Cyclestherida and Cladocera has been named Cladoceromorpha by Ax (1999). The morphological support for Cladoceromorpha is not impressive in quantity, but it is enough to result in its monophyly in the present analysis. One similarity between Cyclestherida and Cladocera is the cyclic alternation between parthenogenetic and sexual reproduction (heterogony; character 58). Another similarity is the directly developing subitaneous eggs (or embryon-

**Fig. 7.** Branchiopod second antennae (a2). **A**: *Caenestheriella mariae* (Spinicaudata, Cyzicidae), frontal view. **B**: *Lynceus brachyurus* (Laevicaudata), right side a2, anterior is up. **C**: *Cyclestheria hislopi* (Cyclestherida), left side a2, ventral. **D**: *Polyphemus pediculus*, left side a2, anterior is up. Abbreviations: a2 = antenna 2; ca = carapace; tl1 = trunk limb 1.


a2
ca
A
1 mm
a2
B
100 µm
a2
C
100 µm
tl1
a2
ca
D
100 µm

ised larvae) in the chamber formed dorsally between the carapace valves and the animal body (character 60; Fig. 13). There are indications that direct development in the two different parts of the lifecycle has had different evolutionary paths, since *Leptodora* and possibly at least one population of *Cyclestheria* have free-living larvae as a part of the lifecycle. This has therefore been covered by two characters, one for the parthenogenetic part of the lifecycle (character 60), one for the sexual (character 59). Based on the preferred tree, direct development (embryonised larvae) can be concluded to have evolved once in the ancestor of Cladoceromorpha in the parthenogenetic part of the life cycle (character 60). The situation in the sexual part of the life cycle is more complicated (character 59). The observation of free-living larvae in a Cuban population of *Cyclestheria* (Botnariuc & Viña Bayés 1977) is difficult to explain, considering that Roessler (1995) explicitly reported already developed individuals hatching from resting eggs from Colombia. Another case of free-living larvae hatching from resting eggs is *Leptodora kindtii* within Cladocera. The most parsimonious solution when this character (59) is mapped on the preferred tree is that the free-living larvae in *Leptodora* have reappeared, analogous to what Scholtz (2000) suggested for the free-living nauplius stage in malacostracan crustaceans, but I find this difficult to accept. It seems more feasible that the free-living larvae of *Leptodora* are a retained primitive feature. This leads to the acceptance of the convergent loss of free-living larvae in the sexual part of the life cycle at least twice within Cladocera, depending on how the phylogeny is resolved. Other supporting characters for Cladoceromorpha are few. One likely synapomorphy is the distal sensilla of the first antennae. This is well-known for females of Cladocera, but the same is seen in Cyclestherida (character 10; Fig. 6D–F), while the first antenna of Spinicaudata and Laevicaudata in different ways has sensilla on a larger part of the appendage (Fig. 6B,C). Also Anostraca and *Lepidocaris* have distal sensilla only on the first antennae (Figs. 1B, 6A). Another possible synapomorphy for Cladoceromorpha is the presence of an ephippium (character 61). However, on the preferred tree, in which cladoceran phylogeny is largely unresolved, ephippia maps most parsimoniously as convergent for Cyclestherida and Anomopoda (where ephippia are present). But if Anomopoda eventually turns out to be the first branch within Cladocera, then one of the most parsimonious optimisations is that an ephippium was present already in the ancestor to Cladoceromorpha, and then lost at least once within Cladocera. A detailed morphological comparison between ephippia in Cyclestherida and Anomopoda is needed (see Fryer 1999). One of the classical similarities between Cyclestherida and Cladocera, the fused compound eyes, which were already pointed out by Sars (1887), has turned out to be difficult to maintain as a synapomorphy. Richter et al. (2007) showed that some spinicaudatans such as *Caenestheriella* sp. have compound eyes which are fused to the same degree as those of *Cyclestheria*, and that ‘fused’ compound eyes therefore is rather a synapomorphy for Spinicaudata and Cladoceromorpha (see above).

## 5.7. Monophyly of Cladocera and phylogenetic position of Cryptopoda, a new cladoceran order from the Jurassic

Cladocera has in recent morphology-based phylogenetic analyses been found to be monophyletic (Martin & Cash-Clark 1995; Olesen 1998, 2000, 2002; Negrea et al. 1999; Richter et al. 2007), which has been confirmed by most molecular works (see summary in Richter et al. 2007). The morphological support of Cladocera may not seem impressive since many characters are reductions, sometimes further modified within Cladocera, but still the support is sufficient to result in a monophyletic Cladocera. One synapomorphy is the reduction of trunk limbs to six pairs (character 18), or even five or four pairs in some taxa. Another synapomorphy is the reduction in size of the carapace to a condition where it covers only the trunk and limbs (head is free; character 4), in some taxa modified further to a dorsal brood pouch (Gymnomera). A couple of synapomorphies relates to the segmentation of the rami of the second antennae. Four exopodal segments clearly is an autapomorphy for Cladocera (character 12); this number is found in all Cladocera, except for Ctenopoda and Chydoridae, which have fewer segments. The phylogenetic status of the segmentation of the second antennae endopod is more complicated (character 13). Here the number of segments varies between two and four within Cladocera. *Leptodora* and the Jurassic *Leptodorosida* have four segments, Onychopoda and Anomopoda three, and Ctenopoda three or two. Based on the preferred tree (Fig. 14), the most parsimonious solution is three antennal endopodal segments ancestrally in Cladocera, later modified to four or two. However, in this case, a less parsimonious solution with four segments of the antennal endopod in the cladoceran ancestor, as seen in *Leptodora* and *Leptodorosida*, may be preferable. Further synapomorphies are the dorsal opening of the female genital system within the carapace (character 6) and the presence of only one pair of ostia in the heart; the latter is in contrast to all other branchiopods, where more pairs are present (character 52; Richter et al. 2007). Some of the cladoceran synapomorphies are losses of various structures present in other branchiopods. For example, since Laevicaudata, Spinicaudata,

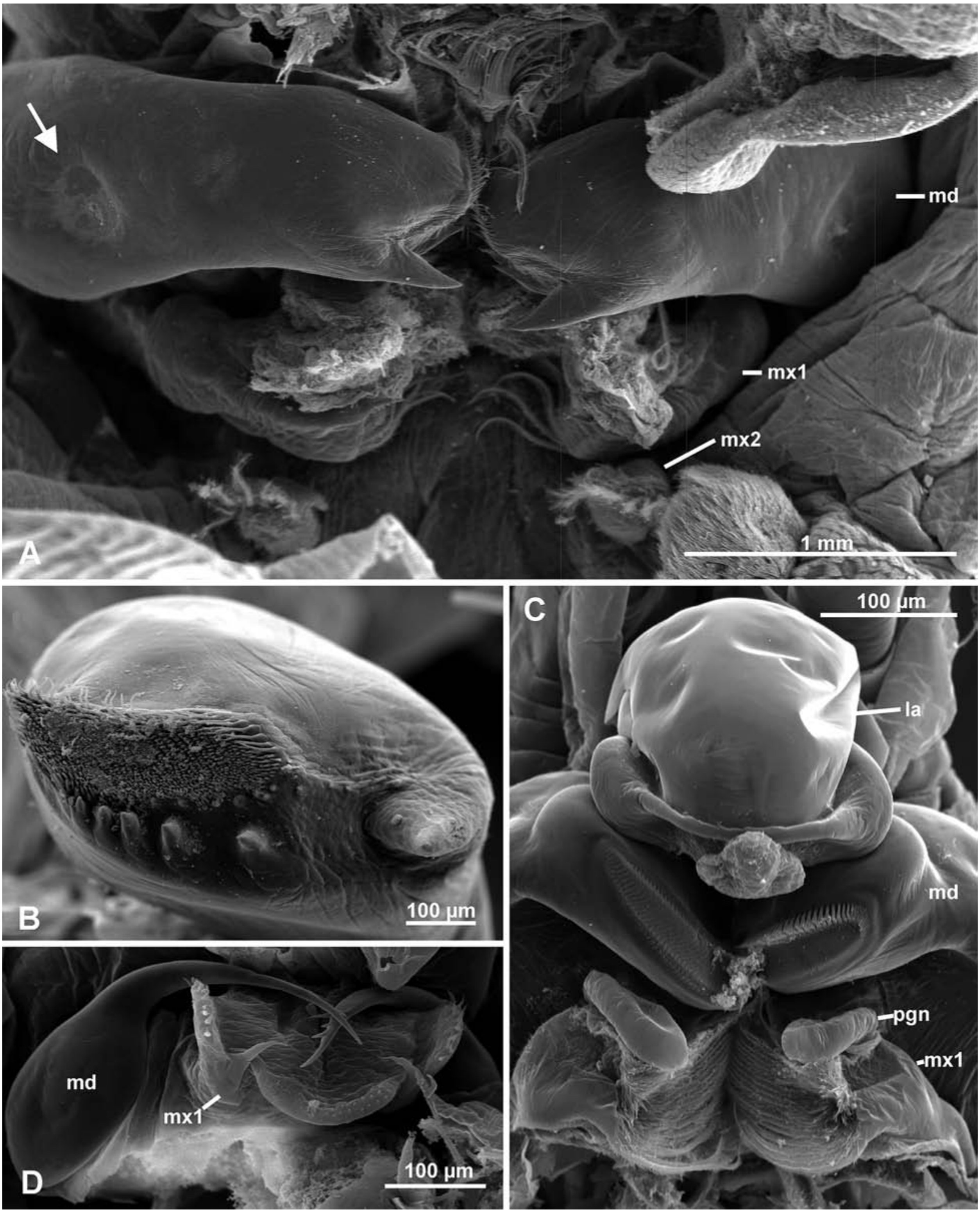


**Fig. 8.** Branchiopod mandibles (md). **A**: *Branchinecta raptor* (Anostraca), ventral (arrow point at 'scar' after mandibular palps). **B**: *Branchinecta raptor*, gnathal edge of left side md. **C**: *Cyclestheria hislopi* (Cyclestherida), ventral. **D**: *Leptodora kindtii* (Cladocera, Haplopoda), mandibles and 'lower lip' with lateral first maxilla lobes. Abbreviations: md = mandible; mx1 = maxilla 1; mx2 = maxilla 2; pgn = paragnath.

Cyclestherida (former 'Conchostraca', but now paraphyletic) all have the exopods of the trunk limbs extending into long dorsal lobes, and females have eggs/embryos attached to/supported by these lobes, both the dorsal lobes of the exopods as well as the connection to/support of eggs/embryos must be assumed lost at some stage in the ancestor to Cladocera (characters 28, 57). Actually, due to the fact that cladocerans deviate so much from all other branchiopods, many modifications must have taken place in the linage leading to

Cladocera, but many of these are difficult to formulate as characters and have therefore not been included.

The fossil record has traditionally not been of much help in elucidating the origin of Cladocera. The available cladoceran fossils have been few and not very well-preserved (Fryer 1991; Smirnov 1971, 1992; Kotov & Korovchinsky 2006). They are mostly from the Cretaceous and the Jurassic/Cretaceous boundary. Most fossil cladocerans can be placed in either Anomopoda or Ctenopoda and are therefore not particularly informative for the origin of Cladocera. However, recently a couple of Jurassic cladocerans has been described which could not be placed in any of the accepted four cladoceran orders, so a fifth order, Cryptopoda, was erected for them (Kotov 2007). One of the species of Cryptopoda, *Leptodorosida zherikhini*, has been included in this analysis since the species is known in enough detail to allow for a meaningful scoring in the matrix. *Leptodorosida zherikhini* shares the following characters with Cladocera: a carapace which is reduced in size to cover body and limbs only (not head) (character 4), four segments in the second antennae endopod and exopod (characters 12, 13), and six pairs of trunk limbs (character 18). It is not possible to say anything more precise about the relationships of *Leptodorosida*. Based on what is known about *Leptodorosida*, its morphology was that of a generalised cladoceran and it may have been very close to the common cladoceran ancestor. There is room for *Leptodorosida* being in a stem-lineage position to Cladocera or to any of the other four cladoceran orders, but there is no unambiguous support for any of these possible positions, so the erection of a fifth cladoceran 'order' by Kotov (2007) was justified. Fryer & Boxshall (2009) suggested that *Leptodorosida* can be accommodated within Ctenopoda, since it shares with this taxon six pairs of homonomous trunk limbs and 'appropriate' mandibles. Certainly, such a position is possible, but no information is available to support a ctenopod affinity with confidence. Six filtratory, homonomous limbs are most likely an ancestral character of Cladocera, and therefore can not be used to link *Leptorosida* to Ctenopoda. The same applies to the grinding type of mandibles in *Leptodorosida*, which seems to be similar to the ctenopod type, but also to the type seen in Spinicaudata or Cyclestherida.

If it is assumed that *Leptodorosida* actually is close to a cladoceran ancestor in morphology, then such an ancestor would have looked the following way: (1) A head free from the carapace with a pair of fornices (cuticular folds) on each side (sometimes confusingly called 'head shield'). As pointed out by Kotov (2007) these folds on the head are probably homologous to similar structures on the head of *Cyclestheria hislopi*, the sister group to Cladocera, and are also present in Laevicaudata and most spinicaudatans. The presence of such in *Leptodorosida* and in many anomopodan cladocerans therefore is a retained primitive feature, lost independently in some cladocerans. (2) A carapace covering only the trunk and the limbs (a cladoceran synapomorphy; character 4). (3) Six pairs of phyllopodous limbs (a cladoceran synapomorphy; character 18), probably not far from the morphology of the trunk limbs in Ctenopoda, but the detailed structure of the trunk limbs of *Leptodorosida* is not known. (4) A pair of second antennae with a very robust limb stem, similar to those seen in various ctenopods and anomopods, and a pair of rami each with four segments, in this respect similar to the condition in *Leptodora*.

## 5.8. Monophyly of raptorial cladocerans

Already Sars (1865) recognised the similarities between the two non-filtratory groups of cladocerans, Haplopoda and Onychopoda, and grouped them under the name Gymnomera. The validity of this taxon has long been discussed. Fryer (1987) abandoned the taxon, but Martin & Cash-Clark (1995) suggested a sister group relationship between Haplopoda and Onychopoda and Olesen (1998) reinstated the term Gymnomera for this grouping, a step not followed by Martin & Davis (2001). In the last decade molecular based phylogenies have often supported Gymnomera (Braband et al. 2002; Swain & Taylor 2003; Stenderup et al. 2006; deWard et al. 2006; Richter et al. 2007). There is a number of morphological synapomorphies for Gymnomera. The two most clear-cut ones may be the modification of the carapace to a smaller, dorsal brood pouch, attached dorsally to the trunk (character 4; Fig. 5), and the stenopodous, four-segmented trunk limbs (trunk limb 1 of *Leptodora* five-segmented; character 22; Figs. 5, 9D,E). Other characters are absence of food groove (character 2), absence of epipods (character 23), lacking dorsal spine row on telson (character 38), non-articulated furcae (character 39), and the in cross-section cylindrical telson (character 36). Also the presence of a limbless abdomen may be a synapomorphy, but then it must be assumed secondarily reduced again in some onychopods (character 1). A number of the mentioned characters are reductions. In summary Gymnomera is a very well-supported taxon.

## 5.9. Some general lines of branchiopod evolution based on current view on phylogeny

### 5.9.1. Adults

Accepting the phylogeny presented in this paper (and elsewhere) and the close relationship between *Rehbachiella* and other Branchiopoda, several conclusions can be reached regarding the morphology of a common ancestor of Branchiopoda and the further evolution of several structures.

The adult branchiopod ancestor probably had a carapace somewhat like that seen in *Rehbachiella*, where the carapace is a simple posterior extension of the naupliar shield. After this point it has undergone a spectacular evolution. It was lost in the sarsostracan lineage (Anostraca and *Lepidocaris*); modified to a more flattened appearance in Notostraca and Kazarcharthra (*Castracollis* uncertain); modified to a large bivalved carapace, capable of enclosing the whole body, in the diplostracan ancestor ('clam shrimp morphology' seen in Laevicaudata, Spinicaudata, Cyclestherida); reduced from the latter condition to cover only the trunk and limbs in the cladoceran ancestor (seen in Anomopoda and Ctenopoda); further reduced/specialised to a dorsal brood pouch in the Gymnomera ancestor (Haplopoda and Onychopoda).

In *Rehbachiella* the second antennae and the trunk limbs operate together as propulsory organs, while feeding is taken care of by the trunk limbs mainly (filter-feeding apparatus; Walossek 1993). And since roughly the same division in function between antennae and trunk limbs must have been the case for both *Lepidocaris* and *Castracollis* (Scourfield 1926; Fayers & Trewin 2003), it is safe to assume that this would have applied also to the branchiopod ancestor. Interestingly, from this stage, evolution has gone in two completely different directions within Branchiopoda with regard to which limbs are involved in feeding versus swimming. In Anostraca the propulsory function of the second antennae has been entirely lost in adults, and these appendages have been recruited for a different purpose (clasping in males). The double function of the trunk limbs in Anostraca (feeding and swimming) has been kept. The same applies to Notostraca, where the second antennae in adults have lost the function as swimming appendages, and, as in Anostraca, the trunk limbs instead have a double function in being both responsible for locomotion and feeding (but no longer filtration). The phylogeny, and especially the position of *Castracollis* as a stem-lineage notostracan, where the second antennae have retained their swimming functions, clearly suggests that the loss of the swimming function of the antennae has taken place independently in Anostraca and Notostraca. The diplostracan lineage went into an entirely different direction. Here the second antennae have kept their fuction as swimming appendages, as seen in Laevicaudata, Spinicaudata, Cyclestherida, and Cladocera. In contrary the propulsory fuction of the trunk limbs has been lost (Laevicaudata is partly an exception, see character 21), and they have become specialised for feeding only, probably due to their partial encapsulation between the carapace valves.

The mandible in the branchiopod ancestor had lost the distal parts (basipod and rami) and retained only the coxal part, which has a gnathal edge occupied mainly by a large molar (no large incisor) (Fig. 8). This morphology is kept essentially unchanged in many branchiopods such as Anostraca, *Lepidocaris*, *Castracollis*, Spinicaudata, Cyclestherida, and, among cladocerans, Ctenopoda and Anomopoda (see Richter 2004), which probably is related to a similar lifestyle as filtrators. Among the exceptions are Notostraca and Kazacharthra, where the gnathal edge bears a row of distinct cusps because of their omnivorous lifestyle, and something similar is seen in Laevicaudata (probably convergent). Within Cladocera, *Leptodora* (Haplopoda) and Onychopoda also have strongly modified mandibular gnathal edges. In *Leptodora*, for example, the mandibles are long, and styliforme, adapted for a predatory lifestyle (Fig. 8D). The second maxillae must be assumed reduced already in the branchiopod ancestor (after *Rehbachiella*) since there is no exceptions to their reduced condition within Branchiopoda. It is more uncertain with the first maxillae, since males of *Lepidocaris* have rather prominent first maxillae probably used for holding the females during mating.

Trunk limbs in the branchiopod ancestor probably looked like a reduced version of a *Rehbachiella* trunk limb. It seems that an average ancestral branchiopod trunk limb was composed of a large, undifferentiated limb corm with six median endites, an unsegmented endopod articulated to the limb corm, a large, flaplike exopod inserting laterally approximately midway at the limb corm, and had a sac-like epipod proximal to the exopod (Fig. 9 shows some aspects). Some of the features of this ancestral limb are unambiguously optimised in the present analysis as being ancestral to branchiopods. This includes for example the unsegmented endopod, articulated to the limb corm, because such is found in most non-cladoceran branchiopods. The precise number of median endites is more uncertain. Six endites are seen in *Lepidocaris* and in Anostraca (at least in larvae), but only five in all other non-cladoceran branchiopods. It is equally parsimonious to assume five or six median endites in the ancestor to Branchiopoda. However, since *Rehbachiella* has about eight median endites, the larger number (six) is preferred as the ancestral branchiopod number. Interestingly,

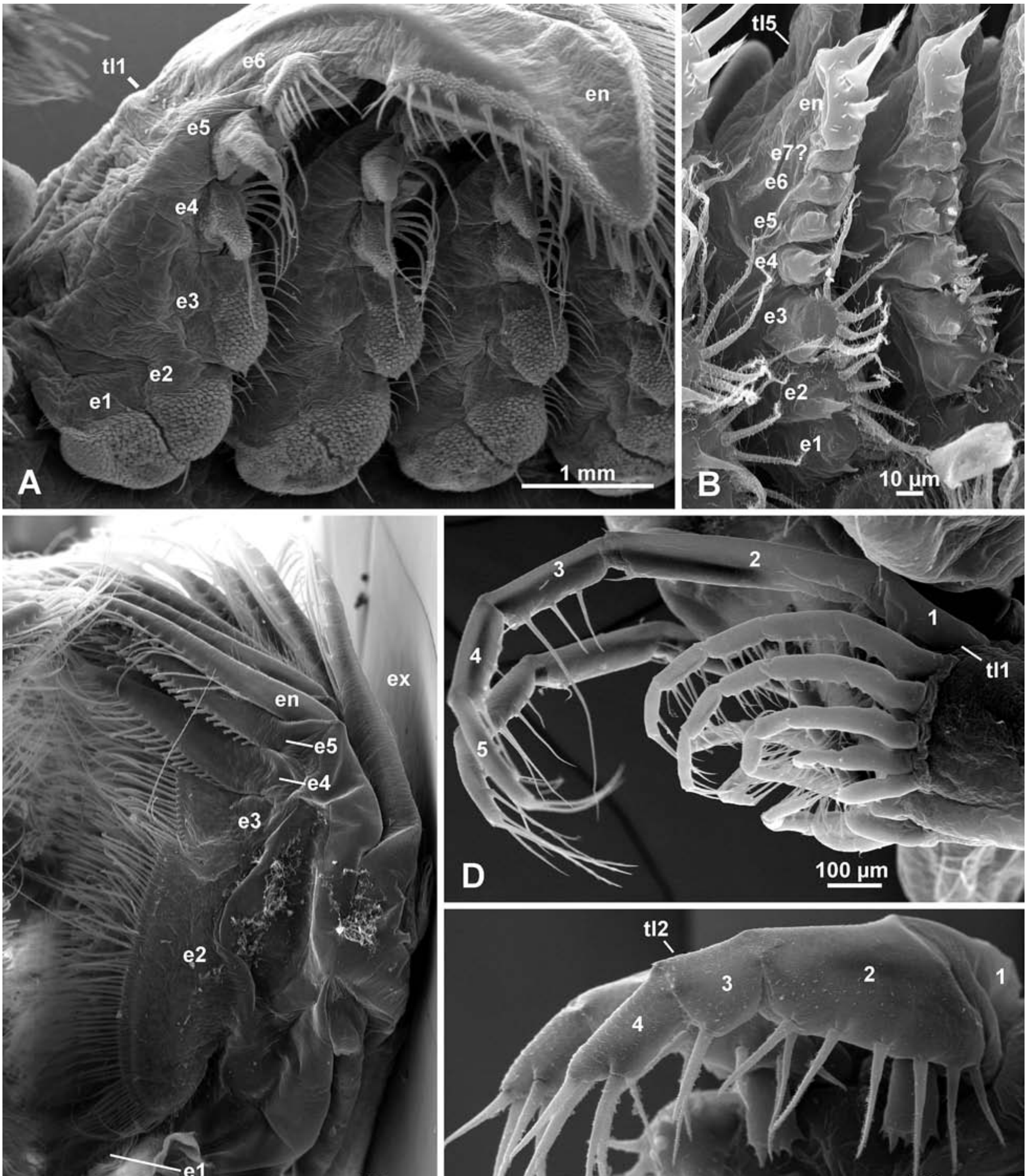


**Fig. 9.** Branchiopod trunk limbs. **A**: *Branchinecta raptor* (Anostraca), median view on left side trunk limbs 1–3. **B**: *Eubranchipus grubii* (Anostraca), median view on left side trunk limbs 5 and 6. **C**: *Lynceus brachyurus* (Laevicaudata), male, right side trunk limb 2, anterior view. **D**: *Leptodora kindtii* (Haplopoda), left side trunk limbs, lateral view. **E**: *Bythotrephes longimanus* (Cladocera, Onychopoda), right side trunk limb 2, anterior view. Abbreviations: e1–e7 = endites 1–7; en = endopod; ex = exopod; tl1 = trunk limb 1; tl2 = trunk limb 2; tl5 = trunk limb 5.

developing trunk limbs of *Eubranchipus* show what can be intepreted as a vestige of a seventh endite (Fig. 9B), which is one more than in adults. From this level a convergent reduction to five endites has taken place within Anostraca and in Phyllopoda.

*Rehbachiella*, Sarsostraca (Anostraca and *Lepidocaris*), *Castracollis* and Calmanostraca (Kazacharthra and Notostraca) have a limbless abdomen, so this was probably also the case for the branchiopod ancestor (Figs. 1, 2). The exact number of limbs in the bran-

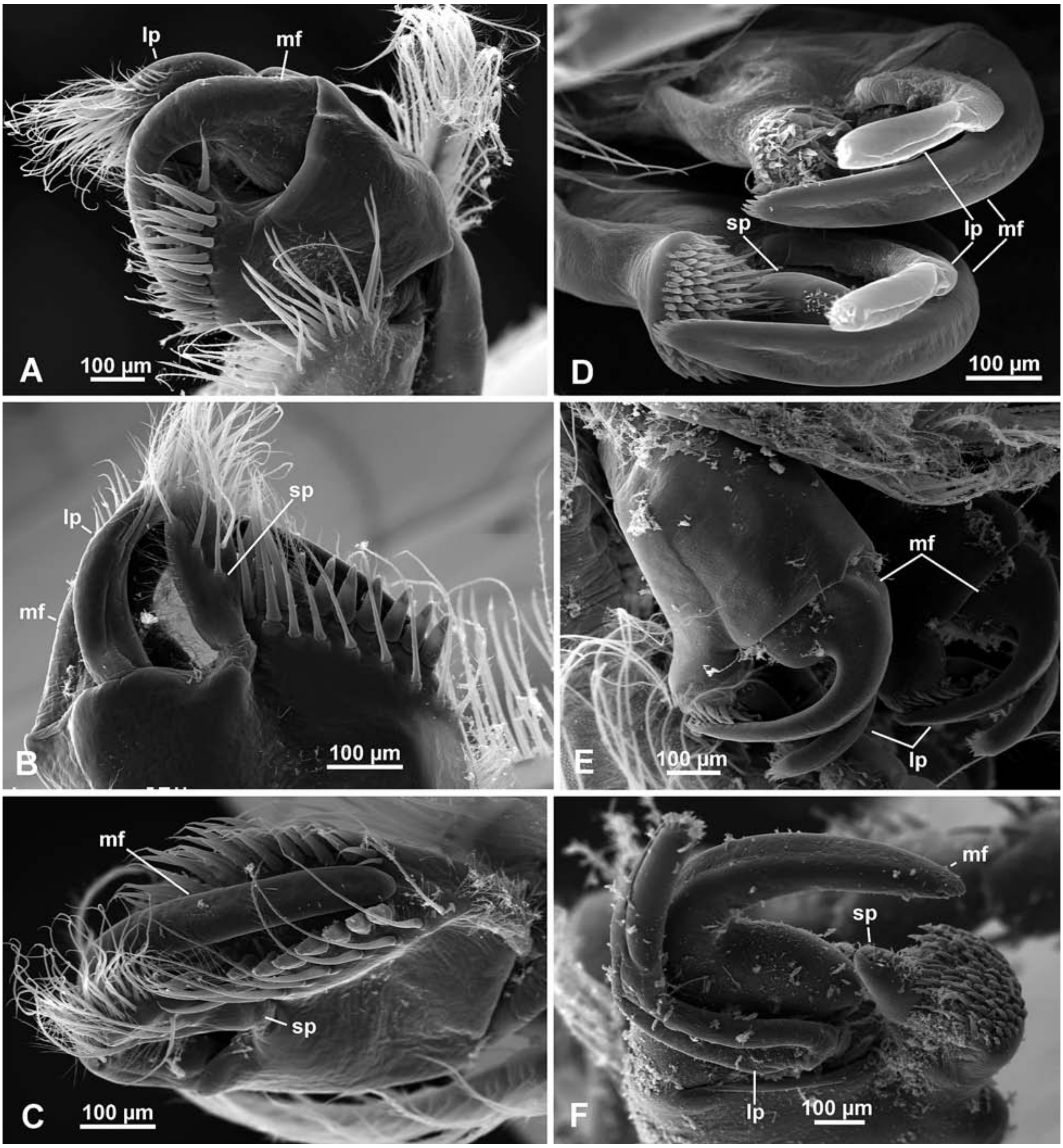


**Fig. 10.** Male claspers of Laevicaudata and Spinicaudata. **A–C**: *Lynceus brachyurus* (Laevicaudata), left side clasper (trunk limb 1), anterior (A), posterior (B), and apical (C) views. **D–F**: *Caenestheriella* sp. (Spinicaudata, Cyzicidae), claspers of right side trunk limbs 1 and 2, left is anterior (D), left side clasper in anterior view (E), and right side clasper (F). Abbreviations: lp = long palp; mf = movable finger (endopod); sp = short palp.

chiopod ancestor is difficult to trace due to so much variation within Branchiopoda in this regard. There is no single most parsimonious optimisation. However, 11–13 pairs of serially similar limbs is a qualified guess since approximately this number is found in a number of taxa: Anostraca and *Lepidocaris* have 11 limb pairs (larger number in *Polyartemia* and *Polyartemiella* clearly secondary), 13 if the limbs modified as brood pouches are included; Kazacharthra has 11 pairs, the same number as Notostraca in the anterior series; Laevicaudata has 10 or 12; *Rehbachiella* has 12 but is not yet fully developed. From this stage, several modifications of the limb series have taken place. In Notostraca and *Castracollis* the limb series have become subdivided in two series (11 limbs in the anterior series) with distinctly different limbs. The anterior series in Notostraca is further subdivided in shorter limb series serving different purposes (e.g., endites on first pair of trunk limbs are feelers, Fig. 2B). In Diplostraca the limbless abdomen (as in Laevicaudata, Spinicau-

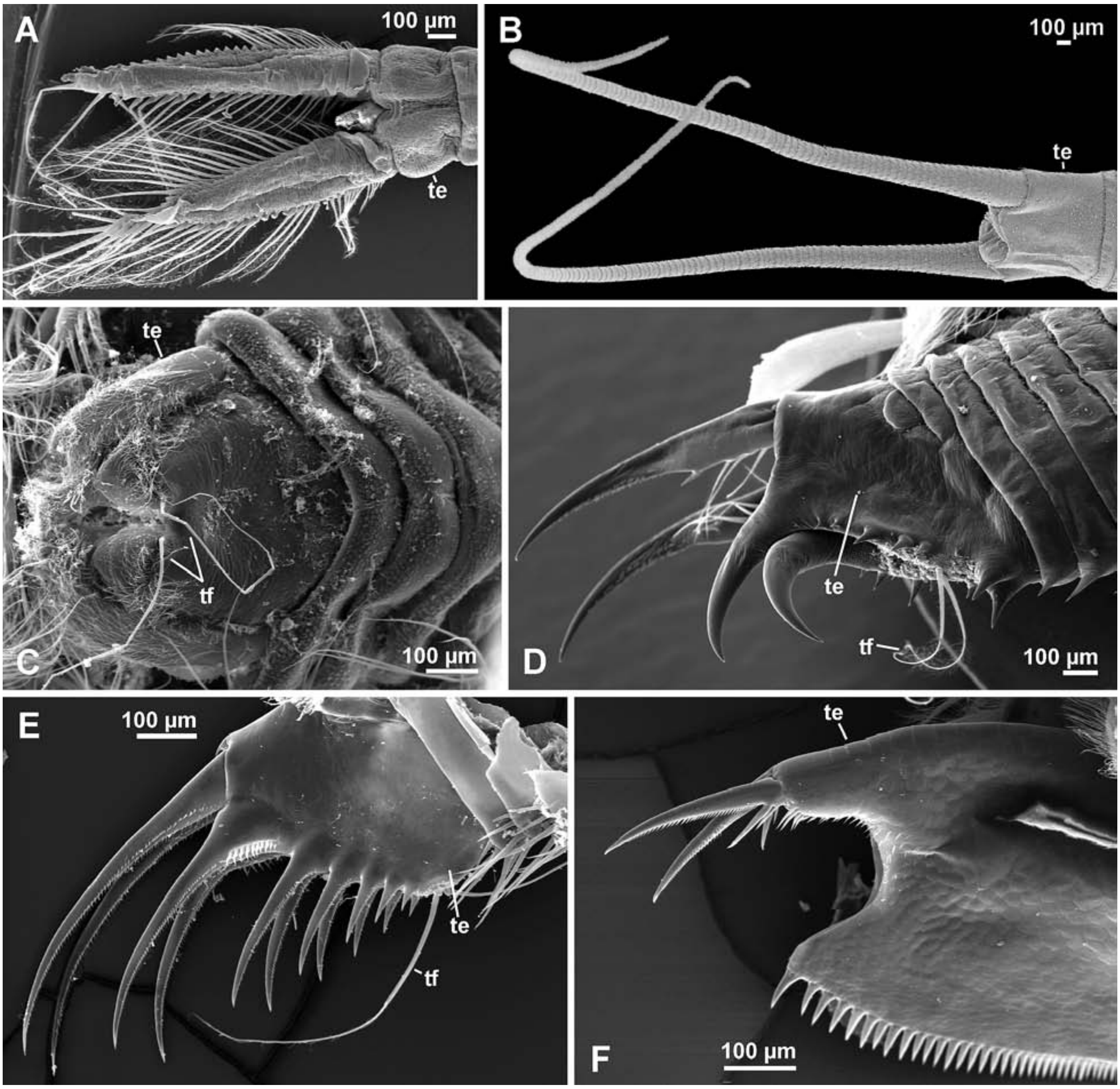


**Fig. 11.** Caudal region of branchiopods. **A**: *Eubranchipus grubii* (Anostraca), late juvenile from ventral, telson and caudal rami (cercopods). **B**: *Triops australiensis* (Notostraca), ventral, telson and caudal rami. **C**: *Lynceus brachyurus* (Laevicaudata), telson seen from dorsal. **D**: *Caenestheria* sp. (Spinicaudata) telson and caudal claws seen from lateral. **E**: *Cyclestheria hislopi* (Cyclestherida), telson and caudal claws seen from lateral. **F**: *Eurycercus lamellatus* (Cladocera, Anomopoda), part of telson and caudal claws seen from lateral. Abbreviations: te = telson; tf = telson filament.

data, and Cyclestherida) has been lost and limbs are thus present along the entire trunk (Figs. 3, 4), but later a limbless abdomen is redeveloped in certain cladocerans (Haplopoda and certain onychopods; Fig. 5A,C), probably by a suppression of limb formation.

The general design of branchiopod trunk limbs has been remarkably conservative during large parts of branchiopod evolution, since basically the same components (limb corm with 5–6 endites, unsegmented endopod, flap-like exopod, and sac-like epipod) are present in all non-cladoceran branchiopods. But obviously there are many specialisations in different taxa. One example is the specialisation of the first pair(s) of trunk limbs in males in Diplostraca to a structure used for clasping or holding the females during mating. The claspers in Laevicaudata, Spinicaudata, and Cyclestherida are similar at the detailed level and consist of largely the same components (Olesen et al. 1996), while those of Cladocera are modified. Another limb specialisation is the slender, naked palps on most trunk limb endites in *Castracollis*. The most distal one of these (on fifth endite) is virtually identical to a similarly placed palp in many spinicaudatans (Fig. 3B). On the preferred tree the most parsimonious solution is convergent evolution of these palps, but I am not convinced that this is correct. The presence of palp(s) may

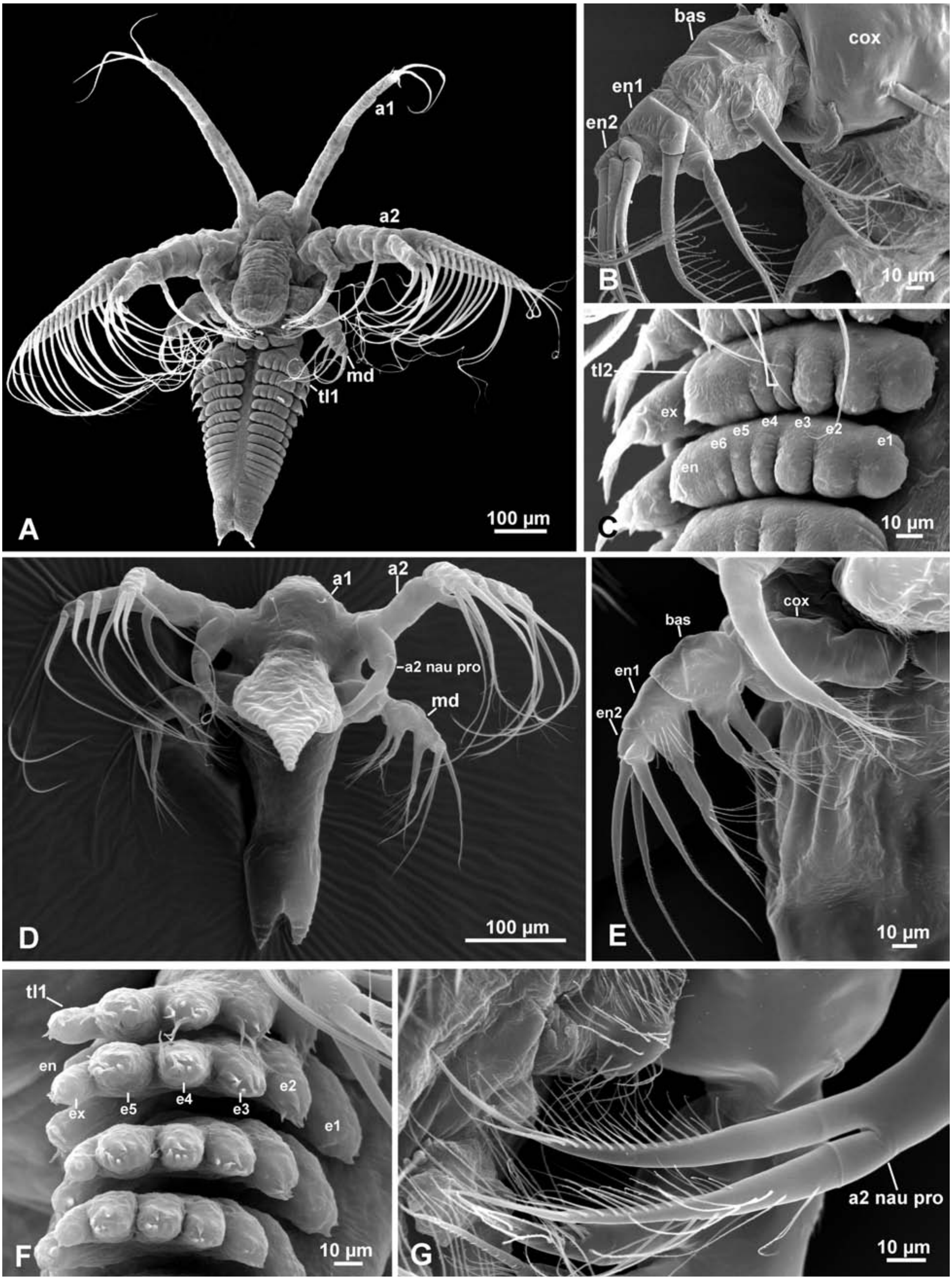


**Fig. 12.** Free-living larvae of Branchiopoda. **A**: *Eubranchipus grubii* (Anostraca), intermediate larva, ventral view. **B**: *Eubranchipus grubii*, mandibular palp, right side. **C**: *Eubranchipus grubii*, early buds of right side trunk limbs 2 and 3. **D**: *Eulimnadia braueriana* (Spinicaudata), intermediate larva (nauplius 4), ventral view. **E**: *Eulimnadia braueriana*, mandible, right side. **F**: *Eulimnadia braueriana*, late larva (nauplius 7), limb buds of right trunk limbs 1–4. **G**: *Eulimnadia braueriana*, bifid naupliar process of antenna 2 in intermediate larval stage. Abbreviations: a1 = antenna 1; a2 = antenna 2; a2 nau pro = antennal naupliar process; bas = basipod; cox = coxa; e1–e5 – endite 1–5; en = endopod; en1 = endopod segment 1; en2 = endopod segment 2; ex = exopod; md = mandible; tl1 = trunk limb 1.

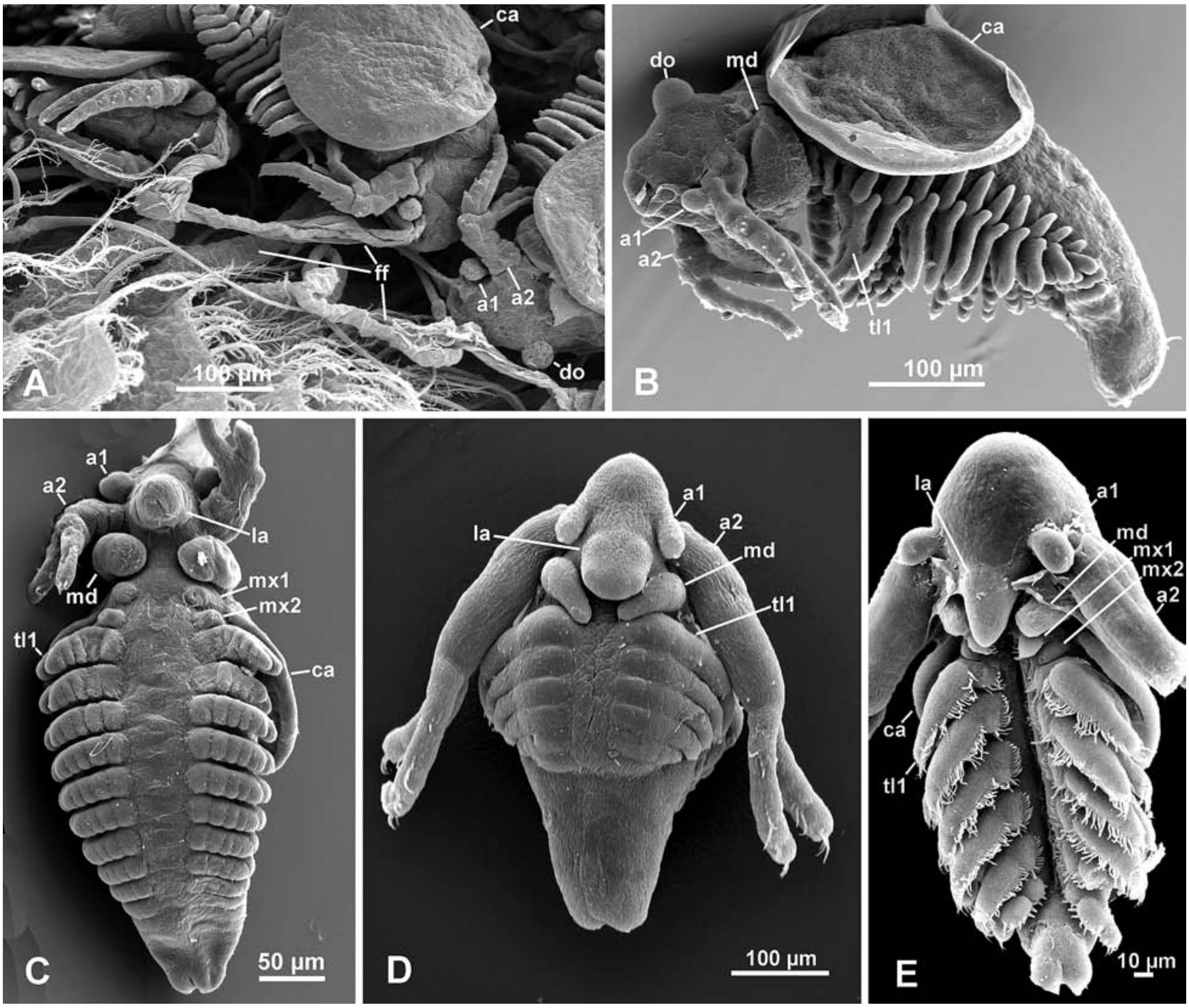


**Fig. 13.** Embryonised larvae of Cyclestherida and Cladocera. **A**: *Cyclestheria hislopi* (Cyclestherida), close-up of late embryos in dorsal brood chamber showing attachment filaments between limb exopods of adult and foreheads of embryos. **B**: *Cyclestheria hislopi*, late embryo removed from brood chamber. **C**: *Cyclestheria hislopi*, intermediate embryo removed from brood chamber. Remains of the connecting filaments between the adult limbs and the embryo can be seen anteriorly. **D**: *Leptodora kindtii* (Cladocera, Haplopoda), intermediate embryo removed from brood pouch. **E**: *Diaphanosoma brachyurum* (Cladocera, Ctenopoda), late embryo removed from brood pouch. Abbreviations: a1 = antenna 1; a2 = antenna 2; ca = carapace; do = dorsal organ; ff = frontal filament; la = labrum; md = mandible; mx1 = maxilla 1; mx2 = maxilla 2; tl1 = trunk limb 1.

rather be a symplesiomorphy lost in a number of taxa.

Among the taxa deviating most strongly from the ancestral branchiopod limb design are the non-phyllopodous, segmented, stenopodous limbs seen in Haplopoda and Onchychopoda (= Gymnomera) modified for a predatory or at least raptorial lifestyle. In these taxa there are four or six trunk limbs consisting of four (Onychopoda) or five (*Leptodora*, at least trunk limb 1) distinct segments, sometimes with an exopod (some Onychopoda), but never with an epipod (Figs. 5, 9D,E). Due to the deeply subordinate position of Onychopoda and Haplopoda in Branchiopoda, it has long been assumed that the segmented limbs in these taxa have been derived from branchiopod-type phyllopodous limbs. Based on a homologisation of the endites in non-cladoceran branchiopods with the segments in *Leptodora*, it was concluded that the segments in *Leptodora* have evolved from phyllopodous limbs where the endites roughly have been transformed into segments (Olesen et al. 2001).

### 5.9.2. Larvae and neoteny

Turning now to branchiopod larvae and how ontogeny has evolved within Branchiopoda, several conclusions can be made based on the phylogeny presented here (and elsewhere). It is well-known that various anostracans have a long and gradual larval development (anamorphic) with more than 20 stages (Benesch 1969) and *Rehbachiella* may have had more than 30 stages before even being fully adult (Walossek 1993). Given

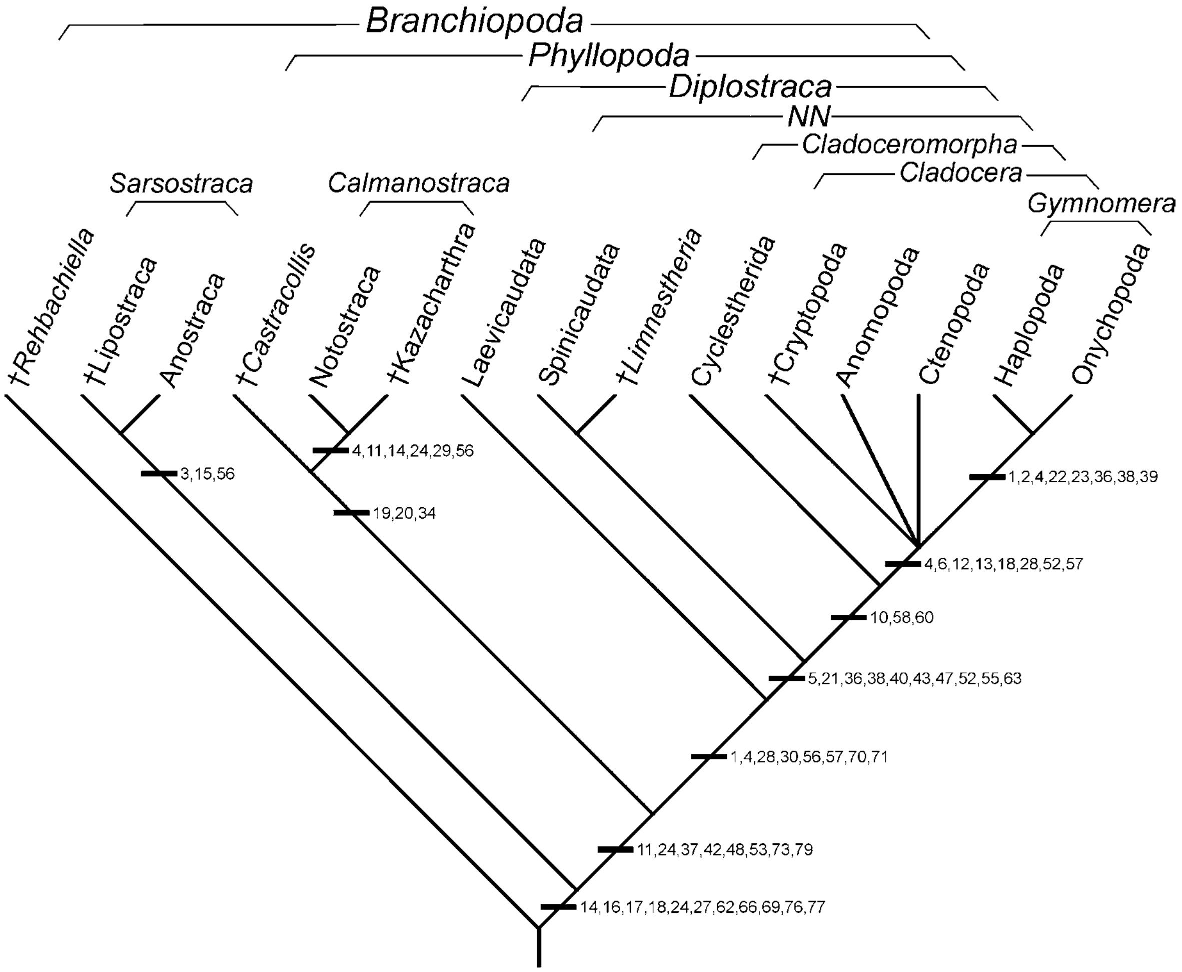


**Fig. 14.** One of the three shortest trees obtained after parsimony analysis (identical to strict consensus tree). Selected character transformations are mapped on the tree (see Tab. 3 for explanation). The "†" symbols indicate that the taxa are extinct.

the phylogenetic position of Anostraca (and *Lepidocaris*) as sister group to the remaining branchiopods, it is clear that the original mode of branchiopod development was gradual with a high number of stages with only small changes between.

The early larval stages of all non-cladocerans are in many respects quite similar. Based on the presented phylogeny, these similarities can be inferred to have been present already in the branchiopod ancestor (after *Rehbachiella*). For example, the many similar components of the naupliar feeding apparatus, such as details of the naupliar process of the second antennae and segmentation and setation of the mandibular palp (among others), in Anostraca, *Lepidocaris*, Notostraca, Laevicaudata, and Spinicaudata, indicate that they must have been present early in evolution (at least Devonian) and after that been remarkably conservative in evolution (Fig. 12). Alongside the conservativeness of the naupliar feeding apparatus, some branchiopod larvae are quite modified in other respects. For example, the larvae of *Lynceus brachyurus* (Laevicaudata), with their peculiar, horn-like first antennae and large, rounded labrum, forming a large ventral plate almost as large as the dorsal shield, are among the most bizarre crustacean larvae (Olesen 2005). Regarding larval clam shrimps, the labrum seems to be one of the body parts which have been subject to most extensive evolutionary experiments. Species are known with one (Olesen & Grygier 2003), three (Olesen & Grygier 2004), or four (*Lynceus biformis*, Olesen & Grygier unpublished data) large spines on the distal margin.

An interesting general question concerns to which extent branchiopod evolution can be explained by heterochronic events (= developmental change in the timing of events, leading to changes in size and shape). Perhaps one of the most well-known examples within Crustacea of an entire taxon suggested to have originated by a hetereochronic event is the idea that Cladocera are neotenic 'conchostracans' (e.g., Schminke 1981). This idea was briefly re-evaluated by Olesen (1999) in the light of the possible sister group relationship between Cyclestherida and Cladocera. This relationship is now well-established and much more is now known about the larval development of various clam shrimps, so it may be time to look at that idea again. Indeed there is a very intriguing general correspondence in morphology between spinicaudatan larvae and some adult cladocerans. For example, late larvae or early juveniles of *Caenestheriella gifuensis* (Spinicaudata, Cyzicidae) or *Eulimnadia braueriana* (Spinicaudata, Limnadiidae) (see Olesen & Grygier 2003, 2004) share with adult cladocerans (for example Ctenopoda) a short carapace not enveloping the head, only six visible trunk limbs, and rather few segments in the antennal rami. The similarities between larval spinicaudatans and adult cladocerans and the commonly accepted notion that both 'Conchostraca' and Spinicaudata sensu Linder (1945) are paraphyletic with respect to Cladocera, seems strongly to suggest neotenic origin of Cladocera. However, as pointed out by Olesen (1999) there is a conflict in logic between assuming that direct development (embryonised free-living larvae) is a synapomorphy for Cyclestherida and Cladocera, and at the same time assuming neotenic origin of Cladocera from spinicaudatan ancestors with free-living larvae. Since Olesen (1999) it has become close to a fact that Cyclestherida and Cladocera are indeed sister groups, which also means that direct development was present in their common ancestor. I therefore conclude that Cladocera probably has not evolved from free-living spinicaudatan larvae by neoteny, at least not the way normally perceived. The shortening of the body and the reduction of the carapace and other structures, typical for cladocerans, must have evolved *after* free-living larvae were lost.

### 5.10. Classification of Branchiopoda based on current phylogeny

The classification presented below is strictly based on the phylogeny presented in this work (Fig. 14). The phylogeny is adequately supported to justify inclusion of all clades in the classification. One uncertainty concerns the monophyly of Diplostraca. As mentioned above morphology supports Diplostraca, whereas molecular data suggest its paraphyly with respect to Notostraca (summarised by Stenderup et al. 2006). Diplostraca has been included in the present classification but future will show whether this is justified. Another uncertainty concerns the intrinsic phylogeny of Cladocera. The present analysis has led to no convincing result, so with the exception of Gymnomera, higher level categories have been avoided. In contrast to many other classications for branchiopods and other crustaceans, fossils have been treated equal to Recent taxa. This seems as the most logical approach and it works for the higher-level classification for branchiopods, but may be unpractical for many other fossil taxa due to lack of detailed information. No Linnean categories have been applied, simply because one runs out of categories when attempting to use the Linnean system. From the 'Branchiopoda' to 'Haplopoda/Onychopoda' eight named levels are needed, and the family level is not even reached.

**Branchiopoda (s.str.)**
- Sarsostraca
    - †Lipostraca
    - Anostraca
- Phyllopoda
    - NN
        - †*Castracollis*
        - Calmanostraca
            - †Kazacharthra
            - Notostraca
    - Diplostraca
        - Laevicaudata
        - NN
            - Spinicaudata
            - Cladoceromorpha
                - Cyclestherida
                - Cladocera
                    - †Cryptopoda
                    - Anomopoda
                    - Ctenopoda
                    - Gymnomera
                        - Haplopoda
                        - Onychopoda

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