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ONYCHOCAUDATA (BRANCHIOPODA: DIPLOSTRACA), A NEW HIGH-LEVEL TAXON IN BRANCHIOPOD SYSTEMATICS

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ABSTRACT

The systematics of Branchiopoda has received much attention in recent years, and a full understanding of the higher-level classification seems close. Based on a number of phylogenetic analyses involving both morphological and molecular data, some higher-level taxon names have been resurrected in the last decades (Phyllopoda, Diplostraca, Cladocera, Gymnomera) and new names for new hypotheses have been suggested (Cladoceromorpha). Herein we suggest Onychocaudata n. tax. as a name for a clade consisting of Spinicaudata and Cladoceromorpha. This clade has in various previous publications received much morphological support (telsonal region and compound eye characters) as well as strong molecular support. We also argue that the name Diplostraca is best retained with its original content ('bivalved branchiopods') since there is still much evidence (especially morphological) for its monophyly and competing hypotheses, e.g., Notostraca and Laevicaudata as sister taxa, are less well supported.

KEY WORDS: Branchiopoda, classification, PhyloCode, phylogeny, systematics

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INTRODUCTION

Branchiopoda comprises about 1120 species (Brendock et al., 2008; Forró et al., 2008; Ahyong et al., 2011) with a large diversity in morphology and habit preference. The group is predominantly found in freshwater, but a recently described branchiopod from shallow marine sediments from the Cambrian, possibly belonging to the branchiopod crown group *sensu* Olesen (2007, 2009), suggests a marine origin (Harvey et al., 2012; see also Walossek, 1993; Olesen, 2007). A few branchiopods have conquered the world oceans secondarily (marine cladocerans, e.g., Rivier, 1998). Most species are filtratory but predators (or raptorial feeders) are known both within Anostraca (Fryer, 1966; Rogers et al., 2006) and Cladocera (Rivier, 1998).

Branchiopod systematics has received intensive attention in the last decades, and a full understanding of the higher-level phylogeny seems close (Olesen, 1998, 2007, 2009; Braband et al., 2002; deWard et al., 2006; Stenderup et al., 2006; Richter et al., 2007). Fryer's (1987) 'flat' taxonomic scheme, with the recent Branchiopoda subdivided in eight taxa being at the same systematic level ('orders') and with a suggestion of abandoning all higher level groupings, was the starting point of a new era in branchiopod systematics. The monophyly of most of Fryer's (1987) orders have later been confirmed, with the exception of his Spinicaudata (introduced by Linder, 1945) from which the aberrant clam-shrimp family Cyclestheridae has later been removed (see Martin and Davis, 2001). Publications after Fryer (1987) starting with Olesen (1998) has attempted to group the branchiopod 'orders' into earlier proposed or new arrangements, which has led to the resurrection of certain taxonomic names (Phyllopoda, Diplostraca, Cladocera, Gymnomera) and to the suggestion of new, e.g., Cladoceromorpha (Ax, 1999). We are far beyond Fryer's (1987) scheme today, but a few important aspects are still controversial. Among the major achievements are that it is now well supported that Anostraca is the sister group to the remaining branchiopods that are grouped together as Phyllopoda, but the precise order in which Notostraca and Laevicaudata branch off is more uncertain. The general morphology-based view is that Notostraca is the first branch after Anostraca resulting in a monophyletic Diplostraca (clams shrimps and water fleas) (Eriksson, 1934; Walossek, 1993; Negrea et al., 1999; Olesen, 1998, 2000, 2007; but see Richter, 2004 for a discussion of alternative relationships), but this is partly opposed by molecular evidence where Notostraca is sometimes placed within Diplostraca as sister group to Laevicaudata, Onychocaudata n. tax, or even to Cladoceromorpha (Braband et al., 2002; deWard et al., 2006; Stenderup et al., 2006; Richter et al., 2007). Perhaps the most enlightening finding in this process of elucidating the main evolutionary lineages in Branchiopoda was the discovery of a sister group relation between the diverse Cladocera and the clam shrimp *Cyclestheria hislopi* (Cyclestherida) (collectively named Cladoceromorpha). Another significant higher-level grouping is Gymnomera (*sensu* Sars, 1865) consisting of the aberrant cladocerans Onychopoda and Haplopoda (raptorial water fleas) (Olesen, 1998, 2009; Richter et al., 2001, 2007; Swain and Taylor, 2003; deWard et al., 2006).

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Notwithstanding some still existing uncertainties in branchiopod phylogeny, a clade consisting of Spinicaudata and Cladoceromorpha as sister taxa has repeatedly been supported based both on morphological and molecular data. The consistent appearance of this clade in many studies addressing a variety of approaches strongly suggests that it is a valid taxon and therefore is important to name (marked 'NN' in the phylogeny presented by Olesen, 2009). In this paper we name the clade 'Onychocaudata' and summarise its morphological and molecular support based on previously published evidence. At the same time we argue for the use of the name Diplostraca with its original content.

SYSTEMATICS

Definitions following PhyloCode principles outlined in Cantino and Queiroz (2007) are provided for two clade names, Onychocaudata n. tax. and Diplostraca. Because of the close relation between these two concepts, it is important to define both at the same time. As reference phylogenies are used those presented in Richter et al. (2007) and Olesen (2007, 2009) (summarised in Fig. 1), which finds support for both taxa (Onychocaudata marked 'NN' in Olesen, 2009). Onychocaudata n. tax. consists of Spinicaudata + Cladoceromorpha and Diplostraca consists of Laevicaudata + Onychocaudata n. tax.

Onychocaudata n. tax.

Clade Definition.—Onychocaudata refers to the crown clade originating from the most recent common ancestor of *Limnadia lenticularis* (Linné, 1761) (Spinicaudata), *Cyclestheria hislopi* (Baird, 1859) (Cyclestherida), and *Daphnia magna* Straus, 1820 (Cladocera), provided that it does not include *Lynceus brachyurus* O. F. Müller, 1776 (Laevicaudata) or *Triops cancriformis* (Bosc, 1801) (Notostraca).

Etymology.—The name Onychocaudata from ho onyx, ónychos (Greek), i.e., claw, and caudatus (Latin), i.e., with a tail; refers to the presence of articulated curved caudal furca, which is one of the morphological characters supporting this clade.

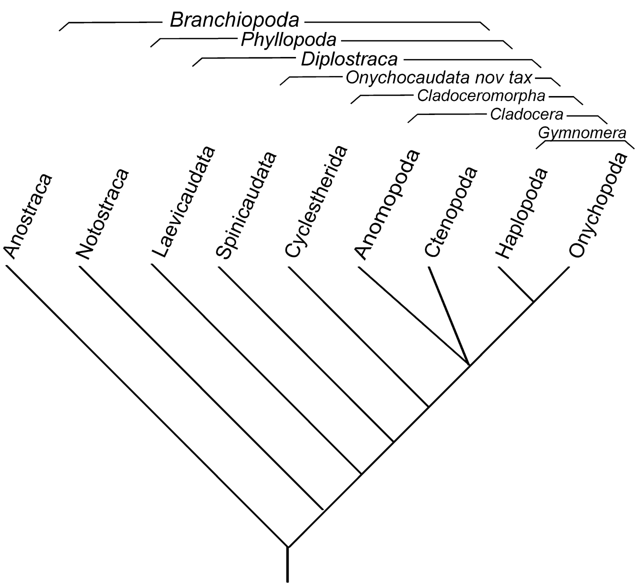

Fig. 1. Phylogeny of Branchiopoda based on Richter et al. (2007) and Olesen (2007, 2009). The phylogeny is essentially similar to the one presented in Olesen (2009) but with fossils excluded.

Diplostraca Gerstaecker, 1866

Clade Definition.—Diplostraca refers to the crown clade originating from the most recent common ancestor of *Lynceus brachyurus* O. F. Müller, 1776 (Laevicaudata), *Limnadia lenticularis* (Linné, 1761) (Spinicaudata), *Cyclestheria hislopi* (Baird, 1859) (Cyclestherida), and *Daphnia magna* Straus, 1820 (Cladocera), provided that it does not include *Triops cancriformis* (Bosc, 1801) (Notostraca) or *Artemia salina* (Linnaeus, 1758) (Anostraca).

Etymology.—The name Diplostraca from diploos (Greek), i.e., doubled, and ostrakon (Greek), i.e., shell; refers to the bivalved carapace which is present in Laevicaudata and Spinicaudata as well as most Cladoceromorpha.

DISCUSSION

Morphological Support for Onychocaudata

The morphological support for Onychocaudata was presented in Richter et al. (2007) and Olesen (2009) and is summarised briefly here.

Telsonal Region.—It has long been known that Spinicaudata, Cyclestherida, and many cladocerans (Ctenopoda and Anomopoda) have a quite similar telsonal region that is laterally compressed, a pair of claw-like and often curved caudal furcae, and with dorsal spines arranged in two rows (chrs. 36, 38, 40 in Olesen, 2009). This is different from Anostraca, Notostraca, and Laevicaudata, where this region is more cylindrical, and terminating in a pair of broad, flattened, setae-bearing cercopods (Anostraca), in a pair of long, slender, superficially articulated appendages (Notostraca), or in a pair of tri-angular lobes (Laevicaudata). It should be noted that all these supporting characters must be considered lost in raptorial water fleas (Gymnomera) (see character optimisations in Olesen, 2009).

Compound Eye Structures.—Richter et al. (2007) showed that the compound eyes of all investigated members of Spinicaudata, Cyclestherida, and Cladocera have exactly five cone cells in their ommatidia (pentapartite cone), which is a very unusual number within Crustacea; laevicaudatans, notostracans, and anostracans have four ommatidal cone cells (chr. 39 in Richter et al., 2007; chr. 47 in Olesen, 2009). Another important eye character concerns the fusion of the separate compound eyes into one globular medially placed eye. This has long been known from Cladocera but Sars (1887) was the first to note that the eyes are fused in *Cyclestheria hislopi* as well. However, in Richter et al. (2007) it was documented that the compound eyes in a number of spinicaudatans are also more or less fused, and that the degree of eye fusion between these and *C. hislopi* are too gradual to be divided into different character states. In representatives of Laevicaudata, however, the eyes are kidney-shaped, and a fusion of the ommatidial part appears only in the ventral area. In Notostraca the two compound eyes are very close together but are not in contact with each other. Compound eyes fused into one globular structure are therefore considered additional support for the Onychocaudata (see Richter et al., 2007; Olesen, 2009).

Table 1. Onychocaudata n. tax. inserted in the classificatory hierarchy of Branchiopoda based on the phylogeny in Fig. 1. The classification is identical to the one presented in Olesen (2009) but with fossils and various high-level taxa to accommodate fossils (Sarsostraca and Calmanostraca) excluded. Sister taxa in Fig. 1 (e.g., Anostraca and Phyllopoda, or Notostraca and Diplostraca) are placed with the same indentation symbolising their sister group relationship. Three taxa (Anomopoda, Ctenopoda, and Gymnomera) are placed with the same indentation indicating an unresolved trichotomy in Fig. 1.

- **Branchiopoda**
  - Anostraca
  - Phyllopoda
    - Notostraca
    - Diplostraca
      - Laevicaudata
      - **Onychocaudata n. tax.**
        - Spinicaudata
        - Cladoceromorpha
          - Cyclestherida
          - Cladocera
            - Anomopoda
            - Ctenopoda
            - Gymnomera
              - Haplopoda
              - Onychopoda

Other Morphological Support.—In the phylogenetic analyses of Richter et al. (2007) and Olesen (2009) a number of other character transformations got optimised as apomorphies for the clade we now name as Onychocaudata. This includes the carapace growth lines, which are present in Spinicaudata and Cyclestherida, lost again in Cladocera (perhaps more than once) (chr. 5 in Olesen, 2009). Another synapomorphy is the presence of small budlike first antennae in larvae or embryos (chr. 63 in Olesen, 2009). Yet another synapomorphy proposed by Richter et al. (2007) and Olesen (2009) is the lack of contribution of the trunk limbs to locomotion as it seen in Cladocera and apparently also in Spinicaudata (chr. 21 in Olesen, 2009). In Anostraca, Notostraca, and most certainly also in the fossil *Rehbachiella* and *Lepidocaris* from the Cambrian and the Devonian respectively, it is well known that the trunk limbs contribute to (*Rehbachiella* and *Lepidocaris*), or are even fully responsible for (Anostraca and Notostraca) locomotion. Also in Laevicaudata, the trunk limbs have a clear contribution to locomotion, despite being large and enclosed between the two valves of the carapace (Sars, 1896; Fryer and Boxshall, 2009).

Molecular Support for Onychocaudata

Much molecular-based phylogenetic work has been conducted on branchiopod crustaceans in recent years, which, combined with the morphology-based phylogenetic work (summarised above), have resulted in many aspects of the high-level phylogeny being relatively well understood, at least compared to other groups of Crustacea (see summary in Richter et al., 2007).

In molecular analyses, a clade for Onychocaudata has often been supported, but not universally. Based on a varying amount of data Spears and Abele (2000), Braband et al. (2002), Stenderup et al. (2006) all find some support for Onychocaudata, and in the more comprehensive analyses of deWard et al. (2006) combining six loci, this clade is also supported. The same is the case in two other works where Branchiopoda are a minor part of more comprehensive, sequence-heavy analyses of the entire Arthropoda (Regier et al., 2010; von Reumont et al., 2012). In the analyses of Richter et al. (2007), which combine sequence information from six loci with a morphological data set, the clade for Onychocaudata is also strongly supported.

Other Recent Classificatory Suggestions for Branchiopoda

Two high-level classifications of Crustacea employing classical Linnean ranking (class, order, etc.), both of which partly address branchiopod systematics, have appeared in recent years (Martin and Davis, 2001; Ahyong et al., 2011). The phylogeny-based branchiopod classification put forward in the present work (Table 1) is basically congruent with that of Martin and Davis (2001) but includes more taxa: Onychocaudata, Cladoceromorpha (Cyclestherida + Cladocera), and Gymnomera (Onychopoda + Haplopoda), all of which have received considerable support since Martin and Davis (2001). The more recent classification of Ahyong et al. (2011) differs from that of Martin and Davis (2001) in excluding Laevicaudata from Diplostraca, which in Ahyong et al. (2011) is restricted to encompass only Spinicaudata, Cyclestherida, and Cladocera (see also Pessaqo et al., 2011). However, in the present classification we prefer to retain Diplostraca with its original and more inclusive content since much evidence support its monophyly (morphology and some molecular datasets, see Richter et al., 2007). Excluding Laevicaudata from Diplostraca would create the need for a new name being synonymous with the original Diplostraca, something which appears very unreasonable, especially because the etymology of ‘Diplostraca’ refers to the ‘bivalved shell (= carapace)’ and therefore is an appropriate taxon name for the ‘bivalved branchiopods’ (clam shrimps and water fleas = Diplostraca). We consider the erection of a new taxon name (Onychocaudata) for those branchiopods with ‘claws on the tail’ to be a more logical step instead of restricting the content of Diplostraca.

Conclusions

Morphological and molecular data strongly supports a hitherto unnamed classificatory concept/hypothesis in branchiopod phylogeny: a clade consisting of Spinicaudata and Cladoceromorpha, which we propose to name ‘Onychocaudata.’ A recent classification has suggested restricting the name Diplostraca to a taxon with the same content as what we propose for Onychocaudata (= Diplostraca excluding Laevicaudata), but since there is still much evidence for a monophyletic Diplostraca with its original content (= Diplostraca incl. Laevicaudata), we prefer to retain use of the name Diplostraca this way. After all, Diplostraca refers to the ‘bivalved shell (= carapace)’ and is therefore an appropriate name for the ‘bivalved branchiopods.’ Continued research into the systematics of Branchiopoda will test the validity of Onychocaudata.

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