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Phylogeny of Branchiopoda (Crustacea) based on a combined analysis of morphological data and six molecular loci

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Abstract

The phylogenetic relationships of branchiopod crustaceans have been in the focus of a number of recent morphological and molecular systematic studies. Although agreeing in some respects, major differences remain. We analyzed molecular sequences and morphological characters for 43 branchiopods and two outgroups. The branchiopod terminals comprise all eight "orders". The molecular data include six loci: two nuclear ribosomal genes (18S rRNA, 28S rRNA), two mitochondrial ribosomal genes (12S rRNA, 16S rRNA), one nuclear protein coding gene (elongation factor 1α), and one mitochondrial protein coding gene (cytochrome *c* oxidase subunit I). A total of 65 morphological characters were analyzed dealing with different aspects of branchiopod morphology, including internal anatomy and larval characters. The morphological analysis resulted in a monophyletic Phyllopoda, with Notostraca as the sister group to the remaining taxa supporting the Diplostraca concept ("Conchostraca" + Cladocera). "Conchostraca" is not supported but *Cyclestheria hislopi* is the sister group to Cladocera (constituting together Cladoceromorpha) and Spinicaudata is closer to Cladoceromorpha than to Laevicaudata. Cladocera is supported as monophyletic. The combined analysis under equal weighting gave results in some respects similar to the morphological analysis. Within Phyllopoda, Cladocera, Cladoceromorpha and Spinicaudata + Cladoceromorpha are monophyletic. The combined analysis is different from the morphological analysis with respect to the position of Notostraca and Laevicaudata. Here, Laevicaudata is the sister group to the remaining Phyllopoda and Notostraca is sister group to Spinicaudata and Cladoceromorpha. A sensitivity analysis using 20 different parameter sets (different insertion–deletion [indel]/substitution and transversion/transition ratios) show the monophyly of Anostraca, Notostraca, Laevicaudata, Spinicaudata, Cladoceromorpha, Cladocera, and within Cladocera, of Onychopoda and Gymnomera under all or almost all (i.e., 19 of 20) parameter sets. Analyses with an indel-to-transversion ratio up to 2 result in monophyletic Phyllopoda, with Laevicaudata as sister group to the remaining Phyllopoda and with Spinicaudata and Cladoceromorpha as sister groups. Almost all analyses (including those with higher indel weights) result in the same topology when only ingroup taxa are considered.

Branchiopoda comprise approximately 1180 described species of mainly freshwater dwelling crustaceans (Adamowicz and Purvis, 2005). It includes taxa with a general, archaic morphology very similar to that of some Cambrian and Devonian crustacean fossils (Anostraca, Notostraca, Spinicaudata), as well as taxa that are highly specialized for predatory, scraping, parasitism, and advanced filtration such as the water fleas (Scourfield, 1926; Fryer, 1968, 1974, 1987, 1991; Martin, 1992; Dumont and Negrea, 2002; Fayers and Trewin, 2003; Olesen, 2004).

Calman (1909) (based on works by G.O. Sars) divided the Recent Branchiopoda into four subtaxa, Anostraca, Notostraca, Conchostraca and Cladocera, a division that was accepted as undisputed until the late 1980s, when Fryer (1987) expressed doubt about the naturalness of a number higher-level taxa (Conchostraca and Cladocera) and recognized eight orders of Recent branchiopods: Anostraca, Notostraca, Laevicaudata, Spinicaudata, Anomopoda, Ctenopoda, Haplopoda and Onychopoda.

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Only a few morphology-based phylogenetic analyses dealing with higher-level phylogeny/classification of Branchiopoda have been published (Olesen, 1998, 2000; Negrea et al., 1999), while molecular systematics has attracted more interest in this taxon (e.g., Hanner and Fugate, 1997; Taylor et al., 1999; Spears and Abele, 2000; Braband et al., 2002; Swain and Taylor, 2003; deWaard et al., 2006; Stenderup et al., 2006). Virtually no other crustacean taxon has seen so much interest from molecular systematists and in no other group does a consensus of relationships of higher taxa seem closer.

Among the most important results of largely all of these recent phylogenetic attempts is the support of various classical groupings such as Cladocera (water fleas), and often also of Phyllopoda (all nonanostracan branchiopods), and Gymnomera (raptorial water fleas), while ''Conchostraca'' and Spinicaudata *sensu* Linder (1945) have turned out to be paraphyletic with respect to Cladocera, as the former spinicaudatan, *Cyclestheria hislopi*, in practically all analyses comes out as sister group to Cladocera. The validity of Diplostraca (''Conchostraca'' and Cladocera) is still being discussed, and especially the position of Laevicaudata is under debate (e.g., Richter, 2004). Diplostraca was recently suggested to be paraphyletic with respect to Notostraca (Stenderup et al., 2006). Branchiopoda itself is supported as monophyletic in various recent combined or molecular analyses (e.g., Giribet et al., 2005; Regier et al., 2005) and has been supported recently based on morphological evidence (Olesen, 2007).

Despite much morphological information being available in older and more recent literature, this type of data is severely underrepresented in recent studies on branchiopod phylogeny. The present work attempts to fill this gap. The morphological data set used in this work builds on Olesen (1998, 2000), but many characters have been reinterpreted and the present data set includes much new information on larval development and internal anatomy. Molecular data from six genes are included in the present study. Morphological and molecular data have been analyzed separately, but also in combination.

The intention of this study is to test the stability of the various suggestions of branchiopod phylogeny based on sensitivity analysis (Wheeler, 1995; Giribet, 2003). Sensitivity analysis applies different weighting schemes (parameter sets) for unobservable processes such as insertions/deletions and substitutions. We are aware that the sensitivity analysis has been criticized as not providing additional evidence for the validity of clades (Grant and Kluge, 2003, 2005), but, in our view, sensitivity analysis nevertheless adds to our understanding of data structure. It is not the dominant goal of the present paper to distinguish between well supported and weakly supported clades based on sensitivity analysis but to provide a better understanding on previous (which are often based on a single model or parameter set) and present results in the light of dependence of different analytical parameters.

Materials and methods

Molecular data

Taxon sampling

For this study molecular sequences from 26 species were newly generated. Voucher specimens from the same locality and identified by the same collector were deposited at Zoological Museum, University of Copenhagen (ZMUC). Data for additional species were taken from GenBank (in many cases provided by previous studies of the authors of the present paper). In total, molecular sequences and morphological characters for 43 branchiopods and two outgroups were included in the analyses (Table 1). The branchiopod terminals comprise all eight ''orders'' with a particular focus on an extended taxon/loci sampling of Notostraca, Laevicaudata and Spinicaudata. All four cladoceran ''orders'' are included but not all of the traditional ''families''. The major focus of our work is on the relationships of the eight higher taxa including testing of their monophyly. As outgroups, representatives of Malacostraca (*Paranebalia longipes*) and of Cephalocarida (*Hutchinsoniella macracantha*) were chosen, both taxa of which were considered close to Branchiopoda by Hessler (1992) and placed in his Thoracopoda, although phylogenetic relationships of higher crustacean taxa are far from being resolved. The choice of outgroups for Branchiopoda is difficult and often creates problems (see also Braband et al., 2002; Stenderup et al., 2006). The small number of outgroups implies that the test of branchiopod monophyly is not particularly rigorous but this seems now very well supported and is not in the focus of the present study.

DNA isolation, amplification and sequencing

Laboratory work was conducted at the Molecular Systematics Laboratory at the American Museum of Natural History Museum (AMNH). Genomic DNA was extracted from ethanol-preserved tissue using the Qiagen DNeasy Tissue Kit, DNeasy Protocol for Animal Tissues (Qiagen, Valencia, CA). Double stranded template, suitable for sequencing, was prepared by polymerase chain reaction (PCR) amplification with the primers listed in Table 2. The 18S rRNA fragment was amplified in three overlapping sections, using the following primer pairs: 18S1F/18S5R, 18S3F/18Sbi, 18Sa2.0/18S9R (Giribet et al., 1996; Whiting et al., 1997). A partial sequence of 28S rRNA was also amplified using three primer pairs: 28Srd1a/28Sb, 28Sa/28Srd5b, and 28Srd4.8a/28Srd7b1, or instead of the two first pairs alternatively (sometimes additionally) 28Srd1a/28Srd4b,

Table 1
List of species included in this study. GenBank accession numbers for each molecular locus. Sequences generated for this study are in bold font type

		18S rRNA	28S rRNA	16S rRNA	12S rRNA	COI	EF1α
Branchinella occidentalis	Paroo area, NSW, Australia	AY744888	AY744895	**EF189600**	AF994485	**EF189664**	NA
Artemia sp.		AJ238061	X01723	AF209051	X69067	NC001620	X03349
Parartemia minuta	Paroo area, NSW, Australia (ZMUC CRU-9939)	**EF189631**	**EF189656**	**EF189613**	AF494484	AF209059 (contracta)	NA
Branchinecta paludosa		AF144206	DQ470650, AY137141	DQ470608	NA	AF209064	NA
Eubranchipus grubeii		AJ293894 (serratus)	DQ470652	DQ470610	NA	AF209061 (spec.)	NA
Thamnocephalus platyurus		AF144217	DQ470653, AF209046	DQ470611	NA	AF209066	NA
Triops cancriformis	Morava flood plain, Austria (ZMUC CRU-9950)	**EF189638**	**EF189663**	**EF189617**	AF494482	**EF189678**	**EF189596**
Triops australiensis	Paroo area, NSW, Australia (ZMUC CRU-9940)	**EF189637**	**EF189662**	**EF189616**	AY050646	**EF189677**	**EF189595**
Triops longicaudatus		AF144219	AY157606	AY115610	AY115600	NA	U90058
Lepidurus apus	Spandauer Forst, Berlin, Germany (ZMUC CRU-9941)	**EF189623**	**EF189647**	DQ470599	AF494483	**EF189669**	AF526293
Lepidurus arcticus		AF070112	DQ470639, AF209047	DQ470597	AJ583701	NA	NA
Lynceus brachyurus		AF070115	DQ470646, AY137136	DQ470604	AF494480	NA	NA
Lynceus biformis	Lake Biwa area, Japan (ZMUC CRU-9942)	**EF189628**	**EF189653**	**EF189611**	AF494481	**EF189672**	**EF446669**
Lynceus tatei	Paroo area, NSW, Australia (ZMUC CRU-9943)	**EF189629**	**EF189654**	**EF189612**	AF494479	**EF189673**	AF526294
Leptestheria kawachiensis	Lake Biwa area, Japan (ZMUC CRU-9944)	**EF189625**	**EF189649**	**EF189607**	AF494477	NA	NA
Leptestheria dahalacensis	Morava flood plain, Austria (ZMUC CRU-9945)	**EF189624**	**EF189648**	**EF189606**	AF494476	**EF189670**	AF526291
Caenestheria lutraria	Paroo area, NSW, Australia (ZMUC CRU-9946)	**EF189618**	**EF189639**	**EF189601**	**EF189597**	**EF189665**	**EF189592**
Caenestheriella gifuensis	Lake Biwa area, Japan (ZMUC CRU-9947)	**EF189619**	**EF189640**	**EF189602**	**EF189598**	NA	NA
Imnadia yeyetta	Morava flood plain, Austria	**EF189622**	**EF189646**	**EF189605**	AY009487	**EF189668**	AF526289
Limnadia lenticularis	Morava flood plain, Austria (ZMUC CRU-9948)	**EF189627**	**EF189651**	**EF189609**	AF494471	**EF189671**	AF063412
Limnadopsis birchii	Paroo area, NSW, Australia	AY744889	**EF189652**	**EF189610**	AF494472	NA	AF526290
Eulimnadia braueriana	Lake Biwa area, Japan (ZMUC CRU-9949)	**EF189621**	**EF189644**	**EF189604**	**EF189599**	**EF189667**	**EF189593**
Cyclestheria hislopi	Jabiru, NT, Australia (ZMUC CRU-9951)	AF144209	**EF189642**	**EF189603**	AF494478	DQ310631	AF526292
Leptodora kindtii	Tegeler See, Berlin, Germany (ZMUC CRU-9952)	**EF189626**	**EF189650**	**EF189608**	AY009488	DQ310659	AF526278
Bythotrephes longimanus		L34043 (*B.cederstroemi*)	DQ470629	DQ470587	AY009493	AF435129	NA

Table 1
Continued

		18S rRNA	28S rRNA	16S rRNA	12S rRNA	COI	EF1α
Cercopagis pengoi	Russia, Caspian Sea (ZMUC CRU-9953)	**EF189620**	**EF189641**	EF158458	AY009494	AF320013	NA
Polyphemus pediculus	Nikolassee, Berlin, Germany	**EF189633**	**EF189658**	DQ470588	AY009495	AY075048	NA
Podon leuckarti		AF532895, AY137189, AY075087	DQ470631	DQ470589	AY009496	AY075051	AF526287
Evadne nordmanni		AF532900, AF532896, AY075084	DQ470632	DQ470590	AY009498	AY075049	AF526288
Cornigerius maeoticus		AY075083	EF158452	EF158455	AY009503	AY075047	NA
Sida crystallina		AF070121, AF070516	DQ470636	DQ470594	AY009490	AF277891	AF526280
Diaphanosoma brachyurum	Nikolassee, Berlin, Germany (ZMUC CRU-9954)	AF144210 (spec.)	**EF189643**	DQ470593	AY009489	**EF189666**	AF526279
Penilia avirostris	Banyuls-sur-Mer, France (ZMUC CRU-9955)	**EF189632**	**EF189657**	DQ470595	NA	**EF189674**	NA
Eurycercus lamellatus		AF070503, AF070109 (longirostris)	EF158453	EF158456	AF494468	NA	AF526285
Pseudochydorus globosus	Nikolassee, Berlin, Germany (ZMUC CRU-9956)	**EF189634**	**EF189659**	**EF189614**	AF494469	**EF189675**	AF526286
Daphnia pulex		AF014011	DQ470613	DQ470571	AF117817	AY380449	NA
Simocephalus vetulus	Lower Oder, Brandenburg, Germany (ZMUC CRU-9957)	**EF189636**	**EF189661**	DQ470576	AY009492	NA	AF526281
Scapholeberis mucronata	Lower Oder, Brandenburg, Germany	**EF189635**	**EF189660**	**EF189615**	AF494465	**EF189676**	AF526282
Ceriodaphnia spec.		NA	DQ470627 (pulchella)	DQ470585 (pulchella)	AF494466 (megops)	DQ310634 (spec.)	AF526283 (megops)
Ilyocryptus spec.		AF070506 (spec.)	EF158454 (agilis)	EF158457 (agilis)	AF494470 (spec.)	DQ310638 (spec.)	NA
Ophryoxus gracilis		AF070117	DQ470619, AF532881	DQ470578	NA	DQ310637	NA
Acantholeberis curvirostris		AF070093	DQ470618	DQ470577	NA	DQ310639	NA
Bosmina coregoni		AY075093	DQ470615 (longirostris)	AY264726	AF494467	AY075057	AF526284
Paranebalia longipes	Bermuda	**EF189630**	**EF189655**	AY744909	NA	NA	NA
Hutchinsoniella macracantha	New Bedford, MA, USA	AF370801	**EF189645**	AF370875	NA	AF370852	AF063411

NA, not available.

Table 2
Primers used in this study

18S rRNA	1F	5′-TAC CTG GTT GAT CCT GCC AGT AG-3′
	5R	5′-CTT GGC AAA TGC TTT CGC-3′
	3F	5′-GTT CGA TTC CGG AGA GGG A-3′
	Bi	5′-GAG TCT CGT TCG TTA TCG GA-3′
	A2.0	5′-ATG GTT GCA AAG CTG AAA C-3′
	9R	5′-GAT CCT TCC GCA GGT TCA CCT AC-3′
28S rRNA	rd1a	5′-CCC SCG TAA YTT AGG CAT AT-3′
	28Sb	5′-TCG GAA GGA ACC AGC TAC-3′
	rd4b	5′-CCT TGG TCC GTG TTT CAA GAC-3′
	28Sa	5′-GAC CCG TCT TGA AAC ACG GA-3′
	28Sbout	5′-CCC ACA GCG CCA GTT CTG CTT ACC-3′
	rd3a	5′-AGT ACG TGA AAC CGT TCA GG-3′
	rd4.8a	5′-ACC TAT TCT CAA ACT TTA AAT GG-3′
	rd7b1	5′-GAC TTC CCT TAC CTA CAT-3′
12S rRNA	12Sai	5′-AAA CTA GGA GTA GAT ACC CTA TTA T-3′
	12Sbi	5′-AAG AGC GAC GGG CGA TGT GT 5′
16S rRNA	16Sa	5′-CGC CTG TTT ATC AAA AAC AT-3′
	16Sb	5′-CTC CGG TTT GAA CTC AGA TCA-3′
COI	LCO1490	5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′
	HCOOUTOUT	5′-GTA AAT ATA TGR TGD GCT C-3′
EF1α	HaF2For1	5′-GGG YAA AGG WTC CTT CAA RTA TGC-3′
	2R53ST	5′-CAG GAA ACA GCT ATG ACG CGA ACT TGC AAG CAA TGT GAG C-3′

28Sa/28SBout and 28Srd3a/28Sb (Schwendinger and Giribet, 2005; Edgecombe and Giribet, 2006; AMNH laboratory). Primer pairs 12Sai/12Sbi (Kocher et al., 1989), 16Sa/16Sb, LCO/HOCOoutout (Folmer et al., 1994; Schwendinger and Giribet, 2005), HaF2-For1/2R53ST (AMNH laboratory) were, respectively, used to amplify fragments of 12S rRNA, 16S rRNA, cytochrome *c* oxidase subunit I (COI) and elongation factor 1α (EF1α).

Amplification was conducted using Ready-To-Go PCR beads (GE Healthcare, Buckinghamshire, UK) to which were added 1 μL per reaction of each 10 μM primer, 21 μL of water, and 2 μL of DNA. The PCR program consisted of an initial denaturing step at 94 °C for 1 min, 35 amplification cycles (94 °C for 15 s, 48 °C for 15 s, 72 °C for 15 s) and a final step at 72 °C for 6 min using an MJ Research Tetrad four-head thermocycler (Bio-Rad, Hercules, CA). Specific conditions (e.g., annealing temperature) were optimized for taxa and primer pairs. PCR products were verified on 1% agarose/TBE electrophoretic gels.

Products were purified using the TeleChem Array-it Kit (TeleChem International, Sunnyvale, CA) by eluting the product in 80 mL binding buffer/20 μL TE buffer, four washing steps, dehydrating in a speed-vac using a Biomek 2000 liquid-handler, and the cleaned product re-suspended in 100 μL water. Alternatively, PCR products were purified using AMpure™ Cleanup (Agencourt, Bioscience Corp., Beverly, MA) by using AMPure, after washing in 70% ethanol using a magnetic plate, re-suspending the PCR product in water, using Beckman-Coulter Biomek 2000 and Biomek Nx liquid-handlers.

Double-stranded sequencing of the PCR products was conducted by the dideoxy termination method (Sanger et al., 1977) using an automated Applied Biosystems Inc. (ABI) Prism™ 3730xl DNA sequencer. The same primers were used as for the PCR. Samples were cycle-sequenced using dye-labeled terminators (ABI Prism™ BigDye™ Terminator Cycle Sequencing Ready Reaction Kit v1.1, Foster City, CA, USA) in a Tetrad 4-head thermocycler. Cycle-sequencing was conducted in an 8 μL reaction, consisting of 1 μL BigDye, 1 μL BigDye Extender (ABI), 1 μL 3.2 μM primer, and 5 μL cleaned PCR product. The cycle-sequencing program consisted of 25 amplification cycles (96 °C for 15 s, 50 °C for 15 s, 60° for 4 min). BigDye-labeled cycle-sequence products were cleaned by isopropanol/ethanol precipitation: 40 μL 70% isopropanol added, centrifuged for 30 min at 2109 ***g***, microtiter plate inverted and centrifuged for 1 min at 43 ***g***, 40 μL ethanol added, centrifuged for 30 min at 2109 ***g***, microtiter plate inverted and centrifuged for 1 min at 43 ***g***, air dried for 30 min, re-suspended in 10 μL ABI Hi-Di Formamide and loaded in microtiter plates on to the ABI 3730xl sequencer. Alternatively to the isopropanol/ethanol precipitation, CleanSeq™ Cleanup (Agencourt) was used for precipitation by adding to the sequencing reaction product, followed by two steps of washing in 85% ethanol using magnetic plates, and re-suspending the dried product in 40 μL 0.5 mM EDTA.

DNA sequence editing

The accuracy of sequences was tested by independently amplifying and sequencing the complementary strands of all fragments. Chromatograms obtained from the automated sequencers were read and contigs made using Sequencher™ Ver. 4.1.4 (Gene Codes Corporation, Ann Arbor, MI, USA). Primer sequences were

removed and consensus sequences were created from the complementary strands.

A total of 87 sequences from 26 species were generated for this study: 21 sequences of 18S rRNA, 25 sequences of 28S rRNA, 18 sequences of 16S rRNA, three sequences of 12S rRNA, 15 sequences of COI and five sequences of EF1α. All new sequences have been deposited in GenBank (see accession codes in Table 1). The length of the successfully sequenced 18S rRNA varied between 1757 bp and 2139 bp, of the sequenced 28S rRNA between 1094 bp and 2548 bp, of the 16S rRNA between 482 bp and 582 bp, of the COI between 780 and 848 bp, of the EF1α between 822 and 975 bp, and of the 12S rRNA between 341 bp and 347 bp.

In addition to our own 87 sequences, 146 sequences were added from GenBank. The taxon sampling was complete for the 16S rRNA and the 28S rRNA (but not always including the entire length), and almost complete (44 of 45 taxa) for the 18S rRNA. A total of 37 sequences were considered for the 12S rRNA, a total 35 for COI and a total of 26 for EF1α (see Table 2). Complete sequences were edited in GDE (Smith et al., 1994), where they were divided according to primer delimited regions and secondary structure features (e.g., Giribet and Wheeler, 2001).

18S rRNA: The complete sequence of the small nuclear ribosomal subunit has been shown in various analyses to be useful for analyzing arthropod relationships. The sequences were divided into 20 fragments (17 fragments analyzed; fragments 4, 8 and 14 were not analyzed because of major length differences, intraspecific variability and several repetitive elements in Cladocera). Length: "large branchiopods" about 1760 bp; Cladoceromorpha about 2100–2200 bp. An average of 1300 bp were included in the analysis.

28S rRNA: The large nuclear ribosomal subunit has also been used in previous analyses of arthropod relationships. Herein, we use an extended part of the 28S rRNA. The sequences were divided into 21 fragments (19 fragments analyzed; fragments 6 and 18 were excluded because of major length differences and intraspecific variability). Length: about 2100–2300 bp (2500 bp in *Paranebalia*). An average of 1454 bp were included in our analyses.

16S rRNA: A fragment of the mitochondrial ribosomal large subunit has been used recently in analyses of branchiopod relationships (deWaard et al., 2006; Stenderup et al., 2006). We divided the sequences into nine fragments; all of them were included in the analyses. An average of 500 bp were included in our analyses.

12S rRNA: The mitochondrial ribosomal small subunit has also been shown to be informative in branchiopod phylogeny (Richter et al., 2001; Braband et al., 2002). The sequences have been divided into eight fragments (six fragments analyzed; fragments 1 and 8 were not analyzed because of the lack of data for most taxa). An average of 503 bp were included in our analyses.

COI: A fragment of 786 bp of the mitochondrial protein coding gene cytochrome *c* oxidase subunit I has been analyzed as a single piece due to the fact that no sequence length variation appears. COI was also previously used in molecular phylogenetic analyses of Branchiopoda (deWaard et al., 2006).

EF1α: Partial sequence of the nuclear protein coding gene EF1α has been shown as useful in a previous analysis of branchiopod relationships (Braband et al., 2002). We excluded the introns and analyzed the exons as a single fragment of 993 bp.

In total, we have included an average of 4747 bp for each taxon, spanning from 1990 to 6373 bp. In a few cases, partitions from congeneric species have been combined into one terminal (see Table 1).

Morphological characters

The character list includes morphological characters from external morphology, anatomy of different organ systems, and developmental characters. An exemplar approach (*sensu* Prendini, 2001) has been used in most cases, which means that characters are scored only for those species where they have been observed. In some cases, observations in other closely related taxa (e.g., congeneric) were scored. We used characters from our own observations as well as from the published literature. In particular, for the characters relating to eye structure, information is included here that is presented for the first time. Histological methods and preparation for SEM were the same as described for example in Olesen et al. (2003).

If higher taxa are mentioned in the character description, this is for the convenience of the reader only and does not imply the scoring of the supposed ground pattern of these higher taxa for the exemplars. We also decided in most cases to divide the character into a high number of states in order to avoid unjustified assumptions. The character list mainly focuses on characters that are informative for the resolution of the relationships between "higher taxa." In particular, characters only important for resolving the relationships within certain species-rich taxa such as Anomopoda were not considered because this fell outside the scope of the present study. Our morphological analysis provides, therefore, less resolution than the molecular partitions.

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

In the following, we use the term "abdomen" as referring to the posterior limb-less body segments (following Walossek and Müller, 1998). The homology between the different "abdomens" in various branchiopods is not completely settled due to lack of detailed

developmental studies, in particular, developmental genetic information addressing this question. Herein, the abdomens in all taxa are treated as potentially homologous. A six-segmented abdomen is present in all species of Anostraca (all scored 0). The number of abdominal segments in Notostraca is variable (Longhurst, 1955) but several limb-less segments are always present in all species (scored 0). In Laevicaudata, Spinicaudata and Cyclestherida, there is no abdomen (Fryer, 1987). The situation in Cladocera is more complicated. An abdomen is present in *Leptodora* (scored 0; see Olesen et al., 2003 for a discussion of potential interpretations of this body region) as well as in *Bythotrephes* and *Cercopagis* (scored 0), whereas no abdomen seems to be present in the other onychopods as well as in Ctenopoda and Anomopoda, but in these latter taxa the tagmatization is often obscured posteriorly (scored 1). The unsegmented posterior part of the body of cladocerans are often referred to as the "postabdomen" (e.g., Flößner, 2000), as the exact homologies to a crustacean telson traditionally has been difficult to establish (see Discussion of chars 31–32).

We considered the single limb-less segment in Leptostraca as abdominal following Lauterbach (1975) and Walossek and Müller (1998), and developmental evidence showing that anlagen of even more limb-less segments may be present (Olesen and Walossek, 2000). Cephalocarida also possess a limbless abdomen (both taxa scored 0).

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

The food groove, a medio-ventral channel formed by the sternites between the limbs, has generally been considered an autapomorphy of Branchiopoda (Walossek, 1993; Olesen, 2004). It is present in almost all branchiopod taxa but absent in the raptorial (macrophagous) cladocerans (Onychopoda and Haplopoda; both scored 1) (Fryer, 1987). A food groove is also lacking in Leptostraca and Cephalocarida (both scored 1) despite the fact that both taxa are filter feeders (Cannon, 1927; Sanders, 1963; Walossek, 1993).

3. Carapace: (0) absent; (1) present

A carapace, or modifications of a carapace (brood pouch in Haplopoda and Onychopoda), is, except in Anostraca, present in all branchiopods. In particular, the early development of the carapace is rather similar in a number of taxa. In *Cyclestheria hislopi*, the carapace develops as a pair of swellings behind the "naupliar" head portion, and in later stages the carapace overgrows the head and becomes bivalved (Olesen, 1999) (see also Fig. 1D). Also in spinicaudatan clam shrimps (Sars, 1896; Olesen and Grygier, 2003, 2004; Pabst and Richter, 2004) and in various cladocerans (Olesen, 1998; Olesen et al., 2003), the carapace develops as a pair of swellings behind the head region (Fig. 1C,E). These similarities in carapace development indicate homology of diplostracan carapaces. The carapace has a modified development in Laevicaudata (Gurney, 1926; Fryer, 1996; Olesen, 2005) with an abrupt shift in morphology from a naupliar dorsal shield to a bivalved juvenile/adult carapace. The early development of the juvenile/adult carapace takes place within the naupliar shield, just behind the head portion (behind the dorsal organ), and is in this respect similar to other Diplostraca. In *Cyclestheria hislopi*, Spinicaudata and in various cladocerans, such as *Leptodora kindtii*, there is a clear distinction dorsally between the head region and the carapace. Walossek (1993, 1995) used this distinction to hypothesize that the type of carapace in Diplostraca (= Onychura) is non-homologous to carapaces in other branchiopods such as Notostraca and the Upper Cambrian branchiopod *Rehbachiella kinnekullensis*, and he suggested a specific term—"secondary shield"—for the diplostracan carapace. A recent study on the carapace development of *Triops cancriformis* (Notostraca) (Møller et al., 2003), however, shows that the development is rather similar to that of diplostracan branchiopods (Fig. 1A,B). Homology between the notostracan carapace and the carapace in various diplostracans seems therefore convincing, which is why we prefer to use the term carapace in all branchiopods. Other evidence in favor of homology between branchiopod carapaces is the fact that the very long and curled ducts of the maxillary glands are placed in the valves of the carapace between the inner and outer carapace integument in most, if not all phyllopods (Cannon and Manton, 1927). Fryer (1996) reached a similar conclusion on the homology of carapaces based on the cephalic origin of all branchiopod carapaces and thereby being in agreement with the "definition" on a carapace put forward by Calman (1909). However, a dorsal "disconnection" between the head region and the carapace as the one seen in various diplostracans ("secondary shield" *sensu* Walossek, 1993), could qualify a synapomorphy, but at the moment we find it difficult to define such a character clearly. We scored all taxa (1) except the representatives of Anostraca (scored 0).

We decided to consider the carapace in Leptostraca as homologous (following Fryer, 1996 and others) (scored 1), whereas a carapace is absent in Cephalocarida (scored 0).

4. Shape of the carapace: (0) carapace covers limbs and head; (1) carapace covers limbs but the head is free; (2) carapace as a dorsal brood pouch; (3) carapace as a dorsal shield not covering the limbs (carapace is fused with head shield)

The carapace covers the limbs and extends over the head in Spinicaudata (Sars, 1896), Cyclestherida (Sars, 1887b), and Laevicaudata (although in the latter taxon, the animals are able to move their head outside the carapace) (Martin and Belk, 1988) (all scored 0). In Ctenopoda and Anomopoda, the carapace covers the limbs but the head is free (scored 1), whereas in Onychopoda and Haplopoda the carapace is a dorsal brood

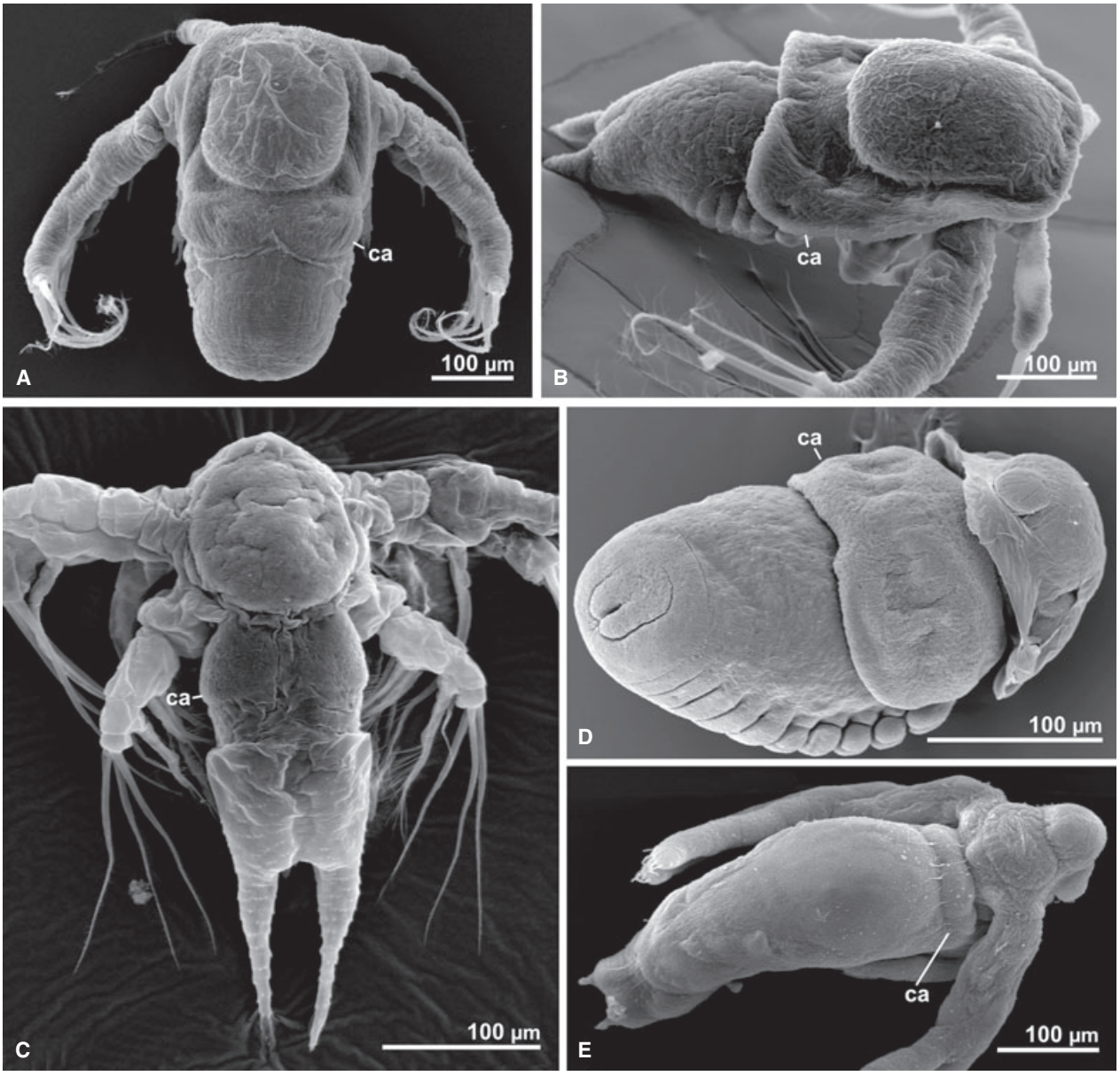

Fig. 1. Branchiopod larvae showing early development of carapace (c). All dorsal or semidorsal view. (A) *Triops cancriformis* (Notostraca), stage 1. (B) *Triops cancriformis* (Notostraca), stage 2. (C) *Caenestheriella gifuensis* (Spinicaudata), stage 3. (D) *Cyclestheria hislopi* (Cyclestherida), stage 4. (E) *Leptodora kindtii* (Haplopoda), stage 3. Partly from Olesen (1999), Olesen et al. (2003), Olesen and Grygier (2004), Møller et al. (2003).

pouch (Olesen et al., 2003). Although the homology of this brood pouch between Haplopoda and Onychopoda has been questioned and differences have been emphasized (Fryer, 1987), the fact remains that only in these two taxa the carapace does not cover the limbs (scored 2). The condition in Notostraca is unique (scored 3), and Anostraca are scored as inapplicable. Leptostraca is scored (0) although the head is not entirely covered by the carapace (Cannon, 1960). Cephalocarida is scored as inapplicable.

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

Representatives of Spinicaudata and Cyclestherida are well known for having carapace growth lines. Each growth line represents the remaining carapace of the previous moult (scored 1). In most cases, the growth lines are present as semicircles surrounding the umbo of the carapace in some distance. In Laevicaudata and Cladocera, growth lines are in most cases absent. However, there is one description of growth lines in Laevicaudata (Linder, 1945), but the significance of this observation is uncertain and has not been confirmed. It does not concern the species of Laevicaudata studied herein, which are therefore scored (0). Growth lines are absent in Ctenopoda. A few species of Anomopoda have growth lines at the carapace (e.g., *Monospilus* and some

species of *Ilyocryptus* but not *I. agilis* considered in our analysis; see Fryer, 1999a). Growth lines are scored absent for Onychopoda, Haplopoda, Notostraca, and for Leptostraca (scored 0). Anostraca and Cephalocarida are scored inapplicable.

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

7. Position of male genital opening: (0) the sperm ducts open at the 12 (or 20th) segment; (1) base of the 11th pair of limbs through a simple pore; (2) paired genital openings behind the 6th 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 3rd abdominal segment; (6) at the base of the 8th thoracopods; (7) at the base of the 6th thoracopods

Oviducts lead from the ovaries to openings at the base of thoracic limbs in Notostraca (Sars, 1896), Spinicaudata (Sars, 1896), and Cyclestherida (Sars, 1887b) (char. 6; all scored 2). In certain Spinicaudata, the eggs originate from epipods (Tommasini and Scanabissi Sabelli, 1989), which is also at the base of the thoracopods. The ovaries lead to openings within the dorsal carapace in Cladocera (Weissmann, 1876–1879; Dumont and Negrea, 2002) (char. 6; scored 1), to an ovisac within the ventral brood pouch in Anostraca (Sars, 1896); (char. 6; scored 0), or to the base of trilobed, flap-like lamellar extensions of the body wall (Laevicaudata) (char. 6; scored 3) (summarized by Martin, 1992). In Leptostraca, the oviducts lead to the coxae of the 6th thoracic limbs (Cannon, 1960) (char. 6; scored 2). In Cephalocarida, the oviducts and testes exit at the posterior face of the protopod of the 6th thoracic limbs (Hessler and Elofsson, 1992); (char. 6; scored 2).

In Anostraca, the sperm ducts open at the 12th (or 20th, depending on the number of trunk limbs) segment (char. 7; scored 0) (Martin, 1992). In Notostraca and Spinicaudata, the genital pores are at the base of the 11th pair of limbs and open through a simple pore (char. 7; scored 1). In Laevicaudata, the situation seems to be uncertain since Sars (1896) described a position apparently similar to the females (see above), whereas Linder (1945) suggested that they open alongside the anal opening (see also Martin, 1992), which, if so, perhaps is similar to the situation in anomopods (see state 4). In *Cyclestheria*, the position of the male genital opening is uncertain. In Ctenopoda, the paired genital openings lie behind the last pairs of limbs (sometimes leading into a double copulatory organ) (char. 7; scored 2). In Onychopoda, the sperm ducts end between limb IV and the anus (Rivier, 1998) (char. 7; scored 3), in *Leptodora* at the 3rd abdominal segment (char. 7, scored 5). Only in Anomopoda, the vasa deferentia are fused and lead to different positions at the telson (char. 7; scored 4) (Sars, 1993; Dumont and Negrea, 2002). In Leptostraca, the male genital opening are at the bases of the 8th thoracic limbs (char. 7; scored 6). For Cephalocarida see char. 6 (char. 7, scored 7).

8. Antennule: (0) present; (1) reduced, only sensillae present

9. Antennule: (0) without lobes; (1) lobate

10. Antennular sensillae: (0) sensillae not restricted to tip; (1) sensillae restricted to the tip

Most adult branchiopods, at least in males, have distinct but sometimes very small tubular antennules (char. 8, scored 0). In the Podonidae (three species in this work), the antennules are always reduced and only two clusters of five sensillae are present (char. 8, scored 1; Richter and Olesen unpublished). In all Spinicaudata, the antennules are along most of their length divided into sensillae-bearing lobes (Olesen et al., 1997) (char. 9, scored 1). In the other branchiopods and in the two outgroups, such lobes are not present (char. 9, scored 0). The Podonidae are scored as inapplicable. Character 10 concerns the position of the sensillae on the antennules. In all cladocerans, at least in females (males can have rather specialized antennules as in *Leptodora* or *Moina*), the antennular sensillae are restricted to the tip (scored 1). The same is seen for Anostraca and females of *Cyclestheria hislopi* (Cyclestherida) (scored 1). Sars (1896) depicted and described the reduced antennules in an adult of *Lepidurus arcticus* (Notostraca) as having a rather swollen distal part with three sensory setae distally and several rows of sensory structures along its side (scored 0). In Spinicaudata and Laevicaudata (see Martin and Belk, 1988), the antennular sensillae are not restricted to the tip (scored 0). In Leptostraca and Cephalocarida, antennular sensillae are not restricted to the tip only (scored 0).

11. Antenna in adults, length of rami: (0) rami of different length, endopod shortest; (1) rami of similar length ("symmetrical")

Adults of Spinicaudata, Laevicaudata, Cyclestherida and Cladocera have antennae with rami that are relatively similar to each other ("symmetrical" rami) (scored 1). In the case of Spinicaudata, Laevicaudata and Cyclestherida, they are many-segmented (at least seven) while fewer segments are present in Cladocera (two to four segments). The exact number of segments in the antennal rami is treated separately in the following characters. Adults of Anostraca and Notostraca have reduced or much modified antennae; therefore, both taxa are scored as inapplicable. In Leptostraca, one antennal ramus is reduced (scored as inapplicable). *Hutchinsoniella* (Cephalocarida) has an antennal exopod with 19 segments and a shorter endopod with only two segments (scored 0).

12. Antennae in adults, number of segments in exopod: (0) seven segments or more; (1) four segments; (2) three segments; (3) two segments

Adult Anostraca and Notostraca have modified or highly reduced antennae so they are scored as inapplicable for this character. Laevicaudata, Spinicaudata and Cyclestherida all have a relatively high number of exopodal segments (at least seven) (scored 0). *Leptodora* (Haplopoda), all Onychopoda, and most species of Anomopoda (only excluding the Chydoridae) have four exopodal segments (scored 1). The Chydoridae have three exopodal segments (scored 2). In Ctenopoda, a varying number of three (*Penilia*, *Sida*; scored 2) and two (*Diaphanosoma*; scored 3) segments are found (see Olesen, 1998; for a summary). Adult *Hutchinsoniella* (Cephalocarida) have 19 segments in the exopod (scored 0). Leptostraca is scored inapplicable as the second antenna is uniramous, and it is uncertain which ramus has been reduced.

13. Antennae in adults, number of segments in endopod: (0) seven segments or more; (1) four segments; (2) three segments; (3) two segments

Adult Anostraca and Notostraca have modified or highly reduced antennae so they are scored as inapplicable for this character. Laevicaudata, Spinicaudata and Cyclestherida all have a relatively high number of exopodal segments (at least seven) (scored 0). *Leptodora* (Haplopoda) has four endopodal segments (scored 1). In all representatives of Anomopoda, Onychopoda, and in the ctenopod *Diaphanosoma*, three endopodal segments are present (scored 2). In other included ctenopods (*Penilia* and *Sida*), the antennal endopod has two segments (Flößner, 2000) (scored 3). Leptostraca has only one antennal ramus and is therefore scored inapplicable for this character. *Hutchinsoniella* (Cephalocarida) has two endopodal segments (scored 3).

14. Mandible gnathal edge: (0) with incisor and molar process; (1) ellipsoid molar process, with pores; (2) with separate teeth

Two different kinds of mandibular gnathal edges exist in branchiopods (Linder, 1945; Richter, 2004). Representatives of Anostraca (Mura, 1995, 1996), Spinicaudata, Cyclestherida (Richter, 2004) and certain Cladocera (Edwards, 1980; Glagolev and Korovchinsky, 1992; Kotov, 1998, 2000a) have a molar process that covers the entire gnathal edge (scored 1). In these taxa, the *pars molaris* consists of several rows of comb-like projections originating from the primary surface of the gnathal edge. The "comb teeth" form the grinding surface at a second, more distal level. The central area of the molar surface is formed as a smooth plate, perforated by numerous small pores. Another type of gnathal edge is found in Notostraca (Fryer, 1988) and Laevicaudata (Martin, 1989; Kotov, 2000b; Richter, 2004). It is characterized by several parallel-oriented teeth (the number varies in Laevicaudata). Each of these teeth possesses a dorsal and a ventral cusp, both connected by a concave ridge. In addition, a smaller tooth-like structure, but different from the other teeth, is present anteriorly, and an incisor or canine-like tooth is present posteriorly. However, there are also differences between the mandibles in Notostraca and Laevicaudata. In Notostraca, the mandibles are distinctly asymmetrical (left and right mandibles being different) while they are symmetrical in Laevicaudata (both scored 2). The mandible in Haplopoda and Onychopoda (e.g., Rivier, 1998) are so different to those of the other taxa that we decided to score them as inapplicable.

Leptostraca possess a gnathal edge with molar and incisor process (e.g., Edgecombe et al., 2003). Sanders (1963) described for *Hutchinsoniella* a molar process with numerous tiny teeth forming a grinding plate and an incisor component with two spines (both outgroups scored 0).

15. Opening of maxillary gland: (0) opening located more or less ventrally; (1) located laterally

The ducts of the maxillary glands commonly open in association with the second maxillae in branchiopods (Cannon and Leak, 1933; Martin, 1992). However, the maxilla is reduced in most taxa, which make the decision on the position of the maxillary gland more difficult. Therefore, we scored only those taxa where the opening has been clearly shown. Studies on the embryology of *Cyclestheria hislopi* (Cyclestherida) and certain ctenopods and anomopods showed that the developing maxillary glands open directly into the ventrally placed early limb buds (Olesen, 1998, 1999; Olesen et al., 2003 for a brief summary) (scored 0). In contrast, Olesen et al. (2003) found evidence that the openings of the maxillary glands in *Leptodora kindtii* (Haplopoda) and *Cercopagis pengoi* (Onychopoda) are placed laterally at the body, close to the bases of the first trunk limbs (scored 1). Such an extreme lateral displacement of the maxillary gland openings is unusual within branchiopods, even though their position has been reported to be slightly lateral (but still basically ventral) in species of both *Triops* (Notostraca) and *Lynceus* (Laevicaudata) (Claus, 1873) (scored 0) (see Olesen et al., 2003).

In Cephalocarida, the position is ventrally at the base of the maxilla (Hessler and Elofsson, 1991). According to Cannon (1960) the position of the maxillary opening in Leptostraca is laterally as well, in the position where the carapace is fused with the thorax. As the situation in Leptostraca appears incomparable with that of *Leptodora* and *Cercopagis*, we scored Leptostraca as inapplicable.

16. Number of trunk limbs: (0) 11; (1) at least 35; (2) 10 or 13; (3) 18–32; (4) 15 or 16; (5) 6; (6) 5; (7) 4; (8) 14; (9) 9

The number of trunk limbs differs greatly between the different branchiopod taxa. No evidence exists that allows to group for example four, five and six pairs of trunk limbs into one state. Most representatives of Anostraca possess 11 pairs of trunk limbs (scored 0) (in some cases 17–19 but not in the species considered here),

the number of trunk limbs in Notostraca varies but at least 35 (according to Dumont and Negrea, 2002) are present (scored 1). In Laevicaudata the number is 12 in females (the opercular lamellae not counted) and 10 in males (Sars, 1896; Martin, 1992) (scored 2), in Spinicaudata between 18 and 32 (Daday, 1914–27) (scored 3), in Cyclestherida 15 in males and 16 in females (scored 4) (Sars, 1887b; Olesen et al., 1997). In Cladocera, four to six trunk limbs are present (Flößner, 2000). Haplopoda, Ctenopoda, and some Anomopoda possess six pairs of trunk limbs (scored 5), other Anomopoda five pairs (scored 6) (see Dumont and Negrea, 2002), and Onychopoda four pairs (scored 7). Leptostraca have 14 pairs of trunk limbs (Cannon, 1960), counting both thoracopods and pleopods (scored 8), and *Hutchinsoniella* (Cephalocarida) has nine pair of trunk limbs, counting also the egg carriers at the 9th thoracic segment (Sanders, 1963) (scored 9).

17. Function of trunk limbs: (0) swimming and feeding; (1) feeding *only* (filter feeding or as raptorial limbs)

In adults of Anostraca and Notostraca, the trunk limbs have a double function in being responsible for both swimming and feeding (scored 0). These taxa lack swimming antennae as adults. In *Lynceus brachyurus* (Laevicaudata), the main locomotory organs are the second antennae. However, swimming takes place with the carapace valves widely opened ventrally, and the trunk limbs apparently contribute significantly to locomotion (Gruner, 1993; Dumont and Negrea, 2002; JO, pers. obs.), which gives the animal an even motion through water without abrupt jumps (scored 0). In Spinicaudata, Cyclestherida and Cladocera, the organs of locomotion are the second antennae, which cause most taxa to swim through water in abrupt jumps (all scored 1, despite trunk limbs in some spinicaudatans, such as *Limnadia lenticularis*, may have a minor contribution to swimming, see Sars, 1896). It should be noted that in some benthic cladocerans, the telson and sometimes certain thoracopods are involved in crawling, but not in swimming (Fryer, 1968, 1974; Flößner, 2000). This is not considered here.

Sanders (1963) reported the trunk limbs of *Hutchinsoniella* (Cephalocarida) to be involved in locomotion as well as feeding (scored 0). Sars (1896) reported that the thoracopods in *Nebalia* (Leptostraca) take no part in locomotion, which was confirmed by Cannon (1927). The pleopods, which are responsible for locomotion in Leptostraca, are not considered in this character.

18. Trunk limb shape: (0) phyllopodous with endites and an unsegmented endopod; (1) stenopodous with maximal four segments (in main axis of limb if biramous)

In most branchiopods, the adult trunk limbs are phyllopodous in the sense that segment borders can only be weakly recognized. Furthermore, in the ''large'' branchiopods (Anostraca, Notostraca, Laevicaudata, Spinicaudata and Cyclestherida), the limbs consist largely of the same components, which is six (Anostraca) or five endites, an unsegmented endopod, a large exopod, and a sac-like epipod, all originating from a mostly undifferentiated limb corm (scored 0) (see Olesen, 2007, for a discussion of branchiopod limb homologies). In Anomopoda and Ctenopoda, most limbs are phyllopodous, but, especially in Anomopoda, limb morphology varies and generalizations are difficult to make (see Fryer, 1968, 1974, 1991; Dumont and Negrea, 2002). However, as at least some of the characteristics mentioned above can be found in trunk limbs of many ctenopods and anomopods, we have scored these as phyllopodous (state 0). In two cladoceran taxa, *Leptodora kindtii* (Haplopoda) and in Onychopoda, the trunk limbs are stenopodous and segmented (state 1). Olesen et al. (2001) showed how the segmented trunk limbs of *L. kindtii* most likely have been derived from phyllopodous limbs during evolution. It was possible to establish precise homologies between the various limb segments of *L. kindtii* to specific parts of phyllopodous limbs, such as the endites. The segmented trunk limbs of some species of Onychopoda have the same number of segments as in *L. kindtii*, which potentially supports homology. The trunk limbs of Leptostraca are also phyllopodous, but the specific structure of the limbs is too different from those of branchiopods to be scored the same way. In contrast to branchiopod phyllopods, leptostracan phyllopods have no endites, they have a segmented endopod, and the protopod is possibly divided into a coxa and basis. The trunk limbs of Cephalocarida bear in some respects more resemblance to branchiopod limbs (e.g., they have endites medially on an undifferentiated/phyllopodous limb corm), but differ from these in possessing a segmented exopod and a so-called pseudoepipod, apparently attached to the proximal segment of the exopod (see Sanders, 1963). Instead of defining two unique states for each outgroup, they are scored as inapplicable.

19. Trunk limb epipods: (0) present; (1) absent

Trunk limb epipods are present on practically all limbs in Anostraca, Notostraca, Spinicaudata, Laevicaudata, *Cyclestheria hislopi* (Cyclestherida), Ctenopoda, and on some trunk limbs in Anomopoda (state 0). Epipods are lacking completely in Onychopoda and Haplopoda (state 0). An epipod is also present on the thoracopods of Leptostraca (state 0). The homology between malacostran and branchiopod epipods has been supported by pdm (apterous) and nubbin expression data (Averof and Cohen, 1997). The trunk limbs of Cephalocarida have a lateral, unsegmented, setose limb part that traditionally has been named a ''pseudoepipod'' (Gruner, 1993). Walossek (1993) suggested this limb part to be actually a part of the exopod. We have scored Cephalocarida as uncertain (?) for this character.

20. Number of trunk limb endites: (0) six (at least during development); (1) five

In some species of Branchinectidae (Anostraca), six endites are present in adults (e.g., *Branchinecta gigas*, see Fryer, 1966; *Branchinecta raptor*, see Rogers et al., 2006). In most adult anostracans, only five endites are visible, at least in some species, due to the fusion of the two most proximal endites (see Møller et al., 2004 and Fig. 2A). In Notostraca, Spinicaudata, Laevicaudata and *Cyclestheria hislopi*, the trunk limbs constantly have five endites (state 1) (Fig. 2B,C,E). In Cladocera, no constant pattern are found; either a much reduced number or endites lack entirely (scored inapplicable). The thoracopods in Leptostraca have no endites (scored inapplicable). The protopod of the trunk limbs in Cephalocarida apparently have five endites, appearing in a more irregular pattern than those in Branchiopoda (state 1) (Sanders, 1963). More similar to Branchiopoda than Cephalocarida are the endites of certain ''Orsten'' fossils such as *Rehbachiella kinnekullensis* (not included in this analysis). *Rehbachiella*, and other ''Orsten'' fossils, have a higher number of endites than six.

21. Shape of trunk limb endites: (0) lobate, not elongate (1) at least endites 4–5 elongate

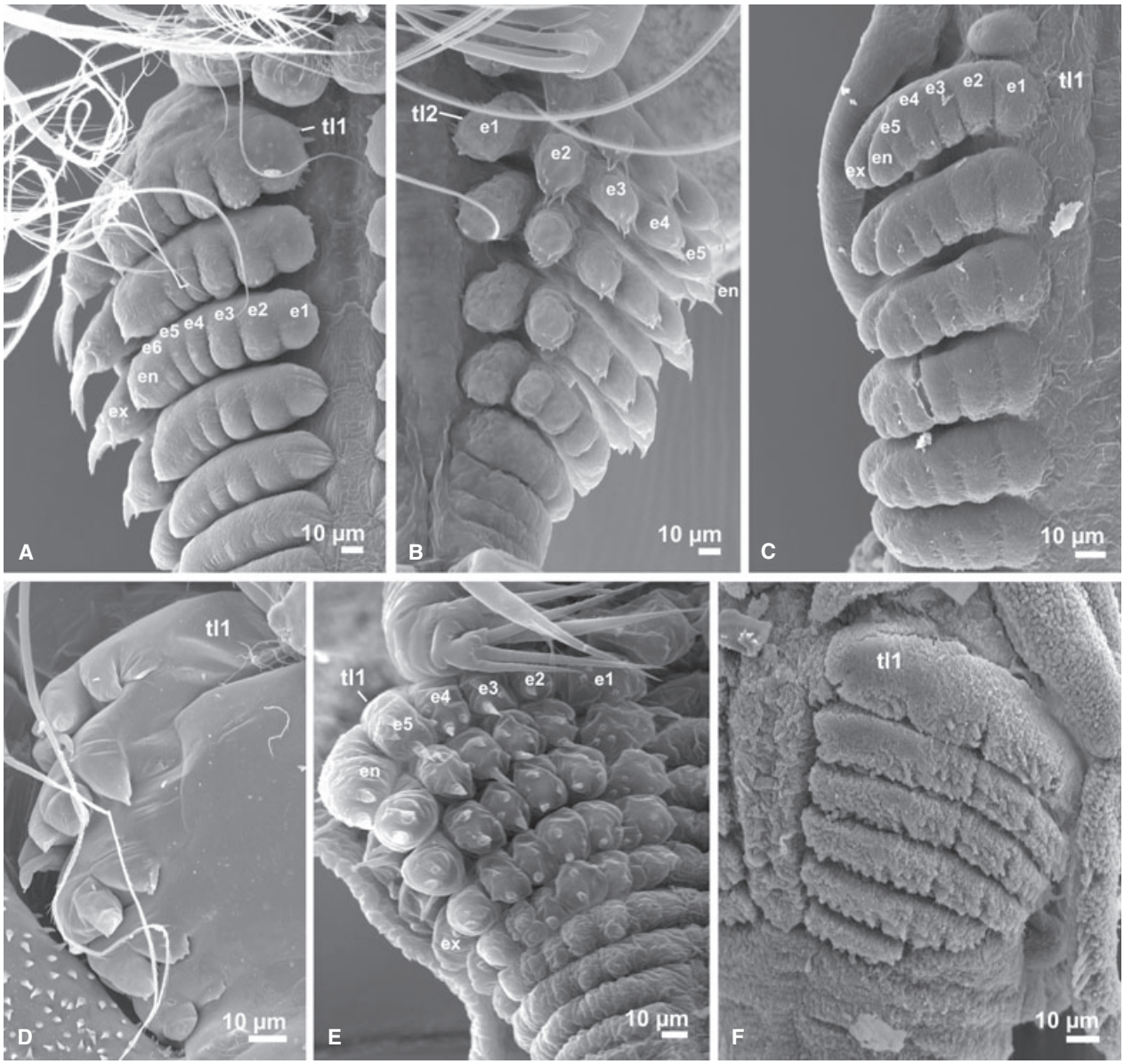

Fig. 2. Branchiopod larvae showing early development of trunk limbs. (A) *Eubranchipus grubii* (Anostraca), intermediate stage. (B) *Caenestheriella gifuensis* (Spinicaudata), intermediate stage. (C) *Cyclestheria hislopi* (Cyclestherida), stage 4. (D) *Lynceus brachyurus* (Laevicaudata). (E) *Triops cancriformis* (Notostraca), stage 3. (F) *Leptodora kindtii* (Haplopoda), stage 2. Abbr. e1-e6, endite 1–6; en, endopod; ex, exopod; tl1-tl2, trunk limb1–2.

In Anostraca, Spinicaudata, and Cyclestherida, the endites are distinct and form broad lobes (scored 0). Linder (1945) pointed out a similarity between Notostraca and Laevicaudata. In Notostraca, endites 2–5 are elongate (flagella-like structures in the first thoracopod but to a lesser extent also in other limbs). In Laevicaudata, at least endites 4–5 are also elongate (to a different degree in different limbs but in some cases very distinct, e.g., Sars, 1896) (both scored 1). The endites in Ctenopoda and Anomopoda (if recognizable) are not elongate (Dumont and Negrea, 2002), in Haplopoda and Onychopoda, endites (at least in the general definition, but see Olesen et al., 2001) are absent (scored inapplicable). Leptostraca are scored as inapplicable because endites are absent. In Cephalocarida, endites are present but never elongate (scored 0) (Sanders, 1963).

22. Trunk limb endites: (0) without palps; (1) with palps

Here only those trunk limbs that are not transformed into claspers are considered. The clasper-bearing limbs are treated as separate characters (see chars 24–26). Only in Spinicaudata, ''palps'' as outgrowths of the endites exist (Daday, 1914–27) (scored 1). These palps seem to be absent in *Limnadia lenticularis* (Sars, 1896). These structures are absent in all other branchiopods (scored 0). Taxa without endites are scored as inapplicable.

23. Trunk limb endopod: (0) more than one segment; (1) unsegmented

Following Walossek (1993) and Olesen (2007), we recognize branchiopod trunk limbs as having an unsegmented endopod, in most cases articulated to the stem of the limb (scored 1). The endopod articulation is clearly present in Notostraca, Laevicaudata, Spinicaudata, Cyclestherida but absent in Anostraca (see Olesen, 2007), but here we still interpret the medio-distal part of the trunk limbs as endopodal. Cladoceran trunk limbs are modified in different ways and are therefore scored as inapplicable. Cephalocarida and Leptostraca have trunk limbs with more than one endopodal segment (state 0).

24. 1st thoracopod as clasper: (0) absent; (1) present

25. 2nd thoracopod as clasper: (0) absent; (1) present

26. Clasper, "movable finger" (endopod): (0) sucker-like structure absent; (1) with sucker-like structure

The striking similarity between the claspers of the male first trunk limb in Laevicaudata and Spinicaudata has been known for a long time (Linder, 1945) but was interpreted as convergent by Botnariuc (1947) (later supported by Fryer, 1987), who observed that different parts of the limbs in the two taxa appeared to be involved in the ontogeny of the claspers. However, although this might weaken the character, a different ontogenetic origin does not exclude the possibility of homology (e.g., Scholtz, 2004). Olesen et al. (1997) and Olesen (1998) suggested only the so-called movable finger (the modified endopod) as being homologous; the remaining similarities between the claspers of Laevicaudata and Spinicaudata were accepted as convergent. Here, we argue that at least parts of the clasper can be homologized. Such a clasper is present on the first limbs in all representatives of Spinicaudata, Laevicaudata, and in *Cyclestheria* (char. 24, scored 1). Some male cladocerans have the first pair of trunk limbs modified to hold the female during mating, but detailed homologies to Laevicaudata, Spinicaudata and Cyclestherida are difficult to establish. Although a homology of the ''copulatory hook'' to the movable finger appears reasonable for us, we decided to score this character as inapplicable in cladocerans because detailed comparative studies are lacking (Flößner, 2000; Dumont and Negrea, 2002).

Only in Spinicaudata, an almost identical clasper is present on the second pair of thoracopods (char. 25, scored 1). Other kinds of claspers (or modifications) on the second pair of limbs that show distinct differences to the one described above have been reported from some Laevicaudata (see Martin and Belk, 1988), but are not present in the species included in this study.

In representatives of Limnadiidae (except *Limnadopis*), the movable finger carries at its distal tip a sucker-like structure (char. 26, scored 1). The structure could be part of a sexual recognition mechanism, although this remains speculative at the moment. Other Spinicaudata have scales and/or spines at the same place (char. 26, scored 0). Similar structures are unknown in Laevicaudata and in Cladocera. There are no claspers or clasper-like structures in Leptostraca and Cephalocarida (chars 24–25 scored 0; char. 26 scored inapplicable).

27. Ejector hooks: (0) absent; (1) present

Almost all Anomopoda (except *Lathonura* and Neothricidae) possess a pair of ejector hooks at the basis of the first trunk limb (Fryer, 1987; Dumont and Negrea, 2002) (scored 1). Their function is to remove accumulated detritus during the feeding process (Fryer, 1963). All other branchiopods and the two outgroups do not possess comparable structures (scored 0).

28. Shape of telson region: (0) cylindrical; (1) laterally compressed

29. Telsonal setae: (0) absent; (1) present

30. Dorsal spines on telson arranged in two rows: (0) absent; (1) present

The following characters relate to the last element(s) of the trunk that we here consider as mainly composed of the original telson. A few comments on homologies are needed before considering the characters specifically. The precise homologies between the posterior body portions and their terminal (caudal) appendages in various taxa of Branchiopoda we consider as uncertain. Adult anostracans have a distinct telsonal segment on which a pair of ''cercopods'' insert. The posterior part of the body in cladocerans is often termed ''postabdomen'' and carries a pair of ''postabdominal claws'', most

certainly homologous to very similar structures in Spinicaudata and Cyclestherida. How the telson and cercopods of Anostraca relates to the postabdomen and postabdominal claws of Cladocera, Spinicaudata and Cyclestherida in terms of homologies are uncertain. Kotov (2006) suggested that the postabdomen represent the fused cercopods of Anostraca, and that setae of the cercopods represent the postabdominal claws and the dorsal postabdominal row of spines, but there is no developmental data available to support this idea. Potentially conflicting evidence comes from an early phyllopod fossil, *Castracollis wilsonae*, where a pair of regular spine rows is present dorsally at the telson, most likely being homologous to the dorsal spine rows of the postabdomen in Cladocera, Spinicaudata and Cyclestherida. Thus, if this terminal segment of *Castracollis* indeed is the original telson (as seen in Anostraca), and if the spine rows on this segment are homologous to those of the cladoceran postabdomen, then these cannot be homologous to the marginal setae of anostracan cercopods, as suggested by Kotov (2006).

We consider the presence of a pair of setae dorsally in all representatives (without exceptions) of Notostraca, Laevicaudata, Spinicaudata, Cyclestherida and Cladocera as an important indicator of the telsonal nature of this body region (char. 29, scored 0). In Cladocera, these setae are often called postabdominal setae but larval stages in *Cyclestheria* (Olesen, 1999), *Leptodora* (Olesen et al., 2003) and *Triops cancriformis* (Møller et al., 2003) have showed that they are telsonal. In this light, the term "postabdomen" is superfluous. In Anostraca, such telsonal setae are missing (char. 29, scored 0) but possibly serially homologous paired setae are present more anteriorly on the abdominal segments, at least of larvae (Møller et al., 2004). The telson (or the portion roughly corresponding to the telson) is cylindrical in cross-section in Anostraca, Notostraca, *Leptodora* and Onychopoda (char. 28; scored 0), whereas it is laterally compressed in Laevicaudata, Spinicaudata, Cyclestherida, Ctenopoda and Anomopoda (char. 28; scored 1). In Spinicaudata, *Cyclestheria*, Ctenopoda and Anomopoda, the telson (= postabdomen) carries two rows of dorsal spines (char. 30, scored 1). A dorsal spine armature occurs also in Notostraca, but it is not arranged in two rows (Longhurst, 1955) (char. 30, scored 0). In Laevicaudata, the telson bears only minute spinules (Sars, 1896; Martin and Belk, 1988) (char. 30, scored 0). As mentioned above two telsonal spine rows are also present in the Devonian *Castracollis wilsonae*, an early phyllopod fossil that may belong to the notostracan stem lineage (Fayers and Trewin, 2003; Olesen, 2007). Leptostraca and Cephalocarida possess cylindrical telsons (char. 28, scored 0) and have no pair of dorsal telsonal setae (char. 29, scored 0), and no spines (char. 30, scored 0).

31. Caudal appendages: (0) articulated; (1) not articulated

32. Caudal appendages shape: (0) straight; (1) curved, claw-like

Paired caudal appendages (e.g., cercopods in Anostraca and postabdominal claws in Cladocera) are present terminally in most branchiopods, sometimes articulated to the terminal segment. As outlined in the previous character, the exact homologies between various branchiopod taxa are uncertain, in particular, the homology between anostracan cercopods and the claw-like structures in the other taxa. Thus, in the present characters, we are aware that we treat potentially non-homologous structures. However, character state 1 for both characters applies only for diplostracan taxa, where the terminal structures most likely *are* homologous. In Anostraca, Notostraca, Spinicaudata, *Cyclestheria*, Anomopoda and Ctenopoda, the caudal appendages are articulated to the telson (char. 31, scored 0), although Fryer (1999a) emphasized that they are not capable of independent movement. In Haplopoda and in Onychopoda, the caudal appendages are not articulated (char. 31, scored 1). The caudal appendages are curved and claw-like in Spinicaudata, *Cyclestheria*, Ctenopoda and Anomopoda (char. 32, scored 1) ("postabdominal claws"). In Notostraca and Anostraca, the caudal appendages are straight (char. 32, scored 1). Within Onychopoda, some species possess straight, other curved claws; in *Polyphemus*, claws are even absent (Rivier, 1998). We decided to score Onychopoda and Haplopoda where the shape of the caudal appendages is somewhat between the two states as inapplicable. In Laevicaudata, only small spines are present (e.g., Sars, 1896; Fryer, 1987; both characters scored inapplicable).

Leptostraca and Cephalocarida possess articulated (char. 31, scored 0) and straight (char. 32, scored 1) caudal appendages (e.g., Sanders, 1963; Sars, 1887a).

33. Neck organ: (0) present, not pronounced; (1) present, pyriforme; (2) absent

The neck organ (dorsal organ) is pyriforme in *Limnadia, Eulimnadia* and *Limnadopsis* (scored 1), whereas it is not pronounced in adults of any other branchiopods (scored 0) (Rieder et al., 1983; Martin, 1992). It is absent in certain adult anomopods and ctenopods (following Dejdar, 1930; Olesen, 1998; scored 2). There are no external neck organs in Leptostraca and Cephalocarida (scored 2).

34. Compound eyes position: (0) externally; (1) internalized

Anostraca possesses stalked eyes (scored 0), whereas all other representatives of Branchiopoda possess eyes in an internal eye chamber (scored 1). The eye chamber is connected with the environment via a channel and an open pore in all Notostraca, Laevicaudata, Spinicaudata, Cyclestherida (Fig. 3A) and in some Cladocera.

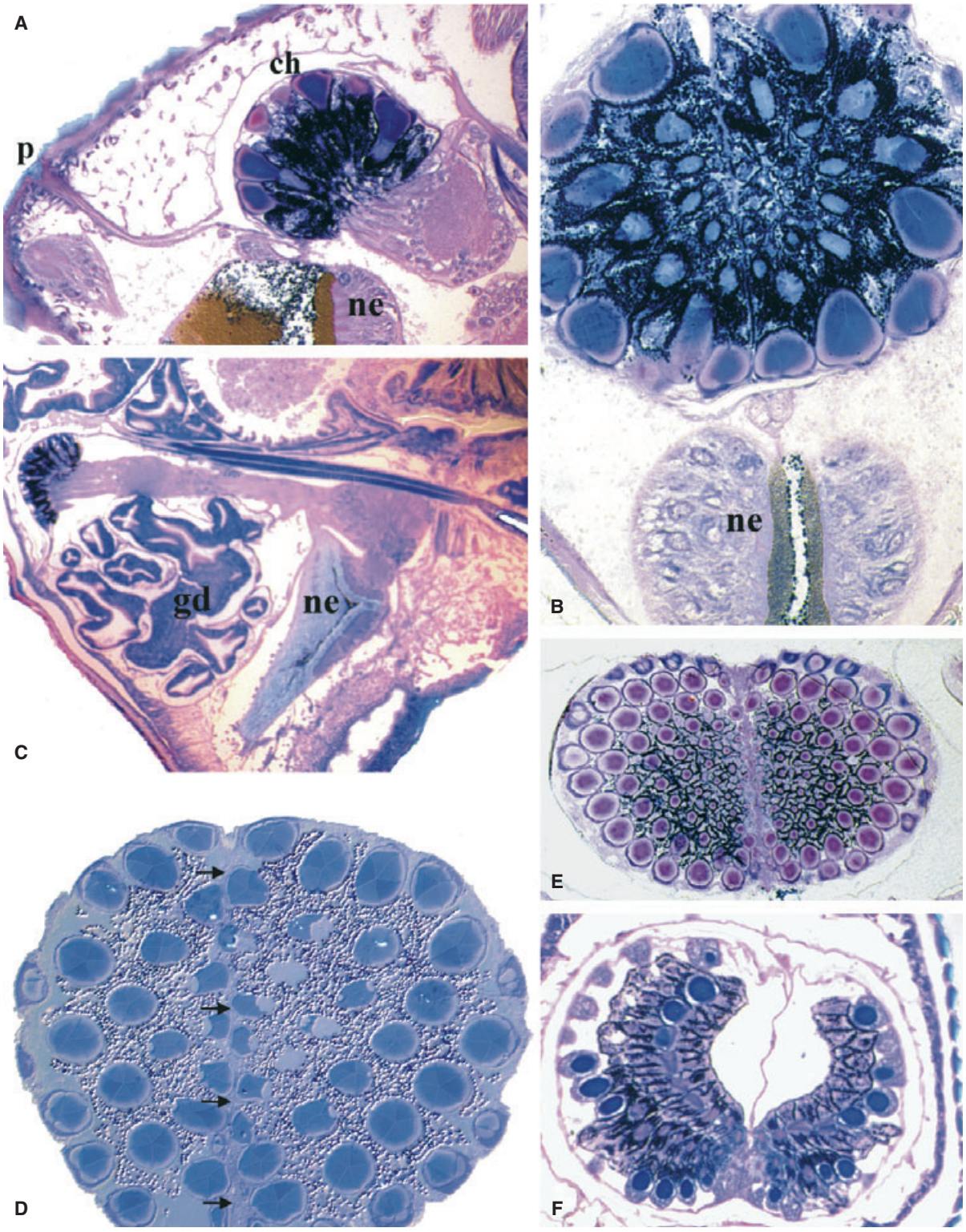

Fig. 3. Compound eyes. (A,B) *Cyclestheria hislopi* (Cyclestherida). (A) Sagittal section showing the internalized compound eye lying in an eye chamber (ch), connected via an eye pore (p) with the environment. (B) Transversal section showing the single globular compound eye close to the nauplius eye (ne). (C,D) *Caenestheriella* spec. (Spinicaudata). (C) Compound eye and triangular nauplius eye (ne) separated by gut diverticles. (D) Transversal section through the single globular compound eye. Arrows mark the line where the originally two compound eyes are fused. (E) *Limnadia lenticularis* (Spinicaudata) with single compound eye made of two semicircles fused in the midline. (F) *Lynceus tatei* (Laevicaudata). Transversal section showing two compound eyes with the ommatidial parts fused in the ventral area only.

35. Compound eyes, ommatidial part: (0) ommatidial part not fused; (1) fused only ventrally; (2) fused to a globular organ

It has been known for a long time (e.g., Leydig, 1860) that the ommatidial parts of the two original lateral compound eyes have been fused into a single, median globular eye in all cladocerans (scored 2). Sars (1887b) described also for *Cyclestheria* a globular compound eye (Fig. 3B), which he saw as similar to that in cladocerans (scored 2). The present study shows that the eye shape in some representatives of Spinicaudata (e.g., *Caenestheriella* sp.; Fig. 3D) shows no significant differences in the shape of the eyes between representatives of Spinicaudata and *Cyclestheria*. In other Spinicaudata (e.g., *Limnadia lenticularis*), the fusion that has taken place is somewhat imperfect (Fig. 3E). However, these differences between the degree of eye fusion between various spinicaudatans and *Cyclestheria* are too gradual to be divided into different character states (therefore all scored 2). In representatives of Laevicaudata, the eyes are kidney-shaped, and a fusion of the ommatidial part appears only in the ventral area (Fig. 3F; scored 1). Also, in Notostraca, the two compound eyes are very close together but are not in contact with each other (scored 0). Obviously, Anostraca are scored as having ommatidial parts not fused (scored 0).

36. Compound eyes, midline of ommatidia (0) absent; (1) present

Although, the compound eye is perfectly globular in all studied species of Anomopoda and to a similar degree in Spinicaudata and *Cyclestheria*, all ommatidia can be referred to either the left or the right of the two original compound eyes (scored 0). This is not the case in Ctenopoda and Onychopoda studied herein (Fig. 4B,C). Here a vertically oriented midline of ommatidia exists, which can not be correlated to the original left or right eye. Instead, it exactly fills the gap between them (scored 1). The condition in *Leptodora* is uncertain because of the very high number of ommatidia (scored inapplicable). This character is scored as inapplicable for all taxa where the ommatidial parts of the eyes are not (completely) fused, i.e., Anostraca, Notostraca, and Laevicaudata.

37. Compound eyes, fusion of lamina: (0) absent; (1) present

38. Compound eyes, fusion of medulla: (0) absent; (1) present

Hanström (1928) showed that in some cladocerans not only the ommatidial parts of the two body sides are fused but also that the two optical neuropils might be fused. However, the exact degree of fusion is different between the different cladoceran taxa. In Onychopoda, Haplopoda (see Kirsch and Richter, in press) and Ctenopoda (Fig. 4B), both optical neuropils (i.e., the distal *lamina ganglionaris* and the proximal *medulla*) are fused to a single structure (own observations) (chars 37–38, scored 1), whereas in Daphniidae (as far as known) only the two laminae are fused but the two medullae are separated from each other (char. 37, scored 1; char. 38 scored 0). In other Anomopoda as well as in *Cyclestheria*, Spinicaudata (Fig. 4A) and all other Branchiopoda, both pairs of neuropils are clearly separated from each other (chars 37–38, scored 0). Fryer (1999b) reported a one-eyed mutant brine shrimp, *Artemia franciscana* (the optic neuropils also fused) and discussed this as an "atavism" of an ancient condition. However, for the scoring of the terminals in this analysis, his "ad hoc" explanation cannot be applied.

In Cephalocarida, compound eyes including optic neuropils are absent (Elofsson and Hessler, 1990). Therefore, all characters have been scored as inapplicable for *Hutchinsoniella*. Leptostraca possess stalked unfused eyes (Sars, 1887a; Cannon, 1960) (chars 34–35 and 37–38, scored 0; char. 36 scored inapplicable).

39. Compound eyes, crystalline cones: (0) tetrapartite; (1) pentapartite

The ommatidial structure in Notostraca (Diersch et al., 1999) corresponds in detail to the one generally suggested for the ground pattern of Crustacea and more inclusive taxa such as Tetraconata (e.g., Richter, 2002). This concerns also the presence of four cone cells contributing to the formation of the crystalline cone and four proximal cone cell processes in the area of the rhabdom (tetrapartite cones) (scored 0). Also for several Anostraca four crystalline cone cells per cone, i.e., a tetrapartite cone, have been described (Nowikoff, 1905; Debaisieux, 1944). The number of cone cell processes can be detected only using TEM (see e.g., Elofsson and Odselius, 1975). A survey of the ommatidial structure in Spinicaudata, Cyclestherida and Cladocera shows that there are five cone cells, i.e., the cones are pentapartite as conducted by the present study (Fig. 4D–F; see also, e.g., Miltz, 1899; Wolken and Gallik, 1965); the presence of five cone cell processes could be shown in a few cases where TEM studies are available (all scored 1). In the representatives of Laevicaudata, only four cone cells contribute to a crystalline cone (Fig. 4G; see also Nowikoff, 1905 for *L. brachyurus*) (scored 0). However, it should be noted that in *Lepidurus apus* (Notostraca), very few crystalline cones are pentapartite (SR, pers. obs.). Also, for *Artemia salina,* a few cones consisting of a different number of portions (i.e., three, five, six) are known (Debaisieux, 1944). These findings, certainly of interest, have not been considered for the scoring of the taxa because they concern only very few ommatidia, whereas the majority of crystalline cones are tetrapartite.

The character has been scored as inapplicable for *Hutchinsoniella*. In Leptostraca, the ommatidia are tetrapartite (Gross and Melzer, 2002).

40. Nauplius eyes, number of ocelli: (0) three; (1) four

41. Nauplius eye shape: (0) globular; (1) triangular

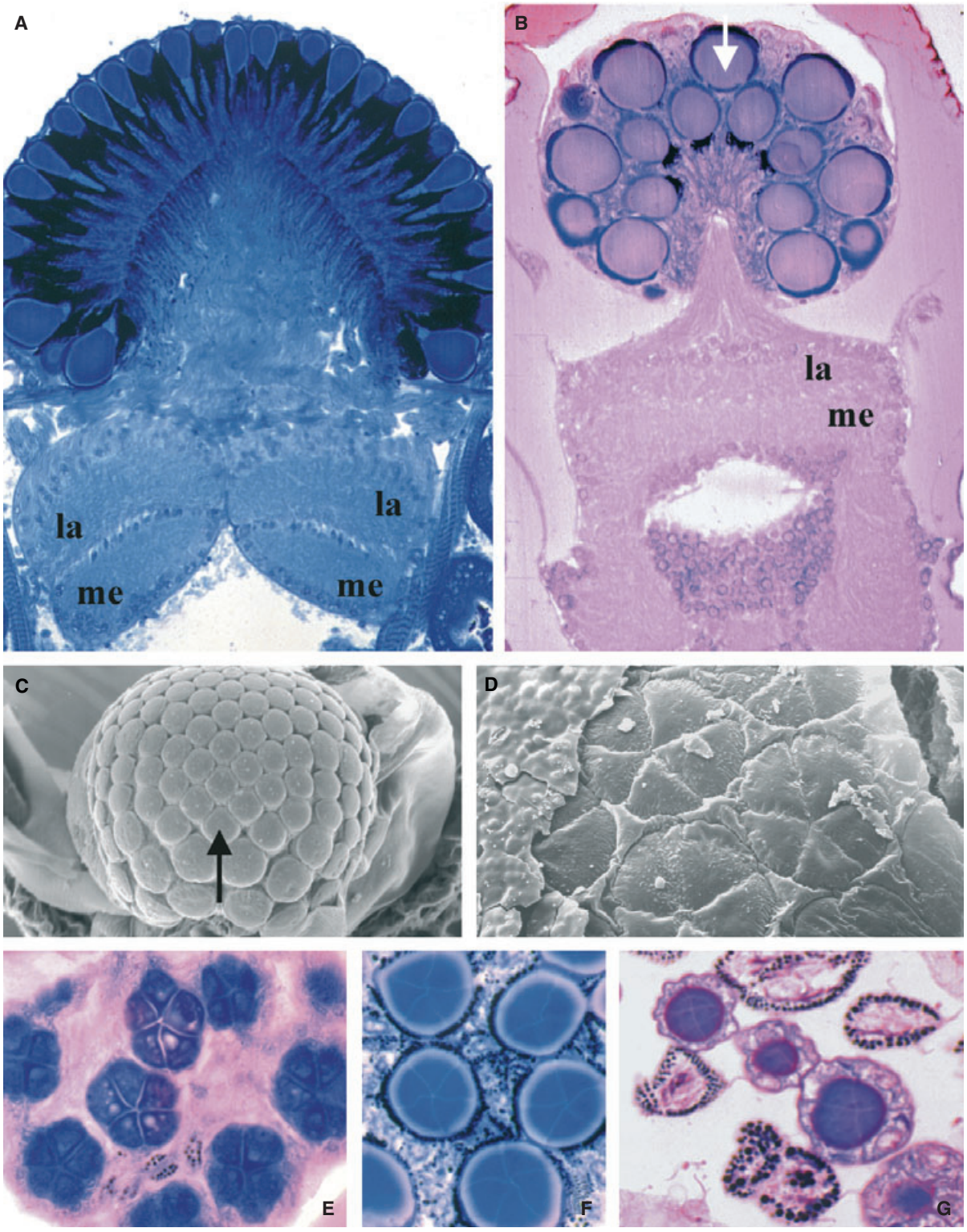

Fig. 4. Compound eyes. (A) *Limnadopsis birchii* (Spinicaudata). Ommatidial part fused to a single globular compound eye but with separated left and right optic neuropils (lamina, medulla). (B) *Sida crystallina* (Cladocera, Ctenopoda) with fused left and right lamina (la) and medulla (me); the arrow points to a crystalline cone representing a row of ommatidia (midline), which cannot be related to the original left or right compound eye. (C) *Polyphemus pediculus* (Cladocera, Onychopoda) with midline of ommatidia (arrow)—SEM picture. (D) *Bythotrephes longimanus* (Cladocera, Onychopoda) with pentapartite crystalline cones—SEM picture. (E) *Caenestheriella* spec. Cone cells with nuclei forming the pentapartite crystalline cones. (F) *Cyclestheria hislopi* with pentapartite crystalline cones. (G) *Lynceus tatei* (Laevicaudata) with tetrapartite crystalline cones.

42. Nauplius eye position: (0) nauplius eye close to compound eye; (1) nauplius eye displaced, space between filled by gut diverticles

In Anostraca, the nauplius eye consists of three ocelli (char. 40, scored 0), whereas in Notostraca, Laevicaudata, Spinicaudata and Cyclestherida four ocelli are present (all scored 1) (Elofsson, 1966; Martin, 1992; Reimann and Richter unpublished). In Anomopoda, a reduction of the nauplius eye is common, but, if recognizable, four ocelli are present consisting of only a few cells each (Elofsson, 1966; Reimann and Richter unpublished). In Ctenopoda, the nauplius eye is even more reduced and it is absent in Onychopoda and Haplopoda (although it has at one occasion been described for the first generation hatching from the resting eggs by Sars, 1873). We scored the representatives of these three taxa as inapplicable for this character (and for chars 41–42). The shape of the nauplius eye is more or less globular in representatives of Anostraca, Notostraca, Laevicaudata, and in *Cyclestheria* (Fig. 3B) (e.g., Sars, 1887b; Elofsson, 1966; Martin, 1992) (char. 41, scored 0). This seems also true for most representatives of Anomopoda (but certainly not for *Simocephalus vetulus*, which is scored as inapplicable) where a nauplius eye is clearly recognizable (Flößner, 2000) (char. 41, scored 0). In Spinicaudata, the nauplius eye has a triangular shape (Fig. 3C; Elofsson, 1966; Reimann and Richter unpublished) (char. 41, scored 1).

In representatives of Notostraca, the nauplius eye and the compound eye lie close together (char. 42, scored 0). In Spinicaudata, they are placed further apart with the extended gut diverticles in between (Fig. 3C; char. 42, scored 1). In Laevicaudata, extended gut diverticles (also called hepatopancreas) are present but are located mainly in the labrum (char. 42, scored 1) and the nauplius and the compound eyes lie close together (char. 42, scored 0). In *Cyclestheria*, the nauplius eye and the compound eye (char. 42, scored 0) also lie close together (Fig. 3A,B; Sars, 1887b). In Anomopoda, the position of the nauplius eye varies from being close to the compound eye to a more distant position but the space between the nauplius and compound eyes is never filled by gut diverticles (Flößner, 2000). Although not completely satisfying we decided to score all Anomopoda where the condition is not clear-cut (based on Flößner, 2000) as inapplicable as we did for the cladocerans without nauplius eye. Anostraca are also scored as inapplicable as the presence of stalked eyes make a comparison with other taxa more difficult.

In Leptostraca and Cephalocarida, nauplius eyes are completely absent and are scored as inapplicable for all nauplius eye characters (chars 40–42).

43. Gut system: (0) anterior diverticles extensive; (1) anterior diverticles small; (2) anterior diverticles absent

Notostraca, Laevicaudata and Spinicaudata (Fig. 3C) have extensive, paired gut diverticles (also called "hepatopancreas" or "midgut glands") originating antero-dorsally at the midgut, closely behind the esophagus (Martin, 1992; Dumont and Negrea, 2002) (scored 0). Anostraca has simple paired pouches (scored 1). In *Cyclestheria*, the midgut diverticles are small and curved (Sars, 1887b) similar to the conditions in many Cladocera ("Leberhörnchen") (scored 1); in other cladocerans anterior diverticles are absent (Sars, 1993; Dumont and Negrea, 2002). Posterior ventral unpaired diverticles like those seen in some Chydoridae are not homologous.

In Leptostraca, several anterior midgut glands are present, some leading into the head (scored 0) (Claus, 1888; Sars, 1896), in Cephalocarida, a pair of relatively small diverticles are present (scored 1) (Elofsson et al., 1992).

44. Structure of the heart, numbers of pairs of ostia: (0) 18; (1) 11; (2) 7; (3) 4; (4) 3; (5) 1

Within Anostraca 18 pairs of ostia have been described for *Artemia salina* and *Branchinecta paludosa* (Sars, 1896; Vehstedt, 1941). The notostracans *Lepidiurus glacialis* and *Triops cancriformis* have 11 pairs of ostia (Claus, 1873; Sars, 1896), the spinicaudatan *Limnadia lenticularis* four, the laevicaudatan *Lynceus brachyurus* three (Sars, 1896) and Cladocera only one pair (e.g., Claus, 1876, 1877; Sars, 1897). *Cyclestheria hislopi* has four pairs of ostia (Sars, 1887b).

Hutchinsoniella has three pairs of ostia (scored 4) (Hessler and Elofsson, 2001), Leptostraca have seven pairs (scored 2) (Claus, 1888 for *Nebalia*).

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

Preuss (1951) emphasized differences in the oogenesis between Anostraca and the remaining Branchiopoda. In Anostraca, oocytes and nurse cells separates early in the development, there are never groups of four cells (Criel, 1989) (char. 45, scored 0). In all phyllopod taxa for which information are available, four cells are formed, which differentiate into one oocyte and three nurse cells (Sars, 1896; Preuss, 1951; Trentini and Sabelli Scanabissi, 1978, 1982; Rossi, 1980; Martin, 1992).

In Leptostraca (Claus, 1888) and in Cephalocarida (Hessler and Elofsson, 1992), there are no nurse cells present as in Branchiopoda (both taxa scored absent).

46. Size of spermatozoa: (0) small; (1) gigantic, with marginal vesicles; (2) gigantic, empty-looking vesicles

Representatives of Onychopoda possess gigantic spermatozoa with smooth surface and marginal vesicles (Wingstrand, 1987) (scored 1). Spermatozoa off almost all other taxa are small (scored 0) (see Roessler, 1995 for *Cyclestheria*), apart from certain Ctenopoda. However, in these species the ultrastructure of the spermatozoa is very different. Therefore, we decided to score *Sida crystallina* and *Diaphanosoma brachyurum* with a separate state (scored 2) following Wingstrand (1978).

The spermatozoa in Leptostraca (Jespersen, 1979) and Cephalocarida (Brown and Metz, 1967) are, despite

other general differences to those of Branchiopoda, small (see also Jamieson, 1991) (scored 0).

47. Spermiogenesis (maturation of spermatids): (0) cystic type of maturation; (1) lumenal type of maturation; (2) vacuolar type of maturation

Three types of maturation have been identified within Branchiopoda (Wingstrand, 1978). In the cystic type of maturation clusters of spermatids mature inside cystic dilations of the intercellular space between vegetative cells. This type of maturation was by (Wingstrand, 1978) found in various species of Anostraca, Notostraca, Spinicaudata, Ctenopoda, and in the anomopod *Ilyocryptus agilis* (scored 0). In the lumenal type of maturation, the spermatids are liberated into the testicular lumen where they mature. This type of maturation is found in various species of Spinicaudata and Ctenopoda (scored 1). Roessler (1995) described the lumenal maturation type in *Cyclestheria hislopi* (scored 1). In the vacuolar type of maturation, the spermatids are phagocytized by vegetative and mature inside private vacuoles. This type of maturation is found in most anomopods (except *Ilyocryptus agilis*) (scored 2). Haplopoda and Onychopoda possess aberrant types of maturation (scored inapplicable). All species except *Cyclestheria hislopi* are scored after Wingstrand (1978).

The type of maturation in Leptostraca and Cephalocarida was not treated by Jespersen (1979) or by Brown and Metz (1967) so we have scored unknown for these two taxa.

48. Protection of cysts/embryos: (0) ventral brood pouch; (1) encapsulated between a subapical lobe and the exopod of the 11th pairs of limbs; (2) carried between carapace and trunk

49. Protection of cysts/embryos: (0) carried under the carapace, attached to dorsal parts of the exopod; (1) carried under the carapace but not attached to the limbs. This character is only applicable for taxa scored 2 for the previous character

All branchiopods protect the cysts or embryos at least for some time before releasing them. Representatives of Anostraca possess a ventral brood pouch at the 12th and 13th thoracic segment (char. 48, scored 0) (Rogers, 2002; Kraus et al., 2004). In Notostraca, the cysts are encapsulated in the 11th pair of limbs between an expansion of a subapical lobe, forming a cup, and the exopod, forming the lid (char. 48, scored 1) (Fryer, 1988). In Laevicaudata, Spinicaudata, Cyclestherida and Cladocera, eggs and embryos are carried under the carapace (char. 48, scored 2). The way in which the cysts are kept under the carapace is different in these taxa, which, however, does not exclude *a priori* a general homology of this state. We included an additional character for better consideration of the differences (char. 49). The cysts are attached to dorsal parts of the exopods in Laevicaudata, Spinicaudata and *Cyclestheria* (char. 49, scored 0), whereas in Cladocera the limbs are not involved in holding the eggs/embryos under the carapace (char. 49, scored 1). Apparently not much is known concerning how the cysts become attached to the exopods in Laevicaudata, Spinicaudata and Cyclestherida. Tommasini and Scanabissi Sabelli (1989) reported for species of *Leptestheria* and *Eoleptestheria* (both Spinicaudata) that the eggs pass *into* the *epipods* from where they later emerge (see also Martin, 1992), probably to become attached to the exopods. The limbs that are involved in carrying the cysts vary slightly in Spinicaudata (different combinations between limb 9 and 15) (Daday, 1914–27), whereas this character seems to be more stable in Laevicaudata (limbs 9 and 10) (Martin, 1992). All other taxa are scored as inapplicable for character 49.

Leptostraca and Cephalocarida also show types of brood protection, but very different from that of any branchiopods. In Leptostraca, the brood is kept until the juvenile phase between the thoracopods (Cannon, 1960), while embryos in Cephalocarida are kept at a specialized egg-carrier leg posterior to the row of normal trunk limbs; each leg carries one embryo (Sanders, 1963; Hessler and Elofsson, 1992). Instead of defining separate and unique character states for each outgroup, we have scored them both as inapplicable for both characters.

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

Cladocerans and *Cyclestheria hislopi* possess two different kinds of eggs, subitaneous and resting eggs whereas almost all other branchiopods possess only one kind of eggs (= cysts) corresponding to the resting eggs (with the exception of *Artemia*, see Dumont and Negrea, 2002). Correlated to the production of two kinds of eggs, *Cyclestheria* and most representatives of Cladocera (a few are asexual, e.g., cited in Taylor et al., 1999) show heterogony or cyclic parthenogenesis (alternation between sexual and parthenogenetic reproduction) (scored 1). In some cases, the sexual part of the life cycle can be suppressed for many generations (see review in Dumont and Negrea, 2002). For some populations of *Triops cancriformis*, parthenogenesis has been described but the situation seems to be more complex (for a recent study see Scanabissi et al., 2005). No heterogony, however, has been described for any notostracan (scored 0). The same is true for *Artemia*, which has some parthenogenetic populations but none with obligate heterogony (scored 0). Representatives of Spinicaudata show complex reproduction systems (Sassaman, 1995; Eder et al., 2000; Weeks et al., 2005) but, again, no representative with heterogony is known (scored 0).

51. Hatching from resting eggs: (0) as free living larvae; (1) as small adults (juveniles)

52. Subitaneous eggs with direct development: (0) absent; (1) present

In Anostraca, Notostraca, Laevicaudata and Spinicaudata, nauplius larvae hatch from the eggs (= resting

eggs) (char. 51, scored 0), whereas in almost all cladoceran juveniles, with no significant morphological differences from the adults, hatch from the resting eggs (char. 51, scored 1) (for a recent review see Olesen, 2004). *Leptodora kindtii,* where a metanauplius hatches from the resting eggs, is a well-known exception (Sars, 1873) (char. 52, scored 0). In Anostraca, Notostraca, Spinicaudata and Laevicaudata, subitaneous eggs with direct development are absent (char. 52, scored 0).

All cladocerans possess in addition to the resting eggs subitaneous eggs with direct development (char. 52, scored 1). The situation is complex in *Cyclestheria*. Development from the subitaneous eggs is always direct, i.e., the embryonized larvae are not released from the brood chamber under the carapace before they have attained an adult morphology (Olesen, 1999) (char. 52, scored 1). Only few reports on the development from the resting eggs in *Cyclestheria* exist, and the results are conflicting. Roessler (1995), based on Colombian populations, reports that juveniles hatch from the resting eggs, which means that the development is direct. In contrast, Botnariuc and Viña Bayés (1977), based on Cuban populations, reported free larvae, looking in most respects like other spinicaudatan larvae. This character (char. 52) is therefore scored polymorphic (0, 1).

Cephalocarida hatch as free living larvae (char. 51, scored 0) and no subitaneous eggs are present (char. 52, scored 0). Leptostraca possess direct development, however, the conditions are very different form those in Cladocera (both characters scored inapplicable).

53. Restings eggs protected by carapace (ephippium): (0) absent; (1) present

When resting eggs are released in Anomopoda, they are protected by an ephippium, a modified carapace exuvia (scored 1). In many species, the ephippium represents only a part of the carapace, whereas in other the entire carapace exuvia forms the ephippium (Scourfield, 1901; Fryer, 1972; Flößner, 2000). In *Cyclestheria hislopi*, an ephippium, corresponding to the entire carapace is present (Roessler, 1995). Fryer (1999a) claimed that the ephippia in *Cyclestheria* and in Anomopoda has ''clearly arisen independently''. However, a thorough morphological comparison is still lacking.

An ephippium is absent in all other branchiopods and in Leptostraca. Anostraca and Cephalocarida are scored as inapplicable because of the absence of a carapace.

The remaining characters deal with larvae or embryonized larvae. We consider the ''embryonic'' phase in Cladocera, and *Cyclestheria* as comparable (homologous) with the larval phase in the ''large'' branchiopods (following Olesen, 2004). There are indications that the ''embryonic'' stages of *Cyclestheria* and Cladocera are ''embryonized'' larval stages (see Olesen, 1999, 2004; Kotov and Boikova, 2001). The ''embryos'' of *Cyclestheria* could be matched to free-living spinicaudatan larvae nearly one-by-one (Olesen, 1999). The development in all taxa takes place outside the body of the mother (either as free larvae or in dorsal brood chamber), which supports comparability further. We therefore—when this is sensible—apply characters for both free-living larvae in the ''large'' branchiopods and embryonized larvae in *Cyclestheria* and Cladocera.

54. Mandibular palp in larvae/embryonized larvae: (0) present; (1) absent

In free-living larvae of Anostraca, Notostraca, Spinicaudata and Laevicaudata, the mandible has a distinct ''palp'' (= segments distal to coxa) with very similar morphology (Olesen, 2004) (scored 0) (Fig. 5A–D). In *Leptodora*, a palp is absent in the embryonized larvae in the parthenogenetic part of the life cycle (Olesen et al., 2003) (Fig. 5F), but present in the free swimming metanauplius hatching from resting eggs (but with a different morphology) (Sars, 1873) (scored polymorphic 0, 1). In all other Cladocera, a palp is lacking (scored 1). In the embryonized larvae of *Cyclestheria hislopi*, a palp is lacking (Olesen, 1999) (Fig. 5E), but it is present in the free living larvae reported from Cuba (Botnariuc and Viña Bayés, 1977) (scored polymorphic 0, 1).

The larval mandible of Cephalocarida has a ''palp'', but with a different morphology from that of Branchiopoda (scored 0). The embryonized larvae in Leptostraca have an undifferentiated palp (scored 0) (Olesen and Walossek, 2000), which shows that ''direct development'' and loss of the palp are not necessarily correlated.

55. Antennae in larvae/embryonized larvae, masticatory process: (0) present; (1) absent

In free-living larvae of Anostraca, Notostraca, Spinicaudata and Laevicaudata, the second antenna has a coxal masticatory process (''naupliar process'') (Fig. 5A–D). In all taxa, the morphology is strikingly similar (Olesen, 2004). In embryos of *Cyclestheria hislopi*, a masticatory process is lacking but it is present in free-swimming larvae of the species (scored polymorphic 0, 1) (Fig. 5E). In all cladocerans, including the free-swimming larvae in *Leptodora*, an antennal coxal masticatory process is lacking (scored 1) (Fig. 5F). In larvae of Cephalocarida, an antennal masticatory process is present (scored 0) (Sanders, 1963), while it is lacking in the embryonized larvae of Leptostraca (scored 1).

56. Anntennule shape in larvae/embryonized larvae: (0) elongate, tubular; (1) as small buds; (2) as horn-like structure

In larvae of Anostraca and Notostraca, the antennules are tubular, more or less elongate, and articulated to the head (scored 0) (e.g., Schrehardt, 1987; Møller et al., 2003, 2004). In the free-swimming larvae of Spinicaudata, the antennules are small, globular, immobile buds (Eder, 2002; Olesen and Grygier, 2003, 2004; Pabst and Richter, 2004), similar to those

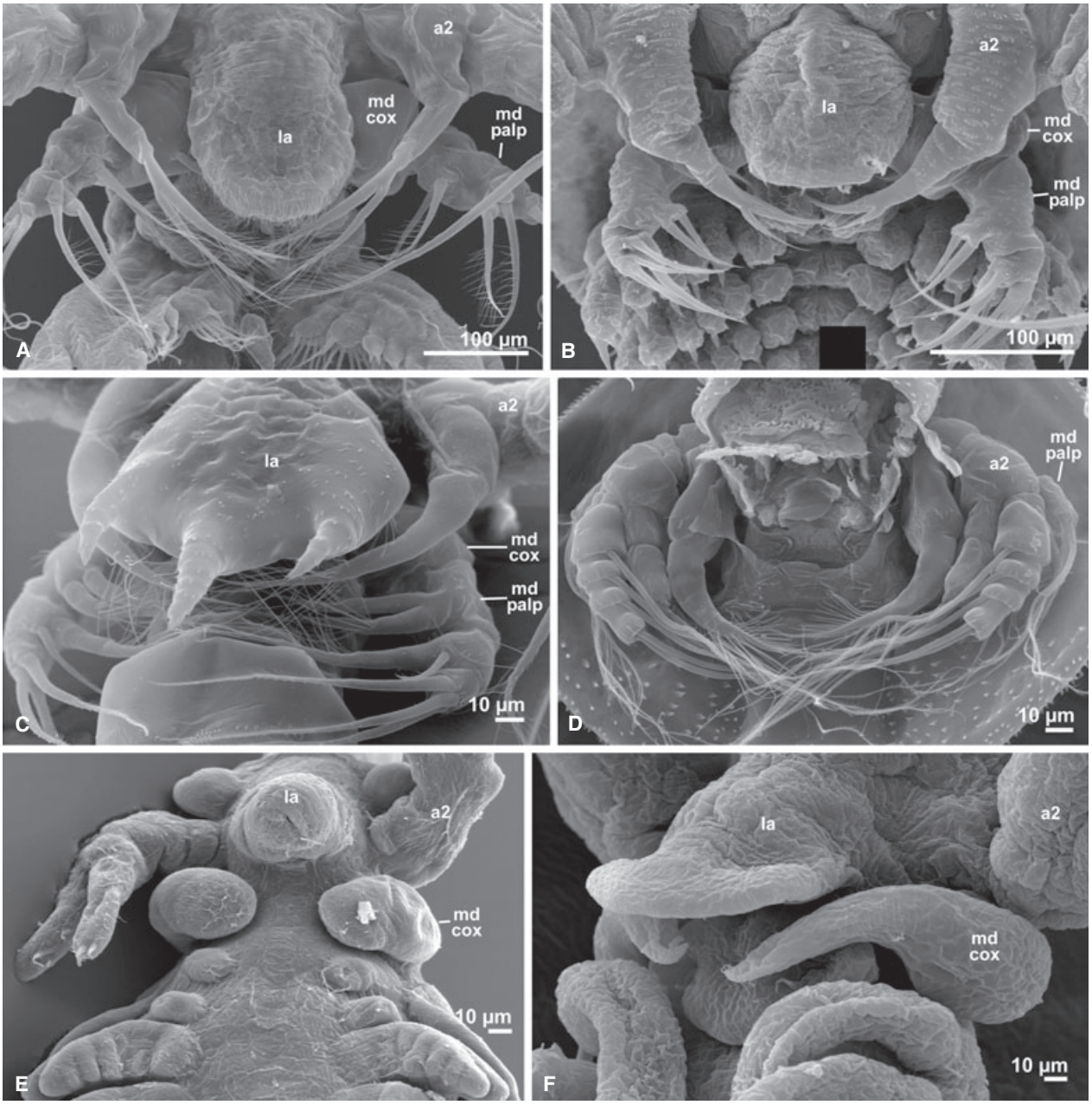

Fig. 5. Branchiopod larvae showing early development of antennal coxal masticatory process and mandibles. (A) *Eubranchipus grubii* (Anostraca), late stage. (B) *Triops cancriformis* (Notostraca), stage 3. *Caenestheriella gifuensis* (Spinicaudata), stage 2. (D) *Lynceus brachyurus* (Laevicaudata), early stage. (E) *Cyclestheria hislopi* (Cyclestherida), stage 4. (F) *Leptodora kindtii* (Haplopoda), stage 4. Abbr. la, labrum; a2, antenna 2; md cox, mandibular coxa; md palp, mandibular palp.

found in the early embryonized larvae of *Cyclestheria hislopi* and of various cladocerans (scored 0) (Kotov and Boikova, 1998, 2001; Olesen, 1998; Olesen et al., 2003). In the Podonidae (Onychopoda), this character is inapplicable as the antennules have been largely reduced, and only the sensillae are visible externally. In larvae of Laevicaudata, the antennules are a pair of large "horns" very different to those of other branchiopod larvae (Gurney, 1926; Olesen, 2005), and these are therefore scored as a separate state (scored 2), despite the juvenile antennules can be recognized inside the larvae antennular horns as small rounded buds, similar to those of Spinicaudata, *C. hislopi* and Cladocera. In Cephalocarida, the antennules in nauplius 1 are elongate with six segments (scored 0) (Sanders, 1963). In embryonized larvae of Leptostraca, the antennules are elongate and undifferentiated (scored 0) (Olesen and Walossek, 2000).

57. Antennules, orientation in larvae/embryonized larvae: (0) remain separate; (1) migrate together (sometimes fusing)

In various species of Onychopoda (but Podonidae scored inapplicable) and Anomopoda the antennular limb buds have a characteristic type of development. The limb buds start their development being widely separate, but later they "migrate" together and sometimes fuse basally medially at the head forming a V-shaped pattern (scored 1) (Olesen et al., 2003). In Ctenopoda (Kotov and Boikova, 1998), Haplopoda (Olesen et al., 2003), *Cyclestheria* (Olesen, 1999), in all other larvae or embryonized larvae of Branchiopoda, as well as in the two outgroups (Cephalocarida and Leptostraca), the limb buds remain separated during development (scored 0).

58. Antennules with one large seta: (0) absent; (1) present only in naupliar larval stages

In free-living larvae of Spinicaudata, Laevicaudata, and also in the free larvae of *Cyclestheria* (see Botnariuc and Viña Bayés, 1977), the antennular buds have a large and characteristic seta (Eder, 2002; Olesen and Grygier, 2003, 2004; Pabst and Richter, 2004; Olesen, 2005). Such setae are absent from free-living larvae of *Leptodora* (Sars, 1873), Anostraca, and Notostraca (Schrehardt, 1987; Møller et al., 2003, 2004). Other cladocerans are scored inapplicable as the embryonized larvae are devoid of setae until late in development. Leptostraca is also scored inapplicable. Cephalocarida is scored absent (Sanders, 1963).

59. Antennules with sensillae at the tip: (0) absent; (1) present

In free-living larvae of Spinicaudata, the antennular limb buds have a group of small sensillae (Olesen and Grygier, 2003, 2004; Pabst and Richter, 2004). Such sensillae are absent in other "large" branchiopods with free-living larvae (Anostraca, Notostraca and Laevicaudata) (scored 0). The descriptions of the larvae of *Cyclestheria* (see Botnariuc and Viña Bayés, 1977) and *Leptodora* (e.g., see Sars, 1873; Sebestyén, 1931) are not detailed enough to be used in this respect (scored "?"). All cladocerans with direct development have been scored inapplicable. Leptostraca is also scored inapplicable. Cephalocarida is scored absent (Sanders, 1963).

60. Antenna in larvae, basis with small segment: (0) absent; (1) present

In free-swimming larvae of Laevicaudata (Olesen, 2005) (Fig. 5D) and some species of Spinicaudata, the basis of the second antennae are subdivided into a small and a large part (Olesen and Grygier, 2004; Pabst and Richter, 2004), but it seems to be undivided in *Eulimnadia braueriana* (Olesen and Grygier, 2003). Such a characteristic subdivision is absent in other free-swimming larvae of Branchiopoda which have been examined by SEM. *Cyclestheria* is scored "?" based on the description by Botnariuc and Viña Bayés (1977), which does not include the necessary details about antennal segmentation. Cladocera is due to the modified developmental stages scored inapplicable, while the situation is unknown for the free-living *Leptodora* larvae. Leptostraca is scored inapplicable. Cephalocarida lacks a characteristic small segment of the antennal basis (scored 0).

61. Antenna in larvae, masticatory process: (0) anterior branch with brush-like setae; (1) with single comb-row

In the free-living larvae of Laevicaudata (Olesen, 2005) (Fig. 5D) and Spinicaudata (Olesen and Grygier, 2003, 2004; Pabst and Richter, 2004), the setae at the anterior branch of the coxal masticatory process are more or less condensed into a single comb-row. In Anostraca and Notostraca (Schrehardt, 1987; Møller et al., 2003, 2004), the setae is arranged more like a brush with setae inserted in an irregular pattern around the process (Fig. 5A,B). Taxa with embryonized larvae (Leptostraca, Cladocera) are scored as inapplicable for this character. *Leptodora* is scored inapplicable because a masticatory process is absent also in the free-living larvae. The character state is unknown for the free larvae in *Cyclestheria*. In larvae of Cephalocarida, the antennal masticatory process is not divided into distinct anterior and posterior branches similar to those of branchiopods and is therefore scored as inapplicable for this character.

62. Antenna in larvae: number of segments in endopod of larvae: (0) portions not separated into clear segments; (1) two clear segments; (2) three segments

In Laevicaudata (Fig. 5D) and Spinicaudata (see Sars, 1896; Monakov and Dobrynina, 1977), the larval antennal endopod is clearly divided into two segments, a smaller one proximally and a larger distally (scored 1). Free-living larvae of *Cyclestheria* were depicted by Botnariuc and Viña Bayés (1977) as having two segments. *Leptodora kindtii* possess a three segmented endopod (scored 2, following Sars, 1873). Olesen and Grygier (2004) demonstrated that the two-segmented endopod in *Caenestheriella gifuensis* is formed by various fusions of a higher number of primordial portions present earlier in the ontogeny. The larval antennal endopod in *Triops cancriformis* (Notostraca) shows a similar, but less clear subdivision into two segments (scored 1), whereas in *Lepidurus arcticus* the endopod is not divided into clear segments (Borgstrøm and Larsson, 1974). In *Eubranchipus grubii*, this limb part is not subdivided this way (scored 0). Taxa with embryonized larvae (Leptostraca and Cladocera) are scored inapplicable. Larvae of Cephalocarida (*Hutchinsoniella*) have two segments in the antennal endopod; they look different (e.g., with more setation) from those of Laevicaudata and Spinicaudata, but are scored the same way (scored 1).

63. Antenna in larvae or embryonized larvae: number of setae on exopod: (0) many; (1) seven; (2) five

In free-living larvae of Laevicaudata and Spinicaudata, the antennal exopod constantly has five setae (scored 2) (Fig. 5D). Anostraca has a much higher number of setae on this limb part, while five or seven are present in Notostraca. Botnariuc and Viña Bayés (1977) illustrated a free-living larvae of *Cyclestheria* with setation, but we are uncertain whether the precise number of setae have been drawn (scored "?"). Taxa with embryonized larvae (Leptostraca, Cladocera) are scored inapplicable for this character. Cephalocarida have many antennal exopod setae (scored 0).

64. Segmentation of antennal exopod in larvae: (0) exopod 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

In free-swimming larvae of Laevicaudata (Fig. 5D) and all investigated species of Spinicaudata, the antennal exopod has a characteristic segmentation. Proximally it has one or two small segments, followed by a larger segment with a seta, again followed by three setae-bearing segments (Olesen and Grygier, 2003, 2004; Olesen, 2005). Olesen and Grygier (2004) demonstrated for *Caenestheriella gifuensis* that this characteristic pattern is the result of fusions of certain primordial portions in the exopod. In larvae of Anostraca and Notostraca, the segments are either of similar size or gets gradually smaller distally. The description of free-living larvae of *Cyclestheria* does not allow for the scoring of this character (scored "?"). *Leptodora* has segments of approximately same size in the free-living larvae (Sars, 1873) (scored 0). All taxa with direct development (Cladocera and Leptostraca) are scored inapplicable for this character. Cephalocarida are scored "0".

65. Mandibular palp, endopod segment 1: (0) two setae; (1) one seta

The segmentation and setation of the mandibular palp (segments distal to coxa) in larvae of branchiopods are strikingly similar and was therefore suggested as a synapomorphy for the crown-group Branchiopoda by Olesen (2004). However, there is some variation in the setation of endopod segment 1. In Anostraca (Fig. 5A), Notostraca (Fig. 5B), and in at least one species of Spinicaudata, *Caenestheriella gifuensis* (Fig. 5C), this segment has two setae, and other examples are mentioned in the literature (see Olesen and Grygier, 2004). Laevicaudata (Olesen, 2005) and the majority of Spinicaudata (Sars, 1896; Eder, 2002; Olesen and Grygier, 2003) have only one seta on this segment. The free-living larva of *Cyclestheria* has been clearly illustrated with only one seta on this segment by Botnariuc and Viña Bayés (1977). *Leptodora* has no mandibular palp and has therefore been scored inapplicable, as has the remaining Cladocera and Leptostraca. Cephalocarida has a larval mandibular palp, but since its segmentation is different from that of Branchiopoda, the character has been scored inapplicable for this taxon.

Analytical methods

Morphological characters, all equally weighted and scored as non-additive, were analyzed using the parsimony program NONA version 2.0 (Goloboff, 1999a) and Winclada version 1.0000 as shell program (Nixon, 1999–2002). The search strategy used tree bisection and reconnection branch swapping (TBR) on a series of 1000 random addition replicates retaining up to 10 cladograms per replicate (commands: h/10; mult* 1000). Jackknife values were calculated using an approximate search with 10 random addition replicates, repeated 1000 times.

Molecular data and molecular/morphological data combined were analyzed using the direct optimization approach (Wheeler, 1996) as implemented in the computer program POY (Wheeler et al., 2003) with parsimony as optimality criterion. Direct optimization allows DNA sequence alignment and phylogenetic analysis to be undertaken simultaneously and dynamically under the same parameters for both procedures. The two protein coding genes were analyzed as "prealigned" because no length variation appeared. A "sensitivity analysis" (Wheeler, 1995) was undertaken to access the sensitivity of phylogenetic results to variation in the analytical parameters (see also Giribet, 2003). A parameter space of two variables (indel/transversion ratio and transversion/transition ratio) was explored: If an indel/transversion ratio of 2 : 1, and a transversion/transition ratio of 1 : 1 is specified, two base substitutions equal a single insertion/deletion. If the transversion/transition ratio is 2 : 1 then a single insertion/deletion equals two transversions or four transitions. In total, 20 different combinations were analyzed for the molecular data only and the same 20 combinations for the combined data set of morphological and molecular data. In these combined analyses morphological data were weighted equal to the highest of the molecular costs (= the indel costs). The sensitivity analysis includes equal weighting of all included characters (i.e., substitutions, indels and morphology), which has been argued to have a logical priority if the characters are proposed as singular historical events (Grant and Kluge, 2005).

The POY analyses were run in parallel on a cluster of 22 dual-processor nodes using MPI software and the parallel version of POY. Each of 10 replicates (-replicates 10) consisted of 10 starting Wagner trees generated through random addition sequence (-buildsperreplicate 10), the best of which is submitted to a combination of SPR and TBR branch swapping. TBR branch swapping was followed by a combination of tree-fusing (Goloboff, 1999b) and ratchetting (Nixon, 1999)

to optimize tree searches. While TBR and SPR allow branch rearrangement within a given tree, tree fusing allows the exchange of branches of identical composition among different trees. The -slop and -checkslop commands were employed to improve cladogram cost calculations from the heuristic operations. "Slop 5" checks all suboptimal trees within 0.5% of the current minimum value during a search, whereas "checkslop 10" checks all suboptimal trees within 1% of the minimum value during a final TBR refinement.

The complete command sequence for a simultaneous analysis under equal weighting (using stepmatrix 111 and morphology weighted 1 is as follows: Poy Branchiopoda_12S.dat Branchiopoda_16S.dat Branchiopoda_18S.dat Branchiopoda_28S.dat -prealigned Branchiopoda_COI.dat Branchiopoda_EF1.dat -weight 1 BranchMorph.dat -terminalsfile Branchiopoda.txt -molecularmatrix 111.txt -noleading -minterminals 10 -parallel -solospawn 22 -norandomizeoutgroup -repintermediate -intermediate -catchslaveoutput -replicates 10 -buildsperreplicate 10 -multirandom -multibuild -slop 5 -checkslop 10 -maxtrees 20 -ratchettbr 10 -ratchettrees 5 -treefuse -fuselimit 100 -fusemingroup 3 -fitchtrees -printtree -plotfile output.tre > output.out 2> output.err

For the combined analyses of all molecular data as well as of molecular and morphological data, all resultant optimal trees for each parameter set (i.e., trees from 20 parameter sets) were combined into a file and were used as input topology (–topology filename) for a second round of tree-fusing. This sensitivity analysis tree fusing (SATF; Boyer et al., 2005) was run for each parameter set as an additional search strategy.

Character congruence was used to choose the two combined analyses that minimize incongruence among partitions (see Wheeler, 1995): (1) molecular data only, and (2) molecular data and morphology. Congruence among partitions was measured by a modified version of the ILD metric (Wheeler and Hayashi, 1998). The value is calculated for each parameter set by subtracting the sum of the scores of all partitions from the score of the combined analysis of all partitions, and normalizing it for the score of the combined analysis (Table 3). The parameter set with the lowest ILD value is the one that maximizes overall congruence and minimizes character conflict among all data (Wheeler, 1995).

Results

Morphological data

The analysis of the 65 morphological characters—all equally weighted and non-additive—(Table 3) resulted in 3360 equally parsimonious trees of 137 steps. The strict consensus is shown in Fig. 6. Jackknife support values are given above the branches. Within Branchiopoda, Phyllopoda (comprising all taxa except Anostraca) is supported. Notostraca is the sister group to the remaining taxa supporting the classical Diplostraca concept (Conchostraca + Cladocera). However, Conchostraca is not supported but *Cyclestheria hislopi* is the sister group to Cladocera (constituting together Cladoceromorpha) and Spinicaudata is closer to Cladoceromorpha than to Laevicaudata. Cladocera is supported as monophyletic. Within Cladocera, Gymnomera comprising Haplopoda and Onychopoda is supported and a sister group relationship between Gymnomera and Ctenopoda. Anomopoda is not supported as monophyletic (but this part of the tree is unresolved).

Combined approach

The combined analysis under equal weighting gives in certain respects similar results to the morphological analysis (Fig. 7). Phyllopoda is monophyletic and the sister group to Anostraca. Within Phyllopoda, Cladocera, Cladoceromorpha and Spinicaudata + Cladoceromorpha are monophyletic. This analysis is different from the morphological analysis in the position of Notostraca and Laevicaudata. Here, Laevicaudata is the sister group to the remaining Phyllopoda, and Notostraca is the sister taxon to Spinicaudata and Cladoceromorpha. Within Cladocera, Haplopoda is the sister taxon to Onychopoda and, contrary to the morphological analysis, Ctenopoda is the sister group to a monophyletic Anomopoda. The analysis using only the molecular data under equal weighting results in almost exactly the same topology as the combined analysis (not shown). The parameter set with the lowest incongruence (measured by the ILD) is that with transversions weighted twice to transitions and indels equally weighted to transversions (Table 4). The results of this analysis differ in certain major respects from the one with all characters equally weighted. Notostraca is the sister group to Diplostraca (as in the morphological analysis) and within Cladocera Anomopoda and Onychopoda are sister groups, i.e., Gymnomera is not supported (Fig. 8). Considering only the molecular data, this parameter set (also the least incongruent if only molecular data are considered) results in a sister group relationship between Notostraca and Spinicaudata, and with Laevicaudata as the most basal clade within Phyllopoda. Cladoceromorpha is supported but with *Cyclestheria* inside Cladocera (not shown). The sensitivity analysis reveals that the results of the least incongruent parameter set are "untypical" concerning the monophyly of Diplostraca and the non-monophyly of Gymnomera. All "neighboring" parameter sets show monophyly of Gymnomera (actually shown by the remaining 19 analyses) and show Laevicaudata in a basal position as sister group to the remaining

Table 3
Morphological data matrix

	1 5 10 15 20 25 30 35 40 45 50 55 60 65
Hutchinsoniella macracantha	010--270000030090-?100000-0000002---------0400?--000-0000000-100-
Paranebalia longipes	0110026000---0-81-0---000-000000200-000---0200?--0--00100--------
Branchinella occidentalis	000--00001---1?0000000100-000000?00-00?00-1????0-000-????????????
Artemia sp.	000--00001---1?0000000100-000000200-00000-100000-000-000000000000
Parartemia minuta	000--00001---1?0000000100-000000?00-00?00-1????0-000-????????????
Branchinecta paludosa	000--00001---100000000100-000000000-00??0-100000-000-00000???000
Eubranchipus grubei	000--00001---1?0000000100-000000000-000??-1??000-000-000000000000
Thamnocephalus platyurus	000--00001---1?0000000100-000000?00-00???-1????0-000-00000????000
Triops cancriformis	001302100?---201000110100-001000010-000100011001-0000000000001200
Triops australiensis	001302100?---2?1000110100-001000?10-00?1000????1-0000??????????
Triops longicaudatus	001302100?---2?1000110100-001000?10-00??0?0????1-0000000000???100
Lepidurus apus	001302100?---2?1000110100-001000?10-0001000??001-000000000???????
Lepidurus arcticus	0013021000---2?1000110100-001000010-00??0?011??1-000000000???0200
Lynceus brachyurus	101003?000100202000110110001l0--011-000100041002000000020101112l1
Lynceus biformis	101003?0001002?200011011000110--?11-00?1000????200000020101112l1
Lynceus tatei	101003?0001002?200011011000110--?11-0001000????200000??????????
Leptestheria kawachiensis	10101210101001?3100101111001110l?1??????1?0????200000001011111210
Leptestheria dahalacensis	10101210101001?3100101111001110l012000111l0??012000000101???12?1
Caenestheria lutraria	10101210101001?3100101111001110l?120???1110????200000??????????
Caenestheriella gifuensis	10101210101001?3100101111001110l?120????110????200000001011111211
Imnadia yeyetta	10101210101001?3100101111101110l012000l?1?0??0120?00000101????2?1
Limnadia lenticularis	10101210101001?3100100111101110l1120001111031??200000001101???12?1
Limnadopsis birchii	10101210101001?3100101111001110l1120001111l0????200000001011111211
Eulimnadia braueriana	10101210101001?3100101111101110l11??????1?0????200000001011011211
Cyclestheria hislopi	101012?00110010410010011000111010120001100l3?01201*11**101???1??1
Leptodora kindtii	0112015001111-15111-----0000101-012-111---2510-211010**100?-?200-
Bythotrephes longimanus	0112013001112-?7111-----0000101-0121111---1511-2111101111--------
Cercopagis pengoi	0112013001112-17111-----0000101-0121111---?5???2111101111--------
Polyphemus pediculus	1112013001112-?7111-----000010--0121111---1511-2111101111--------
Podon leuckarti	1112013101112-?7111-----0000101-01????1---?5?1-21111011----------
Evadne nordmanni	1112013101112-?7111-----0000101-01????1---?511-21111011----------
Cornigerius maeoticus	1112013101112-?7111-----0000101-012111?---?5???21111011----------
Sida crystallina	10110120011231?5100-00--000111012121111---251212111101110--------
Diaphanosoma brachyurum	101101200113210510O-00--000111010121111---2?1212111101110--------
Penilia avirostris	10110120011231?5100-00--00011101?1?????---?5???2111101110--------
Eurycercus lamellatus	10110140011221051O0-00--0011110101?????10-15?022111111111--------
Pseudochydorus globosus	101101?0011221?6100-00--00111101012000?10-?5???211111111??--------
Daphnia pulex	10110140011121?6100-00--00111101212010110015102211111111l--------
Simocephalus vetulus	1011014001112l?6100-00--0011110121201011--15?022111111111--------
Scapholeberis mucronata	101101?0011121?6100-00--00111101212010l?0115?022111111111--------
Ceriodaphnia sp.	101101?0011121?6100-00--00111101012010l?0015?022111111111--------
Ilyocryptus sp.	101101?0011121?5100-00--00111101O1?????0025?00211111111?--------
Ophryoxus gracilis	10110140011112??5100-00--00111101211??????0-?5?0221111111??--------
Acantholeberis curvirostris	10110140011112??5100-00--00111101211??????0-25???211111111?--------
Bosmina coregoni	1011014001112l??100-00--00111101212O??1?0-?5?02211111112??--------

*[0,1]

Phyllopoda. All or almost all (i.e., 19 of 20) analyses show monophyly of Anostraca, Notostraca, Laevicaudata (only genus *Lynceus* considered), Spinicaudata, Cladoceromorpha, Cladocera (Fig. 9), and within Cladocera of Onychopoda and Gymnomera (Fig. 10). Concerning the relationships of the major non-cladoceran taxa, the analyses can be divided into two groups (Fig. 11).

The first group comprises analyses with an indel-to-transversion ratio up to 2; the second group the analyses with higher ratios. The first group of analyses results in monophyletic Phyllopoda, with Laevicaudata as sister group to the remaining Phyllopoda (with the above-mentioned exception) and with Spinicaudata and Cladoceromorpha as sister groups. The second group of analyses results in a "large branchiopod" clade with Anostraca and Laevicaudata as sister groups and Notostraca as sister taxon to both (one exception). This implies that considering only the branchiopod ingroup taxa the topology is the same in almost all analyses (despite two). Choosing the root between Anostraca and Phyllopoda, Laevicaudata branches off first, followed by Notostraca; Spinicaudata is the sister group to Cladoceromorpha (Fig. 11).

Concerning the relationships within Cladocera, the monophyly of Onychopoda and of Gymnomera is the

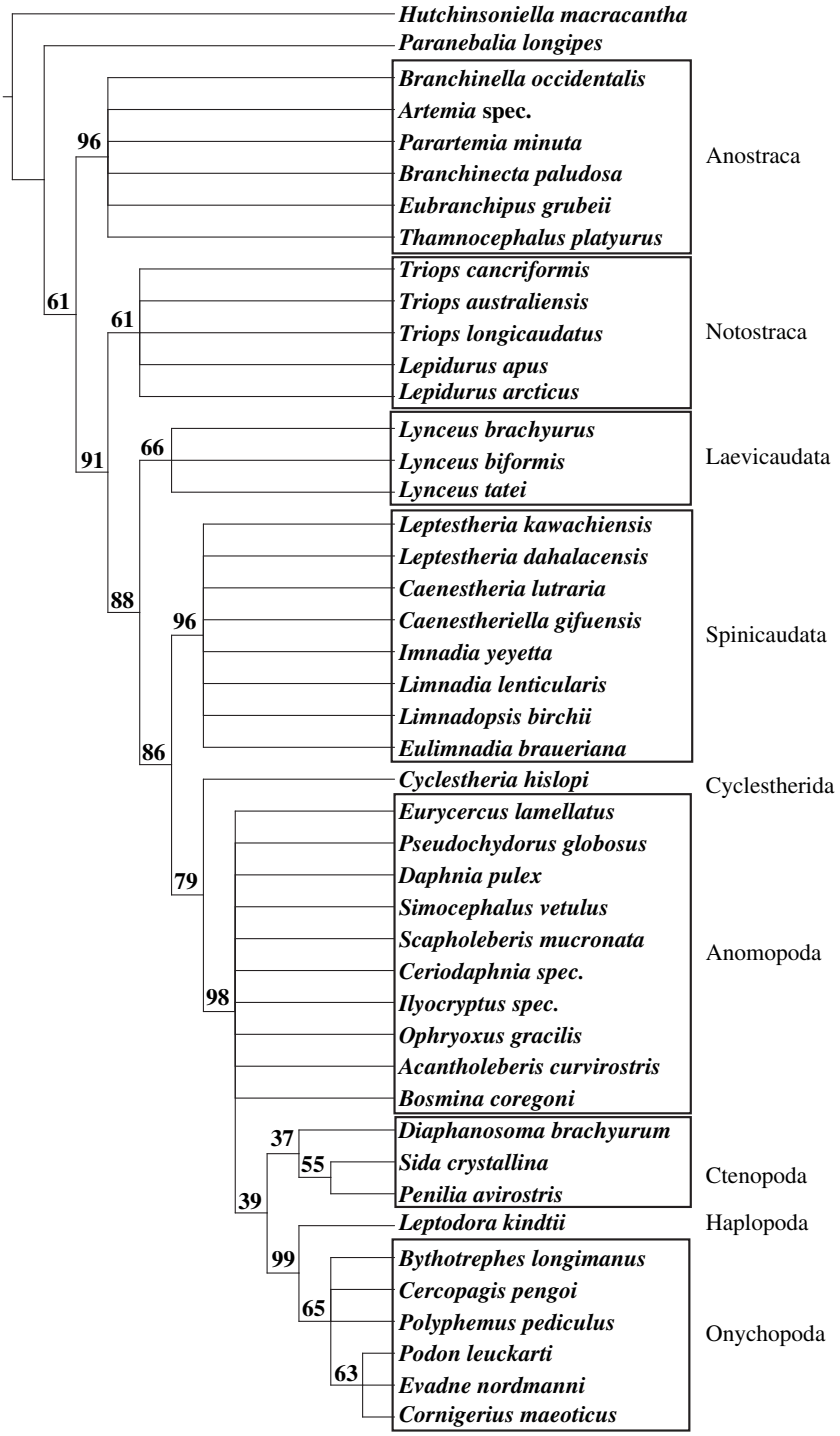

Fig. 6. Strict consensus of the 3360 equally parsimonious trees of 137 steps resulting from analysis of 65 morphological characters (all equally weighted and non-additive). Jackknife support values are given above the branches.

result of 19 analyses. Anomopoda and Ctenopoda are supported by all analyses with indel weights up to 4 (+ the 811 analysis) but not with higher indel weights (Fig. 10). Anomopoda and Ctenopoda as sister groups is only the result of one analysis, whereas a sister group relationship between Ctenopoda and Gymnomera is shown in nine analyses (Fig. 10).

The analyses using only the molecular data are more ambiguous. Anostraca, Notostraca, Spinicaudata and Cladoceromorpha are supported by all analyses. Clado-

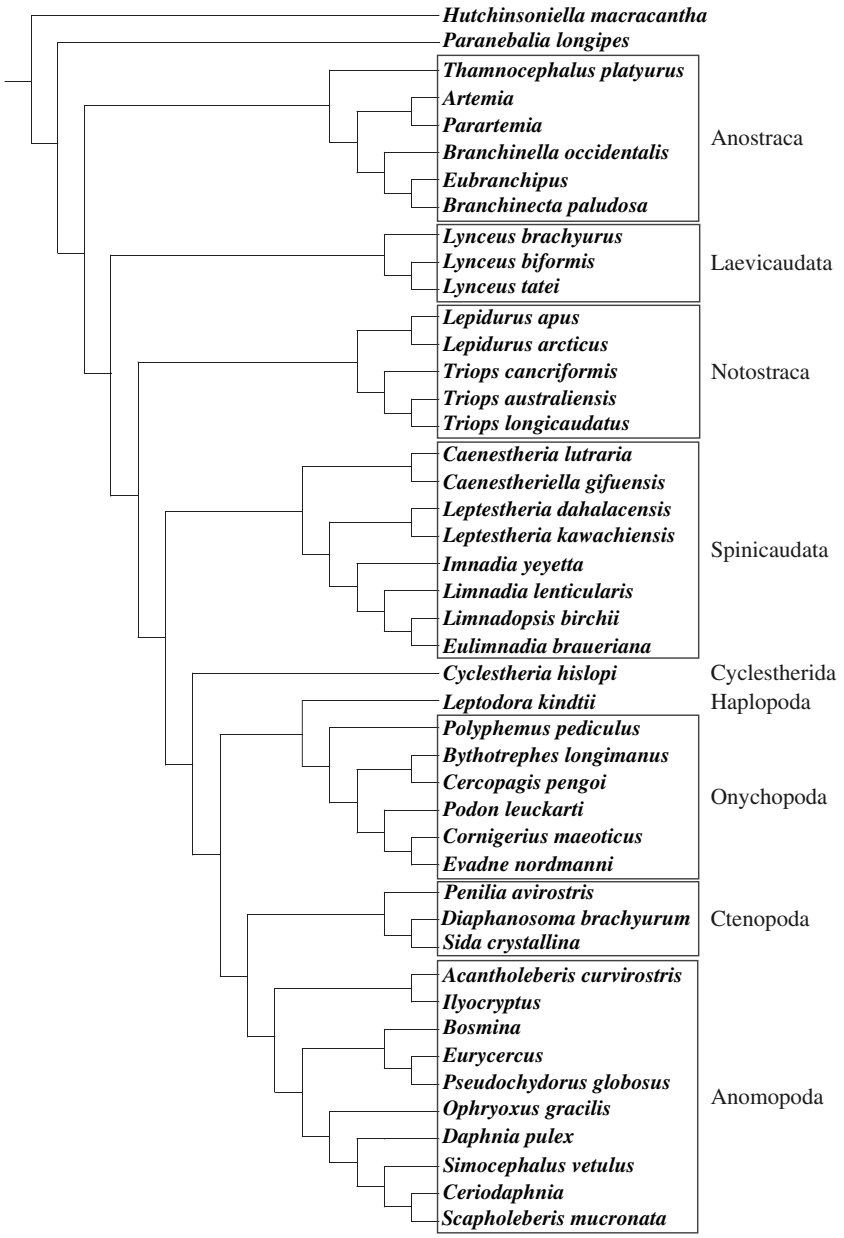

Fig. 7. Most parsimonious cladogram at cost 17148 for the parameter set of equal weighting all characters for six genes and morphology.

cera is only supported by half of the analyses because *Cyclestheria* has a position inside the Cladocera clade in the other analyses. Laevicaudata is only supported by the analyses with lower indel-to-transversion ratios. The described pattern concerning the position of Laevicaudata is the same as in the combined analyses but several analyses result in a sister group relationship between Notostraca and Spinicaudata. The relationships within the Cladocera are much less stable than in the combined analyses. Gymnomera is only supported by three of 20 analyses.

Discussion

In general, molecular systematic publications present phylogenetic hypotheses that are results of the included data and of the analytical techniques used (parsimony, maximum likelihood, Bayesian, often with exclusion of data). In many cases, quite different cladograms are presented in the same publication (based on different analytical techniques or different data partitions). In some cases, the authors prefer a certain cladogram (mainly based on preferred methodology or because of

Table 4
Tree length and ILD values at 20 different parameter set combinations ranging from an indel-to-transversion ratio of 1–16 and transversion-to-transition ratio of 1–8. The parameter set that minimizes ILD is shown in bold font type. Abbreviations for the different partitions are as follows: 12S (12S rRNA), 16S (16S rRNA), 18S (18S rRNA), 28S (28S rRNA), COI (cytochrome *c* oxidase subunit I), EF1 (elongation factor 1α), MOL (molecular data; all molecular loci analyzed simultaneously), MOR (morphology)

Ind: Tv: Ts	12S	16S	18S	28S	COI	EF1	MOL	ILD (MOL)	MOR	MOL + MOR	ILD (MOL + MOR)
111	3144	2660	1328	4230	3418	1845	17148	0,030499184	137	17296	0,030874191
121	**5007**	**4209**	**2040**	**6756**	**4979**	**2557**	**26254**	**0,02689114**	**274**	**26572**	**0,028225199**
141	8566	7169	3393	11545	8019	3971	43978	0,029901314	548	44589	0,030904483
181	15661	13040	6085	20905	14099	6798	79325	0,034503624	1096	80513	0,035137183
211	3581	2932	1604	5490	3418	1845	19432	0,028921367	274	19731	0,029750139
221	5808	4703	2540	8995	4079	2557	30457	0,058278885	548	31046	0,058493848
241	10076	8096	4355	15872	8019	3971	52160	0,033953221	1096	53292	0,033907528
281	18594	14896	7962	29456	14099	6798	95405	0,037733871	2192	97919	0,040053514
411	4119	3288	2016	7406	3418	1845	22779	0,030159357	548	23472	0,035446489
421	6825	5348	3316	12759	4979	2557	37019	0,033361247	1096	38341	0,038105422
441	12045	9409	5855	23272	8019	3971	65123	0,039187384	2192	67788	0,044624417
481	22526	17487	10917	44208	14099	6798	121357	0,043854083	4384	126725	0,049761294
811	4930	3895	2731	10911	3418	1845	28734	0,034941185	1096	30070	0,041370136
821	8361	6587	4742	19642	4979	2557	48928	0,042102681	2192	51757	0,052108893
841	15089	11795	8678	37041	8019	3971	88858	0,047997929	4384	94289	0,056337431
881	28562	22171	16527	71581	14099	6798	168446	0,051696093	8768	179743	0,062517038
1611	6259	4892	4120	17645	3418	1845	40136	0,048759219	2192	42867	0,058226608
1621	11003	8706	7503	33041	4979	2757	71682	0,05151921	4384	77652	0,067982795
1641	20313	16016	14194	63583	8019	3971	133984	0,058872701	8768	145736	0,074600648
1681	38957	30575	27479	124696	14099	6798	250193	0,030332583	17536	282789	0,080091517

concordance with morphological data). In other cases, the authors do not favor any of their particular results. Herein, we refer to previous analyses if at least one of the published cladograms shows a certain relationship, independently of whether or not the authors really "suggest" this phylogenetic hypothesis. Analyses using additional data and different methodology like ours, do not test any of the previous analyses in a strict sense (which should still give the same results using the same data and analytical techniques), but are able to test the stability of traditional and recently published relationships under a combined approach, including a maximum of the currently available data (six loci + morphology).

In our discussion on proposed relationships within Branchiopoda, we start with the most unambiguous part. All of our combined analyses support the monophyly of Anostraca (one exception), Notostraca, Laevicaudata (only the genus *Lynceus* considered), Spinicaudata, Cladoceromorpha, Cladocera (one exception), Gymnomera (one exception) and Onychopoda (one exception). Some of this is not surprising and has never been seriously doubted. However, certain aspects should be discussed in more detail.

Morphological support for Cladocera has still to be considered as not entirely convincing and Fryer (1987) was certainly right in emphasizing the morphological differences between the four major cladoceran taxa. However, doubts on cladoceran monophyly (Fryer, 1999a, 2001, 2002) seem now to be somewhat anachronistic. All recent molecular analyses support the monophyly of Cladocera (Taylor et al., 1999; Spears and Abele, 2000; Braband et al., 2002; deWaard et al., 2006; Stenderup et al., 2006) and only one of our analyses using the combined approach contradicts this view. The monophyly of Cladocera (as well as of Spinicaudata), however, does not necessarily imply that the stem species of the crown-group Cladocera looked like a water flea. It is still possible that certain water flea characters evolved independently from clam-shrimp-like ancestors within the crown-group Cladocera. Also, it is this morphological transition that was implied by the original polyphyly hypothesis (Eriksson, 1934; Schminke, 1981). Whether all cladocerans evolved from an ancestor with cladoceran characters can only be solved by convincingly showing the homology of these characters.

That the monoptypic clam shrimp *Cyclestheria hislopi* has finally turned out to be the sister group to Cladocera may not be completely surprising considering the cyclic-parthenogenetic life cycle and the direct development of the "embryos" known for a long time (Sars, 1887b). Nevertheless, it was not before Olesen et al. (1997) that a possible sister group relationship was discussed. Now, the monophyly of the clade Cladoceromorpha (*sensu* Ax, 1999) has become supported by all available molecular systematic analyses (Taylor et al., 1999; Spears and Abele, 2000; Braband et al., 2002; deWaard et al., 2006; Stenderup et al., 2006), and also the molecular structure of the two nuclear ribosomal genes strongly supports its monophyly (Crease and Taylor, 1998; Taylor et al., 1999). None of our combined analyses (or of the separate analyses) contradicts this view.

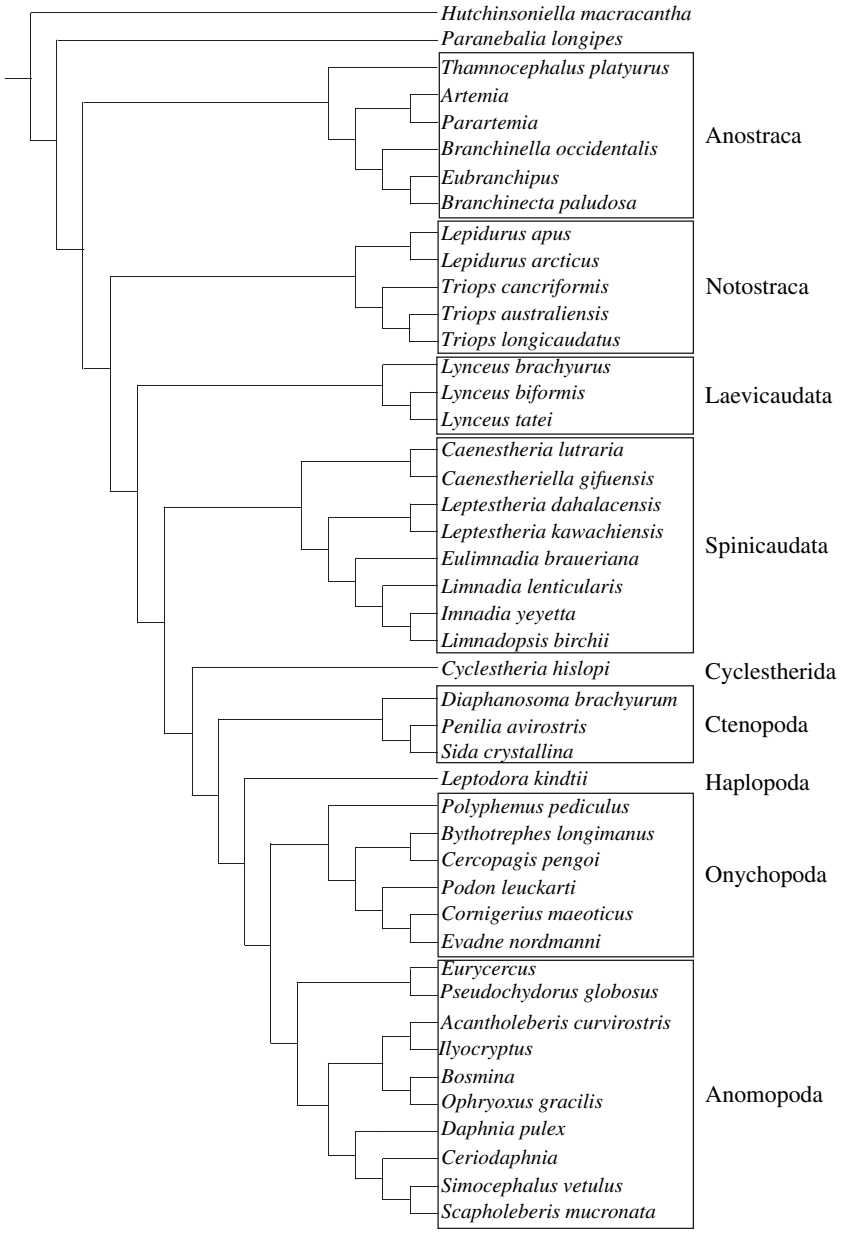

Fig. 8. Most parsimonious cladogram at cost 26254 for the least incongruent data set (indel/transversion cost of 1 and transversion/transition cost of 2) for six genes and morphology.

Traditionally, four major taxa have been recognized within Cladocera (Ctenopoda, Anomopoda, Onychopoda and Haplopoda). Most previous analyses supported the monophyly of Ctenopoda, Onychopoda and Anomopoda—Haplopoda are monotypic. However, Braband et al. (2002) found some evidence that Anomopoda may be paraphyletic and Stenderup et al. (2006) found *Leptodora kindtii* placed within Onychopoda. Our combined analyses support the monophyly of Onychopoda as previous molecular analyses have done (Richter et al., 2001; Braband et al., 2002; deWaard et al., 2006—only those analyses considered with a reasonable number of onychopods included). The monophyly of Anomopoda was the result of the analyses by deWaard et al. (2006) and Stenderup et al. (2006). It is also the result of our combined analyses with lower indel-to-transversion ratios (all up to 4). The same analyses also support the monophyly of Ctenopoda (only Sididae). Our morphological analysis also supports the monophyly of these four cladoceran subgroups. Within Cladocera, a sister group relationship between Haplopoda and Onychopoda, combined as Gymnomera, has been

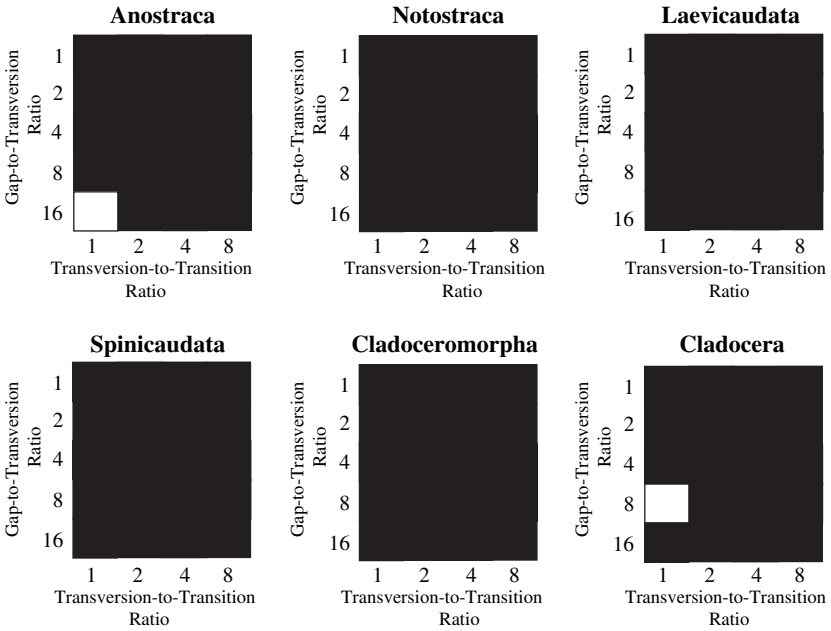

Fig. 9. Navajo Rugs representing the results of the sensitivity analysis including six genes and morphology. Higher branchiopod relationships. Black squares indicate monophyly; white squares indicate non-monophyly.

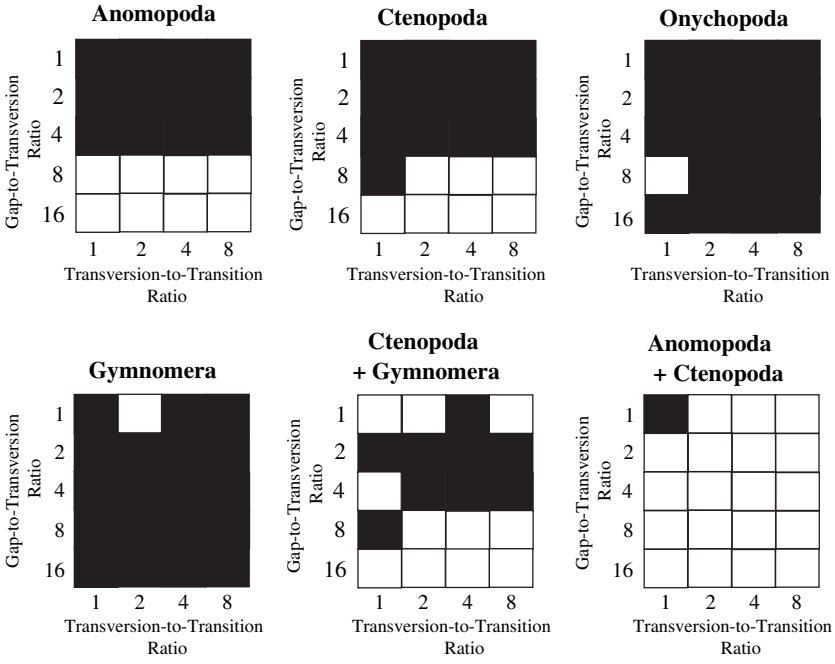

Fig. 10. Navajo Rugs representing the results of the sensitivity analysis including six genes and morphology. Relationships within Cladocera. Black squares indicate monophyly; white squares indicate non-monophyly.

discussed for a very long time (Sars, 1865; Martin and Cash-Clark, 1995; Olesen, 1998; Olesen et al., 2003). Alternatively, a sister group relationship between Haplopoda and all remaining Cladocera (called Eucladocera) has been suggested from a morphological point of view: *Leptodora kindtii* is the only cladoceran with a free swimming larva. Previous molecular analyses have resulted in monophyly of Gymnomera (Schwenk et al., 1998; Richter et al., 2001; Braband et al., 2002; Swain and Taylor, 2003; deWaard et al., 2006; Stenderup

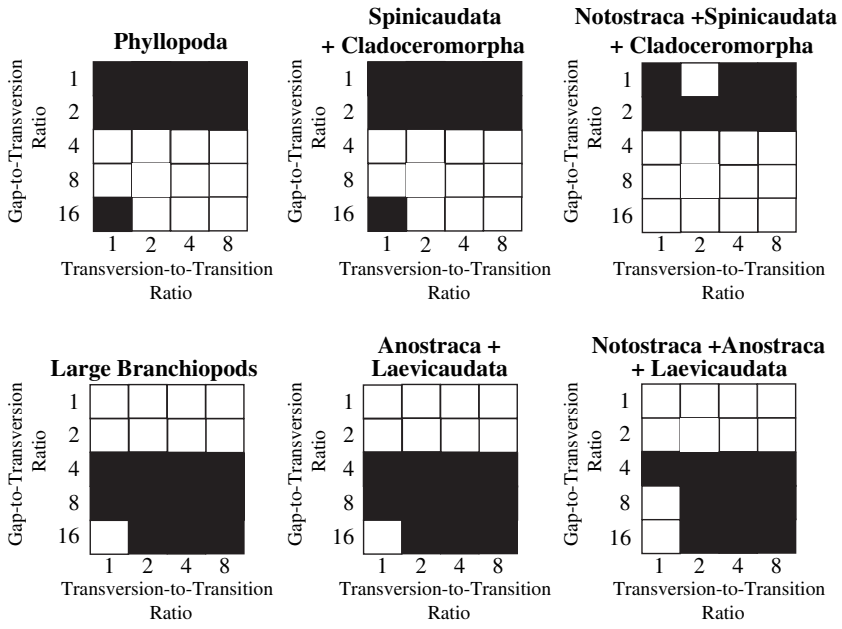

Fig. 11. Navajo Rugs representing the results of the sensitivity analysis including six genes and morphology. Allmost all analyses (despite 121 and 811) result in the same topology if outgroups are not considered. Black squares indicate monophyly; white squares indicate non-monophyly.

et al., 2006) but also the Eucladocera concept has found support in one molecular study (Spears and Abele, 2000). Interestingly enough, 19 of our 20 combined analyses (as well as the morphological analysis) support the monophyly of Gymnomera. The only contradictory analysis (1 of 20 analyses), however, is the one that minimizes incongruence between data partitions (Fig. 8). This shows, at least, that choosing the least incongruent as "optimal" analysis might be in conflict with the stability of clades as provided by a sensitivity analysis. Nevertheless, no other relationship within Cladocera has been the result of so many different analyses (previously and in the present study). Only one additional aspect will be mentioned. A sister group relationship of Ctenopoda and Gymnomera was the result of previous molecular analyses (Schwenk et al., 1998; Braband et al., 2002; deWaard et al., 2006), whereas others show Anomopoda and Ctenopoda as sister groups (deWaard et al., 2006; Stenderup et al., 2006). Our analyses support the former analysis in nine cases and the latter just in one.

Probably most interesting are the relationships between the major branchiopod clades: the "large branchiopod" (used as ecological term) taxa Anostraca, Notostraca, Laevicaudata and Spinicaudata and the water fleas, including *Cyclestheria hislopi* (= Cladoceromorpha). Several previous analyses agree in a split between Anostraca and the remaining taxa, i.e., Phyllopoda (Spears and Abele, 2000; deWaard et al., 2006; Stenderup et al., 2006). Within Phyllopoda, almost all possible relationships have been suggested already in previous analyses: Notostraca as sister taxon to Diplostraca, within Diplostraca Spinicaudata as sister taxon to Cladoceromorpha (Braband et al., 2002), Notostraca as sister taxon to Laevicaudata (Spears and Abele, 2000; Braband et al., 2002) or Laevicaudata as sister taxon to the remaining Phyllopoda, with Spinicaudata as sister taxon to Cladoceromorpha (Braband et al., 2002; deWaard et al., 2006; Stenderup et al., 2006). Also a "large branchiopod" clade as sister taxon to Cladoceromorpha was found in a recent molecular analysis (deWaard et al., 2006). Our morphological analysis supports monophyletic Diplostraca with Notostraca as the sister group. Within Diplostraca, Spinicaudata and Cladoceromorpha together are monophyletic. This is in agreement with previous morphology based analyses of Diplostraca (Olesen, 1998, 2000; but Negrea et al., 1999 suggested Spinicaudata + Laevicaudata as sister groups).

Our combined analyses can be arranged into two groups. The analyses with higher indel-to-transversion ratios (4 or more) almost entirely (one exception) support a "large branchiopod" clade, whereas analyses with indel-to-transversion ratios up to 2 support Phyllopoda with Laevicaudata as sister taxon to the remaining phyllopods, and Spinicaudata + Cladoceromorpha forming a clade. These relationships appear in all of the eight analyses except one, again the one with the least incongruent partitions, which results in a monophyletic Diplostraca. In the analyses supporting the "large branchiopods" Anostraca and Laevicaudata appear as sister taxa. One could speculate that the choice of

outgroups is responsible for these different groupings. Removing the two outgroups and choosing the split between Anostraca and Phyllopoda as the root (based on the analyses with lower indel-to-transversion ratios) results unambiguously in a sister group relationship between Laevicaudata and remaining Phyllopoda (whereas the monophyly of Phyllopoda is obviously the necessary result of the rooting, this is not the case for the position of Laevicaudata). Concerning previously suggested relationships, monophyly of Diplostraca found no support in 19 of 20 analyses and a sister group relationship between Laevicaudata and Spinicaudata is not the result of a single analysis. This is also true for a sister group relationship between Laevicaudata and Notostraca. On the other hand, considering the suggested problematic choice of outgroups as a valid argument, the position of Laevicaudata as sister taxon to the remaining Phyllopoda is the result of 19 of 20 analyses. Interestingly enough, also the remaining branching pattern is the same in 18 of 20 analyses (if the two outgroups are not considered). Spinicaudata is sister taxon to Cladoceromorpha and Notostraca to both these groups. This implies that the topology is (despite the relationships within Cladocera) almost always the same. A similar case of identical topology leading to different phylogenetic hypotheses has been recently discussed for the major euarthropod relationships (Giribet et al., 2005).

In a recent paper, deWaard et al. (2006) stated that all previous molecular analyses "have failed to achieve the Holy Grail: a consensus on branchiopod relationships." This statement should certainly include their own study but also our various analyses did not disclose the Holy Grail—keeping in mind that the biblical Holy Grail was never discovered although it was the desire for centuries. We could show that based on a maximum of available data (six genes and morphology) certain previously proposed relationships are much less sensitive to the inclusion of more data and to varying the analytical parameters than others. At the moment, particular relationships seem to be very stable independently of analytical methodology and amount of included data such as monophyly of Cladocera and Cladoceromorpha, as well as Gymnomera (not to speak about monophyly of Anostraca, Notostraca, Laevicaudata, and Spinicaudata). However, any predictions about how stable these clades will be after inclusion of additional six or more genes should be done very cautiously. The recently proposed position of Laevicaudata as sister group to the remaining Phyllopoda (Stenderup et al., 2006)—although surprising from a morphological point of view—appears much more stable than expected. This is a very interesting conflict between molecular (combined) and morphological data. If the combined analysis holds true, the morphological support of Diplostraca would need to be explained by convergencies or symplesiomorphies.

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