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The disunity of "Mysidacea" (Crustacea)

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Abstract

New studies on malacostracan relationships have drawn attention to issues concerning monophyly of the order Mysidacea, manifested in recent crustacean classifications that treat the taxon as two separate orders, Lophogastrida and Mysida. We present molecular phylogenies of these orders based on complete sequences of nuclear small-subunit ribosomal DNA (18S rRNA), and morphological evidence is used to revise the classification of the order Mysida to better reflect evolutionary history.

A secondary structure model for 18S rRNA was constructed and used to assign putative stem and loop regions to two groups of partitions for phylogenetic analyses. Phylogenies were estimated by maximum-likelihood, Bayesian inference, and maximum-parsimony. The analyses gave strong support for three independently derived lineages, represented by three monophyletic groups, Lophogastrida, Stygiomysida, and Mysida. The family Petalophthalmidae is considered as sister group to the family Mysidae, and Boreomysinae and Rhopalophthalminae are the most early derived of the Mysidae. The tribes contained in the current classification of the subfamily Mysinae are not well-supported by either molecular data or morphology.

Keywords: Crustacea; Mysida; Lophogastrida; Stygiomysida; Phylogeny; Taxonomy; 18S rRNA; Secondary structure

1. Introduction

The Lophogastrida and Mysida are usually regarded as more or less closely related groups of peracarid crustaceans. Although recently ranked as distinct orders of the Peracarida (Martin and Davis, 2001) questions on monophyly (see below) have not changed the most common classifications that treat Lophogastrida and Mysida as subgroups of the "Mysidacea". This also includes the present taxonomy employed by GenBank. The "Mysidacea" contains approximately 1000 species within ca. 160 genera (Meland, 2002). The majority of "Mysidacea" are marine species that have adapted both benthic and pelagic lifestyles. They are distributed from the coastal littoral zone to open ocean waters down to hadal depths. Species are also described from continental fresh water and several taxa are found in groundwater habitats and in marine and anchialine caves.

The most recognized classification of the "Mysidacea" follows that introduced by Hansen (1910). The Lophogastrida contains the families Lophogastridae and Eucopiidae, and the family Gnathophausiidae has additionally been separated from the Lophogastridae (Udrescu, 1984). The Mysida includes the families Petalophthalmidae, Mysidae, and now also the Lepidomysidae and Stygiomysidae (Gordon, 1960; Martin and Davis, 2001). Based on suggested relationships to fossil forms such as the Pygocephalomorpha (Taylor et al., 1998), the Lophogastrida are generally considered to be the most primitive of the "Mysidacea". Support for a more recently derived Mysida is suggested by several morphological characters. In Mysida the carapace forms an extensive respiratory surface, while in the Lophogastrida respiration is primarily a function of epipodal gills. The Lophogastrida have well developed biramous, natatory pleopods in both males and females, while in the Mysida unmodified, uniramous female pleopods are observed. This sexual dimorphism is often considered a derived state (Wilson, 1989). The presence of a proximal statocyst in the

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uropod's endopod in Mysida is also recognized as a derived state that is absent in lophogastrids.

Historically, conflicting ideas on Malacostraca phylogeny have often involved issues concerning monophyly of Mysidacea and Peracarida. In the early 19th century, a Schizopoda concept implied the idea of a close relationship between the orders Euphausiacea and Mysidacea, and a close affiliation with the remaining Peracarida was not recognized (Milne-Edwards, 1837; Dana, 1850). The Schizopoda was also recognized by G.O. Sars (1870), in which he placed the families Euphausidae, Mysidae and Lophgastridae. Boas (1883) introduced a classification with the Euphausiacea and Mysidacea as two distinct orders within the Malacostraca, and following G.O. Sars, the Mysidacea were divided into the suborders Lophogastrida and Mysida. Hansen (1893) took these ideas one step further in considering the Euphausiacea closely allied to the Decapoda and the Mysidacea to the Cumacea, Amphipoda, Isopoda and Tanaidacea. Calman (1904) respectively termed these taxa Eucarida and Peracarida, and the term Schizopoda was formally abandoned. A re-introduction of the Schizopoda was suggested by Land (1981) based on the possession of refractive superposition eyes in Euphausiacea and Mysida. However, later discoveries of such eyes in Anaspidacea, some Dendrobranchiata and some Reptantia (Nilsson, 1990) invalidated these arguments.

With the discovery of groundwater mysids, the establishment of families Lepidomysidae (Clarke, 1961) and Stygiomysidae (Caroli, 1937) seemed justified, but the systematic position of these two families has remained uncertain. Gordon (1960) suggested a close affinity between these families, but recognized several ambiguities in external morphology and was therefore reluctant to assign these taxa to either Lophogastrida or Mysida. Nonetheless, Tchindonova (1981) erected a new suborder Stygiomysida for these groups and revised the entire order Mysidacea accordingly. She also elevated the family Petalophthalmidae and subfamily Boreomysinae to the levels of suborder and family, respectively. More recent discoveries of groundwater species (Bacescu and Iliffe, 1986; Hanamura and Kase, 2002) have lead to the establishment of the tribes Aberomysini and Mancomysini, which are considered to be members of the subfamily Mysinae.

Although both the Lophogastrida and Mysida are generally recognized as monophyletic orders (Martin and Davis, 2001), the phylogenetic relationship between them and their inclusion within the Peracarida remains highly controversial. The controversy led to early proposals of splitting the Mysidacea into separate orders (Schram, 1984; Dahl, 1992), sometimes even by reference to a paraphyletic "Mysidacea" within a "caridoid" malacostracan group (Watling, 1981, 1983, 1999). A molecular study using 28S rRNA (Jarman et al., 2000) presented evidence for a polyphyletic "Mysidacea", suggesting a Mysida-Euphausiacea monophyly and the Lophogastrida grouped with Decapoda and remaining peracarid orders. Close affiliation with the Eucarida has also been suggested based on karyology. Mysida, like the Decapoda show very high chromosome numbers when compared to peracarid taxa (Salemaa, 1986). Mysidacea polyphyly is also suggested in a recent 18S rRNA study on the Peracarida that places the Lophogastrida within Peracarida, but excludes Mysida (Spears et al., 2005). However, morphological inference by Richter and Scholtz (2001) seems to conflict with these molecular findings and points to a basal position of a monophyletic Mysidacea within the Peracarida. Their results also suggest that the Euphausiacea should be removed from the Eucarida, implied by a sister group relationship with the Peracarida. According to De Jong-Moreau and Casanova (2001), foregut morphology additionally supports the unity of the Mysidacea and demonstrates a gradual morphological transition from the Lophogastrida to Mysida through Petalophalmidae and a separate lineage of Stygiomysidae from Lophogastrida ancestors.

Despite the systematic debate concerning the Lophogastrida and Mysida and their relationships with other Eumalacostraca, only few attempts have been made to explore internal relationships within these groups. Studies mainly concerned with the Lophogastrida have proven valuable in inferring phylogeny between the families Lophogastridae, Gnathophausiidae, and Eucopiidae (Casanova et al., 1998). Some results give strong support for treating the Mysida and Lophogastrida as separate, albeit closely related, monophyletic groups (De Jong and Casanova, 1997; Kobusch, 1998). Although both De Jong-Moreau and Casanova dealt with aspects of character evolution of internal morphology, foregut characters were never used in formalized phylogenetic analyses of Lophogastrida and Mysida. A most recent molecular study based on 18S rRNA for selected taxa of the family Mysidae present evidence of non-monophyletic assemblages of Mysidae subfamilies and tribes (Remerie et al., 2004).

In this study, we address hypotheses of phylogeny between and within the orders Lophogastrida and Mysida based on phylogenetic analyses using nuclear small subunit ribosomal DNA sequences (nSSU rRNA or 18S rRNA). Secondary structure models for 18S rRNA are constructed to aid in sequence alignment and to identify sequence segments that can be unambiguously aligned for phylogenetic analysis. Both published and new sequence data are analyzed for 16 of the 20 currently recognized taxonomic subgroups of Lophogastrida and Mysida (Table 1). In terms of taxon sampling, this study is the most comprehensive investigation on "Mysidacea" systematics to date. By including representatives of Eucarida and other Peracarida we also aim at contributing new evidence to the questions of Lophogastrida and Mysida placement within the Malacostraca.

2. Materials and methods

2.1. Taxon sampling

In order to infer relationships between taxa contained within the order Mysidacea *sensu* Nouvel et al. (1999) (Table 1) and other malacostracan taxa, 26 species

Table 1
Taxonomy of the order Mysidacea *sensu* Nouvel et al. (1999), including tribes Aberomysini and Mancomysini for the genera *Aberomysis* and *Palaumysis*, respectively (Bacescu and Iliffe, 1986)

ORDER MYSIDACEA Boas, 1883
Suborder Lophogastrida Boas, 1883[a]
Family Lophogastridae G.O. Sars, 1870[a]
Family Gnathophausiidae Udrescu, 1984[a]
Family Eucopiidae G.O. Sars, 1885[a]
Suborder Mysida Boas, 1883[a]
Family Lepidomysidae Clarke, 1961
Family Stygiomysidae Caroli, 1937[a]
Family Petalophthalmida Czerniavsky, 1882[a]
Family Mysidae Haworth, 1825[a]
Subfamily Boreomysinae Holt & Tattersall, 1905[a]
Subfamily Thalassomysinae Nouvel, 1942
Subfamily Siriellinae Czerniavsky, 1882[a]
Tribe Siriellini Czerniavsky, 1882[a]
Tribe Metasiriellini Murano, 1986
Subfamily Gastrosaccinae Norman, 1892[a]
Subfamily Rhopalophthalminae Hansen, 1910[a]
Subfamily Mysinae Haworth, 1825[a]
Tribe Aberomysini Bacescu & Iliffe, 1986
Tribe Calyptommini Tattersall, 1909[a]
Tribe Erythropini Hansen, 1910[a]
Tribe Heteromysini Norman, 1892[a]
Tribe Leptomysini Hansen, 1910[a]
Tribe Mancomysini Bacescu & Ilife, 1986[a]
Tribe Mysini Haworth, 1825[a]
Subfamily Mysidellinae Norman, 1892[a]

[a] Taxa represented in this study.

representing families, subfamilies and tribes of Lophogastrida and Mysida, and two Caridea species were added to a 26 taxa dataset presented by Spears et al. (2005). We refer to this compiled dataset as "Malacostraca" and use *Nebalia* sp. as an outgroup (see Table 2). A second dataset referred to as "Mysida" consisted of 67 species. Metasiriellini (Murano, 1986), Thalassomysinae (Nouvel, 1942), Aberomysini (Bacescu and Iliffe, 1986), and Lepidomysidae (Clarke, 1961) were not obtainable for molecular analyses. Based on the analyses of the "Malacostraca" dataset, representatives of the Stygiomysidae (Caroli, 1937) were not included in the "Mysida" dataset. A complete species list is presented in Appendix A.

The majority of Mysidacea species were obtained by the first author from cruises in the North Atlantic, Sagami and Tateyama Bay, Japan. Additional specimens were obtained from cruises in fjords around Bergen, Norway. Coastal species were collected using a hand net in the intertidal zone on the Norwegian coast and the west coast of Florida, USA.

Self-supplied Lophogastrida and Mysida material was sorted out by hand directly from nets, epibenthic- or RP-sledges and preserved directly in 96–100% ethanol. Species were later identified by Dr. Torleiv Brattegard and the first author. Additional specimens were kindly donated by several colleagues. Identifications of donated species were verified by the first author. Sequence data from 23 of the Mysida species was taken from GeneBank. With the exception of the smallest species (<2 mm), all mysid samples are archived as ethanol preserved vouchers in the Natural History Collections of Bergen Museum, Norway.

2.2. Extraction and sequencing

DNA was usually extracted from abdominal muscle tissue. Entire animals were used when bodies were less than 2 mm long. Extractions were performed with either a Qiagen© extraction kit or by using a scaled down protocol for the G-NOME® DNA kit (see Spears et al., 2005). To improve DNA yield, ethanol preserved tissue was diluted in sterile H_2O for 12–24 h prior to digesting. Additionally, lengthening incubation time to 24 h significantly increased amount of DNA extract. Extracted DNA was in many cases diluted 1:5–1:10 with ddH_2O when pure extract resulted in unsuccessful PCR runs.

PCR amplifications were carried out in 50 or 100 μl reactions using 1–4 μl DNA template. The 50 μl reactions contained 1 unit of Taq DNA polymerase, 4 μl 10× PCR buffer (Promega©), 2 μl of each primer (10 μM), 4 μl dNTP mix (1.25 mM for each nucleotide), and 36.8 μl ddH_2O. The 100 μl reactions contained 2.5 units of Taq DNA polymerase, 10 μl 10× PCR buffer, 5 μl of each primer (20 μM), 16 μl dNTP mix (1.25 mM for each nucleotide), and 54.5 μl ddH_2O. Amplification reactions were run in either a Peltier Thermal Cycler 2000 (MJ Research, Inc.) or a Perkin Elmer DNA Thermal Cycler 480 (Perkin Elmer, Foster City, CA).

Both strands of the entire nSSU rRNA were amplified either as single PCR products or in overlapping fragments. Primers developed for crustacean studies (Meland and Willassen, 2004; Spears et al., 2005) were dispersed throughout the nSSU rRNA and used both for symmetric PCR amplification and bidirectional sequencing of double-stranded PCR products. PCR cycle conditions were 3 min at 94 °C for initial denaturing; 94 °C, 30 s; 50 °C, 1 min; 72 °C, 2 min for 40 cycles, followed by 72 °C, 10 min for final extension.

PCR products were electrophoresed through an ethidium bromide stained 1% agarose gel and examined under ultraviolet illumination. In the case of low DNA concentration and/or more than one amplification product, the band conforming to the expected sequence length was excised directly from the gel, purified and either sequenced directly or used in a second PCR run for increased concentration. PCR products were purified using commercially available spin columns (Qiagen© and GibcoBRL Life Technologies Concert™ Rapid PCR Purification System). Final DNA concentration was estimated by comparing band intensity with a DNA marker or quantified using a Pharmacia GeneQuant spectrophotometer.

Both strands were cycle sequenced using ABI Big Dye terminators. Products were separated and analyzed with either an ABI 3700 PE automated sequencer or an ABI PRISM® 3100 Genetic Analyzer. Sequence contigs were assembled using Sequencher™ 4.1 and Contig Express in the software package Vector NTI 9. GenBank accession and voucher numbers are listed in Appendix A.

Table 2
Number of nucleotides in three data partitions, stems, loops, and combined (stems + loops) in nuclear small-subunit ribosomal RNA sequences from the Malacostraca-dataset (52 taxa)

Taxon	Loops		Stems		Total	
	Complete	Analyzed	Complete	Analyzed	Complete	Analyzed
Leptostraca						
Nebalia sp	586	(513)	1204	(1113)	1790	(1626)
Stomatopoda						
Gonodactylus sp	596	(514)	1207	(1114)	1803	(1628)
Squilla empusa	594	(513)	1208	(1113)	1802	(1626)
Anaspidacea						
Anaspides tasmaniae	601	(514)	1215	(1113)	1816	(1627)
Amphipoda						
Gammarus oceanicus	855	(529)	1388	(1117)	2243	(1646)
Phronima sp	892	(518)	1362	(1119)	2254	(1637)
Caprella geometrica	852	(533)	1309	(1119)	2161	(1652)
Cumacea						
Spilocuma salomani	761	(504)	1243	(1054)	2004	(1558)
Diastylis sculpta	932	(511)	1285	(1121)	2217	(1632)
Isopoda						
Asellus racovitzai	745	(513)	1382	(1113)	2127	(1626)
Paramphisopus palustris	809	(512)	1536	(1117)	2345	(1629)
Idotea metallica	1063	(509)	1651	(1113)	2714	(1622)
Mictacea						
Thetispelecaris remex	694	(513)	1224	(1119)	1918	(1632)
Lophogastrida						
Eucopia sculpticauda	579	(500)	1191	(1099)	1770	(1599)
Eucopia unguiculata	591	(513)	1202	(1110)	1793	(1623)
Gnathophausia gigas	574	(496)	1184	(1092)	1758	(1588)
Gnathophausia ingens	591	(513)	1201	(1110)	1792	(1623)
Gnathophausia zoea	591	(513)	1200	(1109)	1791	(1622)
Lophogaster typicus	590	(513)	1201	(1110)	1791	(1623)
Mysida						
Amblyops sp	604	(514)	1198	(1114)	1802	(1628)
Anchialini agilis	597	(511)	1191	(1110)	1788	(1621)
Boreomysis arctica	607	(514)	1198	(1114)	1805	(1628)
Boreomysis inermis	607	(514)	1198	(1114)	1805	(1628)
Gastrosaccus psammodytes	601	(512)	1192	(1111)	1793	(1623)
Hansenomysis fyllae	606	(513)	1199	(1114)	1805	(1627)
Hemimysis abyssicola	600	(513)	1194	(1110)	1794	(1623)
Heteromysis formosa	605	(514)	1197	(1114)	1802	(1628)
Leptomysis lingvura adriatica	599	(516)	1189	(1111)	1788	(1627)
Michthyops parva	604	(514)	1197	(1113)	1801	(1627)
Mysidella typica	605	(514)	1196	(1113)	1801	(1627)
Neomysis integer	606	(514)	1195	(1114)	1801	(1628)
Parapseudomma calloplura	604	(514)	1198	(1114)	1802	(1628)
Praunus flexuosus	602	(514)	1196	(1113)	1798	(1627)
Pseudomma frigidum	604	(514)	1198	(1114)	1802	(1628)
Rhopalophthalmus sp	605	(513)	1198	(1114)	1803	(1627)
Siriella armata	598	(512)	1189	(1110)	1787	(1622)
Stygiomysida						
Stygiomysis aemete	710	(511)	1198	(1113)	1908	(1624)
Stygiomysis cokei	723	(511)	1200	(1113)	1923	(1624)
Stygiomysis holthuisi	721	(510)	1200	(1113)	1921	(1623)
Spelaeogriphacea						
Spelaeogriphus lepidops	697	(502)	1330	(1116)	2027	(1618)
Tanaidacea						
Paratanais malignus	873	(518)	1466	(1120)	2339	(1638)
Kalliapseudes sp	882	(511)	1636	(1115)	2518	(1626)
Tanais dulongi	754	(507)	1231	(1110)	1985	(1617)

Table 2 (*continued*)

Taxon	Loops		Stems		Total	
	Complete	Analyzed	Complete	Analyzed	Complete	Analyzed
Thermosbaenacea						
Tethysbaena argentarii	931	(511)	1313	(1113)	2244	(1624)
Euphausiacea						
Meganyctiphanes norvegica	629	(518)	1209	(1113)	1838	(1631)
Nyctiphanes simplex	629	(518)	1210	(1114)	1839	(1632)
Decapoda						
Callinectes sapidus	641	(515)	1209	(1111)	1850	(1626)
Hippolyte pleuracanthus	619	(482)	1173	(1056)	1792	(1538)
Homarus americanus	647	(514)	1201	(1109)	1848	(1623)
Oedignathus inermis	664	(515)	1202	(1104)	1866	(1619)
Palaemonetes vulgaris	626	(485)	1170	(1057)	1796	(1542)
Panulirus argus	644	(513)	1212	(1114)	1856	(1627)

Statistics obtained from PAUP* 4.0b10 (Swofford, 2002).

2.3. Nucleotide sequence and phylogenetic analyses

Multiple sequence alignments on both datasets were carried out with the editing program BioEdit 7.0.1 (Hall, 1999), using an implemented version of ClustalW (Thompson et al., 1994) and by manually adjusting positions in regions where automatic alignment did not perform well. The initial alignment of the Malacostraca dataset was based on suggested stem and loop regions from Spears et al. (2005) and Van de Peer et al. (1997). In the next step we made adjustments in the alignment by eye before we imported the dataset into the program DCSE (De Rijk and De Watcher, 1993), where we added secondary structure notation, verified conserved motifs and manually aligned these to putative homologous stem and loop segments. DCSE was also used to infer base pairings in the Lophogastrida, Stygiomysida, and Mysida sequences. Secondary structures of 18S rRNA were drawn with RNAVIZ 2.0 (De Rijk and De Watcher, 1997). We defined three groups of data partitions in the nexus data-files: secondary structure stems, loops, and ambiguously aligned regions. The ambiguously aligned regions were omitted in the subsequent phylogenetic analyses (Tables 2 and 3). Entropy in 26 of the 68 sequences in the "Mysida" dataset was calculated in BioEdit and mapped onto a secondary structure drawing of *Boreomysis megalops* (Fig. 1).

Maximum parsimony (MP) analyses were conducted using PAUP* 4.0b10 (Swofford, 2002). Trees were found by 1000 replicate heuristic searches using the tree-bisection-reconnection (TBR) branch swapping algorithm with 10 starting trees obtained by stepwise addition. MP searches were performed on unordered equally weighted parsimony informative characters. Nodal support for resulting MP trees was determined through non-parametric-bootstrapping of 2000 pseudoreplicates with 10 heuristic searches in each.

Maximum likelihood analyses were performed in PAUP* on all unambiguously aligned characters using 10

Table 3
Length (in alignment positions) of the Malacostraca and Mysida nuclear small-subunit ribosomal RNA datasets, and length of secondary structure partitions with statistics

	Malacostraca			Mysida		
	Stems	Loops	Combined	Stems	Loops	Combined
Length	1873	1376	3249	1233	673	1906
Ambiguous sites	727	828	1555	12	33	45
Analyzed sites	1146	548	1694	1221	640	1861
Constant sites	410	239	649	804	420	1224
Parsimony uninformative	196	84	280	143	62	205
Parsimony informative	540	225	765	274	158	432
Unique site patterns	712	332	996	398	226	598
Mean nt frequency						
Adenine	0.24	0.24	0.24	0.25	0.26	0.25
Cytosine	0.30	0.21	0.27	0.31	0.19	0.27
Guanine	0.24	0.18	0.22	0.24	0.19	0.23
Thymine	0.21	0.37	0.26	0.21	0.36	0.25

Partitioning of data based on a modified version of a secondary structure model from Van de Peer et al. (1997). Ambiguously aligned nucleotides were excluded in the phylogenetic analyses.

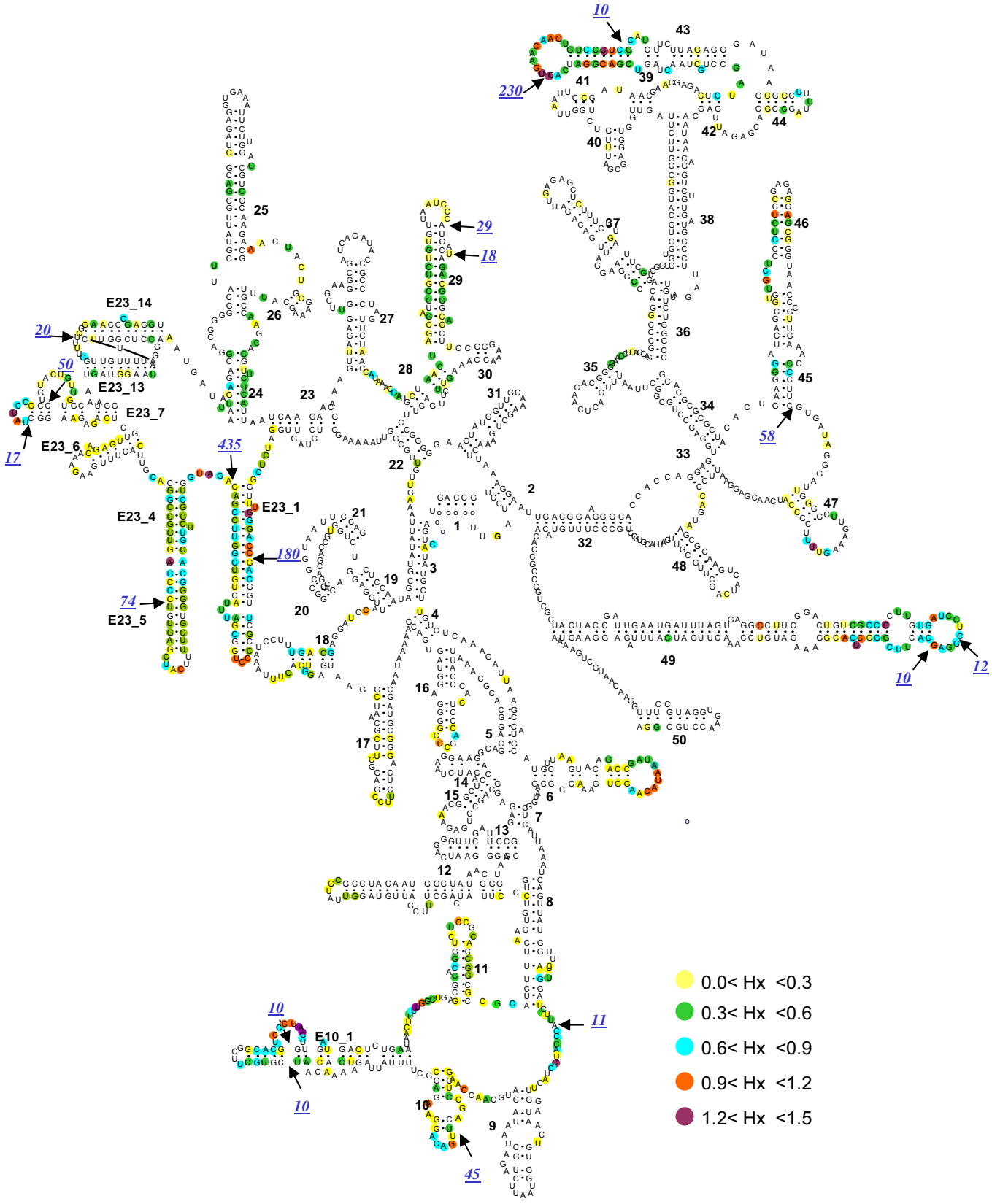

Fig. 1. Putative secondary structure of 18S rRNA in *Boreomysis megalops*, with color coded variability measured as entropy (Hx) from an alignment with a selection of 26 Mysida species (see Appendix A). Arrows point to gapped regions of 10 or more nucleotides found in the Malacostraca-alignment, underscored figures indicate numbers of gaps.

replicate heuristic searches with TBR branch swapping and random stepwise addition of sequences to obtain starting trees. Modeltest 3.7 (Posada and Crandall, 1998) was used to determine an appropriate DNA evolution model for ML by the Akaike Information Criterion (AIC) (Posada and Buckley, 2004). ML phylogeny estimates and model parameter values were optimized in PAUP using a successive-approximation approach (Sullivan et al., 2005).

MrModeltest 2.2 (Nylander, 2004) was used to select models of nucleotide evolution for the Bayesian inference. In one set of runs, we treated all included sites as one linked unit (non-partitioned). In a second set of runs, we treated stems and loops as two groups of partitions with unlinked parameter space (partitioned). Bayesian MCMC analyses were conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). For each analysis (non-partitioned and partitioned data), two independent runs of initially 4 million generations were performed with three hot and one cold chains. Trees were sampled every 200 (Malacostraca) or 100 (Mysida) generations and the average standard deviation of spilt frequencies (SDSF) was monitored throughout the run. The number of runs was successively increased by 0.5 million generations in the case that stationarity was not reached after 4 million generations, as judged by the SDSF of more than 0.02. Additionally, parameter values were evaluated for convergence throughout the run by using the "sump" command in MrBayes and by examining results in Tracer 1.3 (Rambaut and Drummond, 2005). Plots from Tracer were used to determine the appropriate number of trees to be discarded in the "burnin". MrBayes was used to finally summarize model parameters and to calculate Bayesian posterior probabilities for nodes from 50% majority rule consensus trees.

To test for the probabilities of monophyly between traditional taxa of Mysidacea, we made constraint trees expressing several hypotheses of sister group relationships between Lophogastrida, Mysida, and Stygiomysidae. We searched for nodes corresponding to these hypotheses among retained trees (after burnin) from the Bayesian MCMC searches on both non-partitioned and partitioned Malacostraca datasets. Such probability estimates were obtained using the filter command in PAUP*.

3. Results

3.1. Alignment and sequence analyses

Sequences in the two datasets were aligned based on a model of secondary structure of stem and loop regions. Excluded partitions in the Malacostraca alignment (Tables 2 and 3) were basically due to unalignable expansion segments of extreme length particularly in Isopoda and Amphipoda. Nucleotide homologies between Mysida terminals where the same in both alignments.

3.1.1. Malacostraca

Total sequence lengths for Lophogastrida and Mysida species were approximately 1800 base pairs (bp), compared to ca. 1900 in Stygiomysidae. The longest sequence lengths were found in the peracarid taxa, which in some cases has lengths of more than 2500 bp (Table 2). The Malacostraca alignment consisted of 3249 site positions, of which 1555 were excluded from the phylogenetic analysis because they could not be unambiguously aligned. Of the remaining 1694 matrix characters, there were 996 unique site patterns, 649 characters were constant and 765 were parsimony informative (Table 3). Stem and loop regions exhibited heterogeneity in nucleotide frequencies (Table 3). Bias in nucleotide composition was reflected in high cytosine (30%) and low thymine (21%) content in stems, whereas loops showed lower levels of cytosine (21%) and a high level thymine (37%). Stems 8–11 and the E23 region (Fig. 1) displayed variable structure, and were also highly variable in terms of nucleotide composition. Structural variability in stem 43 was also evident and most conspicuous in the extended stem (ca. 100 bp) of *Stygiomysis cokei* compared to other "mysidaceans". In addition, the terminal loop of stem 49 in *S. cokei* exceeded that in lophogastrids and mysids by 14 bp. In general, the peracarid taxa had the longest insertions and the stygiomysids were intermediate in length compared to the remaining taxa (Table 2). Length variability was most conspicuous in the E23-1 region were some peracarids displayed an expanded sequence length of up to 680bp, as opposed to only 40 bp in the remaining taxa. In stem 43, expansions up to 247 bp were observed in peracarids. Comparable length differences of additional 45 bp and a total of 49 bp insertions were seen in the peracarid stems 10 and E10-1, respectively.

3.1.2. Mysida

The "Mysida" alignment consisted of 1906 matrix positions (Table 3). Alignment difficulties motivated the removal of 12 characters in stems and 33 in loops, leaving 1861 characters to be analyzed. There were 598 unique site patterns, 1224 sites were constant and 432 sites were parsimony informative (Table 3). As in the "Malacostraca" alignment, biased nucleotide composition was reflected in a relatively high cytosine content (31%) in stems and high thymine content (36%) in loops (Table 3). Nucleotide type variation of 26 Mysida sequences with complete secondary structure notation was investigated by calculated entropy values (Hall, 1999) and mapped onto the secondary structure of *Boreomysis megalops* (Fig. 1). The stems E10-1, E23, and 43 had the highest variability in the Mysida, as in the other Malacostraca.

Uncorrected sequence divergence between Mysida ranged from 0.56% (*Boreomysis tridens* and *B. arctica*) to 16.2% (*Schistomysis spiritus* and *Metamysidopsis swifti*). Average sequence divergence was $6.2 \pm 2.7\%$. A relatively high sequence divergence was observed between *Schistomysis spiritus* and the remaining Mysida ($12.3 \pm 1.3\%$). High divergence in this species was due to dissimilarity in stem regions E23-1, 17, and E10-1 (Fig. 1). A similar pattern of high sequence divergence in the same region was observed in *Paramysis helleri* ($9.8 \pm 1.5\%$). BLAST searches were

performed on several portions of the nSSU sequences, which resulted in consistent hits on various Mysida nSSU genes found in GeneBank, thereby ruling out our suspicion of non-mysid sequences in the dataset. Sequence divergence between *S. spiritus* and *P. helleri* was 12.7% and the resulting sister group relationship of these species is therefore interpreted as a possible case of long branch attraction (see Fig. 3).

3.2. Phylogenetic analysis

3.2.1. Malacostraca

In the Malacostraca analyses on 765 informative characters, gaps were treated as missing states. The best maximum parsimony (MP) estimate returned four most parsimonious trees having 4041 steps (ci: 0.45, ri: 0.63). Incongruence between these trees was due to an internally unresolved Lophogastrida clade. Bootstrap analysis returned high support for the individual groups Mysida, Stygiomysida and Lophogastrida (Fig. 2), but there was no support for a "Mysidacea" clade comprised exclusively by these three groups.

Maximum likelihood (ML) estimation was based on 1694 characters. Modeltesting suggested a general-time-reversible model (Rodriguez et al., 1990) with gamma distributed substitution rates and an estimated proportion of invariable sites (GTR+*I*+*G*). Model parameter values for the best ML estimate (Fig. 2) are provided in Table 4. The ML phylogeny also suggested that the Mysidacea are polyphyletic. The Mysida was grouped with Stomatopoda and Euphausiacea. The non-Caridea decapods showed a sister group relationship to the Syncarida, and the Caridea fell basal to the Peracarida (excluding Mysida), leaving the Decapoda as paraphyletic. Placement of the Euphausiacea further suggested a polyphyletic Eucarida. However, relationships between these higher taxa may be regarded as unresolved since both MP bootstrap values and Bayesian posterior probabilities on relevant branches are low (see below). Within the Peracarida, there is strong support for a monophyletic Lophogastrida within a Thermosbaenacea + Spelaeogriphacea + Amphipoda + Lophogastrida clade. A sister group relationship between the Stygiomysida and the mictacean *Thetispelecaris remex* received strong support.

MrModeltest suggested a GTR+*I*+*G* model both for the non-partitioned dataset, and for separate runs with stem and loop partitions. MCMC with non-partitioned data was run for 4 million generations. The standard deviation of split frequencies (SDSF) at that point was 0.0061. We discarded the initial 502 trees (100.400 generations) from each run and computed posterior probabilities from 38998 trees. The partitioned analysis was run for 5 million generations (SDSF: 0.022). Likelihoods started to converge after 200.000 generations. Estimated parameters are shown in Table 4.

With the exception of a few unresolved nodes, as reflected in posterior probabilities (Fig. 2), Bayesian linked, unlinked, and ML phylogenies were highly congruent. Strong support for a polyphyletic Mysidacea was made evident in high probability values of separate monophyletic groupings of Lophogastrida, Stygiomysida, and Mysida as found in the ML analyses (Fig. 2). In both Bayesian analyses, none of the trees retained after the burnin contained the splits (nodes) defined by constraints forcing monophyly of "Mysidacea". Thus, given the data observed in 18S rRNA and the model of evolution, the probability of a sister relationship between Lophogastrida and Mysida equals zero. We obtained the same results with other combinations of constrained groups, Lophogastrida + Stygiomysida, Mysida + Stygiomysida, and Mysida + Lophogastrida.

3.2.2. Mysida

With support in the monophyly of Mysida suggested by the analyses of Malacostraca, we conducted separate analyses of 67 Mysida taxa (Stygiomysidae excluded). The inclusions of additional sequence regions (reflected in Table 3), those considered unalignable in the Malacostraca analyses, lead to increased resolution and nodal support in the separate Mysida analyses. In effect, a more reliable picture of internal Mysida relationships allowed for an outgroup selection independent of the Malacostraca results. The Petalophthalmida, including *Hansenomysis fyllae*, lack uropodal statocysts and have seven pairs of oostegites in the female marsupium. These morphological characteristics are regarded as plesiomorphies and *H. fyllae* was accordingly used as an outgroup in the phylogenetic analysis of Mysida.

The MP estimate, based on 432 parsimony-informative characters and gaps treated as missing data, returned two most parsimonious trees (not shown) having 2351 steps (ci: 0.418, ri: 0.627). The two MP trees differed in the placement of *Haplostylus dispar* and *Eurobowmaniella simulans* within the Gastrosaccinae clade. Despite low support in deeper nodes, there was strong support for the subfamily Rhopalophthaminae as a sister group to Boreomysinae, and for monophyletic subfamilies Gastrosaccinae, Siriellinae, and Mysidellinae. The latter was also well supported as the sister group of the tribe Heteromysini. Placement of *Stilomysis grandis* within the tribe Mysini rendered both Mysini and Leptomysini as paraphyletic. Low resolution was observed for the tribe Erythropini, as opposed to the strong support for monophyletic tribes Calyptommini and Mancomysini.

Maximum likelihood (ML) estimates on the Mysida dataset was conducted on combined stem and loop partitions summing to 1861 characters. Modeltest suggested a GTR+*I*+*G* model. Optimized model parameters for the best ML estimate are provided in Table 4. ML agreed with MP results in retrieving monophyletic clades to the level of subfamilies, and also in suggesting a monophyly for the Heteromysini and Mysidellinae, rendering the subfamily Mysinae as paraphyletic. The Erythropini tribe appears to be polyphyletic due to placement of the tribe Calyptommini and a *Meterythrops robusta* + *Parerythrops spectabilis* clade forming a sister group relationship with the Mancomysini. In addition to the Leptomysini placement of *S. grandis*, as suggested by MP, paraphyly in the tribe Mysini was seen in

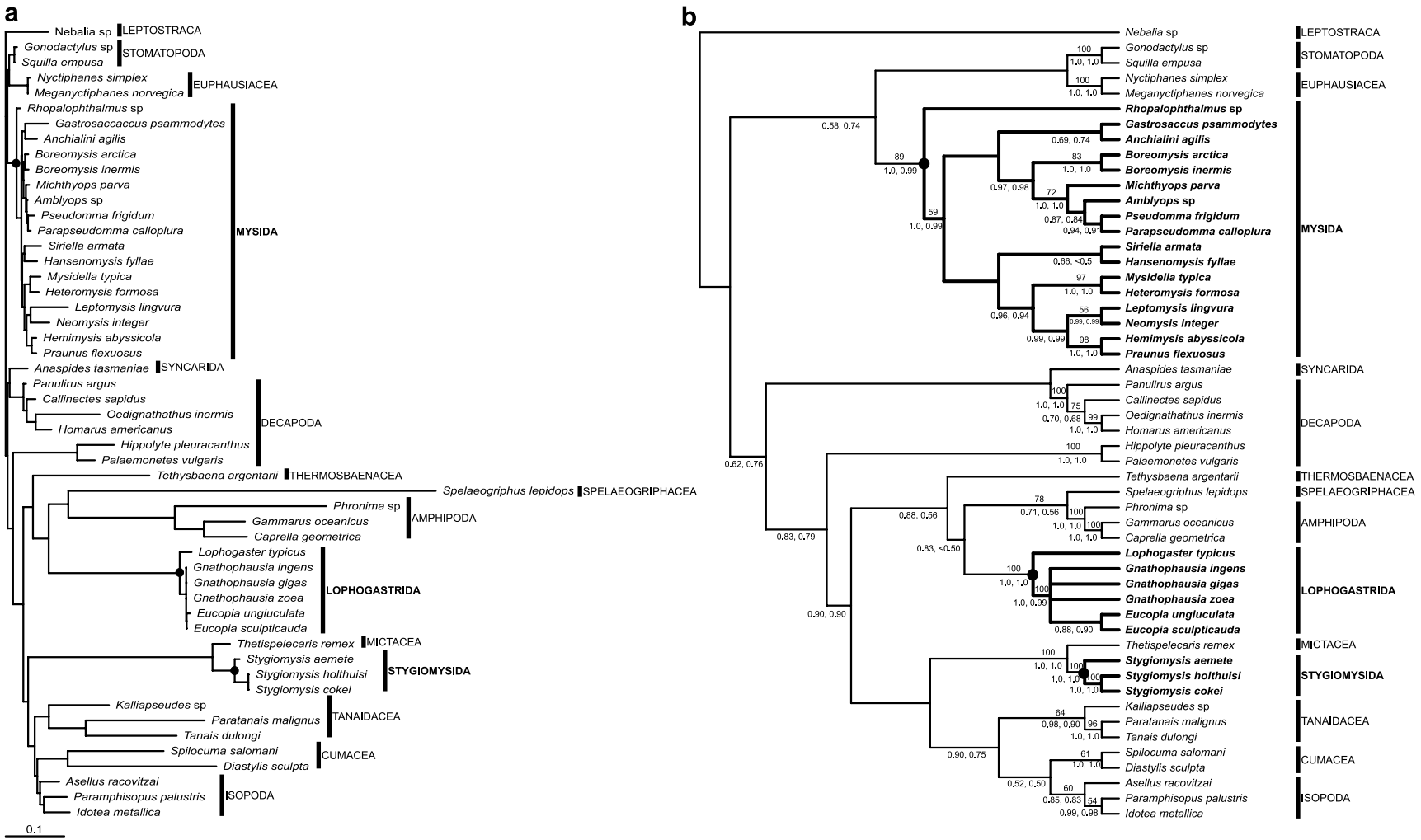

Fig. 2. Phylogram (a) and cladogram (b) of malacostracan Crustacea based on combined stem and loop partitions (see Tables 2,3) of the nuclear small-subunit ribosomal DNA. Topology and maximum likelihood ($\ln L = -20043.47$) estimated in PAUP* 4.0b10 (Swofford, 2002) assuming a GTR+*I*+G model suggested by the Akaike Information Criterion in Modeltest version 3.07 (Posada and Crandall, 1998). Sidebars indicate higher taxa within the Malocostraca and highlighted nodes and branches indicate taxa previously classified as Mysidacea. Numbers above branches indicate non-parametric bootstrap values $\geqslant 50\%$ based on parsimony heuristic searches of 1000 pseudoreplicates, with 10 random sequence additions in each. Pairs of numbers below branches indicate Bayesian posterior proportions of 50%-majority-rule consensus trees from two Markov-Monte-Carlo chain runs in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). First numbers from analyses with stem and loop partitions combined (linked) and second number from analyses with separate partitions (unlinked).

Table 4
Models and parameter values for stem, loop, and combined (stem + loop) nuclear small-subunit ribosomal RNA partitions estimated from ML and Bayesian phylogentic analyses on two datasets (Malacostraca: 52 taxa and Mysida: 67 taxa)

	Bayesian			Maximum likelihood
	Stems (1146 bp)	Loops (548 bp)	Combined (1694 bp)	Combined(1694 bp)
Malacostraca				
Model	GTR + *I* + G	GTR + *I* + G	GTR + *I* + G	GTR + *I* + G
ln *L*	−20025.3		−20090.67	−20043.47
freqA	0.2337 ± 0.00008	0.2489 ± 0.00018	0.2390 ± 0.00006	0.2391
freqC	0.3052 ± 0.00011	0.2138 ± 0.00017	0.2761 ± 0.00007	0.2752
freqG	0.2410 ± 0.00009	0.1813 ± 0.00011	0.2205 ± 0.00005	0.2195
freqT	0.2202 ± 0.00008	0.3561 ± 0.00025	0.2644 ± 0.00006	0.2662
R_{AC}	0.9747 ± 0.00063	0.9416 ± 0.00158	0.9659 ± 0.00044	0.9072
R_{AG}	3.8096 ± 0.00377	4.3095 ± 0.00801	4.0253 ± 0.00256	3.7698
R_{AT}	1.1777 ± 0.00101	0.8366 ± 0.00112	1.0831 ± 0.00058	1.0007
R_{CG}	0.5977 ± 0.00037	0.8156 ± 0.00176	0.6753 ± 0.00034	0.6421
R_{CT}	2.4900 ± 0.00266	1.7715 ± 0.00377	2.1770 ± 0.00152	2.0319
R_{GT}	0.9504 ± 0.00078	1.3252 ± 0.00212	1.0733 ± 0.00057	1.0000
I	0.1148 ± 0.00124	0.2548 ± 0.25483	0.1473 ± 0.00087	0.1539
α	0.5930 ± 0.00370	0.6502 ± 0.65017	0.5848 ± 0.00256	0.5840
	Stems (1221 bp)	Loops (640 bp)	Combined (1861 bp)	Combined (1861 bp)
Mysida				
Model	GTR + *I* + G	GTR + *I* + G	GTR + *I* + G	GTR + *I* + G
ln *L*	−14513.44		−14674.66	−14542.66
freqA	0.2671 ± 0.00013	0.3044 ± 0.00020	0.2720 ± 0.00007	0.2705
freqC	0.3061 ± 0.00013	0.1708 ± 0.00015	0.2612 ± 0.00008	0.2639
freqG	0.2170 ± 0.00010	0.1848 ± 0.00012	0.2062 ± 0.00006	0.2045
freqT	0.2098 ± 0.00010	0.3400 ± 0.00024	0.2606 ± 0.00008	0.2611
R_{AC}	0.8058 ± 0.00070	0.8795 ± 0.00156	0.7859 ± 0.00046	0.7470
R_{AG}	3.9339 ± 0.00563	4.5707 ± 0.00810	4.3858 ± 0.00337	3.9610
R_{AT}	1.3544 ± 0.00184	1.1042 ± 0.00143	1.3890 ± 0.00097	1.2979
R_{CG}	0.4566 ± 0.00039	0.5439 ± 0.00137	0.4540 ± 0.00028	0.4294
R_{CT}	2.5157 ± 0.00402	1.6179 ± 0.00399	1.9126 ± 0.00181	1.7307
R_{GT}	0.9335 ± 0.00013	1.2837 ± 0.00209	1.0728 ± 0.00081	1.0000
I	0.4876 ± 0.00099	0.3925 ± 0.00194	0.4519 ± 0.00061	0.5018
α	0.6974 ± 0.01036	0.4622 ± 0.00467	0.5227 ± 0.00257	0.5907

Models were selected by the Akaike Information Criterion using Modeltest 3.7 (Posada and Crandall, 1998) for ML and MrModeltest 2.2 (Nylander, 2004) for Bayesian analyses. Parameters optimized by PAUP* 4.0b10 (Swofford, 2002) in ML and MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) in the Bayesian analyses. GTR = general-time-reversible model; *I* = proportion of invariable sites; G = gamma-distributed sites; freq (A, C, G, T) = nucleotide frequencies; *R* = relative substitution rates between the listed nucleotides; α = shape parameter of the gamma-distribution.

a *Holmesimysis costata* + *Alienacanthomysis macropsis* + *Neomysis integer* clade falling basal to a terminal monophyly of the remaining Mysini species and tribe Leptomysini. Based on MP bootstrap support values, the resolution of these clades was not robust and a slightly different picture was shown by Bayesian reconstruction (Fig. 3). The Rhopalophthalminae and Boreomysinae are placed at the base of the tree followed by the Gastrosaccinae and then the Siriellinae, which show a sister group relationship to Mysinae and subfamily Mysidellinae.

Results from MrModeltest suggested a GTR+*I*+G model both for the non-partitioned data and for the separate partitions of stems and loops in the Mysida dataset. MCMC with linked partitions was run for 2.7 million generations (SDSF: 0.006067) and likelihood estimates leveled off after 250.000 generations. The analysis of non-partitioned data was run for 6.5 million generations (SDSF: 0.020336) as the two runs did not converge until after 4 million generations. Estimated parameters are shown in Table 4. Variability in secondary structures and base pairing patterns in the sequences were judged too heterogeneous to allow for evolutionary models using a doublet model for paired bases.

The two variants of Bayesian analyses resulted in highly congruent trees (Fig. 3). The lowest posterior probabilities were observed in deeper nodes. The topology of the Bayesian tree agreed with the tree inferred with ML, with one exception and was slightly less resolved. The Rhopalophthalminae and Boreomysinae fell basal to the remaining taxa, but unlike with both MP and ML they were not retrieved as sister groups. Unlike ML, the Bayesian analyses did not support a monophyletic Mysidellinae + Heteromysini + Mysini + Leptomysini clade, which gave a well supported monophyly ($P = 1.0$) only by the inclusion of Siriellinae and Erythropini + Calytommini. Both ML and Bayesian results agreed on a monophyletic Mysini + Leptomysini clade ($P = 1.0$). By the inclusion of the *H. costata* + *A. macropsis* + *N. integer* group, Bayesian analyses also recovered a monophyletic Mysini, but with low support (P = linked: 0.67, unlinked: 0.71). Lower

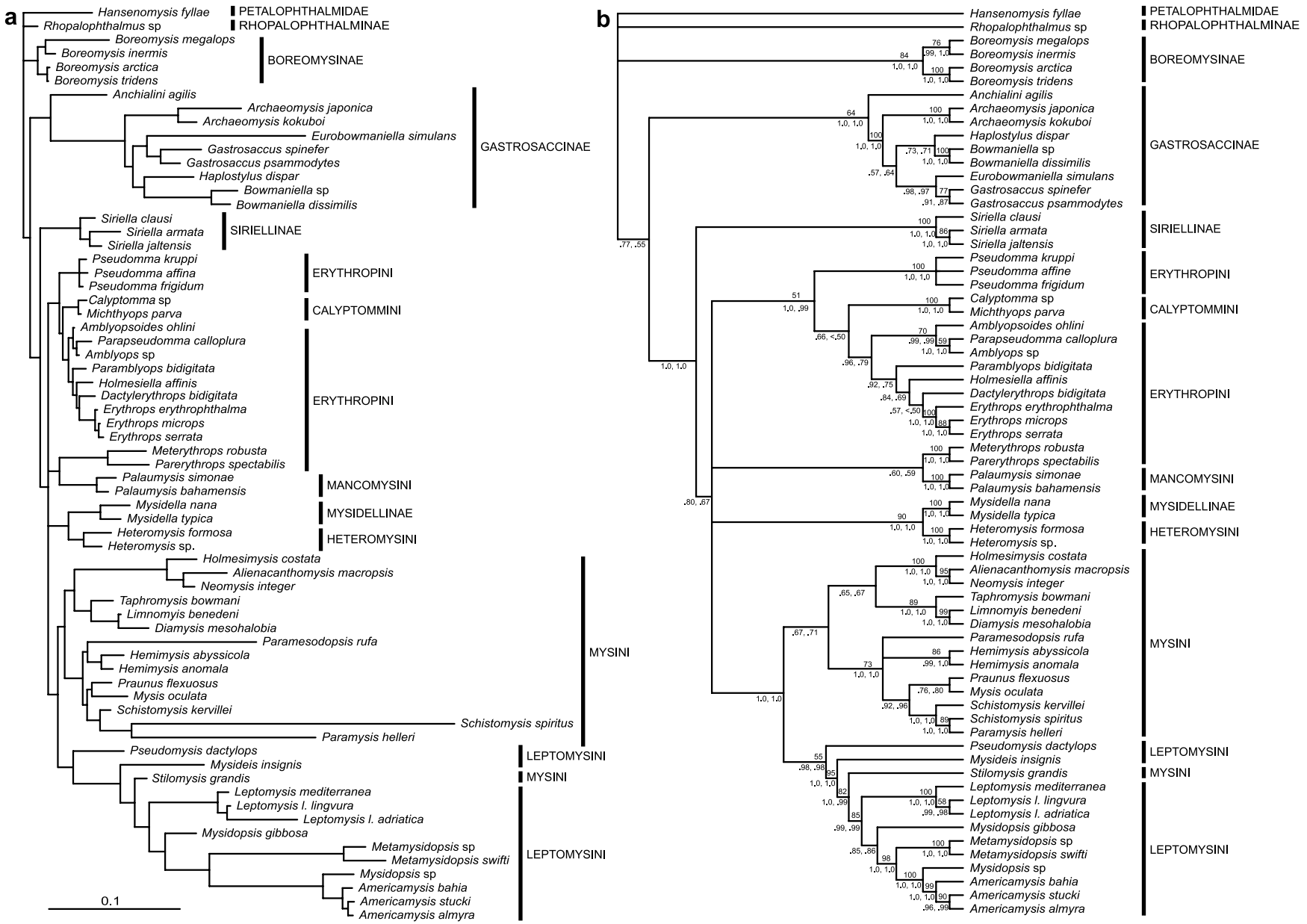

Fig. 3. Phylogram (a) and cladogram (b) of the Mysida estimated with Bayesian inference from combined stem and loop partitions (see Table 3) of the nuclear small-subunit ribosomal DNA. These are 50% majority rule consensus trees of Bayesian MCMC samples (2.5 of 2.7 million generations) assuming a GTR+*I*+G model suggested by the Akaike Information Criteria in MrModeltest version 2.2 (Nylander, 2004). Sidebars indicate higher taxa within Mysida (Table 1). Numbers above branches indicate non-parametric bootstrap values $\geqslant 50\%$ based on parsimony heuristic searches of 2000 pseudoreplicates, with 10 random sequence additions in each. Pairs of numbers below branches indicate Bayesian posterior proportions of a 50%-majority-rule consensus trees from two Markov-Monte-Carlo chain runs in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). First numbers from analyses with stem and loop partitions combined (linked) and second number from analyses with separate partitions (unlinked).

posterior probabilities were observed in the unlinked analyses on internal nodes within the Erythropini and Gastrosaccinae, corresponding to low MP bootstrap values. As observed in the ML analysis, Erythropini paraphyly was suggested due to the sister group relationship with Mancomysini and placement of the Calyptommini, albeit with low posterior probabilities (*P* values linked: 0.60, 0.66; unlinked: 0.59, <0.50). Congruent with both MP and ML, Bayesian analyses produced a paraphyletic Mysinae by the inclusion of the subfamily Mysidellinae within the Mysinae.

4. Discussion

In the present study we have conducted phylogenetic analyses of the "Mysidacea". Analyses were based on nearly full-length sequences of the gene coding for the small ribosomal subunit (18S rRNA). The sequences were produced from species representing 16 of 20 previously recognized families, subfamilies and tribes of Lophogastrida and Mysida *sensu* Nouvel et al. (1999) (Table 1). All applied phylogenetic methods indicate a polyphyletic "Mysidacea" containing three well supported lineages that cannot be traced to a unique most recent common ancestor, namely the Lophogastrida, Mysida, and Stygiomysida.

Turning first to the Mysida and Lophogastrida, the idea of a non-monophyletic Mysidacea is certainly not new (Martin and Davis, 2001), and our study supports recent studies using 18S and 28S rRNA genes (Spears et al., 2005; Jarman et al., 2000) on three major points: (1) Lophogastrida and Mysida are not sister taxa. (3) Lophogastrida is placed within the Peracarida (3) Mysida fall outside the Peracarida.

Phylogenetic hypotheses drawn upon morphological evidence often position the Lophogastrida and Mysida as monophyletic sister groups within the Peracarida (Schram and Hof, 1998; Richter and Scholtz, 2001). However, Sieg (1983), with reference to the so called "caridoid facies" (Calman, 1904), perceived the characters defining the Mysidacea as plesiomorphic, and he suggested that the Mysida and Lophogastrida have been derived from separate peracarid ancestors. In a recent study on the Mysidacea circulatory system, Wirkner and Richter (2007) present distinct ostia patterns of the heart as evidence for a Mysidacea monophyly and also for a peracarid affinity based on "myoarterial formation" characters. These characters cannot be interpreted as plesiomorphic and our results of a non-monophyly between Lophogastrida and Mysida therefore suggest these ostia patterns as evolutionary convergences. Where our results support the idea of polyphyly (Siewing, 1953; Sieg, 1983), we additionally find no evidence for a Peracarida affinity of Mysida. But we do find a sister group relationship between Amphipoda and Lophogastrida (Siewing, 1953; Spears et al., 2005). Watling (1983, 1999) suggested a paraphyletic Mysidacea and an alliance of the group with Syncarida and Eucarida rather than Peracarida. In line with Watling (1999), our results clearly suggest that the cardinal mark of Peracarida, the development of coxal epipodites into oostegites (Dahl, 1983) may be homoplastic. Other character states that have been used to characterize the Peracarida, such as the presence of a lacinia mobilis, are also found in Euphausiacea and a few decapod larvae (Dahl and Hessler, 1982; Richter et al., 2002). This indicates that the lacinia mobilis is either symplesiomorphic or that it must have evolved more than once within the Eumalacostraca. On a similar note, Casanova et al. (2002) recognized ontogenetic similarities in carapace development between Euphausiacea, Decapoda, and Mysidacea that might also point to a shared history of ontogenetic pathways, and it is tempting to speculate in terms of heterochrony with retention of 'mysis larva' juvenile traits, which could be considered ancestral in adults of Mysida and Lophogastrida.

In comparing the "Mysidacea" to the remaining Malacostraca sequences, our observations of hypervariable regions in 18S rRNA confirmed the findings of Spears et al. (2005). Length variability was most evident in the long expansion segments found in stem regions E23-1 and 43 in Isopoda and Tanaidacea. Unlike Spears et al. (2005: fig. 3), we included Caridea and Astacidea taxa in our analyses, which resulted in a polyphyletic Eucarida. Agreement was seen in the Euphausiacea forming a clade with the Mysida and Stomatopoda, but the Decapoda and Syncarida were placed in a separate clade, basal to the remaining Peracarida. We would like to point out that support values in the deeper nodes of the "Malacostraca" trees (Fig. 3) were low, and our analyses on 18S rRNA do not allow for too much confidence in the resolution of the more basal clades. On the other hand, within the Peracarida clade we find our results in complete agreement with Spears et al. (2005), where there is strong support for a monophyletic Lophogastrida within a Thermosbaenacea + Spelaeogriphacea + Amphipoda + Lophogastrida clade. As our results concerning Peracarida and Eucarida relationships are highly congruent with results presented by Spears et al. (2005) and thoroughly discussed therein, we will not elaborate further on the placement of Mysida and Lophogastrida within the Eumalacostraca, but draw attention towards our inclusion of *Stygiomysis* species, suggesting a close relationship of the Mysida family Stygiomysidae to the Mictacea.

4.1. Stygiomysida

The family Stygiomysidae is a small group of stygobitic mysids comprising six described species endemic to anchialine caves in Central America and Mediterranean waters. Stygiomysids are vermiform mysids, diagnosed by a reduced carapace, third and fourth pair of thoracopods modified as gnathopods, the protopod of the uropod is produced into a long distomedial process, and the female marsupium is composed of four pairs of oostegites on thoracopods five to eight.

The Stygiomysidae have been considered closely related to the family Lepidomysidae, also consisting of cavernicolous mysids with similar distribution to *Stygiomysis* species. Shared characteristics of these two families are non-natatory, biramous male and female pleopods; transverse lamellae arising from the posterior sternal margins of abdominal somites three, four and five; and a posteriorly directed prolongation of the protopodite of the uropod (Gordon, 1960).

Placement of Stygiomysidae and Lepidomysidae based on morphological characters has not been trivial (Fage, 1941; Nath and Pillai, 1971; De Jong-Moreau and Casanova, 2001). Shared characters with "Mysidacea" groups include absence of podobranchia (Stygiomysidae, Lepidomysidae, Mysida); absence of the uropodal statocyst (Lophogastrida, Stygiomysidae, Lepidomysidae, Petalophthalmidae); distal suture on the uropodal exopod (Lepidomysidae, Petalophthalmidae, Rhopalophthalminae, Siriellinae); and seven pairs of oostegites (Lophogastrida, Lepidomysidae, Petalophthalmidae, Boreomysinae). Attributing these characters equal weight would suggest an intermediate placement between Lophogastrida and Mysida. Such interpretations lead Tchindonova (1981) to erect Stygiomysida, comprising the families Stygiomysidae and Lepidomysidae, as a third suborder of the "Mysidacea". Tchindonova's suggested revision has been followed (Meland, 2002 *in part*), but has to date not been properly addressed in classification of the Mysidacea. In effect, based on the absence of podobranchiae and reduced (compared to Lophogastrida) male and female pleopods, recent classifications have followed Gordon's (1960) placement of Stygiomysidae and Lepidomysidae within the Mysida (Nouvel et al., 1999; Martin and Davis, 2001). A similar classification is also implied in a recent foregut analysis of "Mysidacea", suggesting that the Lophogastrida are ancestral to both Stygiomysida and Mysida (De Jong-Moreau and Casanova, 2001) and that the Stygiomysida are retaining archaic foregut features inherited from lophogastrid-like ancestors. This relationship is not supported by our study.

Previous phylogenetic studies involving Mysida have not specifically addressed character states in Stygiomysidae or Lepidomysidae (Sieg, 1983; Richter and Scholtz, 2001; Watling, 1981). To our knowledge, by including representative *Stygiomysis* species as separate terminals, ours is the first attempt to address phylogenetic relationships of these cavernicolous mysids within the Eumalacostraca. Our results, regardless of methods used, exclude the Stygiomysidae from the Mysida, and a suggested affinity with Mictacea is equally supported in all of our analyses.

As with the Lophogastrida, most of the characters previously used in attributing the Stygiomysidae an affinity to Mysida (Gordon, 1960) are plesiomorphic "caridoid facies" characters. It is interesting to note properties of the female pleopods. Pleopods in Stygiomysidae and Lepidomysidae are sexually undifferentiated and consist of protopodites armed with simple, platelike endopods and multisegmented exopods (Kallmeyer and Carpenter, 1996: figs. 5A–G). In Lophogastrida, the pleopods are also biramous in both females and males, but the endopods and exopods are articulated. In the Mysida, the pleopods are sexually dimorphic. With the exception of some Gastrosaccinae, all females have uniramous pleopods retained as simple, non-articulated setose plates. Gordon (1960) and Tchindonova (1981) suggested a close affinity between Stygiomysidae and Lepidomysidae and we consider them to be sister groups. A synapmorphy is observed in the chitinous lamina between the pleopods, formed by backward extensions of the posterior sternal margin of the abdominal third fourth and fifth somites (Kallmeyer and Carpenter, 1996: fig. 5H). We observe that 18S rRNA in *Stygiomysis* species contain expansion segments, constituting more than 100 nucleotides that are not found in Lophogastrida and Mysida. These segments are not easily aligned with the even larger expansions (>300 nucleotides) found in isopods and amphipods and were excluded from the phylogenetic analyses. By discarding unalignable segments of nucleotides we have certainly muted some phylogenetic signal within the shallower branches, but despite the exclusion of potentially informative characters, the stygiomysids are nonetheless clearly grouped within the Peracarida, excluding sister group relationships with the Mysida. There is also no support for a sister group relationship with the Lophogastrida.

The suggested relationship between Stygiomysida and *Thetispelecaris remex* is new, and we find no cited evidence for this relationship in the morphological literature. For convenience, we are referring to *T. remex* as a Mictacea. In the traditional view, the order Mictacea contains the genera *Hirsutia*, *Mictocaris*, and *Thetispelecaris* (Martin and Davis, 2001). However, Gutu and Iliffe (1998) included *Mictocaris halope* only in the Mictacea and proposed a new order, Bochusacea, for species of *Hirsutia* and *Thetispelaecaris.* In another paper (Gutu, 1998), the Mictacea and Spelaeogriphacea are classified as suborders of the order Cosinzeneacea. The clear separation of *Spelaeogriphus lepidops* (Cosinzeneacea, Spelaeogriphacea) and *T. remex* (Bochusacea) in our trees may imply support to Gutu's splitting of Mictacea *sensu lato.*

Compared to Stygiomysida the diagnostic characters of Mictacea, such as a carapace, stalked eyes (in part), antennal scale, and pleopods are for the most part considered to be peracarid plesiomorphies (Bowman et al., 1985). Apomorphies defining the Mictacea include the reduction of the lacinia mobilis of the right mandible and the absence of an epipod on the first maxilliped (see Richter and Scholtz, 2001). The strong support in 18S rRNA for a sister group relationship with *Stygiomysis* is not evident in morphology, but a few characters do seem potentially interesting in supporting the suggested monophyly.

The paragnaths in Stygiomysida and Mictacea are anteriorly produced as palpiform lobes. Although the phylogenetic value of this character is possibly limited, as it can be interpreted as an adaptation to feeding habits, the similarity in this feature is nonetheless remarkable. *Thetispelecaris*

and *Hirsutia* are considered deposit feeders (Ohtsuka et al., 2002; Just and Poore, 1988), and an extended third thoracopod may aid in grasping and manipulating large detritus particles. On the other hand *Stygiomysis* species have large robust second to fifth thoracopods taking the form of gnathopods, and raptorial behavior has been observed in *S. aemete* (Wagner, 1992), but considering a preference for soft-bottom substrates a detritus feeding habit is a potential feeding strategy as well. In any case, the extended paragnaths can also be interpreted as, opposed to adaptations, phylogenetic apomorphies that are utilized for different modes of feeding.

As our results are the first to indicate phylogenetic relationships between Stygiomysida and Mictacea, intriguing evidence is now presented for pursuing this topic. Future analyses will require more genes and more morphology studies of *Mictocaris*, *Thetispelecaris*, *Hirsutia*, *Stygiomysis*, *Spelaeomysis*, and *Spelaeogriphus*.

4.2. Mysida

Monophyly of the order Mysida (Stygiomysidae excluded) was strongly supported in the Malacostraca analyses and in our second analyses we focused on phylogenetic relationships between higher Mysida taxa. This was accomplished by a broader taxon sampling of mysids and excluding all non-Mysida from the dataset. Low sequence divergence between Mysida species made alignment less difficult and allowed us to re-include the previously excluded hypervariable regions, as the unalignable expansion segments found in peracarid taxa were absent in Mysida. The inclusion of additional characters increased resolution and nodal support both in MP bootstrap values and Bayesian posterior probabilities (Fig. 3), giving us a more reliable picture of internal relationships within the Mysida. The most obvious improvement from the first analyses is seen in a closer agreement of monophyletic clades with the current classification of the order Mysida.

Morphological character states in Mysida that are also shared with Peracarida taxa are the absence of thoracopodal branchia, where instead respiration is a function of the inner wall of the carapace (Wägele, 1994; Richter and Scholtz, 2001) and the lacinia mobilis being present on both the left and right mandibles (Richter et al., 2002). Mysida autapomorphies are the female pleopods that take on the form of rudimentary uniramous plates and the following foregut characters (Kobusch, 1998): (1) a bulbous cardiac chamber with prominent dorsal fold, (2) prominent lateralia armed with strong spines on the anterior margins and teeth/spines on the posterior part, and (3) the funnel consisting of a separate lamina dorsales posterior and lamella ventrales, and a relatively small valvula postero ventralis.

4.2.1. Petalophthalmidae

Hansenomysis fyllae is clearly supported as a member of Mysida in the Malacostraca-analyses and an early derivation of the Petalophthalmidae is indicated by seven pairs of oostegites, undivided propodal segments of the thoracopods' endopods, and the absence of a uropodal statocyst. With reference to these "primitive" morphological characters, the placement of the Petalophthalmidae as a relatively derived Mysida in the Malocostraca tree (Fig. 2) is not easily understood. A sister group relationship with Siriellinae would require secondary loss of statocysts in Petalophthalmidae and independent events of evolving anterior oostegites in Petalophthalmidae and Boreomysinae. An alternative, but even more problematic interpretation would be several independent evolutionary events of statocyst gains and oostegitte reductions in all other Mysida taxa. Therefore, based on morphological plesiomorphies coupled with low 18S rRNA support for branching in the deeper nodes of Mysida in the Malacostraca trees, we rooted the Mysida tree with *H. fyllae*, suggesting the family Petalophthalmidae ancestral to the remaining Mysida. If our results of a non-monophyletic Mysidacea are correct morphological autapomorphies are seen in the reduction of the first and second (in *Pethalophthalmus)* thoracopod exopods. We interpret these reductions as being derived independently of that found in Lophogastrida. Additionally, the Petalophthalmidae do not have a lacinia mobilis. We consider these and other mandible modifications, such as the reduction of the spine row to one strong spine, to be derived states within the Mysida. A shared plesiomorphy is observed with Rhopalophtalminae, Boreomysinae, and Siriellinae in the uropod exopods being divided by a suture. The combination of shared character states between Lophogastrida and Mysida led Tchindonova (1981) to remove Petalophthalmidae from the Mysida and place it as a separate suborder representing an intermediate group between lophogastrids and mysids. Based on foregut morphology De Jong-Moreau and Casanova (2001) implied a similar intermediate placement of Petalophthalmidae. In their study, *Petalophthalmus armiger* exhibited more common features with the Lophogastrida than with the family Mysidae, but *Hansenomysis pseudofyllae* had more features in common with the Mysida genera *Boreomysis* and *Leptomysis*. In accepting a monophyletic Mysidacea they suggested Petalophthalmidae as a transitional form of mysid between Lophogastrida and the more derived Mysida. Although we do not accept a monophyletic Mysidacea, our results are not in conflict with the character interpretations of Tchindonova (1981) and De Jong-Moreau and Casanova (2001) regarding the placement of Petalophthalmidae. As 18S rRNA gives support for *H. fyllae* within a monophyletic Mysida, we interpret both the molecular and morphological evidence to point more in the direction of a primitive lineage of Mysida that evolved independently of the Lophogastrida. Due to high inter-generic morphological diversity in the Petalophthalmidae, increased support for the proposed hypothesis will require testing of Petalophthalmidae monophyly by the inclusion of additional genera and the foregut characters will have to be analyzed in a phylogenetic context that includes additional Malacostraca taxa.

4.2.2. Boreomysinae

Support for the current classification of the Boreomysinae within the family Mysidae is observed and the basal placement is justified on morphological grounds by the presence of plesiomorphic character states, such as seven pairs of oostegites and that all male pleopods are biramous. The remaining Mysidae taxa have two or three pairs of oostegites and a varying degree of reductions in the male pleopods. The presence of a suture on the uropod exopods is plesiomorphic, but the proximal, opposed to distal, placement of the suture in Boreomysinae is autapomorphic. Based on these characters Tchindonova (1981) lifted the Boreomysinae to the rank of family. We consider this reclassification unnecessary and retain the subfamily Boreomysinae within the family Mysidae. The Mysidae is thereby defined by the presence of uropodal statocysts.

4.2.3. Rhopalophthalminae

An early derivation of Rhopalophthalminae is indicated by 18S rRNA in an unresolved basal placement. Monophyly is supported in morphology by a distal suture on the uropods' endopods, which is unique for Rhopalophthalminae. Strong support for an early derived Mysidae is the organic composition of the uropodal statoliths, also found in the Boreomysinae. In the remaining Mysidae taxa the statoliths are mineralized with either fluorite or calcium carbonate (Ariani et al., 1993). In addition, a basal placement is suggested by the retention of a suture on the uropods' exopods, but the presence of unequally developed male pleopods would suggest a closer affinity with the more derived Mysida. Despite uncertain placement, the presence of uropodal statocysts firmly establishes the Rhopalophthalminae as a true Mysidae.

4.2.4. Gastrosaccinae

The relative placement of the subfamily Gastrosaccinae is in agreement with results presented by Remerie et al. (2004). The Gastrosaccinae are defined by the first abdominal somite of the female having the pleural plates developed into a pair of lateral lamellae that take part in the formation of the brood pouch. Based on morphological evidence, Hanamura (1997) grouped the Gastrosaccinae into two separate lineages, representing burrowing and pelagic genera. The derived first abdominal somite is apparently an adaptation for protecting the marsupium during burrowing, explaining the reduction observed in the pelagic genera *Anchialina*, *Paranchialina*, and *Pseudanchialina*. In our analyses, the pelagic Gastrosaccinae are represented by *Anchialina agilis*, and our remaining taxa represent burrowing genera. Gastrosaccinae monophyly is well supported in our Bayesian analyses, but less supported in MP, due to the uncertain affinity of *A. agilis* with the remaining Gastrosaccinae. Diagnostic for the burrowing Gastrosaccinae lineage are the biramous male pleopods and an elongated exopod on the male third pleopod. The group is consistently supported as a strong clade in our 18S rRNA phylogenies. Remerie et al. (2004) emphasized the development of male and female first pleopods for classifying the Gastrosaccinae, proposing a biramous state ancestral to uniramous. They erroneously stated that females of the genera *Bowmaniella*, *Archaeomysis*, and *Gastrosaccus* have uniramous first pleopods (Remerie personal communication). However, these genera, as well as *Haplostylus* and *Eurobowmaniella*, have biramous pleopods, while in *Anchialina* the female pleopods are uniramous. Our analyses present additional support for a "*Gastrosaccus* group" defined by the biramous female first pleopod and biramous male pleopods (Remerie et al., 2004), but the results give limited support for internal relationships within this group.

We are reluctant to draw conclusions on homology between the biramous state of the second to fifth female pleopods found in *Archaeomysis* and *Bowmanniela* (Hanamura et al., 1996: Fig. 4) and that observed in Lophogastrida (identical to male pleopods) and Stygiomysida (Bowman, 1976: Figs. 26–30). We believe that the condition of female pleopods in the *Gastrosaccus*-group is independently evolved and therefore represents an autapomorphic state, unique for the Gastrosaccinae. Our main concern is uncertainty in establishing statements of homology when identifying protopods, exopods and endopods of female pleopods. In this regard, a comparative morphological study of pleopod development would undoubtedly benefit future research on Mysida evolution.

4.2.5. Siriellinae

The Siriellinae are diagnosed by the presence of spirally coiled pseudobranchia on the male pleopods. In our Bayesian analyses, Siriellinae display a strongly supported monophyletic relationship with the Mysinae tribes and family Mysidellinae (discussed below). Siriellinae share an anteriorly produced labrum with the Gastrosaccinae, but the 18S rRNA phylogeny indicates that this state is homoplastic. The Siriellinae retain some plesiomorphic character states, such as a transversal suture and spiny armature on the uropod's exopod.

4.2.6. Mysinae and Mysidellinae

In our analyses the subfamily Mysinae (Hansen, 1910) is represented by the tribes Calyptommini, Erythropini, Heteromysini, Leptomysini, Mancomysini and Mysini.

Opposed to the other Mysida families, the Mysinae is devoid of defining autapomorphies and is largely defined by plesiomorphic character states. Classification of the tribes themselves is largely based on a combination of shared character states:

Calyptommini: male pleopods uniramous, antennal scale terminating in an apical spine.

Erythropini: first male pleopods biramous with non-articulated endopod, antennal scale terminating in an apical spine.

Heteromysini: third thoracopod forming a gnathopod, male pleopods uniramous.

Leptomysini: first male pleopods biramous with non-articulated endopod, antennal scale entire.

Mancomysini: male pleopods uniramous, reduced antennal scale.

Mysini: first and second male pleopods uniramous and third to fifth biramous.

With the exception of the unique state of male pleopods defining the Mysini, autapomorphies for each of the other tribes have not been identified, and the lack of well defined tribes has led to a problematic classification of the Mysinae, reflected in 18S rRNA by high sequence divergences between Mysinae taxa, seen as variable branch lengths, most conspicuous in Mysini and Leptomysini (Fig. 3). In effect, due to low support values and placement of a few individual taxa, the 18S rRNA phylogenies fail to recognize the tribes Erythropini, Mysini, and Leptomysini as monophyletic. There is, however, strong support for a Leptomysini + Mysini monophyly, and the observed polyphyly of each of these tribes is solely due to the Mysini *Stilomysis grandis* nested within the Leptomysini clade. Relying on male pleopod characters to divide these tribes there is no morphological evidence for this placement and we can by no means justify questioning the monophyly of Leptomysini based on 18S rRNA alone, even more so due to "misplacement" of one species.

The Mysini, in terms of morphology, is the most diverse group of Mysida. The Mysini genera are characterized by highly divergent exo- and endopods of the third to fifth male pleopods. Although useful for identification, these characters are highly heterogenous and problematic to recognize as homologous states. With the exception of the rudimentary first and second male pleopod, we are unable to recognize a single male pleopod state as synapomorphic for Mysini. This is also reflected in antennal scale, telson and uropod character states, which are often used in combination to define the other tribes, but again due to large amounts of homoplasy these characters are uninformative in defining the Mysini. Despite limited phylogenetic value of morphological characters 18S rRNA does suggest, albeit with low support values, a close affiliation of the represented Mysini genera, which are divided into three well supported groups. The "*Holmesimysis* + *Alienacanthomysis* + *Neomysis*", defined by only having the fourth male pleopod developed as biramous; a "*Taphromysis* + *Limnomysis* + *Diamysis*" group, which constitutes brackish to freshwater species; and a third group containing "*Paramesodopsis* + *Hemimysis* + *Praunus* + *Mysis* + *Schistomysis*". These groups are in close agreement with Remerie et al. (2004), but we do not find the polyphyly reflected in their groups Mysini-A and Mysini-B. This being said, our MP analyses fail to construct a monophyly of these three groups, and ML suggests the Mysini as paraphyletic, placing the "*Holmesimysis* + *Alienacanthomysis* + *Neomysis*" group basal to a "Mysini + Leptomysini" group.

Being the largest (>250 species) and most diverse of Mysida taxa, the majority of Mysini constitute shallow water mysids that have successfully dispersed throughout both coastal marine and freshwater habitats. Considering large environmental differences in shallow water habitats, local adaptation resulting in the observed morphological diversity is expected. It is interesting to note how the higher diversity within the Mysini, relative to the other taxa, is reflected in genetic distances branch length variability in 18S rRNA. These data are unable to resolve phylogenetic relationships within the Mysini, but we also recognize that the use of external morphology to construct a natural classification is equally problematic. In effect, we find no good evidence not to treat the Mysini genera as a monophyletic assemblage. Emphasizing the evolutionary success of these shallow water mysids to highly diverse environments we are nonetheless confident in that future studies based on more genes, giving a much wider range of genetic variation at several taxonomic levels, coupled with internal anatomy will reveal more on the evolutionary pathways of the Mysini.

The majority of Erythropini are hyperbenthic, usually found below depths of 200 m. The Erythropini share male pleopod characters with the Leptomysini, but are otherwise distinguished from other Mysinae by what can be considered an autapomorphy in developed "walking legs" composed of a distinct carpus and divided propodus segments on the pereopods. In our analyses the placement of *Calyptommona* and *Michthyops* indicates the Erythropini as non-monophyletic, but based on very low support values in all of our analyses an unresolved basal placement of Calyptommini within the Erythropini is suggested. The Calyptommini genera *Michthyops* and *Calyptomma* share all of the characters defining the Erythropini, but are unique in having uniramous first to fifth pleopods in both males and females. Comparable to Mancomysini, but unlike Heteromysini and Mysidellinae (discussed below) the fourth pleopods of Mancomysini and Calyptommini are sexually dimorphic. *Palaumysis* have long distal setae and in Calyptommini they are divided by an articulation. In our analyses the Calyptommini genera are clearly nested within a polyphyletic Erythropini. This placement suggests that the uniramous state of the male pleopods is independently derived in Calyptommini and Mancomysini. Following Tattersall (1909, 1911) and the classification proposed by Tattersall and Tattersall (1951) we recognize the genera *Michthyops* and *Calyptomma* as belonging to the Erythropini.

Our study suggests a sister group relationship between a strongly supported Mancomysini and the two Erythropini genera, *Parerythrops* and *Meterythrops*. The establishment of the tribe Mancomysini for *Palaumysis simonae* was originally based on the absence of an antennal scale, but recent discoveries of two new *Palaumysis* species revealed the presence of a rudimentary scale (Hanamura and Kase, 2002; Pesce and Iliffe, 2002). Reduced antennal scales are also found in some Erythropini genera and based on this character a close relationship with Erythropini has been suggested (Bacescu and Iliffe, 1986). Although sharing general Erythropini characters, molecular support for this relationship is weak. In abandoning the tribe Calyptommini the resulting non-monophyletic Erythropini is thereby most

likely due to elevated sequence divergence in *Parerythrops* and *Meterythrops* (long branches in Fig. 3a). As for the Mancomysini, we do recognize a close affiliation between the Erythropini and Mancomysini, but based on the existing morphological and molecular evidence we do not agree with the Nouvel et al. (1999) classification of *Palaumysis* as Erythropini.

The placement of the subfamily Mysidellinae as a sister group to the tribe Heteromysini, renders the subfamily Mysinae as paraphyletic. The suggested monophyly of Heteromysini and *Mysidella* is supported in morphology by rudimentary male and female pleopods as uniramous plates, and elongated cylindrical male genital organs. The use of these characters for classification has been addressed by several authors (Ledoyer, 1989; Bowman and Orsi, 1992; Bravo and Murano, 1996), leading to the transfer of *Mysidetes* and *Pseudomysidetes* from Leptomysini to the Heteromysini, thereby excluding the enlarged pereopod 2 as a defining character for the tribe Heteromysini. In our analyses on 18S rRNA, the close relationship between *Heteromysis* and *Mysidella* emphasizes the strength of uniramous male pleopods and male genital organs as uniquely derived morphological characters, and give ample support for redefining the Heteromysini to include the aforementioned Leptomysini genera as suggested by Bowman and Orsi (1992). Consequently we find no good evidence for the respective classification of *Mysidetes* and *Pseudomysidetes* within Leptomysini and Mysini, as suggested by Nouvel et al. (1999). In addition, the mouthpart modifications (labrum, mandible, and maxillae) used to assign Mysidellinae the rank of subfamily does not seem to be justified.

5. Revised classification

Remerie et al. (2004) urged a taxonomic revision of Mysida that reflects monophyletic lineages and the evolutionary history of taxa. We have expanded on their perspective by covering a much more complete representation of "mysidacean" and malacostracan diversity. Our results add weight to their conclusions and also to previous findings of non-monophyletic Mysidacea (Spears et al., 2005). We suggest a taxonomic revision of taxa previously included in the order Mysidacea *sensu* Nouvel et al. (1999) as follows:

Order Lophogastrida Boas, 1883
- Family Lophogastridae G.O. Sars, 1870
- Family Gnathophausiidae Udrescu, 1984
- Family Eucopiidae G.O. Sars, 1885

Order Stygiomysida Tchindonova, 1981
- Family Lepidomysidae Clarke, 1961
- Family Stygiomysidae Caroli, 1937

Order Mysida Boas, 1883
- Family Petalophthalmidae Czerniavsky, 1882
- Family Mysidae Haworth, 1825
  - Subfamily Rhopalophthalminae Hansen, 1910
  - Subfamily Boreomysinae Holt and Tattersall, 1905
  - Subfamily Gastrosaccinae Norman, 1892
  - Subfamily Siriellinae Czerniasky, 1882
  - Subfamily Erythropinae Hansen, 1910
  - Subfamily Mancomysinae Bacescu and Iliffe, 1986
  - Subfamily Heteromysinae Norman, 1892
  - Subfamily Mysidellinae Norman, 1892
  - Subfamily Mysinae Haworth, 1825
  - Subfamily Leptomysinae Hansen, 1910

For taxa not included in our study, the published morphological descriptions are sufficient to address their placement within our revised classification. We find no support for the tribe Aberomysini (Bacescu and Iliffe, 1986), as morphological evidence clearly indicates placement of *Aberomysis murani* within the Erythropini (Nouvel et al., 1999). We find no evidence for retaining the subfamily Thalassomysinae (Nouvel, 1942). The genus *Thalassomysis* is solely based on female morphology. Following Tattersall (1939) when establishing the genus, we place *Thalassomysis* within the Erythropini. On the same note, due to the absence of described males, the monotypic subfamily Mysimenziesinae (Tchindonova, 1981) is considered poorly justified. Following other authors, we retain *Mysimenzies hadalis* within the Erythropini (Bacescu, 1971; Nouvel et al., 1999).

For increased resolution within and stronger support for the suggested subfamilies future studies should concentrate on an increased gene sampling to represent several taxonomic levels of variation. Finally, we believe that increased efforts towards research concentrating on pleopod development will have an important impact on understanding Lophogastrida, Stygiomysida, and Mysida evolution.

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ber 30. Mysida Web Site. http://tidepool.st.usm.edu/mysids. Deprez, T. 2005. NeMys. World Wide Web electronic publication. www.nemys.ugent.be, version (8/2006). This research was funded by a post doctoral fellowship from the Norwegian Research Council (158922/S40).

Appendix A

List of species used in the present study, with geographic origin and GenBank accession number

Taxonomy	Accession No.	Locality	Voucher specimen
Order Lophogastrida Boas, 1883			
Family Eucopiidae G.O. Sars, 1885			
Eucopia unguiculata (Willemoes-Suhm, 1875)	AY781418	Gulf of Mexico, DeSoto Canyon	
Eucopia sculpticauda Faxon, 1893	AM422473	Mid-Atlantic Ridge (55 °36′26″N, 36 °34′13″W)	ZMBM77814
Family Gnathophausiidae Udrescu, 1984			
Gnathophausia ingens Dohrn, 1870	AY781416	Gulf of Mexico	
Gnathophausia gigas Willemoes-Suhm, 1873	AM422475	Mid-Atlantic Ridge (52 °57′56″N, 34 °38′25″W)	ZMBM77815
Gnathophausia zoea Willemoes-Suhm, 1873	AM422474	Mid-Atlantic Ridge (56 °14′58″N, 34 °35′23″W)	ZMBM77816
Family Lophogastridae G.O. Sars, 1870			
Lophogaster typicus Sars, 1857	AM422476	Norway: Fanafjorden	ZMBM77817
Order Stygiomysida, Tchindonova, 1981			
Family Stygiomysidae, Caroli, 1937			
Stygiomysis aemete Wagner, 1992	AM422477	Dominian Republic: Pedernales	
Stygiomysis cokei Kallmeyer and Carpenter, 1996	AM422478	Mexico: Yukaton, Sotuta	
Stygiomysis holthuisi (Gordon, 1958)	AM422479	Mexico: Qunitana Roo, Mayan Blue	
Order Mysida Boas, 1883			
Family Petalophthalmidae Czerniavsky, 1882			
* *Hansenomysis fyllae* Hansen, 1887	AM422480	Iceland: Iceland Basin	ZMBM77818
Family Mysidae Haworth, 1825			
Subfamily Boreomysinae Holt and Tattersall, 1905			
Boreomysis arctica Krøyer, 1861	AM422481	Norway: Fensfjorden	ZMBM77819
* *Boreomysis megalops* Sars, 1872	AM422483	Norway: Hjeltefjorden	ZMBM77820
Boreomysis inermis (Willemoes-Suhm, 1874)	AM422482	Iceland: N. Atlantic,	ZMBM77821
Boreomysis tridens Sars, 1870	AM422484	Norway: Trondheimsfjorden	ZMBM77822
Subfamily Siriellinae Czerniasky, 1882			
Siriella armata (Milne-Edwards,1837)	AJ566105	Italy: Adriatic Sea	
* *Siriella clausi* Sars, 1877	AJ566107	Italy: Adriatic Sea	
Siriella jaltansis Czerniavsky, 1868	AJ566106	Italy: Adriatic Sea	
Subfamily Gastrosaccinae Norman, 1892			
Anchialina agilis (G.O. Sars, 1877)	AJ566089	Belgium: Continental shelf	
* *Archaeomysis japonica* (Hanamura, Jo and Murano, 1996)	AJ566084	Japan: Otsuchi Bay	
Archaeomysis kokuboi Ii, 1964	AJ5666085	Japan: Otsuchi Bay	
Bowmaniella sp.	AJ566086	Ecuador: Valdivia Beach	
* *Bowmaniella dissimilis* (Coifmann, 1937)	AM422485	USA: FL, St. George Island	ZMBM77823
* *Eurobowmaniella simulans* (W. Tattersall, 1915)	AM422486	India: Goa	ZMBM77824
Gastrosaccus psammodytes O. Tattersall, 1958	AJ566087	South Africa: Algoa Bay	
* *Gastrosaccus spinifer* (Goës, 1863)	AJ566088	Netherlands: Westerschelde	
Haplostylus dispar Panampunnayil, 1997	AM422487	Australia: Albany	ZMBM77825
Subfamily Rhopalophthalminae Hansen 1910			
* *Rhopalophthalmus* sp.	AM422488	South Africa: Durban	ZMBM77826
Subfamily Erythropinae Hansen 1910			
* *Amblyops* sp	AM422491	Japan: Sagami Bay	ZMBM77829
Amblyopsoides ohlini (W. Tattersall, 1951)	AM422492	Iceland: Iceland Basin	
Calyptomma sp.	AM422489	Iceland: Iceland Basin	ZMBM77827
* *Dactylerythrops bidigitata* W. Tattersall, 1907	AM422493	Iceland: Iceland Basin	ZMBM77830
Erythrops erythrophthalma (Goës, 1863)	AM422494	Norway: Svalbard, Heløysund	ZMBM77831
Erythrops microps (Sars, 1864)	AM422495	Norway: Hjeltefjorden	
* *Erythrops serrata* (Sars, 1863)	AM422496	Norway: Hjeltefjorden	ZMBM77832
Holmesiella affinis Ii, 1937	AM422497	Japan: Tateyama Bay	ZMBM77833
Meterythrops robusta Smith, 1879	AM422498	Norway: Svalbard, Hinlopen	ZMBM77834
* *Michthyops parva* (Vanhöffen, 1897)	AM422490	Iceland: Iceland Basin	ZMBM77828
Paramblyops bidigitata W. Tattersall, 1911	AM422499	Iceland: Iceland Basin	ZMBM77835
Parapseudomma calloplura (Holt & Tattersall, 1905)	AY624302	Japan: Sagami Bay	ZMBM68271
Parerythrops spectabilis Sars, 1885	AM422500	Norway: Jan Mayen	ZMBM77836
Pseudomma affine Sars, 1870	AY624283	Iceland: Iceland Basin	ZMBM68252
Pseudomma frigidum Hansen, 1908	AY624288	Norway: Jan Mayen	ZMBM68257
* *Pseudomma kruppi* W. Tattersall, 1909	AY624290	Japan: Tateyama Bay	ZMBM68259

Appendix A (*continued*)

Taxonomy	Accession No.	Locality	Voucher specimen
Subfamily Leptomysinae Hansen, 1910			
Americamysis almyra (Bowman, 1964)	AM422501	USA: FL, Pine Island	
Americamysis bahia (Molenock, 1969)	AJ566095	USA: West Coast	
* *Americamysis stucki* Price et al., 1994	AM422502	USA: FL, Tampa Bay	
* *Leptomysis lingvura adriatica* (Sars, 1866)	AJ566098	Italy: Adriatic Sea	
Leptomysis lingvura lingvura (Sars, 1866)	AJ566099	Belgium: Continental shelf	
* *Leptomysis mediterranea* Sars, 1877	AM422503	Portugal: Fuzeta	
* *Metamysidopsis* sp.	AJ566096	Ecuador: Valdivia Beach	
Metamysidopsis swifti Bacescu, 1969	AM422504	USA: FL, St. George Island	ZMBM77837
Mysideis insignis (Sars, 1864)	AM422505	Norway: Fensfjorden	ZMBM77838
* *Mysidopsis* sp.	AJ566094	Ecuador: Valdivia Beach	
* *Pseudomysis dactylops* W. Tattersall, 1951	AM422506	Japan: Tateyama Bay	ZMBM77839
Subfamily Mysinae Haworth, 1825			
Alienacanthomysis macropsis Holmquist, 1981	AM422507	USA: CA, Sauilito	ZMBM77840
Diamysis mesohalobia Ariani and Wittmann, 2000	AJ566100	Italy: Adriatic Sea	
* *Hemimysis abyssicola* Sars, 1869	AM422508	Norway: Korsfjorden	ZMBM77841
Hemimysis anomala Sars, 1907	AJ566104	Austria: Danube river	
Holmesimysis costata (Holmes, 1900)	AM422509	USA: CA, Monteray Bay	ZMBM77842
Limnomysis benedeni Czerniavsky, 1882	AJ566101	Austria: Danube river	
Mysis oculata (Fabricius, 1780)	AM422510	Norway: Svalbard, Duvefjorden	ZMBM77843
* *Neomysis integer* (Leach, 1815)	AY781420	Netherlands: Westerschelde	
* *Paramesopodopsis rufa* Fenton, 1985	AJ566108	Tasmania: Taroona Beach	
Paramysis helleri (Sars, 1877)	AM422511	Portugal: Quinta Dolago	
* *Praunus flexuosus* (Müller, 1776)	AM422512	Norway: Fanafjorden	ZMBM77844
Schistomysis kervillei (Sars, 1855)	AJ566103	Belgium: Continental shelf	
Schistomysis spiritus (Norman, 1860)	AJ566109	Netherlands: Voordelta	
Stilomysis grandis (Goës, 1863)	AM422513	Norway: Svalbard, Hinlopen	ZMBM77845
* *Taphromysis bowmani* Bacescu, 1961	AM422514	USA: FL, Tampa Bay	
Subfamily Heteromysinae Norman, 1892			
Heteromysis sp	AM422515	Japan: Tateyama Bay	ZMBM77846
* *Heteromysis formosa* Smith, 1873	AY781419	USA: MA, Woods Hole	
Subfamily Mancomysinae Bacescu and Iliffe, 1986			
Palaumysis simonae Bacescu and Iliffe, 1986	AM422516	Palau Islands	
Palaumysis bahamensis Pesce and Iliffe , 2002	AM422517	Bahamas: Long Island	
Subfamily Mysidellinae Norman, 1892			
* *Mysidella typica* Sars, 1872	AM422518	Norway: Hjeltefjorden	ZMBM77847
Mysidella nana Murano, 1970	AM422519	Japan: Tateyama Bay	
Order Leptostraca Claus, 1880			
Nebalia sp	L81945	NA	
Order Stomatopoda Latreille, 1817			
Gonodactylus sp.	L81945	NA	
Squilla empusa Say, 1818	L81946	NA	
Order Anaspidacea Calman, 1904			
Anaspides tasmaniae Thomson, 1893	L81948	NA	
Order Amphipoda Latreille, 1816			
Caprella geometrica Say, 1818	AY781423	USA: MA, Woods Hole	
Gammarus oceanicus Segerstråle, 1947	AY781422	USA: MA, Woods Hole	
Phronima sp.	AY781424	NA	
Order Cumacea Kröyer, 1846			
Diastylis sculpta G.O. Sars 1871	AY781431	NA	
Spilocuma salomani Watling, 1977	AY781432	USA: FL, St.George Island	
Order Isopoda Latreille, 1817			
Asellus racovitzai (Williams, 1970)	AY781426	USA: FL, Wakulla	
Idotea metallica Bosc, 1802	AY781427	USA: MA, Woods Hole	
Paramphisopus palustris (Glauert, 1924)	AY781425	Australia: Perth, Lake Monger	
Order Mictacea Bowman, Garner, Hessler, Iliffe and Sanders, 1985			
Thetispelecaris remex Gutu and Iliffe, 1998	AY781421	Bahamas: Blue Hole	
Order Tanaidacea Dana, 1849			
Kalliapseudes sp.	AY781430	USA: MI, Ocean Springs	
Paratanais malignus Larsen, 2001	AY781429	Australia: New South Wales, Botany Bay	

(*continued on next page*)

Appendix A (*continued*)

Taxonomy	Accession No.	Locality	Voucher specimen
Tanais dulongi (Audouin, 1826)	AY781428	Mexico: Alvarado Lagoon	
Order Thermosbaenacea Monod, 1927			
Tethysbaena argentarii Stella, 1951	AY781415		
Order Spelaeogriphacea Gordon, 1957			
Spelaeogriphus lepidops Gordon, 1957	AY781414	South Africa: Table Mountain, Bat Cave	
Order Euphausiacea Dana, 1852			
Meganyctiphanes norvegica Sars, 1857	AY781434	NA	
Nyctiphanes simplex Hansen, 1911	AY781433	USA: CA, La Jolla Canyon	
Order Decapoda Latreille, 1802			
Callinectes sapidus Rathbun, 1896	AY781436	USA: FL, FSU Marine lab	
Hippolyte pleuracanthus (Stimpson, 1871)	AY743956	USA: VA, Chesapeake Bay	
Homarus americanus Milne-Edwards 1837	AF235971	NA	
Oedignathus inermis (Stimpson, 1860)	Z14062	NA	
Palaemonetes vulgaris (Say, 1818)	AY743941	USA: MA, Woods Hole	
Panulirus argus Latreille, 1804	AY781435	USA: FL, Florida Keys	

Revised Mysida classification as suggested in this study. Remaining classification follows Martin and Davis (2001). Voucher specimens are deposited at the Natural History Museum, University of Bergen, Norway. NA indicates unavailable data. Entries with asterisk (*) were provided with secondary structure notation and used in the variability plot in Fig. 1.

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