Relationships of the Sphaeromatidae genera (Peracarida: Isopoda) inferred from 18S rDNA and 16S rDNA genes

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Abstract. The Sphaeromatidae has 100 genera and close to 700 species with a worldwide distribution. Most are abundant primarily in shallow (< 200 m) marine communities, but extend to 1.400 m, and are occasionally present in permanent freshwater habitats. They play an important role as prey for epibenthic fishes and are commensals and scavengers. Sphaeromatids' impressive exploitation of diverse habitats, in combination with diversity in female life history strategies and elaborate male combat structures, has resulted in extraordinary levels of homoplasy. We sequenced specimens from 39 genera for nuclear 18S rDNA and mitochondrial 16S rDNA genes, comprehensively reviewed the effects of alignments on tree topology, and performed Garli and MrBayes analyses. These data consistently retrieved clades (genus groups), *Sphaeroma*, *Exosphaeroma*, *Cymodoce*, *Ischyromene*, *Cerceis*, and *Dynamenella* and the monogeneric clade of *Gnorimosphaeroma*. We define the major clades using morphological characters, attribute sampled taxa to consistently and strongly supported ones and suggest placement of unsampled genera based on their morphological characteristics. Within each clade, we also highlight unresolved and poorly sampled genera. We point out taxonomic problems in hopes of encouraging further phylogenetic exploration. Although we identify clades containing consistent generic groups and are confident that some groups will prove stable and reliable, we feel our sampling is insufficient to propose nomenclatural changes at this time.

Key words. Sphaeromatidae, 18S rDNA, 16S rDNA, *Gnorimosphaeroma*, *Sphaeroma*, *Exosphaeroma*, *Cymodoce*, *Ischyromene*, *Cerceis*, *Dynamenella*, phylogeny.

1. Introduction

The Sphaeromatidae Latreille, 1825 is an isopod family whose species are readily recognised and widely encountered in shallow-water marine environments, and as such came to the attention of the taxonomists early in the history of carcinology (e.g., Leach 1814, 1818; Say 1818; Milne Edwards 1840; Dana 1852). In the early 1900s through to roughly the 1930s large numbers of species and genera were described, notably from southern Australia by Baker (literature can be sourced from Poore (2002) and Keppel H. Barnard from South Africa (see Kensley 1978). The next era of description can be taken to be 1980 with the prolific work over a short period

(1980–1984) of the English duo Keith Harrison and David Holdich followed on by Bruce (1992–2009), bringing the total to 100 accepted sphaeromatid genera and close to 700 species (Bruce & Schotte 2010).

The family received its first revision by the eminent Danish carcinologist Hans Jacob Hansen in 1905. The classification that Hansen (1905) proposed identified three large groups within the family, and within these groups he identified a further five groups for which he gave family-group names (as tribes). This classification was used largely unchanged until the late 20th century, although by the year 2000 the number of genera and spe-

cies had more than doubled. Later, other group names, not using accepted formal nomenclature, were also presented: Colobranchiatae Richardson, 1909 and the Pentabranchiatae Miller, 1975. The three major divisions were eventually formalized by BOWMAN (1981) and IVERSON (1982), with all groups named as subfamilies and, other than the Cassidininae Hansen, 1905, no status given to the other family-group names proposed by Hansen. Of these other names only the Monolistini Hansen, 1905 (tribe) was used (e.g., RACOVITZA 1910), often informally as a group name within the Cassidininae, for the cave-dwelling sphaeromatids from the Balkans, notably by SKET (e.g., 1964, 1986) and a few others (SBORDONI et al. 1980; STOCH 1984). The Ancinidae Dana, 1852 and Tecticipitidae Iverson, 1982 were elevated to family level by BRUCE (1993). These two families, together with the monophyletic Sphaeromatidae (WETZER et al. 2013) and the unplaced genus *Paravireia* Chilton, 1925, constitute the superfamily Sphaeromatoidea Wägele, 1989 of BRANDT & POORE (2003). HANSEN's (1905) divisions of the family was perceptive and were eventually given formal nomenclatural status in the 1980s (see WETZER et al. 2013; El. Suppl. 1) and all genera known to date were placed into their five respective subfamilies in the key and generic listing of HARRISON & ELLIS (1991). This scheme was last formally presented by ROMAN & DALENS (1999).

WÄGELE (1989), as part of an overall phylogenetic reappraisal of the Isopoda and the only attempt to establish and test for groups within the Sphaeromatidae, presented in a brief 'Hennigian analysis' of a dataset of 30 morphological characters which included overall body shape, cephalothorax, mandible, pereopod, pleopod, uropod, pleon, and brood pouch characters for the family; an unspecified number of genera (in some instances reference was to groups, e.g., "Gruppe *Cassidina*") and genera were not coded into a matrix. Many of the characters used in that phylogeny have since been shown not to be of phylogenetic significance, notably flat body shape, uropods forming part of the body outline, presence or absence of dorsal processes, loss of the thickened folds (fleshy transverse ridges) on pleopods 4 and 5, and presence or absence and form of pleotelson sinuses. At the generic level it also became apparent that dorsal processes, once considered to be axiomatically of generic significance (despite HANSEN's 1905 cautions) were inappropriate in terms of generic unity (e.g., see BRUCE 1997; BRUCE & HOLDICH 2002; LI 2000). Some 'groups,' such as the subfamily Cassidininae, are clearly not monophyletic, as recognized by WÄGELE (1989) himself, while some other groups are confirmed monophyletic by our analysis.

In the 1990s and later the generic revisions of BRUCE (e.g., 1994a,b, 1995, 1997, 2003; BRUCE & HOLDICH 2002) increasingly demonstrated that the critical purported subfamily characters – fleshy folds on pleopods 4 and 5 – were repeatedly lost within genera in the family and divisions based on those characters alone could no longer be upheld. Descriptions of new genera and generic revisions (e.g., BRUCE 1993, 1994a,b, 1995, 1997, 2003, 2005; POORE

1994) did not correspond with the existing infra-family concepts. With 100 genera and roughly 700 species no alternative arrangement was offered, though definable generic groups were recognized by BRUCE (1994, 1995). Infra-family groups were not used by POORE et al. (2002).

While several works dealing with the phylogeny of the Isopoda and former Flabellifera have been published (e.g., WÄGELE 1989; BRUSCA & WILSON 1991; WILSON 2003, 2009; BRANDT & POORE 2003; WETZER 2001, 2002) only BRANDT & POORE (2003) questioned the integrity of the Sphaeromatidae itself, concluding that the family was paraphyletic. WETZER et al. (2013) using 18S rDNA data demonstrated that the Sphaeromatidae is unequivocally monophyletic. The Sphaeromatidae, previously split into as many as six subfamilies, with the three largest divisions being based on pleopod morphology, is here revisited using DNA sequences from two genes (complete nomenclature summarized in WETZER et al. 2013, Table 1). We examine the viability of supra-generic groupings and the phylogenetic implications of these groups on classification within the family using combined 18S rDNA and 16S rDNA datasets. Our work further investigates within-clade relationships, mostly based on more extensive 16S rDNA sampling, and discusses morphological characters in the context of our genetic findings.

2. Methods

Taxon sampling. Ideally the type species of each of the Sphaeromatidae genera would be sequenced, as many of the large genera are not monophyletic or may have become a "catch-all genus" (e.g., *Cymodoce* Leach, 1814). In the perfect world, specimens from the type species would also come from the type locality. Prior to data acquisition and analysis, we divided the family Sphaeromatidae into perceived and plausible morphological groups of genera. Some of these groups had long been recognized, e.g., those genera related to *Cerceis*. Some groups had been previously defined, e.g., the '*Ischyromene*-group' (BRUCE 1995). The basis for the present division lays in a DELTA (DALLWITZ 1980; DALLWITZ et al. 2006) phylogenetic generic morphological data set developed and in progress by NLB. These perceived divisions were then effectively assessed by the molecular analysis, and where upheld those data were used to present the morphological characterization of the major clades. Not all of the original groups held up as initially perceived (e.g. *Gnorimosphaeroma* separated from *Exosphaeroma*-like genera into a mono-generic clade). Other groups lacked sequence data.

Most specimens reported here were collected during expeditions to Australia (Great Barrier Reef, southeastern Queensland), East Africa (Kenya, Mombasa; Tanzania, Zanzibar), Singapore, Samoa and Palau. NLB collected specimens from around Australia and New Zealand, and RW contributed specimens from eastern Pacific shores

(Chile, USA). Colleagues from all around the world (see Acknowledgements) sent many carefully collected specimens. All identifications were done by or verified by NLB. Currently there are 100 genera recognized in Sphaeromatidae. We were successful in sequencing specimens from 39 genera of the 52 genera collected and obtained, and in many instances several species and multiple individuals (El. Suppl. 1). In most instances multiple individuals were extracted, amplified, and sequenced for 18S rDNA and 16S rDNA genes. When type species were sequenced, these are indicated in El. Suppl. 1. Only in a few instances were 18S rDNA sequences incomplete (e.g., *Plakarthrium* Chilton, 1883a) or not of the highest quality. This is reported in the 'Results' when unusual and unlikely placements could not be explained.

Our 18S rDNA dataset has 122 Sphaeromatidae sequences: 44 species in 33 genera. Fifty-seven of these sequences were generated for this project. This dataset contains one species of *Ancinus* Milne Edwards, 1840 (Ancinidae), five Valvifera species representing four families and twelve species of Serolidae (outgroup). The outgroup is as previously used in Wetzer et al. (2013).

Our 16S rDNA dataset has 201 Sphaeromatidae sequences: 94 species, in 46 genera, representing 179 sequences which are new for this project. The dataset includes two new *Ancinus* sequences and 45 Valvifera and Serolidae taxa (outgroup). The total aligned dataset was 634 bp long.

The concatenated 18S rDNA + 16S rDNA dataset (98 sequences) is based on 37 genera and 56 species, plus two Ancinidae, three Valvifera and six Serolidae, the later three treated as outgroup. For 114 specimens both the 18S rDNA and 16S rDNA sequences came from the same individual (El. Suppl. 1). The combined dataset is smaller in terms of number of taxa compared to the separate 18S rDNA and 16S rDNA analyses, but still it is by far the most extensive sampling and sequencing of the family to date.

Specimen and sequence numbering scheme. All sequences used in the analyses are included with complete collection data in El. Suppl. 1. Unfortunately, the present Genbank (Benson et al. 2008) numbering scheme does not readily allow one to identify multiple gene fragments as coming from a single specimen. "RW numbers" (e.g., RW99.999) are collecting event identifiers. During DNA extraction from a single specimen, a unique 3 or 4-digit numeric identifier is appended to the locality identifier. This numeric tag readily allows association of the DNA in the spin tube, coming from a specific specimen, the collecting event, the locality, taxon name, and generated sequences (regardless of gene fragment). If a sequence used in our analyses came from Genbank, it too is assigned a 3–4 digit identifier for consistency. These unique identifiers are used here to assist the reader in identifying specimens from specific localities and collecting events and are helpful when nomenclature or taxonomic identification are troublesome. Identifiers either precede the taxon name or are reported in brackets following the taxon identifica-

tion. Only in a few instances did we combine sequences from conspecifics in the combined 18S rDNA and 16S rDNA analyses. In these cases, the 3–4 digit identifier is separated by an underbar and are identified in Figs. 1 and 2. Nexus data has been submitted to TreeBASE (submission ID 21399) and will be added to Open Tree of Life upon publication. Specimens and DNA are deposited in the Natural History Museum of Los Angeles County (LACM) Collections and can be retrieved by GenBank, lot, or specimen number indicated in El Suppl. 1.

Clade names used. Here we refer to clades based on the taxa that could be most extensively sampled. For example, we were able to include multiple specimens and species for the genera *Exosphaeroma* Stebbing, 1900, *Cymodoce* Leach, 1814, *Ischyromene* Racovitza, 1908, *Dynamenella* Hansen, 1905 in our analyses. As a result, these best characterize the species in the clade. The present use of these names does not imply any nomenclatural status nor their future applicability, as we are fully aware as additional taxa are included, some relationships are likely to change.

From tissue to analysis. Specimen preservation, tissue extraction, 18S rDNA primers, amplification, sequence editing, sequence assembly as well as alignment protocols are detailed in Wetzer et al. (2013). Isopod collecting and preservation methods are described in Wetzer 2015. Most material was fixed and preserved in 95% ethanol and stored in 4°C whenever possible. Specimens were extracted with a QIAGEN DNeasy Kit (Qiagen, Valencia, CA) and the manufacturer's protocol was followed. Polymerase chain reaction (PCR, Sakai et al. 1988) was carried out with standard PCR conditions [2.5 µl of 10 × PCR buffer, 1.5 µl of 50 mM MgCl2, 4 µl of 10 mM dNTPs, 2.5 µl each of two 10 pmol primers, 0.15 Platinum Taq (5 units/µl), 9.6 µl double-distilled water, and 1 µl template] and thermal cycled as follows: an initial denaturation at 96°C for 3 minutes followed by 40 cycles of 95°C for 1 minute, followed by 46°C for 1 minute, 72°C for 1 minute, and a final extension at 72°C for 10 minutes. A minimum of four 18S rDNA primer pairs were needed to amplify the gene. In some instances, five or even six pairs were used. Primer sequences are listed in Wetzer et al. (2013). In all instances both directions of the gene were sequenced. The long insertions especially in the V4 and V7 regions (see Nelles et al. 1984; Wägele et al. 2003; Spears et al. 2005) were frequently difficult to sequence through and even though alternate overlapping primers were used, a few sequences have missing data. Sequence length for the 18S rDNA gene varied from 1,748–2,746 bp. 16S rDNA was amplified with universal 16Sar and 16Sbr primers (Palumbi et al. 1991; Wetzer 2001) resulting in ~ 550 bp fragments. PCR products were visualized by agarose (1.2%) gel electrophoresis with Sybr Gold (Invitrogen, Carlsbad, CA). PCR product was purified with Sephadex (Sigma Chemical, St. Louis, MO) on millipore multiscreen filter plates, and DNA was cycle sequenced with ABI Big-dye ready-reaction kit and

following the standard cycle sequencing protocol with one quarter of the suggested reaction volume.

As in the WETZER et al. (2013) analyses which included only 19 Sphaeromatidae species, here we similarly explored all three MAFFT (Multiple Alignment Program for amino acid or nucleotide sequences, KATOH et al. (2002, 2005) alignment algorithms. Separate datasets were created using LINS, EINS, or GINS alignment protocols for 18S rDNA and 16S rDNA sequences. Separate analyses were run eliminating poorly aligned and divergent regions with GBlocks (CASTERESANA 2000; TALAVERA & CASTERESANA 2007). We used default settings for all GBlocks parameters except for allowed gap positions, which we toggled to "with half" (i.e., only positions where 50% or more of the sequences have a gap are treated as a gap position).

Phylogenetic congruence among mitochondrial 16S rDNA and nuclear 18S rDNA genes was assessed using WIENS' (1998) protocol when genes were combined. No areas of strongly supported incongruence were observed among gene trees. Seventeen different datasets were assembled and analyzed. JModelTest v1.0.1 (POSADA 2009; DARRIBA et al. 2012) was used to select the appropriate model of evolution for each gene partition under the Akaike Information Criterion AIC (POSADA & BUCKLEY 2004). The general time reversible model of evolution (TAVARÉ 1986), with proportion of invariable sites and gamma distribution, was selected for each gene (GTR + G + I). Both maximum likelihood (ML) and Bayesian methods of phylogenetic inference were applied. ML analysis was performed in GARLI under default settings for the genetic algorithm, except that searchreps = 10. Clade support was assessed using the non-parametric bootstrap procedure (FELSENSTEIN 1985) with 1000 bootstrap replicates. Bayesian analysis coupled with Markov chain Monte Carlo (BMCMC) inference was performed in MrBayes v3.1.2 (RONQUIST & HUELSENBECK 2003; RONQUIST et al. 2012). Four independent BMCMC analyses were run in the CIPRES Science Gateway portal (MILLER et al. 2010), each consisting of four chains. Each Markov chain was started from a random tree and run for 2×10^7 cycles, with sampling every 1000th generation. Sequence evolution model parameters were estimated independently for each data partition starting as unknown variables with uniform default priors. Convergence and mixing were monitored using Tracer v1.5 (RAMBAUT & DRUMMOND 2009). All sample points prior to reaching stationary levels were discarded as burn-in. The posterior probabilities for individual clades obtained from separate analyses were compared for congruence and then combined and summarized on a 50% majority-rule consensus tree.

Trees presented were selected as best representing all of the different datasets and analyses performed. Tree selection was based on internal relationships being upheld most often regardless of the analytical method used or data permutations performed. Parameters for the phylogenetic trees presented are as follows: Fig. 1 is based on 98 taxa, 5174 characters in total, 2089 constant characters, 2866 parsimony-informative characters, 219 autapomorphic characters. Fig. 2 contains the same 98 taxa as Fig. 1 and the same 5174 characters and is a 50%-majority-rule consensus of 18,002 trees. Figs. 3A, 4A, 5A, 6A, 7A, 8A, and 9A are 18S rDNA Garli BestTrees with MrBayes support values indicated on branches (110 taxa, 1841 bp characters, 854 constant characters, 873 parsimony-informative characters, 114 autapomorphic characters). Figs. 3B, 4B, 4C, 5B, 6B, 7B, 8B, 9B, 10 are 16S rDNA Garli BestTrees with MrBayes support values indicated on branches data matrix (246 taxa, 633 bp, 166 constant characters, 428 parsimony-informative characters, 39 autapomorphic characters).

MrBayes support values are indicated on all phylogenetic trees except Fig. 1. Nodes are considered strongly supported if pP > 0.95. No support values are indicated in instances where maximum likelihood and Bayesian phylogenies are not congruent. Where readily available, dorsal and lateral line drawings from the primary literature have been added to terminal branches identified to the level of species. Sources are identified in the Acknowledgments.

3. Results and discussion: relationships within Sphaeromatidae

This paper infers a Sphaeromatidae phylogeny based molecular data. Key morphological features, i.e., existing morphological knowledge accumulated in the DELTA database (see Methods), is for the first time attributed to genetically derived clades We present new molecular data, draw on morphological characters that support molecular findings, and discuss taxonomic problems and anomalies that need further review. Hence each section offers new insights and suggests new research opportunities.

Figs. 1 and 2 show the entire Sphaeromatidae and are based on the 18S rDNA + 16S rDNA combined datasets. Figs. 3A – 9A show the 18S rDNA datasets, and Figs. 3B – 9B, 10 are based on the 16S rDNA data; all show specific clades. The GARLI best tree (Fig. 1) and the MrBayes tree (Fig. 2) both based on the combined dataset (18S rDNA + 16S rDNA) most consistently captured deep nodes and internal generic relationships. Both of these analyses included the serolids, *Plakarthrium*, and did not apply GBlocks or profile alignments. Tree selection was based on internal relationships being upheld most often regardless of the analytical method used or data permutation performed. Branch lengths and posterior probabilities are indicated on the figures. Despite the long hypervariable regions and subsequent alignment difficulties, removing these regions with GBlocks produced trees we rejected as they no longer retained deep node support and the backbone of the Sphaeromatidae collapsed. Deep nodes are based primarily on combined 18S rDNA + 16S rDNA and 18S rDNA data. 16S rDNA data most consistently and robustly provides within clade relationships. We had also generated more 16S rDNA se-

quences than 18S rDNA sequences with 16S rDNA sequences increasing within clade resolution.

The phylogeny presented herein is based on the results of the molecular analyses depicted in Figs. 1 and 2. Morphological characters defining clades are presented with the relevant molecular results such that together these data will contribute to our future understanding and research of the family. Genera for which there was no genetic representation and lacking clear morphological affinities, remain as *incertae sedis*. All Sphaeromatidae genera are summarized in section 7. Appendix (Sphaeromatidae genera list) and organized according to our findings. A small number of genera (approximately 10% of all genera) are regarded as *incertae sedis* due to lack of descriptive data or simply a lack of clear morphological clues as to their phylogenetic affinities. Examples of the former are *Botryias* Richardson, 1910 and *Hemisphaeroma* Hansen, 1905. Examples of the latter are *Xynosphaera* Bruce, 1994b, a commensal of Alcyonacea (soft corals), with reduced morphology, and the genera *Artopoles* Barnard, 1920 (see Bruce 2001) and *Cassidinella* Whitelegge, 1901 (see Bruce 1994a).

The remaining genera form three basal clades – clade 1 (*Gnorimosphaeroma*) is always basal and the sister taxon to clade 2 and clade 3 (Figs. 1 and 2). Morphologically this clade is defined by pleopod and epistome morphology. The remaining clades are diagnosed, and the characters used are present in most taxa. Again, while some characters are secondarily lost or inconsistent, genera are placed on the overall balance of characters, with penial and pleopodal morphology, which show high consistency within genera, proving critical.

The hypothesis of relationships presented here is likely to undergo further refinement. Clades 2 and 3 equate to the subfamilies Sphaeromatinae and Dynameninae and while we are confident that they will remain stable, the generic composition and resolution of the relationships within the individual major clades is likely to change with the addition of taxa. In large part this is because many of the larger genera are not monophyletic, such as the large genus *Cymodoce*. This is evident on a morphological basis, but has been further demonstrated in the sequence data presented here, with species within such apparently classic 'Sphaeroma-like' genera, such as *Gnorimosphaeroma* Menzies, 1954, *Sphaeromopsis* Holdich & Jones, 1973 and *Exosphaeroma*, splitting into separate clades. Furthermore, the second author (NLB) is aware that there are numerous *de novo* genera in museum collections that remain to be described, and that exploration of deep-water hard-bottom habitats (< 1000 m of depth) will yield yet more new genera. There are many genera and species that remain inadequately described (notably species described by W.H. Baker from southern Australia, Keppel H. Barnard from South Africa and by Harriet Richardson from the USA), and consequently the relationships of these genera cannot be assessed on morphological criteria. Revision of such genera and description of new genera will inevitably change our understanding about the relationships between and within these clades.

3.1. Sphaeromatidae Latreille, 1825

Molecular results. The monophyly of the Sphaeromatidae was confirmed in Wetzer et al. (2013) and is not further discussed.

Diagnosis. The diagnosis presents the distinguishing characters that define the monophyletic Sphaeromatidae from the other families of both the superfamily Sphaeromatoidea and the suborder Sphaeromatidea. Characters in bold italics are diagnostic.

Cephalon not fused with pereonite 1; ***pereonites 2 – 7 with coxal plates fused or with weak sutures***; pleonite 1 tergite usually discrete, ***pleonites 2 – 5 fused bearing partial sutures, pleonite 5 indivisibly fused to pleonite 4***; lateral suture lines variously indicated. Pleotelson entire, separate or partly fused with pleonite 5. ***Frontal lamina and clypeus fused, forming epistome***; labrum present. Mandible stout, usually with multicusped incisor; lacinia mobilis short, multicusped, usually present on left mandible; spine row present; molar process forming flat nodulose, grinding or smooth crushing surface, or chitinised lobe. ***Maxillule mesial lobe with 3 or 4 long pectinate and 1 robust seta***; lateral lobe gnathal surface with 9 – 13 stout, simple and/ or serrate spines. Maxilliped ***endite elongate***, bearing terminal plumose robust setae, usually with variously ornamented robust setae, usually with single coupling hook; palp articles 2 – 4 usually expanded to form lobes. Pereopods ambulatory, usually robust; pereopod 1 not chelate, not expanded, may be lobed (e.g., *Moruloidea* Harrison, 1984b; *Monolistra* Racovitza, 1910); dactylus usually with distinct secondary unguis. Pleopods contained within chamber formed by the strongly vaulted (domed) pleotelson, rami biramous, pleopods 1 – 3 usually lamellar, occasionally pleopod 1 indurate, occasionally operculate; pleopods 1 – 3 with plumose marginal setae; pleopods 4 and 5 with or without thickened ridges, ***exopod of pleopod 5 with distal scaled patches***. Uropods anterolateral in position on pleotelson, ***endopod fused to peduncle, may be reduced to a stub***; ***exopod articulating, may be reduced, set laterally into endopod when present***, often absent.

Remarks. Although the family has proved a challenge to define, in particular because of the high level of homoplasy that is present, most sphaeromatids are readily recognized. In part this is because many species have the ability to roll into a ball or fold themselves 'closed' clam shell-like. Most species appear calcified and have a rugose appearance when compared to families such as the smooth-bodied Cirolanidae and few genera have the discoidal shape of the Serolidae.

In almost all the Sphaeromatidae genera antennular articles are as follows: article 1 longest and widest; article 2 shortest but almost as broad as article 1; article 3 somewhat longer, however much narrower than the preceding articles. Expanded or broad antennular articles is an apomorphic character. All Sphaeromatidae
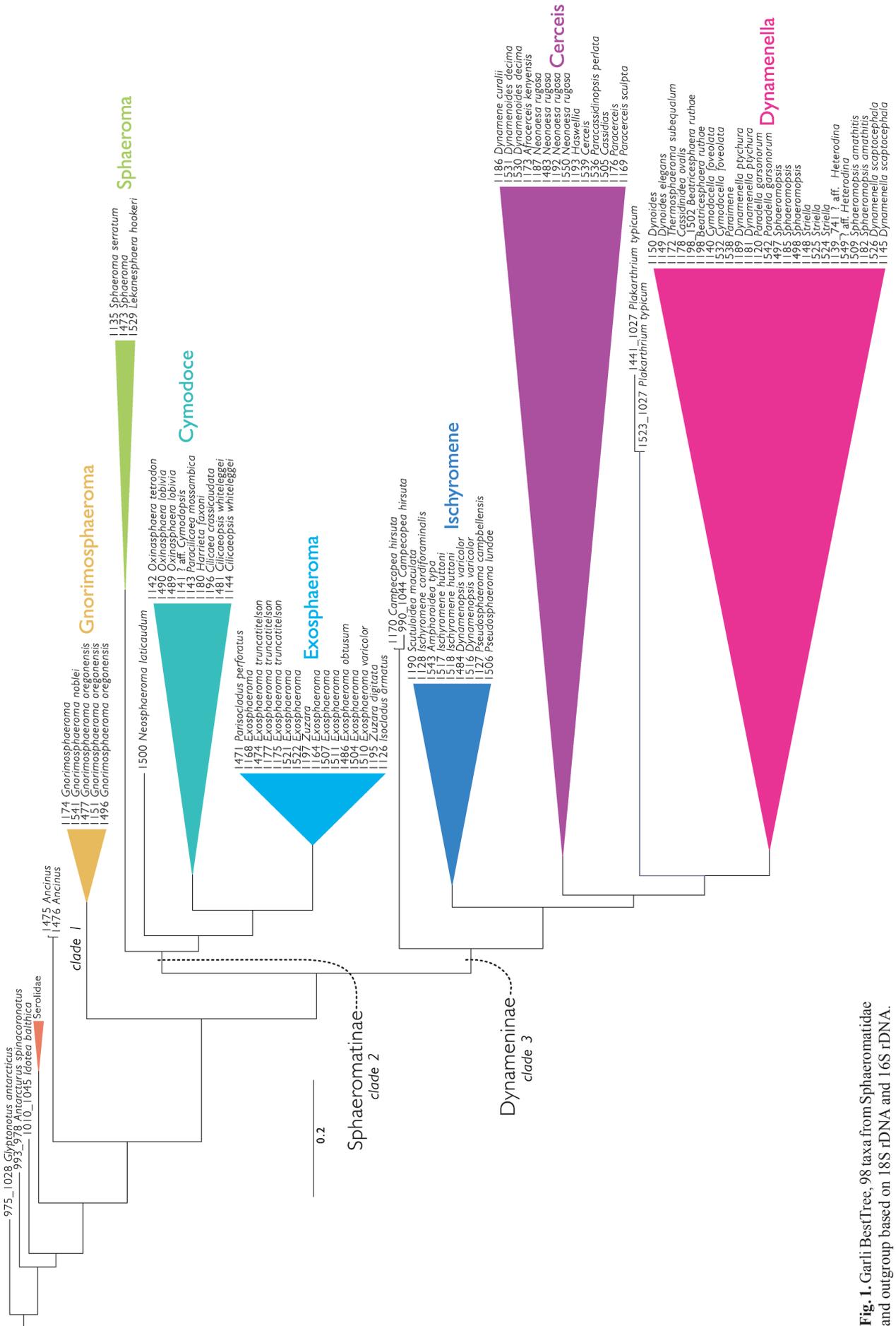
Fig. 1. Garli BestTree, 98 taxa from Sphaeromatidae and outgroup based on 18S rDNA and 16S rDNA.
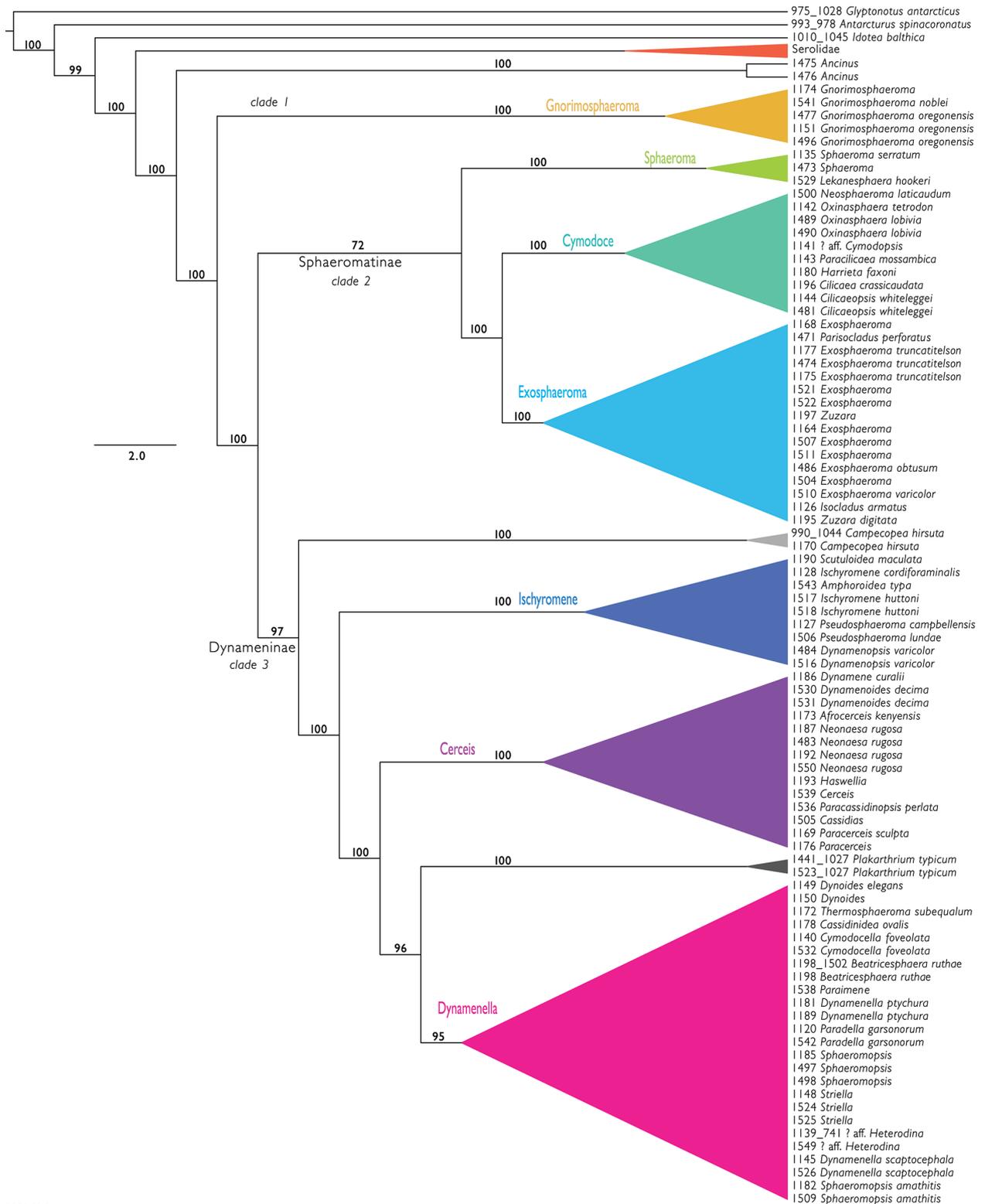
have the pleonites at least partly fused to each other, and all sphaeromatids have the uropodal endopod fused to the peduncle or variously reduced to absent. Similarly, the exopod can be large, and variously reduced to absent.

Characters that distinguish the Sphaeromatidae from the related families Ancinidae, Tecticipitidae and also the Serolidae are summarized in Table 1.

3.2. Clade 1: *Gnorimosphaeroma* clade
Fig. 3A,B

Molecular results. In all of our 18S rDNA and 18S rDNA + 16S rDNA phylogenies *Gnorimosphaeroma* is the most basal lineage within the Sphaeromatidae. With 25 species currently described (SCHOTTE 2015) the genus is restricted to the western shores of North American and the eastern

Table 1. Sphaeromatidea Wägele, 1989: Morphological characters that distinguish the Sphaeromatidae from the related families Ancinidae, Tecticipitidae and Serolidae. Characters indicated in **bold** are synapomorphies.

Character / Taxon	Seroloidea	Tecticipitidae	Ancinidae	Sphaeromatidae
Head	partly fused to pereonite 1	not fused	partly fused to pereonite 1	not fused
Mandible incisor	cultrate, without cusps	cultrate, without cusps	cultrate, with or without cusps	**gnathal, multicusped**
Maxilliped endite	quadrate	quadrate	quadrate	**elongate, distally rounded or acute**
Maxilliped endite distal margin	without robust and slender setae	with slender setae	without or few slender setae	**with many robust and simple setae**
Pereopod 1 propodus	swollen, dactylus prehensile	swollen, dactylus prehensile	swollen, dactylus prehensile	**not swollen, dactylus not prehensile**
Pleonites	3 (1, 2 free; 3–5 fused)	4-fused	1 or 2	4 usually (many reductions to 0)
Uropods	biramous, articulated	biramous, endopod fused	uniramous, fused endopod absent	various, endopod fused when present

shores of Asia. The genus is unusual among sphaeromatids as it contains fresh-, brackish-, and salt water species (see Menzies 1954). Only few sphaeromatid genera have a broad salinity range. Our study has exemplars of two East Pacific species: marine *G. orgeonensis* (Dana, 1853) and brackish/freshwater species *G. noblei* Menzies, 1954 both from the west coast of North America.

18Sr DNA + 16Sr DNA analyses (Figs. 1, 2): In the combined analyses the freshwater *G. noblei* and *G. oregonensis* are sister clades.

18Sr DNA analyses (Fig. 3A): In these analyses 1151 + 1496 + 1477 *G. oregonensis* cluster San Juan and Whidbey Island (Washington) specimens together and are derived with respect to the two freshwater specimens (1541 [Tomales Bay, Marine County, California, freshwater] and 1174 [San Gregorio Creek, San Mateo County, California, freshwater]) which are basal to 1151 + 1496 + 1477.

16Sr DNA analyses (Fig. 3B): A total of 7 sequences were available. Sequences 1174 + 1541 are *G. noblei* from San Gregorio Creek (salinity not measured) and Tomales Bay, head of bay were salinity was 20 ppt, respectively. The other five sequences are fully marine *G. oregonensis* collected in the intertidal of British Columbia and Washington State, San Juan and Whidbey Islands. Marine specimens clade together and are sister group to the *G. noblei* clade.

Morphological characters. The genus and clade is characterized by lamellar uropodal rami, the exopod being shorter than the endopod; the pleonal sutures run from the free lateral margins of the pleon, pleotelson posterior margin arcuate, entire, not thickened; pleopods 4 and 5 are without folds, but otherwise similar to those of *Sphaeroma* Bosc, 1801 (now the accepted authority for the genus – see Low 2012) and *Exosphaeroma*. Generally, there are few distinguishing characters, in essence *Gnorimosphaeroma* superficially differs little from those species of *Exosphaeroma* with an arcuate pleotelson. *Gnorimosphaeroma* is distinguished by the shorter uropodal endopod and pleonal sutures running to the free lateral margin of the pleon (vs posterior pleon margin).

Genera included. *Gnorimosphaeroma* Menzies, 1954.

Remarks. Menzies (1954) erected *Gnorimosphaeroma* for *Exosphaeroma oregonensis* Dana, 1853. Although his diagnosis and accompanying figures for the type species, are reasonably detailed, until at least the type species, *Exosphaeroma oregonensis* is fully redescribed and the genus itself re-diagnosed uncertainty will remain over the systematic position of the genus. It should be noted that all of Dana's isopod specimens were lost when the sloop Peacock sank at the bar of the Colombia River (see Bruce 2009: p. 211), so there is no type material for *Exosphaeroma oregonensis*. Type locality is Puget Sound, Washington State.

Similar genera are *Bilistra* Sket & Bruce, 2004 and *Neosphaeroma* Baker, 1926 (see Harrison & Holdich 1984). However, in our molecular analyses *Neosphaeroma* is basal to the *Cymodoce* clade (see below). We had no *Bilistra* sequences, and thus morphological relationships between these genera and the genera *Sphaeroma* and *Exposphaeroma* are unclear, only *Gnorimosphaeroma* can be attributed to this clade.

3.3. Clade 2 (equivalent to Sphaeromatinae Latreille, 1825)

Molecular results. Clade 2 is supported in all of our analyses (Figs. 1, 2). The bootstrap support (= bs) for Clade 2 is 72%. In the Bayesian analyses *Neosphaeroma* is included within *Cymodoce*. In the Garli analyses *Neosphaeroma* is the sister taxon to *Cymodoce*. Within Clade 2 the genus *Sphaeroma* is the sister taxon to the *Cymodoce – Oxinasphaera* Bruce, 1997 clade + the *Exosphaeroma* clade. The *Sphaeroma*, *Cymodoce* and *Exosphaeroma* clades each have 100% bs.

Morphological characters. Epistome long, anteriorly extended between antennula bases. Pleon of four visible pleonites. Pleopod 1 exopod truncate or sub-truncate (not rounded); endopod triangular to sub-triangular. Pleopods 1 and 2 lamellar. Pleopods 4 and 5 with transverse thickened ridges (when present). Pleopods 1–3 rami subequal in size.
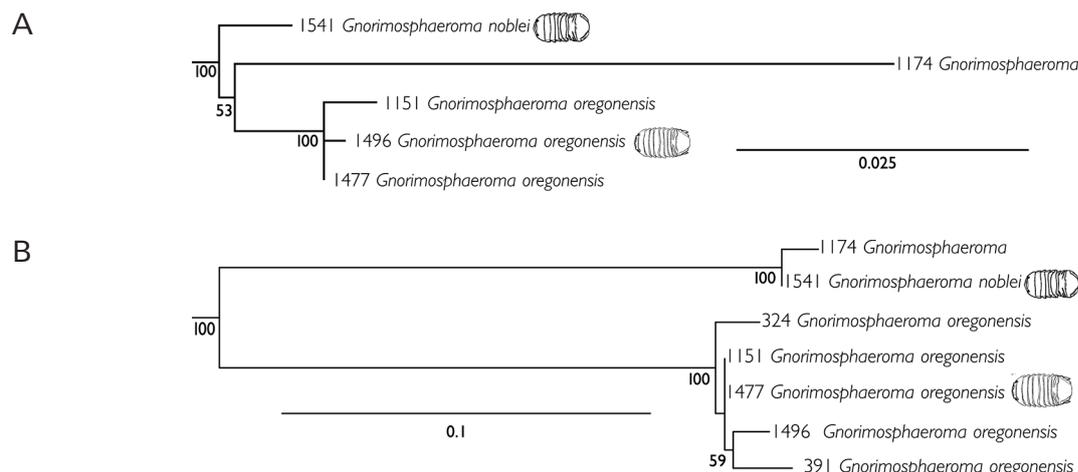
Fig. 3. *Gnorimosphaeroma*. **A**: 18S rDNA Garli BestTree with MrBayes support values indicated on branches. **B**: 16S rDNA Garli BestTree with MrBayes support values indicated on branches.

Remarks. There are three clades within the Clade 2 *sensu stricto*: *Sphaeroma*, *Cymodoce* and *Exosphaeroma* (Figs. 1, 2). The *Sphaeroma* and *Exosphaeroma* clades, are characterised by biramous, lamellar uropods, maxilliped without distinct lobes, pleotelson posterior margin entire (or with shallow, open, ventral exit channel), separate penial processes.

The *Cymodoce* clade is distinctive, distinguished by numerous derived morphological characters, such as excised pleotelson posterior margin, maxilliped palp with 'finger-like' lobes, uropodal exopod reduced (e.g., *Oxinasphaera*) or uropodal endopod reduced (e.g., *Cilicaea* Leach, 1818, *Paracilicaea* Stebbing, 1910b and females with metamorphosed mouthparts [where known; *Dynameniscus* Richardson, 1905 not metamorphosed]. Species within the *Cymodoce* clade have the inferior margin of the merus, carpus and propodus of pereopod 1 with a pattern of large, evenly spaced robust setae that does not occur in any of the other groups of genera.

3.3.1. *Sphaeroma* clade
Fig. 4A,B,C

Molecular results. *18S rDNA + 16S rDNA analyses* (*Figs. 1, 2*): *Sphaeroma* Bosc, 1801 is a large genus that today has 41 species. Most species of the genus can roll up tightly into a sphere. Over time some species formerly placed in *Sphaeroma* have been recognized as belonging to other genera such as *Lekanesphaera* Verhoeff, 1943, *Isocladus* Miers, 1876, *Exosphaeroma* and *Gnorimosphaeroma*, and have been removed from *Sphaeroma*. Our combined 18S rDNA and 16S rDNA analyses all resulted in a strongly supported the clade regardless of the alignment or analysis method.

***18S rDNA analyses* (*Fig. 4A*)**: These included five sequences which in all analyses resulted in two distinct clades. All members of the genus *Sphaeroma* are the sister taxon to the clade containing exemplars of *Lekanesphaera* (100% bs). The two specimens of *S. serratum* (Fabricius, 1787) [1135+973] from Portugal and Spain,

respectively, form the sister taxon to 1473 *Sphaeroma* sp. collected on the opposite side of the Atlantic (South Carolina, USA). They notably form a long branch, but have 100% bs.

GenBank AF279600 *Lekanesphaera hookeri* (Leach, 1814) (989 on tree) sequenced by Dreyer & Wägele (2002) is the sister taxon to 1529 *L. hookeri* from Greece. These three taxa form a well-supported clade and the species identifications are likely valid. 1529 *L. hookeri* was collected from a "spring in brackish lake". This finding is interesting as the implication is another freshwater invasion – once in *Gnorimosphaeroma*, then again in the *Sphaeroma* clade with *Lekanesphaera* and again separately in the *Dynamenella* clade in *Thermosphaeroma* Cole & Bane, 1978 which is discussed later.

***16S rDNA analyses* (*Fig. 4B,C*)**: For these analyses we generated ten sequences for this project. Eleven sequences were previously published in GenBank mostly by Baratti et al. (2011). In most analyses *Sphaeroma* breaks up into two distinct clades with the Baratti et al. (2011) 16S rDNA *S. terebrans* Bate, 1866 sequences forming a clade that is distinct from a second clade containing *Sphaeroma quoyanum* Milne Edwards, 1840, *S. walkeri* Stebbing, 1905, *S. quadridentatum* Say, 1818 and *Lekanesphaera hookeri*.

Clade A: Baratti et al. (2011) extensively sampled *Sphaeroma terebrans* from the Seychelles, East Africa, Brazil, and Florida with 16S rDNA, COI and histone 3 genes. Their combined Bayesian analysis retrieves a clade containing Florida + Brazil sequences which together form the sister taxon to an African clade. Additionally, their sequences identified only as '*Sphaeroma*' are an undescribed species [1601, 1609, 1608]. Adding our 812 *S. terebrans* sequence from South Carolina to the Baratti sequences retrieves a sister taxon relationship with 1603 *S. terebrans* from Florida, and together these form the sister taxon to the Brazilian specimen [1602]. The Baratti *S. terebrans* are all mangrove borers (Baratti et al. 2011; Baratti et al. 2005; Messana 2004). They acknowledge large genetic distances between populations
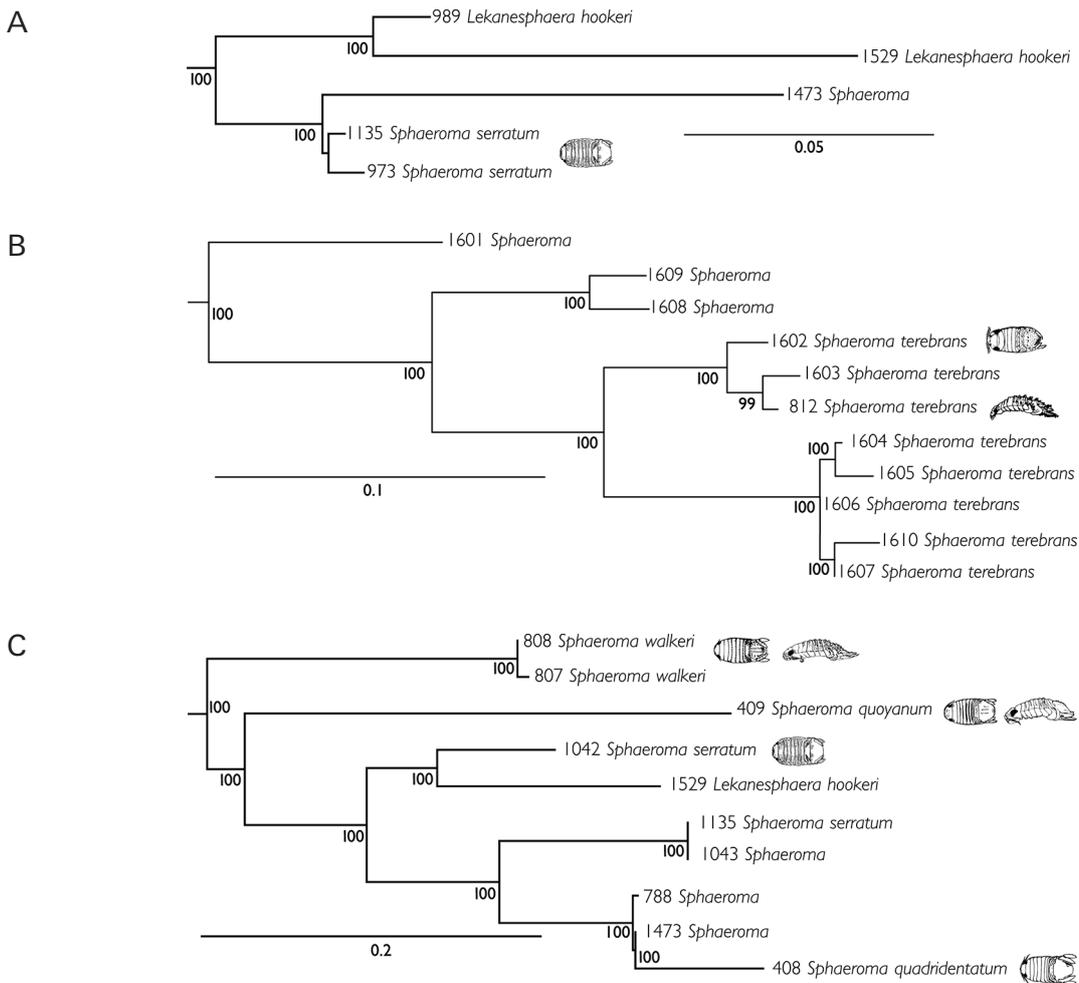
Fig. 4. *Sphaeroma*. **A**: 18S rDNA Garli BestTree with MrBayes support values indicated on branches. **B**: Clade 1, 16S rDNA Garli BestTree with MrBayes support values indicated on branches. **C**: Clade 2, 16S rDNA Garli BestTree with MrBayes support values indicated on branches.

that could suggest that these may be a species complex whose taxonomic status needs further evaluation. Within clade A bs is 100% for all specimens identified as *S. terebrans*.

Clade B: Based on 16S rDNA data, *Sphaeroma* is not monophyletic. The *S. terebrans* clade is distinct from a second clade containing *Sphaeroma quoyanum*, *S. walkeri*, *S. quadridentatum*, and *Lekanesphaera hookeri*. We do not have 18S rDNA *S. terebrans* sequences in our dataset, which quite possibly could change tree topology.

Sphaeroma walkeri [807 and 808] are both from Singapore. 408 *S. quadridentatum* and 409 *S. quoyanum* sequences are from specimens without locality data (donated by S. Shuster). *Sphaeroma* sp. [1473] is from South Carolina, 788 *Sphaeroma* (Florida), 1135 *S. serratum* (Portugal), and 1529 *L. hookeri* (Greece). 1042 *S. serratum* and 1043 *Sphaeroma* sp. are from the coast of France (Genbank, Michel-Salzat et al. 2000). 1529 *Lekanesphaera* may be misidentified, or the identification is correct and this is additional evidence that the genus *Sphaeroma* is not monophyletic. *S. quadridentatum* is the sister taxon to 788 + 1473 *Sphaeroma* (100% bs). Together this clade is the sister taxon to 1135 *S. serra-*

tum + 1043 *Sphaeroma* (100% bs). These in turn together form the sister taxon to 1042 *Sphaeroma serratum* + 1529 *L. hookeri* (100% bs). The sister clade to all these is 409 *S. quoyanum* (100% bs). Basalmost in the clade 808 + 807 *S. walkeri* (100% bs), with 100% bs to its sister group.

Morphological characters. Typically, smooth bodied, weakly or not sexually dimorphic; body can conglobate. Pereopods with superior margin with few to many long setae (shared with *Exosphaeroma*). Uropodal rami lamellar, usually subequal (shared with *Exosphaeroma*); exopod lateral margin usually smooth (*Benthosphaera* Bruce, 1994, *Bilistra* Sket & Bruce, 2004) or weakly to distinctly serrate (*Sphaeroma*, *Lekanesphaera*). Pleon of four visible somites (shared widely). Pleotelson posterior margin rounded or arcuate (never with exit channel, notches or foramen) – shared with *Exosphaeroma* and *Gnorimosphaeroma*; but not *Cymodoce* clade.

Genera included. *Benthosphaera* Bruce, 1994c. *Bilistra* Sket & Bruce, 2004. *Lekanesphaera* Verhoeff, 1943. *Sphaeroma* Bosc, 1801.

Remarks. Bruce (1994c: p. 400) and Sket & Bruce (2004) discussed a group of genera morphologically similar to *Sphaeroma*, primarily based on characters that appear to be plesiomorphic. These genera were: *Apemosphaera* Bruce, 1994b, *Benthosphaera*, *Bilistra*, *Exosphaeroma*, *Exosphaeroides* Harrison & Holdich, 1983, *Lekanesphaera*, *Neosphaeroma* and *Sphaeroma*. The present analysis shows that this clade is restricted to the genera given above, *Exosphaeroma* forming a separate clade, and *Neosphaeroma* (a poorly characterized genus of doubtful monophyly) nesting within the *Cymodoce* clade. Note: According to Low (2012) the correct authority for *Sphaeroma* is Bosc, 1801 and predates the long accepted Latreille (1802).

3.3.2. *Cymodoce* clade
Fig. 5A,B

Molecular results. *18S rDNA + 16S rDNA analyses* (*Figs. 1, 2*): The *Cymodoce* clade is strongly supported and is the sister clade to the well supported *Exosphaeroma* clade. In the MrBayes analyses the sister relationship of *Cymodoce + Exosphaeroma* lacks strong support and is possibly the result of inadequate taxon sampling. In the GARLI analysis *Neosphaeroma* is basal to the *Cymodoce* clade.

18S rDNA analyses (*Fig. 5A*): Ten sequences were available representing seven genera and eight species. Relationships are all strongly supported. 1489 + 1490 *Oxinasphaera lobivia* Bruce, 1997 from Queensland form the sister taxon to 1142 *O. tetradon* Schotte & Kensley, 2005 (Tanzania). 1196 *Cilicaea crassicaudata* Haswell, 1881 (Singapore) is the sister taxon of 1500 *Neosphaeroma laticaudum* (Whitelegge, 1901) (New South Wales). 1500 *N. laticaudum* has a long branch length and although strongly supported as included in the *Cymodoce* clade in the 18S rDNA GARLI analyses and the combined 18S rDNA + 16S rDNA Bayesian analyses (Fig. 2), it comes off basal to the *Cymodoce* clade in the 18S rDNA + 16S rDNA GARLI analyses (Fig. 1). There are three described species of *Neosphaeroma*. Two species are valid, and the third, *N. pentaspinis* Baker, 1926, is *incertae sedis*, probably or possibly a *Gnorimosphaeroma*. Genetic sampling both species might resolve their placement.

1143 *Paracilicaea mossambica* Barnard, 1914 (Kenya) is the sister taxon to 1180 *Harrieta faxoni* (Richardson, 1905) (Florida) (100% bs). Together they form the sister taxon to 1141 ? aff. *Cymodopsis* (Kenya) which is recognized to be at a minimum a new species or possibly a new genus (100% bs). Basalmost in the clade are sister taxa 1144 *Ciliaeopsis whiteleggei* (Stebbing, 1905) (Tanzania) and 1481 *C. whiteleggei* (Fiji) (100% bs).

16S rDNA analyses (*Fig. 5B*): The 16S rDNA gene fragment alone does not consistently reveal the deeper backbone of this otherwise strongly supported clade, but regardless of the analyses performed the following relationship are always supported. Taxa identified as *Oxinasphaera* have 100% bs. All of the Zanzibar specimens to-

gether form the sister taxon to the Mombasa specimens, and this entire group is the sister taxon to specimens from Queensland. At the species level, morphological determinations are more challenging between *O. tetrodon* and *O. penteumbonata* Benvenuti, Messana & Schotte, 2000 and these are interspersed with "*Oxinasphaera* sp." that could only be confidently identified to the level of genus. The sister clade to *Oxinasphaera* contains *Neosphaeroma*, *Paracassidinopsis* Nobili, 1906 and *Platynympha* Harrison, 1984. Notably this group has a long branch which may be the result of our poor sampling (see below "Genera Included" for proposed genera belonging to this clade), poor sequence quality, or misidentification/undescribed species. 1515 *Platynympha longicaudata* (Baker, 1908) (South Australia) should be regarded with caution as is not the best quality sequence. Four individual specimens from two localities (South Australia and Victoria) had been extracted/amplified and only 1515 yielded a useable sequence. 1519 *Paracassidinopsis perlata* (Roman, 1974) (Tanzania) is a high-quality sequence from a small whole individual. Annotations in the collecting notes indicate that the same lot contained immature '*Cymodoce*' and *Oxinasphaera*. Based on its position within the clade our identification appears correct, but based on the specimen's small size, the "*Paracassidinopsis perlata*" taxon label should be used cautiously. All *Neosphaeroma laticaudum* (1131, 1500, and 1513) are from the same New South Wales collecting event.

The sister taxon to this clade is 1128 *Ischyromene cordiforaminalis* (Chilton, 1883b) (New Zealand) with a long branch and no branch support. It is suspected that this is a long branch problem and the 16S rDNA gene fragments' inability to resolve the phylogeny at this level. This is a high-quality sequence, but its placement is absurd. The combined 18S rDNA + 16S rDNA phylogenies (Figs. 1, 2), as well as the 18S rDNA phylogeny (Fig. 7A) firmly places 1128 *Ischyromene cordiforaminalis* in the *Ischyromene* clade.

The genera *Cymodoce*, *Cilicaea*, *Paracilicaea* and *Cilicaeopsis* together are composed of more than 118 described species, many of which are *incertae sedis* and do not belong to the respective genera *sensu stricto*. Sequences for only a few species were available here. As is evident from the groupings in Fig. 5A, species descriptions are difficult to apply and consistent identification was difficult. Together they are supported with 89% bs. All specimens in the clade containing 734, 750, 1143 *Paracilicaea mossambica* Barnard, 1914 and 728, 736, 755 *Cymodoce* are from Kenya. 830 *Cymodoce tribullis* Harrison & Holdich, 1984 (Queensland) with a long branch is the sister taxon to the clade containing 742, 749, and 758 *Cymodoce* (Mombasa and Zanzibar) with the latter having 90% bs. These two clades together are the sister taxon to 1180 *Harrieta faxoni* (Florida).

Specimens 764 + 1144 *Cilicaeopsis whiteleggei* are from Zanzibar, and 1481 *C. whiteleggei* is from Fiji. (Note: *Cilicaeopsis whiteleggei* is a group of cryptic species with at least six species or more.) Bootstrap value for *Cilicaeopsis* sequences is 100%. 1196 *Cilicaea crassicau-*

A

1481 *Cilicaeopsis whiteleggei*
1144 *Cilicaeopsis whiteleggei*
1141 *? aff. Cymodopsis*
1180 *Harrieta faxoni*
1143 *Paracilicaea mossambica*
1500 *Neosphaeroma laticaudum*
1196 *Cilicaea crassicaudata*
1142 *Oxinasphaera tetrodon*
1489 *Oxinasphaera lobivia*
1490 *Oxinasphaera lobivia*

0.025

B

1481 *Cilicaeopsis whiteleggei*
764 *Cilicaeopsis whiteleggei*
1144 *Cilicaeopsis whiteleggei*
1196 *Cilicaea crassicaudata*
809 *Cilicaea latreillei*
747 *Paracilicaea uncinata*
1141 *? aff. Cymodopsis*
739 *Paracilicaea*
1130 *Cymodoce aculeata*
1132 *Cilicaea*
1180 *Harrieta faxoni*
830 *Cymodoce tribullis*
758 *Cymodoce*
749 *Cymodoce*
742 *Cymodoce*
1143 *Paracilicaea mossambica*
736 *Cymodoce*
735 *Paracilicaea mossambica*
728 *Cymodoce*
750 *Paracilicaea mossambica*
734 *Paracilicaea mossambica*
755 *Cymodoce*
1128 *Ischyromene cordiforaminalis*
1131 *Neosphaeroma laticaudum*
1500 *Neosphaeroma laticaudum*
1513 *Neosphaeroma laticaudum*
1519 *Paracassidinopsis perlata*
1515 *Platynympha longicaudata*
1490 *Oxinasphaera lobivia*
1489 *Oxinasphaera lobivia*
730 *Oxinasphaera*
732 *Oxinasphaera penteumbonata*
731 *Oxinasphaera*
1138 *Oxinasphaera tetrodon*
740 *Oxinasphaera tetrodon*
766 *Oxinasphaera penteumbonata*
763 *Oxinasphaera*
761 *Oxinasphaera tetrodon*
765 *Oxinasphaera tetrodon*
1142 *Oxinasphaera tetrodon*
760 *Oxinasphaera penteumbonata*
759 *Oxinasphaera tetrodon*
762 *Oxinasphaera*

0.2

Fig. 5. *Cymodoce*. **A**: 18S rDNA Garli BestTree with MrBayes support values indicated on branches. **B**: 16S rDNA Garli BestTree with MrBayes support values indicated on branches.

data, 809 *C. latreillei* Leach, 1818 are both from Singapore, and 739 *Paracilicaea* from Mombasa and 1130 *Cymodoce aculeata* Haswell, 1881 from New South Wales. 1130 was identified as *Cymodoce aculeata* (New South Wales). 1132 *Cilicaea* is also from New South Wales.

Some clades are strongly supported, others not. As already noted above, too few taxa were sequenced to reassign identifications based solely on the molecular analyses and some rearrangements would be expected as more genera and more sequence data are added.

Morphological characters. Body often setose, pleon and pleotelson variously with processes, nodules or spikes; pleotelson posterior margin variously excavate. Males and females strongly dimorphic; males often with, sometimes without prominent pleonal process; females with 'metamorphosed' mouthparts. Maxilliped endite articles with moderate to long finger-like lobes. Pereopods 1–3 inferior margin (merus, carpus and propodus) with series of prominent, close-set and straight serrate (bi-serrate) robust setae. Penial processes mutually adjacent, elongate;

appendix masculina elongate (reflexed in *Cilicaea*; or 'very long'). The uropodal rami are usually unequal, often with endopod largely or entirely reduced, and the exopod round in section (not lamellar). Some undescribed '*Paracilicaea*' have biramous uropods (NLB pers. obs).

Genera included. *Bregmotypta* Bruce, 1994 – epistome, pereopods and pleopods approximate most closely with *Cymodoce*; females are not known. *Calcipila* Harrison & Holdich, 1984 – ovigerous females are not known. *Ceratocephalus* Woodward, 1877. *Cercosphaera* Bruce, 1994 – has metamorphosed females, placing it in *Cymodoce* clade, but shares few other few other characteristics; pereopod setation also fits with *Cymodoce. Cilicaea* Leach, 1818. *Cilicaeopsis* Hansen, 1905. *Cymodoce* Leach, 1814. *Dynameniscus* Richardson, 1905 – type species redescribed by Kensley & Bruce (2001), but affinities are not clear, but placed into the *Cymodoce* clade; mouthparts not metamorphosed. *Harrieta* Kensley, 1987. *Koremasphaera* Bruce, 2003 – ovigerous females not known. *Kranosphaera* Bruce, 1992 – relationships unclear; body folding at pereonite 5 and uropods suggest *Moruloidea* group; mouthparts, pleopods and penial processes basically as for *Cymodoce* group; pereopods effectively accord with neither group, lacking the row of large serrate setae (*Cymodoce* group) or pereopod 1 with propodal heel (*Moruloidea* group); uropodal exopod absent. *Oxinasphaera* Bruce, 1997. *Paracilicaea* Stebbing, 1910a. *Parasphaeroma* Stebbing, 1902. *Pooredoce* Bruce, 2009.

Remarks. Fifteen genera are included in the group, showing a diverse range of body appearances. The relationships between the genera within this group remain unclear. The larger genera such as *Cymodoce, Cilicaea* and *Paracilicaea* all include species that need to be housed in other mostly new genera. Pleopods are generally similar to *Sphaeroma* clade; penial processes are mutually adjacent (i.e., basally in contact, but separate) and long, extending beyond pleopod peduncle (vs. narrowly separated and short).

Bregmotypta Bruce, 1994, *Kranosphaera* Bruce, 1992 and *Ceratocephalus* Woodward, 1877 are included on the basis of maxilliped, pereopod, penial and pleopod morphology (*Ceratocephalus* female with metamorphosed mouthparts). No specimens of these genera were available for molecular analysis.

3.3.3. *Exosphaeroma* clade
Fig. 6A,B

Molecular results. *18S rDNA + 16S rDNA analyses* (***Figs. 1, 2***): The *Exosphaeroma* clade is monophyletic for the taxa presently included, well supported (100%) and is the sister taxon to the *Cymodoce* clade.

18S rDNA analyses (***Fig. 6A***): Of all of the 18S rDNA clades, the *Exosphaeroma* clade maintains the least internal consistent structure. Internal structure of this clade is also not well supported and with different alignments and analysis permutations does not always return the same relationships. This is contrary to the 16S rDNA findings (see below). 1166 *Sphaeramene polytylotos* Barnard, 1914 and 1471 *Parisocladus perforatus* (Milne Edwards, 1840) are sister taxa (100% bs). 1474 and 1177 *Exosphaeroma truncatitelson* Barnard, 1940 are both from Namibia and always are sister taxa, although not strongly supported (52% bs). For 1486 *Exosphaeroma obtusum* (Dana, 1853) (New Zealand) and 1522 *Exosphaeroma* (Namibia) a sister relationship is recovered only rarely. In this analysis it was recovered with 100% bs. Sequencing through the hypervariable region was problematic for both of these sequences, and they are not of the highest quality, although BLAST searches for each sequence was reasonable. 1197 *Zuzara* Leach, 1818 (South Australia), 1507 + 1164 *Exosphaeroma* (Victoria) is always recovered as a clade. The implication is that 1197 may actually be *Exosphaeroma*. The lot specimen 1197 came from contained what appeared to be single sphaeromatid genus, but specimen 1197 was a small individual not an adult male, but still large compared to most sphaeromatids, hence this may be an identification issue.

16S rDNA analyses (***Fig. 6B***): In all analyses the *Exosphaeroma* clade is always monophyletic for the 34 sequences generated. "*Exosphaeroma*" may appear morphologically simple, smooth bodied, and able to conglobate. At closer examination their dorsums can be highly diverse (many are smooth, others ornate and covered in tubercles, and there are two forms of pleotelson morphology – those with a simple arcuate rim, others with a ventrally thickened rim some with a produced apex; similarly, uropods can be simple, with sub-parallel margins and rounded apex, or expanded as in the *Exosphaeroma* '*amplicauda* group' of species (see Wall et al. 2015). It is therefore to be expected that they appear genetically diverse, some with long branches and others not yet named.

Beginning with the most derived clade A, 1499 *Exosphaeroma obtusum* and 815 + 816 + 1504 *Exosphaeroma* (all New Zealand) form the sister taxon to 714, 1510 *E. varicolor* Barnard, 1914 (Chile). 663 + 1126 *Isocladus armatus* (Milne Edwards, 1840) (New Zealand) together forms the sister taxon to 1486 *E. obtusum* (New Zealand). *E. obtusum* as presently defined needs to be revisited. Together this group is the sister taxon to 1195 and 829 *Zuzara digitata* Harrison & Holdich, 1984 (Queensland). Clade A has 100% bs.

In clade B, 1164, 1507, and 1511 *Exosphaeroma* are all from the same collecting event (Pt. Addis, Victoria). They form the sister clade to material identified as 818 *Zuzara* (Melbourne, Victoria). Basalmost in the clade is 1197 *Zuzara* (Ceduna, S. Australia). Clade B is well supported (100% bs).

All specimens contributing to clade C are from Namibia. 1166, 1472, 1552, and 1838 *Sphaeramene polytylotos* together form the sister taxon to 1471 *Parisocladus perforatus*. 1177, 1474 *E. truncatitelson* as presently defined needs to be revisited. Clade C has 100% bs.

Specimens in clade D are all from Southern California, except 780 *Exosphaeroma* which is from La Paz,
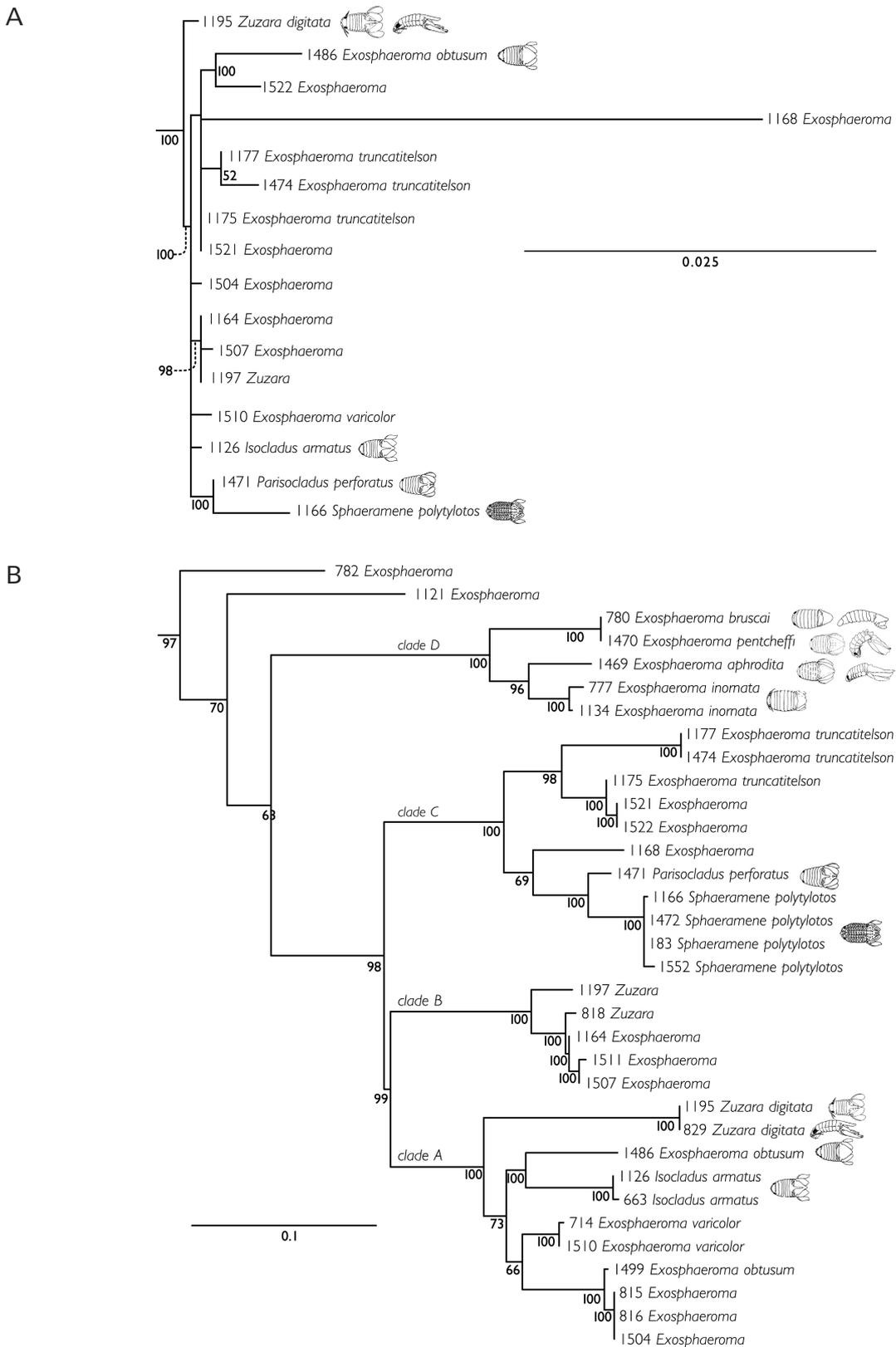
Fig. 6. *Exosphaeroma*. **A**: 18S rDNA Garli BestTree with MrBayes support values indicated on branches. **B**: 16S rDNA Garli BestTree with MrBayes support values indicated on branches.

Baja California Sur, Mexico and is the southernmost exemplar in the clade. 1134 and 777 *E. inornata* form the the sister taxon to 1469 *E. aphrodita* Boone, 1923 (San Diego). 1470 *E. pentcheffi* Wall, Bruce & Wetzer, 2015

(Los Angeles, and dorsally ornately ornamented) is the sister taxon to 780 *Exosphaeroma* sp., possibly *E. bruscai* Espinosa-Pérez & Hendrickx, 2001 (La Paz, Baja California Sur, dorsum smooth). Clade D is strongly sup-

ported (100% bs). 1121 *Exosphaeroma* is from the Pacific coast of Baja California Norte and in dorsal appearance would readily be recognized as *E. inornata* Dow, 1958, but genetically it is clearly not, and hence potentially an undescribed species. Most basal in the clade is 782 *Exosphaeroma* from the Gulf of California, Baja California Sur, also an undescribed species.

Morphological characters. Penial processes are narrowly separated, but longer than *Sphaeroma* clade. Mouthparts are not metamorphosed in females. Posterior margin of pleotelson entire, with or without shallow exit channel (except *Zuzara* has complex pleotelson posterior margin). Pleopods are generally similar to *Sphaeroma* clade, though loss of transverse ridges on pleopods 4 and 5 is common. Uropods lamellar, usually subequal in size, occasionally with large, expanded rami [e.g., *Ptyosphaera*; *Exosphaeroma amplicauda* (Stimpson, 1857)].

Genera included. *Apemosphaera* Bruce, 1984. *Exosphaeroides* Holdich and & Harrison, 1983. *Exosphaeroma*, Stebbing, 1900. *Isocladus* Miers, 1876. *Parisocladus* Barnard, 1914. *Ptyosphaera* Holdich & Harrison, 1983. *Sphaeramene* Barnard, 1914 – lack of data, but appearance of uropods and pleotelson align with genera such as *Isocladus*. *Stathmos* Barnard, 1940 (BRUCE 2001). *Zuzara* Leach, 1818.

Remarks. The monophyly of *Exosphaeroma* is far from assured. Subjectively three groups can be perceived; (1) those related to the type species *E. gigas* (Leach, 1818), which have an exclusively Southern Hemisphere distributions, (2) those species that with broad uropods and produced pleotelson apex (typified by *Exosphaeroma amplicauda*, see WALL et al. 2015), and (3) species similar to *Exosphaeroma inornata*, possibly restricted to the Northern Hemisphere. A particular problem with this genus is the large number of minimally described species, and, therefore, it is not possible to provide a more detailed morphological characterisation of this clade; furthermore, it is probable that some species will prove to be 'species complexes' (see BRUCE 2003; WALL et al. 2015).

Distinguishing of the genera *Zuzara* Leach, 1818 and *Isocladus* Miers, 1876 from *Exosphaeroma* Stebbing, 1900 is equally unclear. *Exosphaeroma* differs from *Isocladus* in lacking a dorsal process on pereonite 7 of males; females of the two genera are effectively indistinguishable using generic criteria. *Zuzara* males also have the dorsal process but also have a short process and notch on the median point of the pleotelson posterior margin. Both these characters are absent from females, leaving them again indistinguishable at the generic level from *Exosphaeroma*. *Exosphaeroma* remains a paraphyletic taxon defined at present by the absence of these derived characters. This is further supported by both *Zuzara* and *Isocladus* being embedded in clades that also have *Exosphaeroma* (Fig. 6B).

3.4. Clade 3 (equivalent to Dynameninae Bowman, 1981)

Molecular results. Clade 3 is strongly supported (bs 97%) and in turn contains the strongly supported *Ischyromene*, *Cerceis* Milne Edwards, 1840 and *Dynamenella* clades (Figs. 1, 2). Both *Campecopea* Leach, 1814 and *Plakarthrium* (Plakarthriidae Hansen, 1905) are included here with *Campecopea* as the sister taxon to the other clades. Recall as noted earlier, the *Plakarthrium* sequence is incomplete and the placement of the taxon in our phylogeny is dubious.

Morphological characters. (*Dyamenella* and *Cerceis* are sister clades and together form the sister taxon to *Ischyromene*. Exceptions to the common clade state are noted in [parentheses].) Pleotelson complex with sinuses, excisions, upturned; or secondarily simple (as in *Sphaeromopsis* and *Thermosphaeroma*); pleonal sutures short, extend from the posterior margin [long in *Cerceis*, extend from lateral margin]. Epistome *usually* without mesial constriction [rarely with]. Maxilliped palp articles weakly lobate. Pleopods 4 and 5 with transverse ridges on both rami (when present); pleopod 2 appendix masculina basal [medial to distal in *Cerceis* clade]. Penial processes close set (but otherwise variable). In *Cerceis* and related genera the appendix masculina is even distally placed; also rami of pleopod 1 or 1 and 2 may be deeply serrate.

Remarks. Clade 3 includes three large clades, each rich in defining and characterizing derived characters, but have few shared characters. The *Dyamenella* + *Cerceis* – *Ischyromene* clades share a single character – both rami of pleopods 4 and 5 have transverse ridges when present.

This is the former "Eubranchiatinae". BOWMAN (1981) designated a type genus and established the name Dynameninae, 1981, but with no diagnosis. HARRISON & HOLDICH (1982a) and BRUCE (1993) equally did not offer a diagnosis to the subfamily. Type genus is *Dynamene* Leach, 1814, type species *Oniscus bidentata* Adams, 1800 [= *Dynamene bidentata* (Adams, 1800)]. *Dynamene* is an atypical genus for this clade in being strongly sexually dimorphic.

3.4.1. *Ischyromene* clade
Fig. 7A,B

Molecular results. *18S rDNA + 16S rDNA analyses* (*Figs. 1, 2*): *Ischyromene*, *Scutuloidea*, *Pseudosphaeroma*, *Dynamenopsis* and *Amphoroidea* Milne Edwards, 1840 representing 7 species were available and consistently produced a strongly supported *Ischyromene* clade (100% bs) with *Campecopea* being its sister group.

18S rDNA analyses (*Fig. 7A*): 1517+1518 *Ischyromene huttoni* (Thomson, 1879) (Chile) is the sister taxon to 1492 *I. huttoni* (New Zealand) (100% bs). Together they form the sister taxon to 1543 *Amphoroidea typa* Milne Edwards, 1840 (Chile) (79% bs). 1484+1516
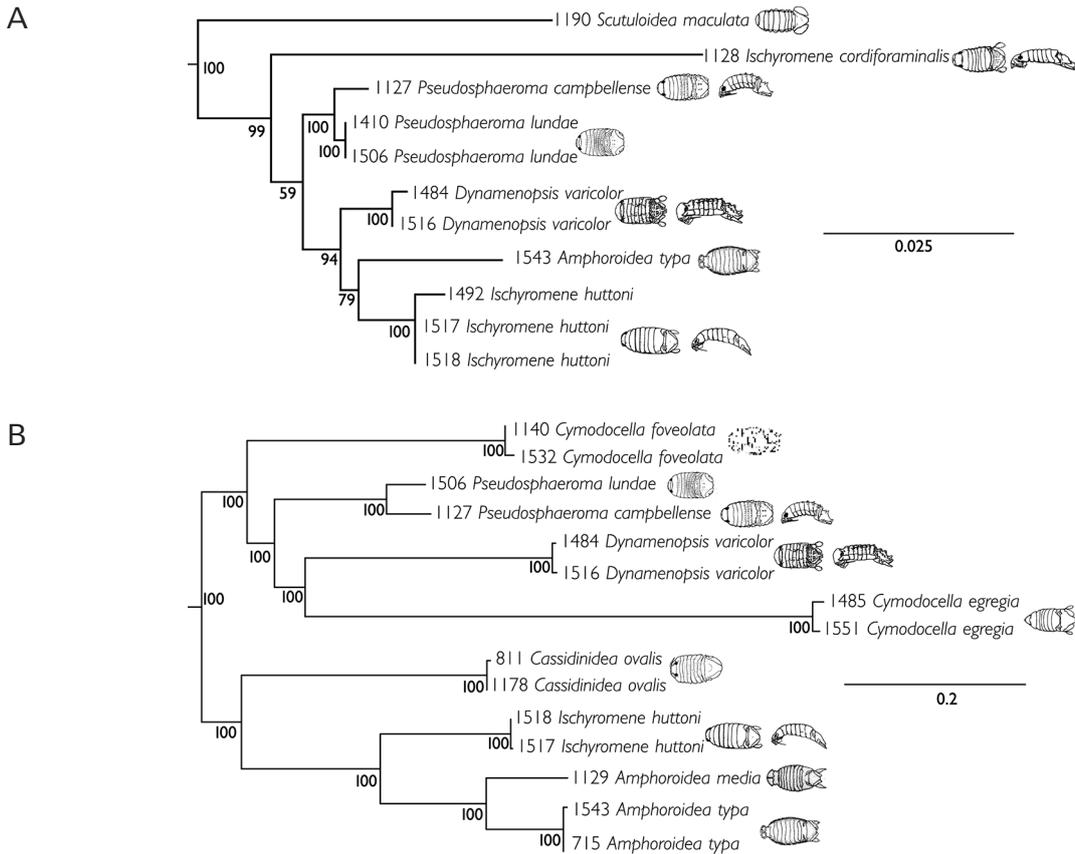
Fig. 7. *Ischyromene*. **A**: 18S rDNA Garli BestTree with MrBayes support values indicated on branches. **B**: 16S rDNA Garli BestTree with MrBayes support values indicated on branches.

Dynamenopsis varicolor (New Zealand) is the sister taxon to the aforementioned clade (94% bs). 1127 *Pseudosphaeroma cambellensis* Chilton, 1909 (New Zealand) is the sister taxon to 1410 + 1506 *P. lundae* (Menzies, 1962) (Chile) (100% bs). There is not strong support for the *Pseudosphaeroma + I. huttoni / D. varicolor / A. typa* clade. 1128 *Ischyromene cordiforaminalis* (New Zealand) is basal and with a long branch. 1190 *Scutuloidea* is basal to all.

16S rDNA analyses (Fig. 7B): 715 + 1543 *Amphoroidea typa* (Chile) together form the sister taxon of 1129 *A. media* (New Zealand) (100% bs). Together they are the sister group to 1517 + 1518 *Ischyromene huttoni* (Canal Darwin, Chile) (100% bs). 811 + 1178 *Cassidinidea ovalis* (Say, 1818) (South Carolina, USA) is the sister taxon to the *I. huttoni – Amphoroidea* clade in this particular analysis (100% bs). In most 16S rDNA analyses *Cassidinidea* is basal within *Ischyromene*, which contradicts it placement in the combined 18S rDNA + 16S rDNA analyses in the *Dynamenella* clade (Figs. 1, 2) and see discussion under *Dynamenella* clade below. 1485 + 1551 *Cymodocella egregia* (Chilton, 1892) (New Zealand) has a long branch and forms the sister taxon to 1484 + 1516 *Dynamenopsis varicolor* (New Zealand) (100% bs). 1506 *Pseudosphaeroma lundae* (Chile) and 1127 *P. campbellense* Chilton, 1909 (New Zealand) are sister taxa (100% bs). 1140 + 1532 *Cymodocella foveolata* Menzies, 1962 (Coquimbo, Chile) is basalmost in the clade (100% bs). Based on the avail-

able molecular data, *Ischyromene* as presently defined, is not monophyletic. Missing from the 16S rDNA phylogeny is 1128 *Ischyromene cordiforaminalis* (New Zealand), which artifactually appears in the *Cymodoce* clade (Fig. 5A). See earlier *Cymodoce* clade discussion.

In all 16S rDNA analysis specimens identified as *Cymodocella* include 1140 + 1532 *Cymodocella foveolata* (Coquimbo, Chile), 1517 + 1518 *I. huttoni* (Canal Darwin, Chile), and 1128 *I. cordiforaminalis* (North Island, New Zealand). In all combined gene 18S rDNA + 16S rDNA analyses and in all 18S rDNA analyses, the *C. foveolata* are members of the *Dynamenella* clade. The contradiction of these data is attributed to the influence of the extremely variable 18S rDNA V4 and V7 regions. The Chilean *C. foveolata* and *I. huttoni* are separated by nearly 1,900 km. All of the sequences are complete and of good quality. Based on morphology, *Cymodocella* would be expected to be within the *Ischyromene* clade.

Morphological features. Antennula peduncle article 2 is always relatively long (> 40% length of article 1); article 3 is short (equal in length or shorter than article 2) [compared to most other genera; e.g., the *Cymodoce*, *Cerceis* and *Cilicaeoposis* genus groups]. Pereopods secondary unguis with 2 accessory cusps. Pleopod 1 endopod medial margin is indurate (exopod may also be indurate and operculate). Pleopods 2 and 3 endopod distinctly longer than exopod. Pleopods 3 and 4 exopods always lacking a

transverse suture. Short pleonal sternite present. Appendix masculina basally attached, extends beyond the pleopodal rami. Maxilliped endite distal margin with clubbed robust setae. Brood pouch of ovigerous females with a posterior pocket. Sexual dimorphism weak or absent.

This group of genera was recognised by Bruce (1995), and has several consistent and distinctive characters. The antennula morphology is unique (the only similar arrangement is in some genera with strongly flattened antennula peduncles), as is the morphology of pleopods 1–3, with pleopod 1 endopod with a thickened mesial margin, occasionally pleopod 1 exopod operculate or thickened and operculate, and pleopods 1–3 with the endopod distinctly longer than the exopod; all included genera have a characteristic secondary unguis (robust seta) on the dactylus, which has two secondary cusps and is described as being bifid.

Only in this clade some genera show a high degree of pleonite fusion – *Austrasphaera* entirely lacks any indication of pleonal sutures, in *Marguerrita* the pleon and pleotelson join is indicated laterally only, and in *Juletta* the pleon and pleotelson is medially fused.

The only exception to these morphological characters is *Pseudosphaeroma*, which shows none of the *Ischyromene*-clade characters.

Genera included. *Amphoroidea* Milne Edwards, 1840. *Amphoroidella* Baker, 1908. *Austrasphaera* Bruce, 2003. *Cassidinopsis* Hansen, 1905. *Cymodocella* Pfeffer, 1887. *Diclidocella* Bruce, 1995. *Dynamenopsis* Baker, 1908. *Ischyromene* Racovitz, 1908. *Juletta* Bruce, 1993. *Margueritta* Bruce, 1993. *Maricoccus* Poore, 1994. *Pedinura* Bruce, 2003. *Pseudosphaeroma* Chilton, 1909. *Scutuloidea* Chilton, 1883a – existing descriptions are inadequate; *S. kutu* has medial appendix masculina; but pereopod dactylus is most similar to the *Ischyromene* clade, as is epistome.

Remarks. This clade has a predominantly Southern Hemisphere distribution, and most species are small in size (< 5 mm) with the exception of some cold-water taxa such as *Amphoroidea*.

3.4.2. *Cerceis* clade
Fig. 8A,B

Molecular results. *18S rDNA + 16S rDNA analyses* (*Figs. 1, 2*): This is a consistent grouping. We were able to sample 10 genera and 14 species out of the 16 genera we hypothesize to be contained in this clade. In all analyses the *Cerceis* clade is always strongly supported (100% bs) and *Dynamene* and *Dynamenoides* are always basal to all other Cerceis genera (99% bs).

18S rDNA analyses (*Fig. 8A*): Our analyses contained representatives of 10 genera. 1169 *Paracerceis sculpta* (Holmes, 1904) (Gulf of California, Sonora, Mexico) and 1176 *Paracerceis* Hansen, 1905 (Gulf of California, Baja California Sur) form the sister clade to 1505

Cassidias Richardson, 1906 (Singapore) (100% bs). The former taxa together form the sister taxon to 1536 *Paracassidinopsis perlata* (Kenya) (99% bs). In our analyses 1539 *Cerceis* (Queensland) is the sister taxon to 1414 *Pseudocerceis* Harrison & Holdich, 1982b (Queensland) (76% bs). Together they are the sister taxon to 1193 *Haswellia* Miers, 1884 (New South Wales) (100% bs). 1192+1550 *Neonaesa rugosa* Harrison & Holdich, 1982b (Queensland) forms a clade with 1483 *N. rugosa* (Fiji), then with 1187 *N. rugosa* (Tanzania) (100% bs). Basal to *Neonaesa* is 1173 *Afrocerceis kenyensis* Müller, 1995 (Kenya) (99% bs). Basalmost in the *Cerceis* clade is the subclade comprising 1186+1544 *Dynamene curalii* Holdich & Harrison, 1980 (Queensland) and 1530+1531 *Dynamenoides decima* Hurley & Jansen, 1977 (New Zealand) as sister taxa (100% bs).

16S rDNA analyses (*Fig. 8B*): As in the 18S rDNA analyses *Neonaesa* is the sister taxon to *Afrocerceis*, however for this gene they are the most derived with *Haswellia* basal to the pair (78% bs). 754 *Cerceis* (Kenya) is the sister taxon to 831 *Cerceis* (Queensland) (100% bs). 1179 *Cerceis pravipalma* is from Singapore and 1539 *Cerceis* from Queensland (100% bs). The genus *Cerceis* is well supported (100%). 1530+1531 *Dynamenoides decima* and 1124 *D. vulcanta* Hurley & Jansen, 1977 (New Zealand) form the sister taxon to 1536 *Paracassidinopsis perlata* (Kenya) (75% bs). 810 *Cilicaea latreilli* (Singapore) is a near match to 1176 *Paracerceis* (Baja California Sur, Mexico) and is possibly a misidentified juvenile *Paracerceis* (70% bs). *P. sculpta* is known to have become established in harbors and ports worldwide: 1133 *P. sculpta* is from a marina in Los Angeles, California. 1169 *P. sculpta* is from Sonora, Mexico. 1505 *Cassidias* (Singapore) is the sister taxon to 1534 an undescribed species of *Cassidias* (Palau). *Cassidias* is the strongly supported sister taxon of *Paracerceis* (100% bs). Both 1190 *Scutuloidea maculata* Chilton, 1883 and 1533 *Cassidinopsis admirabilis* Hurley & Jansen, 1977 are from New Zealand, and 745 is an undescribed genus from Kenya. Their relationship is not strongly supported and placement of these within the *Cerceis* clade is not well understood.

Morphological characters. Pleopod 1 exopod longitudinal axis distinctly oblique to longitudinal axis of endopod, rami not collinear. Pleopod 2 with appendix masculina medial to distal in position. Pleopods 1 and 2 exopod distal margin usually deeply serrate (*) or not serrate (^). Pleonal sternite usually prominent (i.e., long). Pereopod 1 inferior margin usually with prominent straight robust setae. Female with metamorphosed mouthparts (shared with *Cymodoce* clade). In some genera the anterior margin of the head over-rides the antennula and antennal peduncles.

Genera included. **Afrocerceis* Müller, 1995. *^Cassidias* Richardson, 1906 – mouthparts metamorphosed. **Cerceis* Milne Edwards, 1840. *^Discerceis* Richardson, 1905. **Eterocerceis* Messana, 1990. **Exocerceis* Baker, 1926. *^Geocerceis* Menzies & Glynn, 1968. **Haswellia*
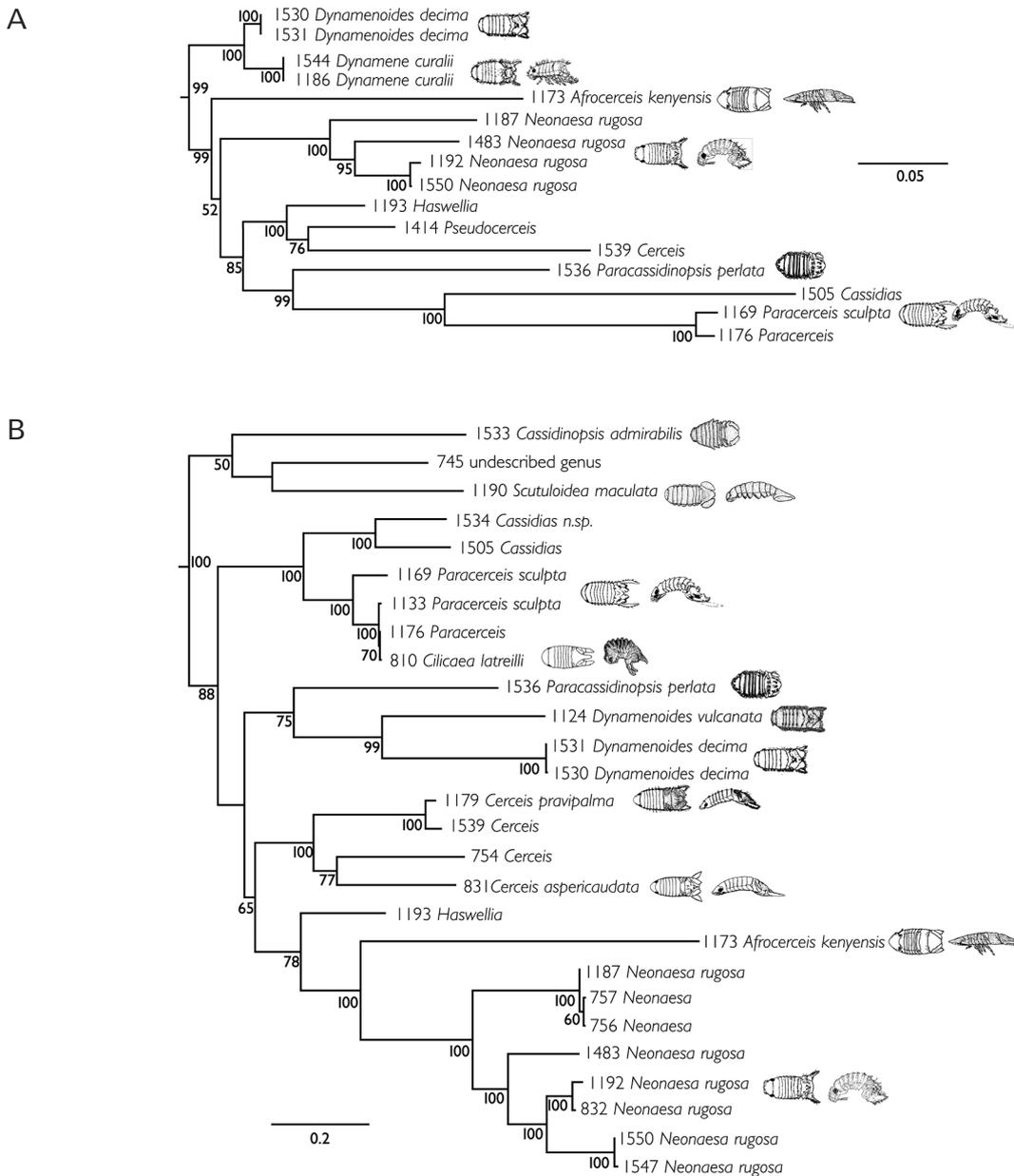
Fig. 8. *Cerceis*. **A**: 18S rDNA Garli BestTree with MrBayes support values indicated on branches. **B**: 16S rDNA Garli BestTree with MrBayes support values indicated on branches.

Miers, 1884. *Holotelson* Richardson, 1909 – existing figures are inadequate; NUNOMURA & IKEHARA (1985) would definitely suggest placement within the *Cerceis* clade. ^*Neonaesa* Harrison & Holdich, 1982b. ^*Paracassidinopsis* Nobili, 1906. *Paracerceis* Hansen, 1905. *Platycerceis* Baker, 1926. ^*Platynympha* Harrison, 1984. *Pseudocerceis* Harrison & Holdich, 1982b.

Remarks. This clade includes a group of fifteen distinctive genera such as *Cerceis*, *Afrocerceis* and *Haswellia*, typified by a greater or lesser degree by its marginal serration on pleopods 1 and 2; the axis of pleopod 1 exopod is strongly oblique to both endopod and peduncle, and the appendix masculina has a medial to distal point of attachment. The epistome of several genera has a medial constriction, in some instances appearing the same as that of the *Sphaeroma* clade. Females of all genera have metamorphosed mouthparts, a character shared with the *Cymodoce* clade.

Dynamene Leach, 1814 and *Dynamenoides* Hurley & Jansen, 1977 clade as sister clade to *Cerceis* clade – so here they are included in the clade on the basis of pleopod morphology and female mouthparts. *Dynamene* has metamorphosed mouthparts – characteristic also of *Cymodoce* and *Oxinasphaera*.

In the molecular analysis *Paracassidinopsis* is included in the *Cerceis* clade, but *Paracassidinopsis* has few *Cerceis* clade morphological characters and appears more like an aberrant *Dynamenella*. Its epistome is not medially constricted, penial process is like the '*Dynamenella* clade' form, but pleopods are collinear and are otherwise not similar.

3.4.3. *Dynamenella* clade
Figs. 9A,B, 10

Molecular results. *18S rDNA + 16S rDNA analyses* (*Figs. 1, 2*): In all analyses, except a single MrBayes analysis, *Dynoides* is always basalmost in the *Dynamenella* clade, and *Dynamenella* is the most derived and the clade has 95% bs. For the combined analysis we had representatives of the nine genera. Striking is that *Sphaeromopsis* falls into two distinct clades. The genera *Paradella* and *Dynamenella* need to be revisited with regional taxonomy overriding phylogenetic relationships. Specimens 1140 + 1532 identified as *Cymodocella foveolata* from Coquimbo, Chile are always included in this clade. Using GBlocks to remove 1841 bp (37%) of the hypervariable regions does not change the outcome.

***18S rDNA analyses* (*Fig. 9A*)**: 1145 + 1526 *Dynamenella scaptocephala* Messana, 1990 (Kenya) forms the sister taxon to 1182 + 1509 *Sphaeromopsis amathitis* Holdich & Jones, 1973 (Kenya) (100% bs). Together they form the sister taxon to 1137 *Dynamenella* (Washington State, USA) (63% bs). The three 1148, 1524, and 1525 *Striella* (Baja California Sur, Mexico) specimens form the sister taxon to the long branched 1512 *Sphaerompsis serriguberna* Holdich & Harrison, 1981 (Queensland) (70% bs). 1147 *Pistorius bidens* Harrison & Holdich, 1982b (Kenya) and 1527 *P. bidens* (Queensland) together form sister clade relationship by a long branch to 1120 + 1542 *Paradella garsonorum* Wetzer & Bruce, 2007 (Baja California Norte and Baja California Sur, respectively) (72% bs). The strongly supported (100 % bs) clade 1139 + 1548 + 1549 "? aff. *Heterodina* sp." (Kenya) forms the sister taxon to 1538 *Paraimene* Javed & Ahmed, 1988 (Kenya), but with low support (58% bs). Our "? aff. *Heterodina* sp." is an undescribed genus that differs from *Heterodina* by having a small, anteriorly acute epistome that does not extend anteriorly, not visible dorsally, and with large flattened antenna peduncle. Specimens are small and there are no males in this sample. 1181 and 1189 *Dynamenella ptychura* (Queensland) are always sister specimens, but their exact position in the clade is not definitive as in different analyses they have a tendency to move within the *Dynamenella* clade (not shown). Specimens 1185, 1497, and 1498 *Sphaeromopsis* (Ecuador) always form a clade together and never with the specimens identified as *Sphaeromopsis* from Queensland or Kenya.

1198 *Beatricesphaera ruthae* Wetzer & Bruce, 1999 (Atlantic, Costa Rica) in this analysis is the sister taxon to 1140 + 1532 *Cymodocella foveolata* (Coquimbo, Chile). As already noted under the 18S rDNA and 16S rDNA combined analyses above, these animals never group with *I. huttoni* from Darwin Channel, Chile or *I. cordiforaminalis* (New Zealand), yet in all of the 16S rDNA analyses (discussed in *Ischyromene*) they always belong to the *Ischyromene* clade. *B. ruthae* collected in 1986 and preserved in 70% ethanol are by far the oldest specimens in our dataset. Multiple extractions and sequencing attempts finally did yield a complete, high-quality sequence for both genes, but with long branches and tendency to move around in the clade. 972 *Cassidinidea* (Dreyer & Wägele Genbank AF255693, collecting locality not indicated) and 1178 *C. ovalis* (South Carolina, USA) form a sister taxon to 1172 *Thermosphaeroma subequalum* Cole & Bane, 1978 (Texas, USA).

In all 18S rDNA analyses 1149 + 1150 *Dynoides* (California, USA) (not shown) have a long branch, are basal to *Dynamenella*, but in some analyses appear in unlikely pairings with other long-branched taxa, e.g., *Plakarthrium typicum*.

***16S rDNA analyses* (*Figs. 9B, 10*)**: *Dynamenella* and *Paradella* are the most derived genera in the clade and nodes are mostly well supported. 411 *Paradella* (specimen gift from S. Shuster, locality unknown) is the sister taxon to 797 *Dynamenella* (Singapore) (95% bs). Together these are the sister taxon to 1542 *P. garsonorum* (Baja California Norte, Mexico) (100% bs). The sister clade 783 + 1120 *P. garsonorum* (Baja California Sur) is well supported (100% bs). 410 *P. dianae* (Menzies, 1962) (S. Shuster, locality unknown) forms the sister clade (90% bs). 733, 738, and 746 *P. harrisoni* Müller, 1995 are all from Kenya. 1181 + 1189 + 1540 *D. ptychura* Harrison & Holdich, 1982 (Queensland) together form the sister taxon to 1148 + 1524 + 1525 *Striella* (Baja California Sur) (79% bs).

1185 + 1497 + 1498 *Sphaeromopsis* (Ecuador) form the sister taxon to the *Dynamenella*, *Paradella*, *Striella*. As in the 18S rDNA alone and the 18S rDNA + 16S rDNA combined analyses, the Ecuadoran *Sphaeromopsis* are more closely related to *Dynamenella pychura* (Queensland) than *Sphaeromopsis* from Kenya and Tanzania. The African *Sphaeromopsis* [729, 741, 748, 768, 1182, 1509] are more closely allied to *D. scaptocephala* [753, 1145, 1526] also from Kenya (94% bs). As presently identified *Sphaeromopsis* is not monophyletic. These are likely two distinct and separate genera in need of reassignment. The sister taxon to the African *Sphaeromopsis* and *D. scaptocephala* is 1538 *Paraimene*, also from Kenya (100% bs).

Thermosphaeroma with eight species occurs in freshwater springs in the southwest U.S. and northern and central Mexico. It is endemic to thermal springs in Texas and New Mexico, as well as in Chihuahua, Durango, Coahuila and Aguascalientes, Mexico. The genus has interesting North American post-Cretaceous biogeographic implications with diversification during receding ocean levels. The genus is supported with 100% bs.

775 *Paraimene tumulus* (Atlantic, Costa Rica) is not closely related to 1538 *Paraimene* from Africa.

In our 16S rDNA analyses *Cassidinidea ovalis* pairs with *I. huttoni* (Canal Darwin, Chile) in the *Ischyromene* clade rather than as expected within the *Dynamenella* clade. Here again we believe the resolution of the 16S rDNA marker may be misleading and inaccurate at this taxonomic level. Based on morphology, 18S rDNA and the combined 18S rDNA + 16S rDNA markers *Cassidinidea* clearly belongs with members of the *Dynamenella* clade.
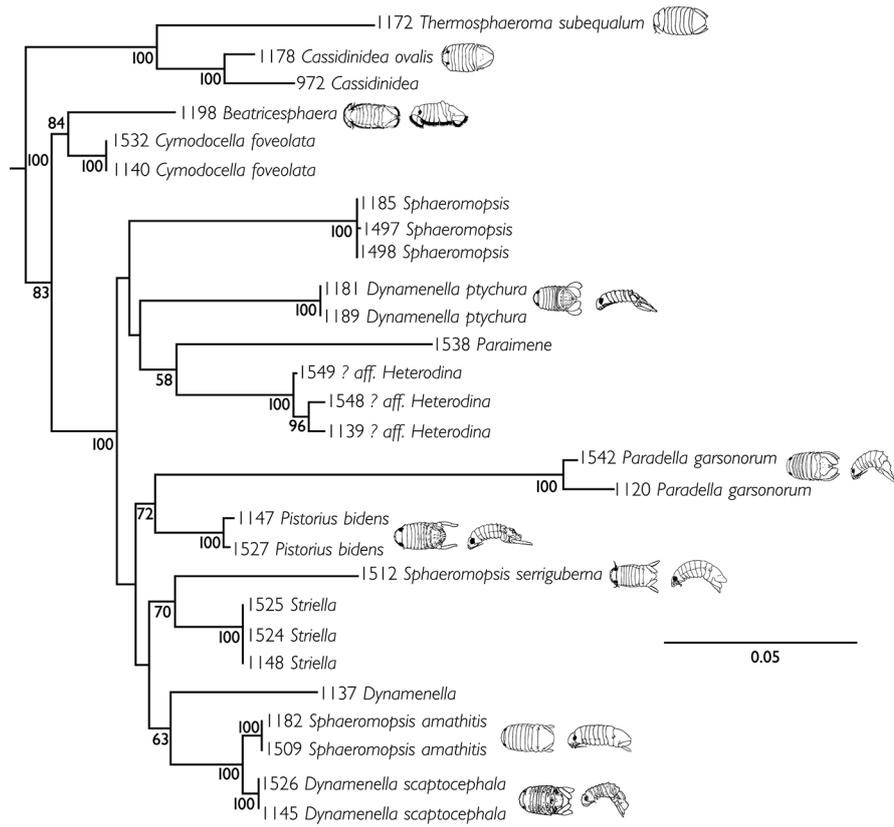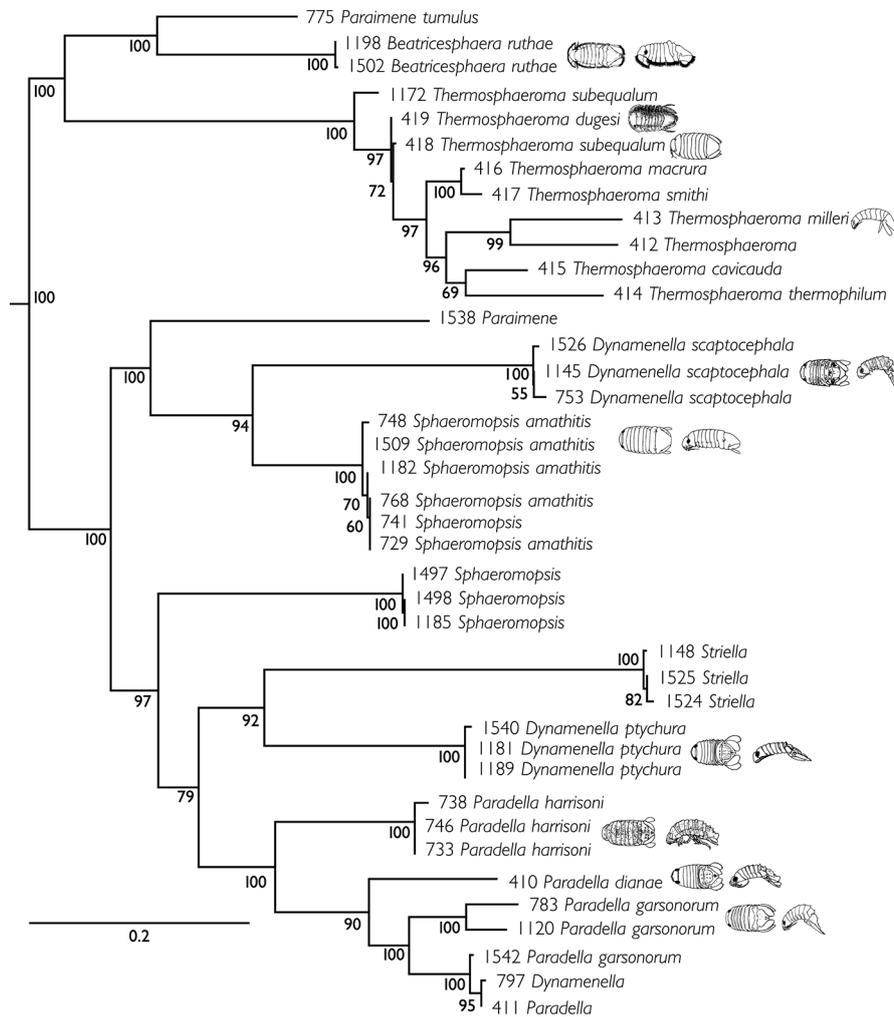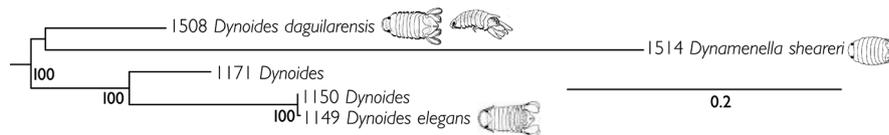
Fig. 10. *Dynoides*. 16S rDNA Garli BestTree with MrBayes support values indicated on branches.

Also in the 16S rDNA analyses the species level structure of *Dynoides* (Fig. 10) is always strongly supported, but deeper node resolution is lost (not shown). 1150+1149 *Dynoides elegans* (Southern California, USA) is the sister taxon to 1171 *Dynoides* (Baja California Sur, Mexico). 1508 *D. daguilarensis* (Hong Kong) is the sister taxon to 1514 *D. sheareri* – specimens identified as *Dynamenella sheareii* (San Juan Island, Washington, USA). The later with a long branch. Based on these analyses 1514 *D. sheareri* would be attributed to *Dynoides* rather than *Dynamenella*.

Beatricesphaera is always in or near the *Dynamenella* clade in all 18S rDNA and some 16S rDNA analyses. In 16S rDNA analyses 741 ? aff. *Heterodina* is not included in the *Dynamenella* clade, but rather is sometimes the sister taxon to *Amphoridea* (*Ischyromene* clade). Trees not shown.

Morphological characters. Pleopod 1 endopod has a characteristic shape, endopod oblique, apex acute, distolateral margin concave, posteromesial angle projecting ('heel') [*Beatricesphaera*, *Cassidinidea*, *Dynoides*, *Thermosphaeroma*]. Pleopod 1 peduncle mesial margin forming narrowly produced lobe in some genera [* = present]. Epistome long but lacking medial constriction. Penial processes basally adjacent (i.e., not fused) or basally, partially or entirely fused. Pleonal sutures to posterior margin (pleonites occasionally wholly fused).

Genera included. *Beatricesphaera* Wetzer & Bruce, 1999. *Cassidinidea* Hansen, 1905. *Cliamenella* Kussakin & Malyutina, 1987. **Dynamenella* Hansen, 1905. *Dynoides* Barnard, 1914. **Heterodina* Schotte & Kensley, 2005. **Makarasphaera* Bruce, 2005. **Paradella* Harrison & Holdich, 1982a. **Paraimene* Javed & Ahmed, 1988. **Pistorius* Harrison & Holdich, 1982b – pleopods indicate belonging to the *Dynamenella* clade, supported by perforate pleotelson; pereopods also compatible (i.e., undistinguished). *Sphaeromopsis* Holdich & Jones, 1973 – pleotelson and pereopods as like other sand dwelling species, but penes and pleopods clearly indicate clade. **Striella* Glynn, 1968 – pleon sutures, penial processes, and pleopods 1 and 2 are of the *Dynamenella* form. *Thermosphaeroma* Cole & Bane, 1978. *Tholozodium* Eleftheriou et al., 1980 – is a specialised sand dweller, with highly setose pereopods and also an anteriorly produced epistome; pleopod 1 is of *Dynamenella* form, as is

pleopod 2, but the appendix masculina is mid-length in attachment; overall form indicates *Dynamenella* clade.

Remarks. In contrast to the *Ischyromene* and *Cerceis* clades, few characters are consistently present throughout the included genera. *Dynamenella* and related genera have a typical pleopod 1 and pleopod 2 morphology, and the penial processes are always mutually adjacent, and often fused to various degrees from basally to entirely fused including the fused vasa deferentia. Many genera have a perforate pleotelson. The genus *Sphaeromopsis* is superficially similar to the Sphaeromatinae but the morphology of the penial processes and pleopods 1 and 2 shows clear *Dynamenella* clade characteristics. *Thermosphaeroma* appears morphologically more closely related to genera such as *Bilistra*.

3.4.4. *Campecopea*

Molecular results. *18S rDNA + 16S rDNA analyses* (*Figs. 1, 2*): In our analyses *Campecopea* is the sister taxon to the remaining clade 3 taxa. *Campecopea* was represented by a single species [*C. hirsuta* (Montagu, 1804)]. 18S rDNA of 1044 *C. hirsuta* had been previously generated by D. Bouchon (GenBank AJ388076) and was paired with 16S rDNA 990 *C. hirsuta* (GenBank AF279601). 1170 *C. hirsuta* sequences are from a Canary Island specimen. This strongly supported pair in these combined analyses is always basal to the *Dynamenella* clade. The genus presently contains five species and *C. hirsuta* is the type species of genus.

18S rDNA analyses (*not shown*): In these analyses *Campecopea* is still basal but with much weaker support. 990+1170 *C. hirsuta* is the sister taxon to 991 *C. lusitanica* (GenBank AF279602, previously generated by H. Dreyer).

16S rDNA analyses (*not shown*): Here *Campecopea* clades with other long-branch taxa in biologically inexplicable relationships, but not unexpected based on characerics of this genetic marker.

Morphological characters. Pleopods 1 and 2 with rami collinear, subequal in size. Maxilliped palp articles weakly lobate. Epistome short, without medial constriction. Uropodal endopod absent. Pleotelson entire or perforate. Sexual dimorphism distinct.

Remarks. Bruce & Holdich (2002) in their revision of *Campecopea* concluded that the genus was incerta sedis. The present analyses place the genus as the sister clade to the *Dynamenella* clade, supporting its position apart from other sphaeromatid genera.

← **Fig. 9.** *Dynamenella*. **A**: 18S rDNA Garli BestTree with MrBayes support values indicated on branches. **B**: 16S rDNA Garli BestTree with MrBayes support values indicated on branches.

3.5. Sphaeromatidae clades incertae sedis

A further four "groups" of genera are based only on morphological characters. These groups lacked any representation in the molecular analysis, but the morphological characters that unite each group are unlikely to be homoplasious (e.g., reflexed and robust antennula articles in *Moruloidea* group; maxilliped article 2 and lateral head margins expanded in *Cassidina* group). The phylogenetic validity of these "groups" remains to be tested by either morphological or molecular analyses.

3.5.1. *Cassidina* group

Molecular results. Our 18S rDNA 1488 *Paracassidina dama* Bruce, 1994 sequence is basal to the *Gnorimosphaeroma* clade in all analyses (not shown). This is not unexpected since we had no other representatives for the group and including other genera will most likely result in a different topology. There was no 16S rDNA sequence available and hence the genus was not included in the combined analyses.

Morphological characters. Body margins expressed laterally (not ventrally) giving an overall flat appearance. Head lateral margins expanded, not set into pereonite 1. Epistome visible in dorsal view. Pereonites with coxal extensions. Pleonal sternite prominent. Pleon of 3 segments, laterally unfused. Antennula peduncle articles 1 and 2 flattened. Maxilliped article 2 expanded, articles 3 and 4 finger-like medial lobes, article 5 elongate. Pereopod 1 modified, with 1 or more elongate articles and elongate dactylus; accessory unguis slender. Pleopod 1 rami subequal in width, distally rounded, usually collinear (from BRUCE 1994).

Genera included. *Agostodina* Bruce, 1994; *Cassidina* Milne Edwards, 1840; *Chitonopsis* Whitelegge, 1902; *Paracassidina* Baker, 1911.

Remarks. These genera, together with the next "group" are at the core of the former "Cassidininae".

3.5.2. *Leptosphaeroma* group

Molecular results. Only 16S rDNA for *Platysphaera* was available.

Morphological characters. Epistome not visible in dorsal view. Head set into pereonite 1, not laterally expanded. Pereonites without coxal extensions. Pleonal sternite absent. Pleonites all fused and pleon with a single segment, laterally unfused. Antennula peduncle articles 1 and 2 flattened, forming continuous outline. Maxilliped articles with weak medial lobes. Pereopods all ambulatory. Penial processes partly or wholly fused. Pleopod 1 endopod reduced or absent; pleopod 2 appendix masculina basal (see BRUCE 1994).

Genera included. *Chitonosphaera* Kussakin & Malyutina, 1993; *Discidina* Bruce, 1994; *Leptosphaeroma* Hilgendorf, 1885; *Paraleptosphaeroma* Buss & Iverson, 1981; *Platysphaera* Holdich & Harrison, 1981.

Remarks. All are strongly flattened genera, sharing few uniting characters with the "*Cassidina*-group" (see above).

3.5.3. *Moruloidea* group

Molecular results. No species were sequenced for this group.

Morphological characters. Antenna with peduncular articles 4 and 5 robust, reflexed. Male pereopod 1 propodus with inferoproximal lobe (= 'heel'). Uropodal exopod reduced. Rugose and heavily calcified dorsum. Fold 'purse-like' at pereonite 5, with coxae 5 overlapping both anteriorly and posteriorly.

Genera included. *Moruloidea* Baker, 1908; *Caecocassidias* Kussakin, 1967 (see BRANDT 1998); *Waiteolana* Baker, 1926; *Ceratocephalus* Woodward, 1977 (see BRUCE 1994).

Remarks. Pleopods are of the *Sphaeroma* clade form as is the setation of the pereopods. Apart from *Moruloidea* and *Caecocassidias* Kussakin, 1967 (see BRANDT 1998) all genera can be satisfactorily placed in the *Sphaeroma* clade genera on morphological criteria. At least one species, *Cymodopsis beageli* Brandt, 1998 may belong to this group though it lacks the reflexed antenna peduncle. It is plausible that *Kranosphaera* Bruce, 1992 also belongs with this group. Characters for *Waiteolana* Baker, 1926 are unclear; maxilliped palp not as produced as in *Cymodoce* clade *s.str*, but pleopod morphology is as in clade 2 (Sphaeromatinae).

3.5.4. *Monolistra* group

Molecular Results. No species were sequenced for this group.

Morphological characters. This is probably a monophyletic clade, as all have similar pleopod, antennule, and antenna morphology.

Genera included. *Caecosphaeroma* Dollfus, 1896; *Monolistra* Gerstaecker, 1856; *Merozoon* Sket, 2012.

Remarks. This group comprises three aquatic cave-dwelling genera, *Caecosphaeroma* in France, *Monolistra* and *Merozoon* in central Europe (SKET 1986). *Monolistra*, a large genus of about 20 species and many subspecies, has been split into five subgenera (see SKET 1986). The affinities of these genera in relation to marine genera remain unapprised, though it is likely that the genera form a monophyletic group.

3.6. Sphaeromatidae genera incertae sedis

The genera listed below cannot reliably be placed in the proposed groupings and are considered incertae sedis. Genera in normal type face are morphologically reasonably well described and their placement is hypothesized. Bold-faced genera lack unambiguous morphological characters to place them. For all these genera no specimens were available for molecular analysis. Genera are listed alphabetically.

Artopoles Barnard, 1920: the only 'clue' is that pleopod 1 is generally similar to those of *Dynamenella* clade (Bruce 2001). Pereopod morphology is unique.

Botryias Richardson, 1910: No data – minimally described; remains unplaced.

Cassidinella Whitelegge, 1901: Good data (see Bruce 1994a) but still not clear to which group this genus belongs; probably in the *Sphaeroma* clade *s.l.*

Caecosphaeroma Dollfus, 1896: Closely related to *Monolistra*.

Cercosphaera Bruce, 1994c: Has metamorphosed females, but shares few other characteristics; pereopod setation also fits with *Cymodoce*.

Cymodetta Bowman & Kühne, 1974: There are no obvious character links; likeliest and most similar is the *Dynamenella* clade.

Cymodopsis Baker, 1926: The status of the poorly known *Cymodopsis* Baker, 1926 is unclear, and the genus is not monophyletic. The type species remains effectively undescribed, and several species are inappropriately placed in the genus.

Hemisphaeroma Hansen, 1905: Genus needs detailed redescription. At present its affinities are entirely uncertain.

Monolistra Gerstaecker, 1856: Probably monophyletic, all with similar pleopod and antennula and antenna morphology; all are European cave taxa

Naesicopea Stebbing, 1893: Few data; probably in with the *Cymodoce* group.

Syncassidina Baker, 1928: Possibly belongs in with the *Dynamenella* clade.

Xynosphaera Bruce, 1994c: A commensal or parasite of soft corals; no real morphological clues to where it belongs except *Ischyromene* and *Cerceis* groups can be excluded – i.e., *Sphaeroma* clade in the broadest sense.

4. Conclusions

Sphaeromatid isopods are ideal for addressing life history, ecology, biogeography, and phylogenetic hypotheses, because: they exhibit extreme morphological diversity; they are readily collectable in many habitats; some genera are speciose, while others are monotypic; and described genera include biogeographically widespread as well as regionally endemic species. However, we demon-strate here that many (perhaps most) of the large genera are not monophyletic.

The importance of and interest in sphaeromatids extends beyond systematics because of their diversity in life histories, reproductive behavior, and sexual polymorphism (e.g., polychromatism: Bocquet et al. 1950, 1951; Tinturier-Hamelin 1962, 1963; biogeography: Carlton 1987; sense organs: Brandt 1988; life history, physiology, and reproductive behavior: Holdich 1968, 1976; Shuster 1981a,b; Jormalainen & Shuster 1997, 1999; male sexual polymorphism: Shuster 1987; Shuster & Wade 1991a; Shuster & Sassaman 1997; sex ratio: Heath & Ratford 1990; Shuster et al. 2001; parental care: Shuster 1992; Thiel 1999, 2000, 2001, 2003).

Variation in brood pouch morphology among females (Harrison 1984b) and extreme sexual dimorphism among males (wide variation in uropod shape, size and ornamentation; cephalic shape, size and ornamentation; and variation in body size and growth rate; Hurley & Jansen 1977; Shuster 1987, 1992) make sphaeromatids excellent organisms for studying mating system evolution. However, this research direction (and similar comparative questions) can only be pursued with a robust phylogeny in hand.

With the exception of *Gnorimosphaeroma* (clade 1) the family divides into two large clades, these corresponding to the Sphaeromatinae (clade 2) and the Dynameninae (clade 3). The morphological support for these two clades is the presence of thickened transverse ridges on both rami of pleopods 4 and 5 (Dynameninae) or the endopod only (Sphaeromatinae). These characters are consistent, but also repeatedly lost within genera and also in those taxa occupying freshwater, and to a lesser degree, estuarine habitats.

Our major clades supported by molecular data are recognizable morphologically. The concept of the subfamily Cassidininae (flat bodied, 'simple' pleopods, flat uropods with reduced exopod and whatever else has been used over the years) is not upheld, but unfortunately we have few sequences for these taxa (the genera and species are mostly sub-tidal benthic, and some didn't yield molecular sequences). Evaluation, description and redescription of morphological characters including brood pouch characters will go a long way in aiding taxonomists in identifying this beautifully diverse group of crustaceans.

5. Acknowledgements

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7. Appendix: Sphaeromatidae genera list

Currently recognized Sphaeromatidae genera list containing recognizable clades. The World Register of Marine Species (http://www.marinespecies.org on 2017-05-05) currently records 100 genera in the family. Genera marked with * denote that at a minimum of one species and one individual is represented in our dataset. In most instances multiple species and multiple individuals were sequenced, and whenever possible for both genes. Based on our molecular phylogeny, genera are organized into monophyletic clades and these are numbered (see Figs. 1, 2). At present it is possible to place 76 of the 100 (76%) genera. Obvious morphological characters and other annotations augment the list. Groups missing from our analysis include representatives of the *Moruloidea* group, *Cassidina* group, *Leptosphaeroma* group (and the randoms) about another 13 species.

Clade 1 – *Gnorimosphaeroma*
1 *Gnorimosphaeroma* Menzies, 1954

Clade 2 – Sphaeromatinae
Sphaeroma **clade**
2 *Benthosphaera* Bruce, 1994
3 *Bilistra* Sket & Bruce, 2004
4 *Lekanesphaera* Verhoeff, 1943
5 *Sphaeroma* Bosc, 1801
Neosphaeroma **clade**
6 *Neosphaeroma* Baker, 1926
Cymodoce **clade**
7 *Bregmotypta* Bruce, 1994
8 *Calcipila* Harrison & Holdich, 1984
19 *Ceratocephalus* Woodward, 1877
10 *Cercosphaera* Bruce, 1994
11 *Cilicaea* Leach, 1818
12 *Cilicaeopsis* Hansen, 1905
13 *Cymodoce* Leach, 1814
  *?aff. *Cymodopsis* (Kenya; an undescribed species, possible new genus. See *Cymodopsis* under *incertae sedis* genera (intentionally not numbered).
14 *Dynameniscus* Richardson, 1905
15 *Harrieta* Kensley, 1987
16 *Koremasphaera* Bruce, 2003
17 *Kranosphaera* Bruce, 1992
18 *Oxinasphaera* Bruce, 1997
19 *Paracilicaea* Stebbing 1910b
20 *Parasphaeroma* Stebbing 1902
21 *Pooredoce* Bruce, 2009
Exosphaeroma **clade**
22 *Apemosphaera* Bruce, 1994
23 *Exosphaeroides* Holdich & Harrison, 1983

24 *Exosphaeroma* Stebbing, 1900
25 *Isocladus* Miers, 1876
26 *Parisocladus* Barnard, 1914
27 *Ptyosphaera* Holdich & Harrison, 1983
28 *Sphaeramene* Barnard, 1914
29 *Stathmos* Barnard, 1940
30 *Zuzara* Leach, 1818

Clade 3 – Dynameninae
Campecopea **clade**
31 *Campecopea* Leach, 1814 – sister clade to all Dynameninae.
Ischyromene **clade**
32 *Amphoroidea* H. Milne Edwards, 1840
33 *Amphoroidella* Baker, 1908
34 *Austrasphaera* Bruce, 2003
35 *Cassidinopsis* Hansen, 1905
36 *Cymodocella* Pfeffer, 1887
37 *Diclidocella* Bruce, 1995
38 *Dynamenopsis* Baker, 1908
39 *Ischyromene* Racovitza, 1908
40 *Juletta* Bruce, 1993
41 *Margueritta* Bruce, 1993
42 *Maricoccus* Poore, 1994
43 *Pedinura* Bruce, 2003
44 *Pseudosphaeroma* Chilton, 1909
45 *Scutuloidea* Chilton, 1883
Cerceis **clade** – comprising two clades: *Dynamene* + *Cerceis*
46 *Afrocerceis* Müller, 1995
47 *Cassidias* Richardson 1906
48 *Cerceis* Milne Edwards, 1840
49 *Discerceis* Richardson, 1905
50 *Dynamene* Leach, 1814
51 *Dynamenoides* Hurley & Jansen, 1977
52 *Eterocerceis* Messana, 1990
53 *Exocerceis* Baker, 1926
54 *Geocerceis* Menzies & Glynn, 1968
55 *Haswellia* Miers, 1884
56 *Holotelson* Richardson, 1909
57 *Neonaesa* Harrison & Holdich, 1982
58 *Paracassidinopsis* Nobili, 1906
59 *Paracerceis* Hansen, 1905
60 *Platycerceis* Baker, 1926
61 *Platynympha* Harrison, 1984
62 *Pseudocerceis* Harrison & Holdich, 1982
Dynamenella **clade** – comprising two clades: *Dynoides* + *Dynamenella*
63 *Beatricesphaera* Wetzer & Bruce, 1999
64 *Cassidinidea* Hansen, 1905
65 *Cliamenella* Kussakin & Malyutina, 1987
66 *Dynamenella* Hansen, 1905
67 *Dynoides* Barnard, 1914
68 *Heterodina* Schotte & Kensley, 2005
69 *Makarasphaera* Bruce, 2005

70 *Paradella* Harrison & Holdich, 1982
71 *Paraimene* Javed & Ahmed, 1988
72 *Pistorius* Harrison & Holdich, 1982
73 *Sphaeromopsis* Holdich & Jones, 1973
74 *Striella* Glynn, 1968
75 *Thermosphaeroma* Cole & Bane, 1978
76 *Tholozodium* Eleftheriou, Holdich & Harrison, 1980

Incertae sedis genera

Three morphologically defined groups lacked molecular representation and at present cannot be associated with any of our clades. The remaining genera lack descriptive data or do not show any clear morphological indication as to where they belong in the schema presented here. The *Cassidina* group and the *Leptosphaeroma* group were defined by BRUCE (1994).

Cassidina group

77 *Agostodina* Bruce, 1994
78 *Cassidina* H. Milne Edwards, 1840
79 *Chitonopsis* Whitelegge, 1902
80 *Paracassidina* Baker, 1911

Leptosphaeroma group

81 *Chitonosphaera* Kussakin & Malyutina, 1993
82 *Discidina* Bruce, 1994
83 *Leptosphaeroma* Hilgendorf, 1885
84 *Paraleptosphaeroma* Buss & Iverson, 1981
85 *Platysphaera* Holdich & Harrison, 1981

Moruloidea group

86 *Caecocassidias* Kussakin, 1967
87 *Moruloidea* Baker, 1908
88 *Waiteolana* Baker, 1926

Monolistra group

89 *Caecosphaeroma* Dollfus, 1896
90 *Monolistra* Gerstaecker, 1856
91 *Merozoon* Sket, 2012. The description of the genus (and species) is based on a fragment so affinities cannot be assessed other than one in this group of genera.

The following genera cannot be reliably placed in the proposed groupings and are considered *incertae sedis*. Genera in normal type face are morphologially reasonably well described and their placement is hypothesized. Bold-faced genera lack unambigious morphological characters to place them. For the genera below no specimens were available for molecular analysis.

92 *Artopoles* Barnard, 1920 – the only 'clue' is that pleopod 1 is generally similar to those of *Dynamenella* clade. Pereopod morphology is unique.
93 **Botryias Richardson, 1910** – minimal morphological data; remains unplaced.
94 *Cassidinella* Whitelegge, 1901 – good data, but still not clear what its phylogenetic affiliation is; probably in the Sphaeromatinae sensu latu, but not confident.
95 *Cymodetta* Bowman & Kuhne, 1974 – descriptions are fine, just no obvious character links; likeliest and most similar is the *Dynamenella* clade.
96 **Cymodopsis Baker, 1926** – the status of this poorly known genus (with eight species) is unclear. As presently constituted the genus is not monophyletic. The type species remains effectively undescribed, and several species are inappropriately placed in the genus.
97 **Hemisphaeroma Hansen, 1905** – lack of descriptive data for this monotypic freshwater genus precludes assessment of its affinities.
98 *Naesicopea* Stebbing, 1893 – few data; some specimens held at Muséum national d'Histoire naturelle (Paris, NLB personal observation); probably in with the *Cymodoce* group.
99 *Syncassidina* Baker, 1928 – to *Dynamenella* clade?
100 **Xynosphaera Bruce, 1994c** – commensal or parasite of soft corals; no real morphological clues to where it belongs except *Ischyromene* and *Cerceis* groups can be excluded – i.e., excluded from the 'Sphaeromatinae' in the broad sense.

Electronic Supplement Files

at http://www.senckenberg.de/arthropod-systematics

File 1: wetzer&al-sphaeromatidaephylogeny-asp2018-electronic supplement-1.xls — Sequences from GenBank and new sequences generated by this project and used in analyses.

File 2: wetzer&al-sphaeromatidaephylogeny-asp2018-electronic supplement-2.doc — Available family-group names in the Sphaeromatidae.