



*Exosphaeroma inornata* Dow, 1958 (Isopoda: Sphaeromatidae), specimens showing intraspecific color variation, Cabrillo Beach, Los Angeles, California (Photo: Leslie Harris)

# 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 latter 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 MgCl<sub>2</sub>, 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, KATO 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; TALLAVERA & 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  $2 \times 10^7$  cycles, with sampling every 1000<sup>th</sup> 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 aut-

pomorphic 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, *Plakarthritis*, 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

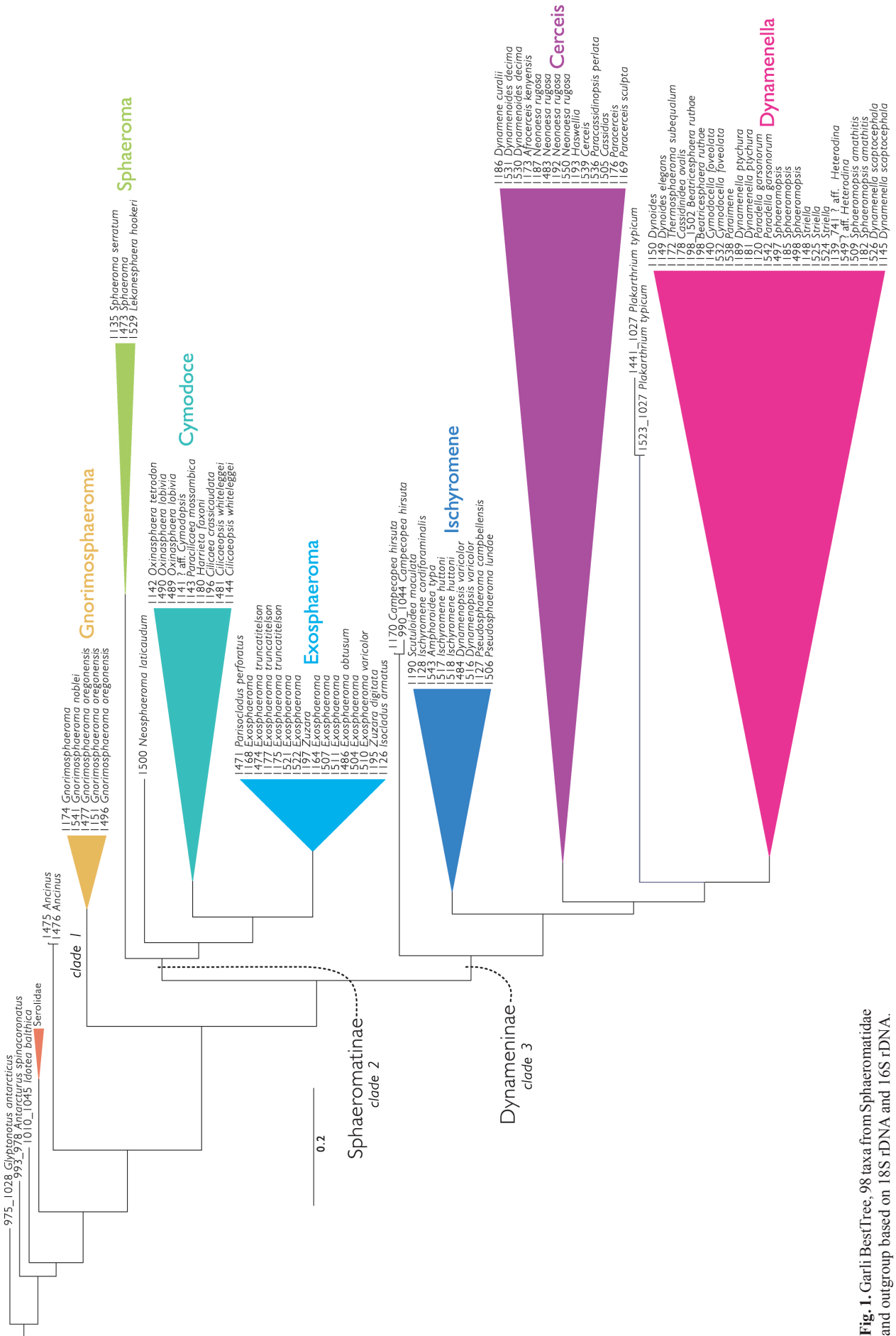
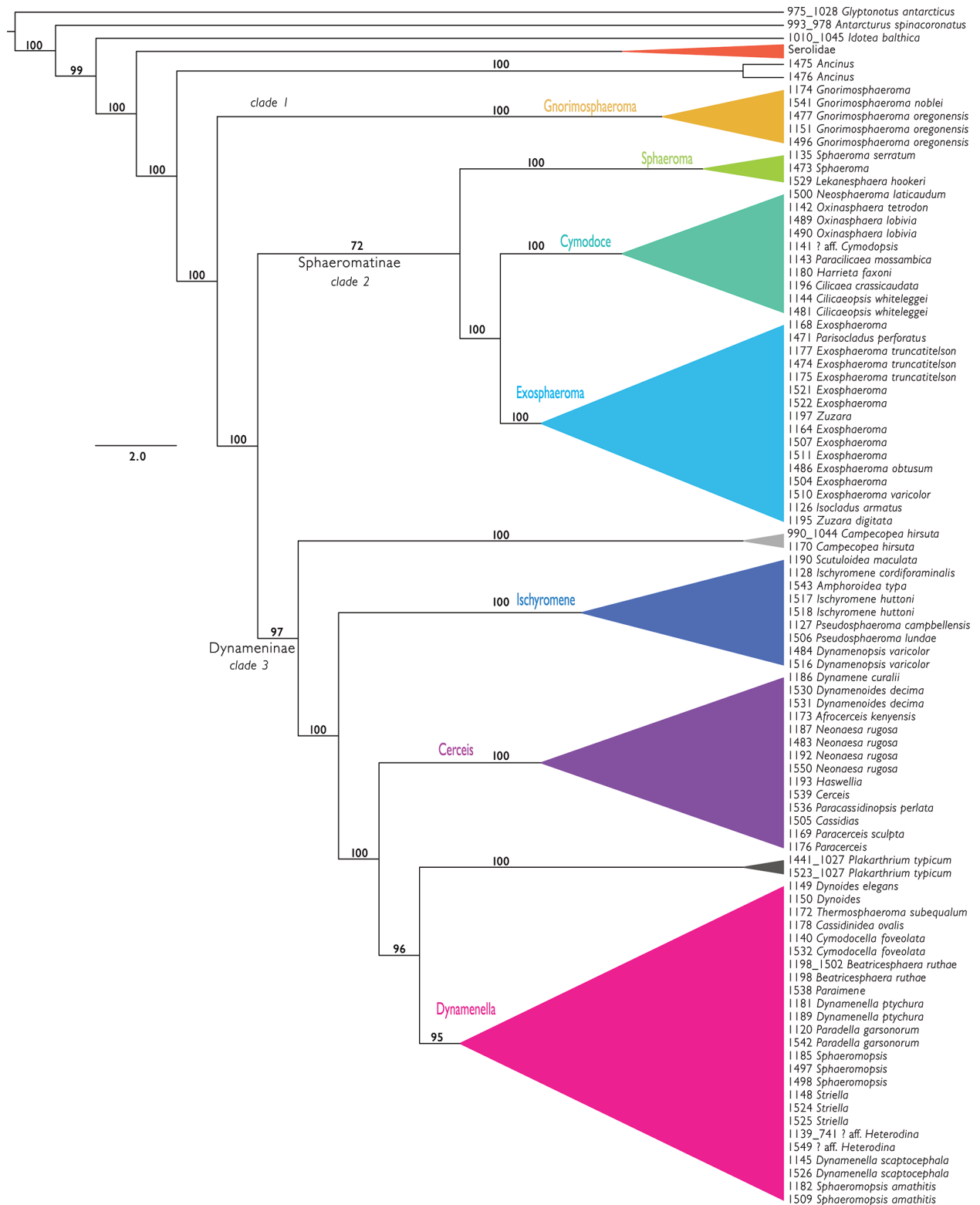


Fig. 1. Garti BestTree, 98 taxa from Sphaeromatidae and outgroup based on 18S rDNA and 16S rDNA.





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 Serolioidea. Characters indicated in **bold** are synapomorphies.

Character / Taxon	Serolioidea	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	<b>gnathal, multicusped</b>
Maxilliped endite	quadrate	quadrate	quadrate	<b>elongate, distally rounded or acute</b>
Maxilliped endite distal margin	without robust and slender setae	with slender setae	without or few slender setae	<b>with many robust and simple setae</b>
Pereopod 1 propodus	swollen, dactylus prehensile	swollen, dactylus prehensile	swollen, dactylus prehensile	<b>not swollen, dactylus not prehensile</b>
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. oregonensis* (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.

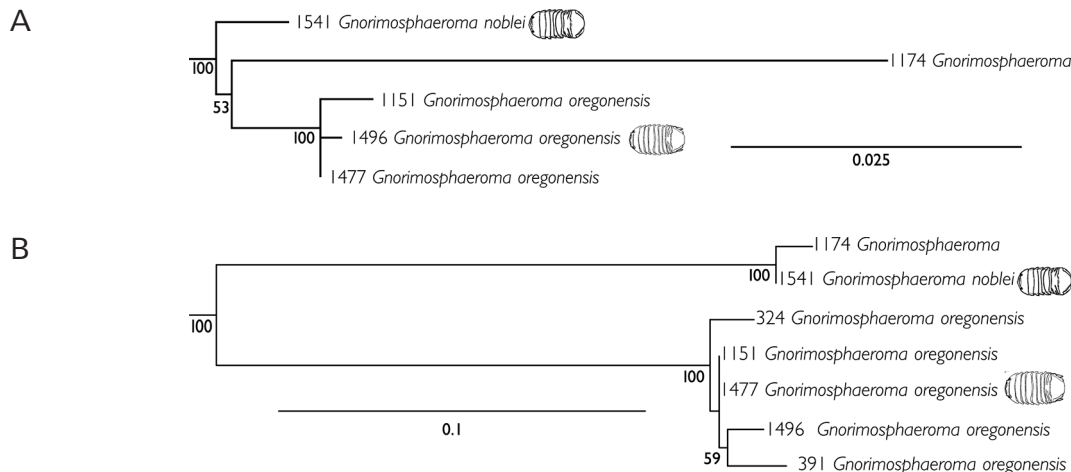
**Remarks.** MENZIES (1954) erected *Gnorimosphaeroma* for *Exosphaeroma oregonensis* Dana, 1853. Although his diagnosis and accompanying figures for the type species, are reasonably detailed, until at least the type species, *Exosphaeroma oregonensis* is fully redescribed and the genus itself re-diagnosed 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 *Exosphaeroma* 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., *Oxinaspheera*) or uropodal endopod reduced (e.g., *Cilicæa* Leach, 1818, *Paracilicæa* 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 clade regardless of the alignment or analysis method.

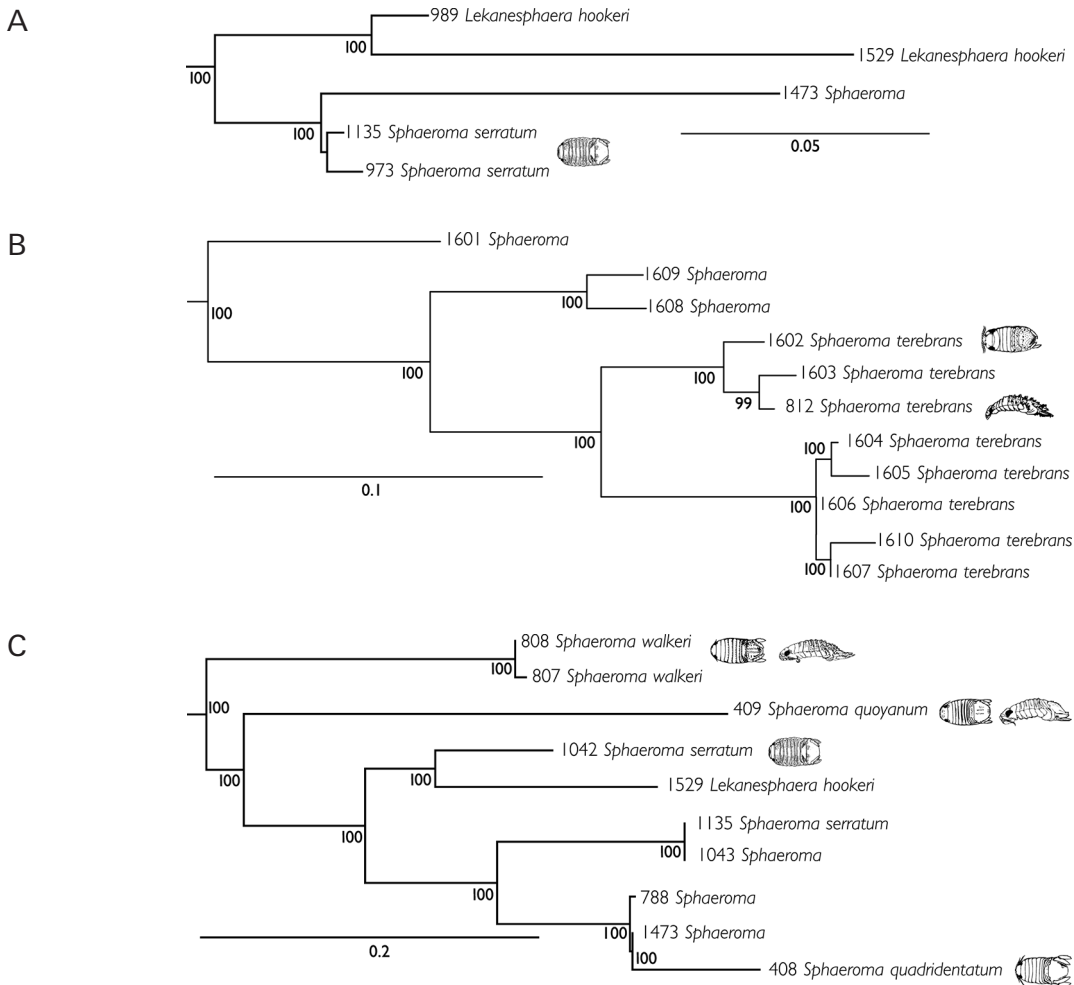
**18S rDNA analyses (Fig. 4A):** These included five sequences which in all analyses resulted in two distinct clades. All members of the genus *Sphaeroma* are the sister taxon to the clade containing exemplars of *Lekanesphaera* (100% bs). The two specimens of *S. serratum* (Fabricius, 1787) [1135+973] 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: *Ape-mosphaera* 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 *Cilicaeopsis whiteleggei* (Stebbing, 1905) (Tanzania) and 1481 *C. whiteleggei* (Fiji) (100% bs).

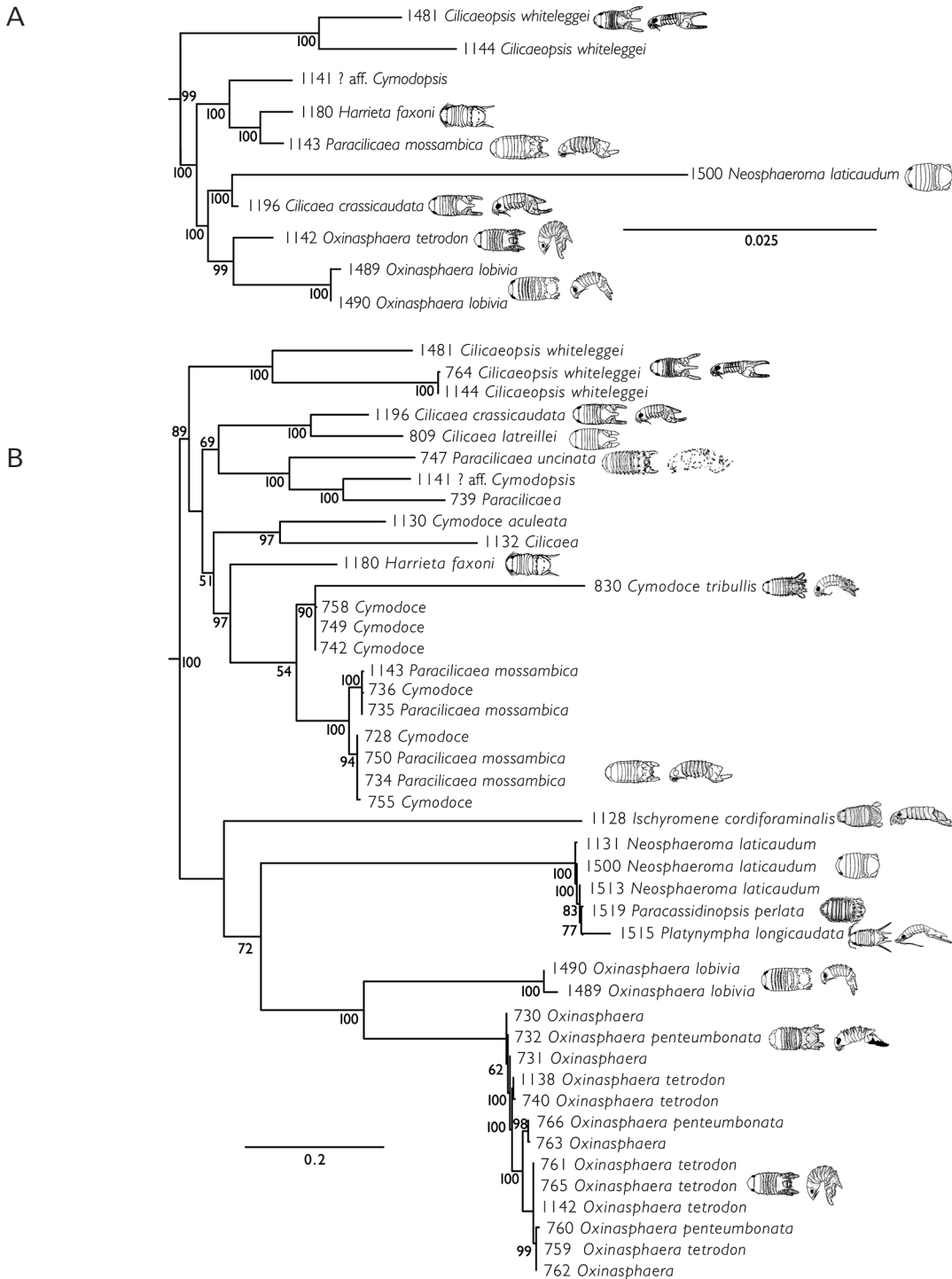
**16S rDNA analyses (Fig. 5B):** The 16S rDNA gene fragment alone does not consistently reveal the deeper backbone of this otherwise strongly supported clade, but regardless of the analyses performed the following relationships are always supported. Taxa identified as *Oxinasphaera* have 100% bs. All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



**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 characteristics; pereopod setation also fits with *Cymodoce*. *Cilicaea* Leach, 1818. *Cilicaeopsis* Hansen, 1905. *Cymodoce* Leach, 1814. *Dynameniscus* Richardson, 1905 – type species re-described by KENSLEY & BRUCE (2001), but affinities are not clear, but placed into the *Cymodoce* clade; mouthparts not metamorphosed. *Harrieta* Kensley, 1987. *Koremaphaera* 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.

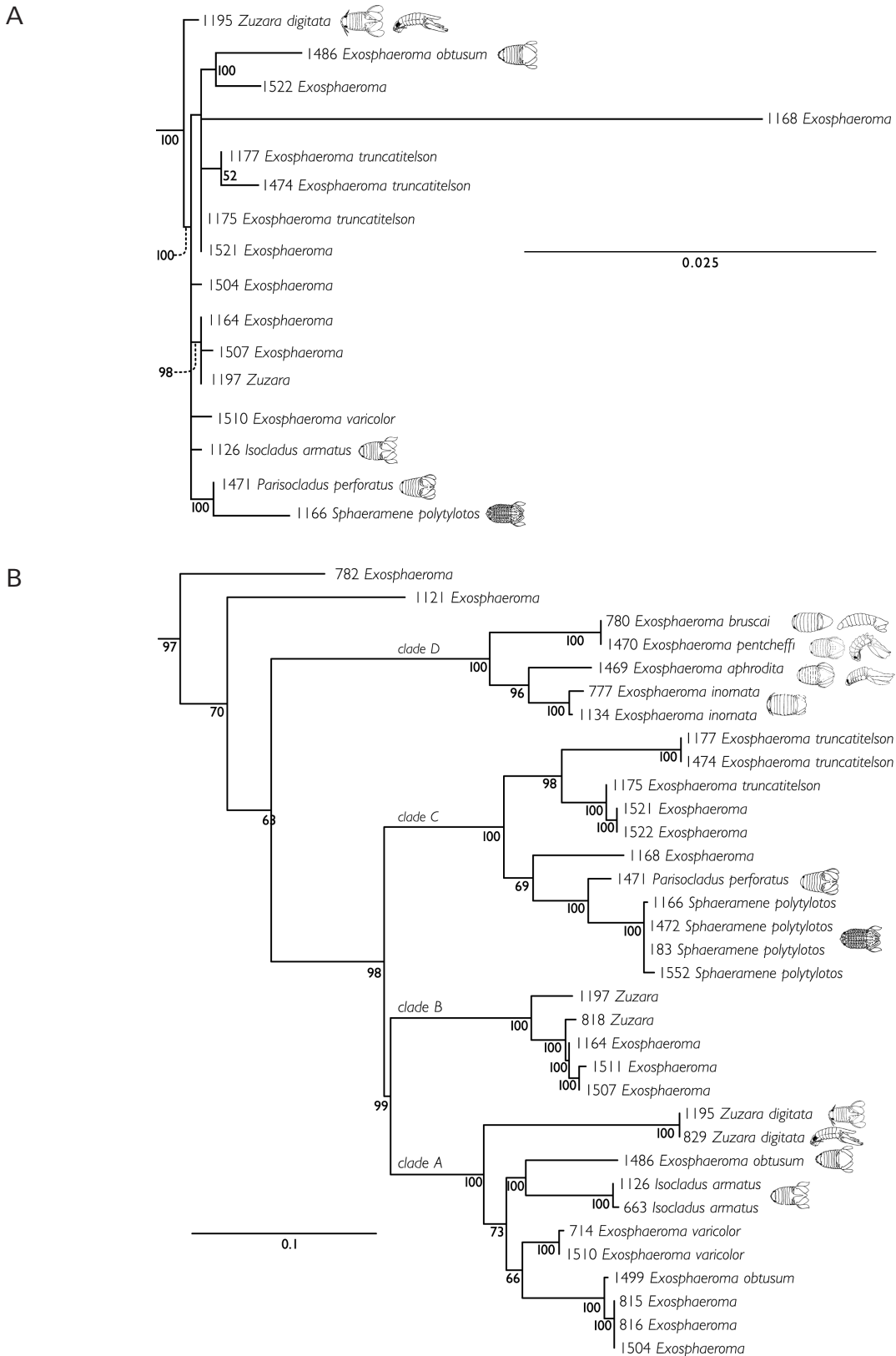
Beginning with the most derived clade A, 1499 *Exosphaeroma obtusum* and 815+816+1504 *Exosphaeroma* (all New Zealand) form the sister taxon to 714, 1510 *E. varicolor* Barnard, 1914 (Chile). 663+1126 *Isocladus armatus* (Milne Edwards, 1840) (New Zealand) together forms the sister taxon to 1486 *E. 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 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.

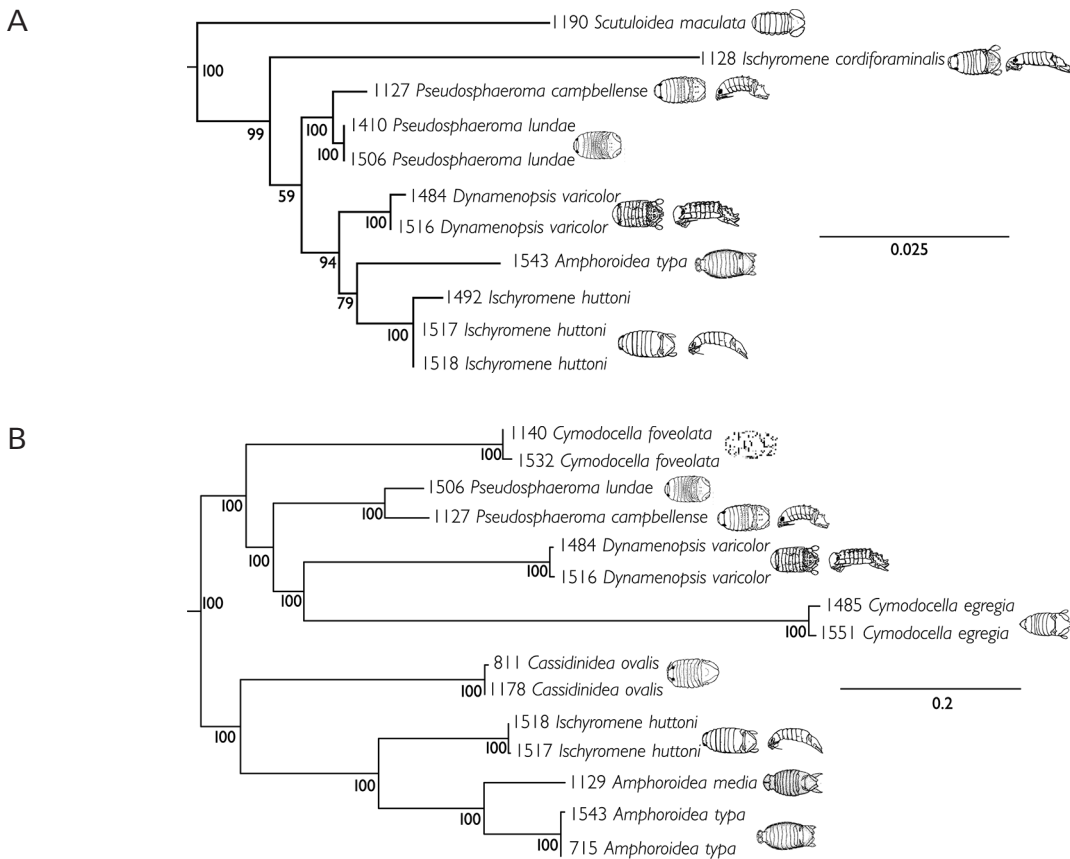
This is the former “Eubranchiatinae”. BOWMAN (1981) designated a type genus and established the name *Dynameninae*, 1981, but with no diagnosis. HARRISON & HOLDICH (1982a) and BRUCE (1993) equally did not offer a diagnosis to the subfamily. Type genus is *Dynamene* Leach, 1814, type species *Oniscus 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 tyta* 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 campbellense* 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 *Cassinidea 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 *Cassinidea* is basal within *Ischyromene*, which contradicts its 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 *Cilicæoposis* 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 *Margueritta* 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).

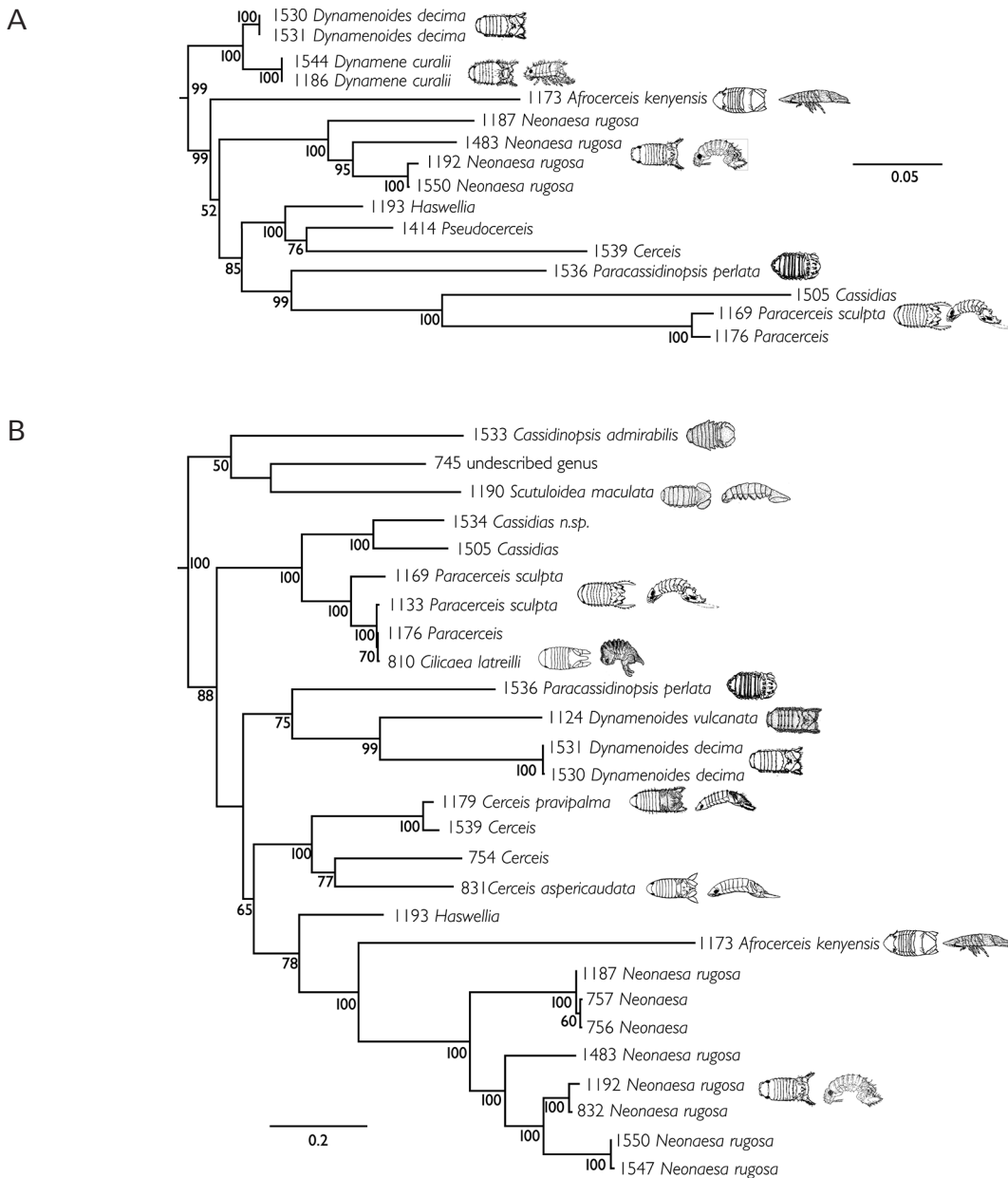
**18SrDNA analyses (Fig. 8A):** Our analyses contained representatives of 10 genera. 1169 *Paracerceis sculpta* (Holmes, 1904) (Gulf of California, Sonora, Mexico) and 1176 *Paracerceis* Hansen, 1905 (Gulf of California, Baja California Sur) form the sister clade to 1505

*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 *Cilicacia 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. ^*Paracassinopsis* Nobili, 1906. \**Paracerceis* Hansen, 1905. \**Platy-cerceis* 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 *Paracassinopsis* is included in the *Cerceis* clade, but *Paracassinopsis* 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 *Sphaeromopsis 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., *Plakarthritis 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 ptychura* (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).

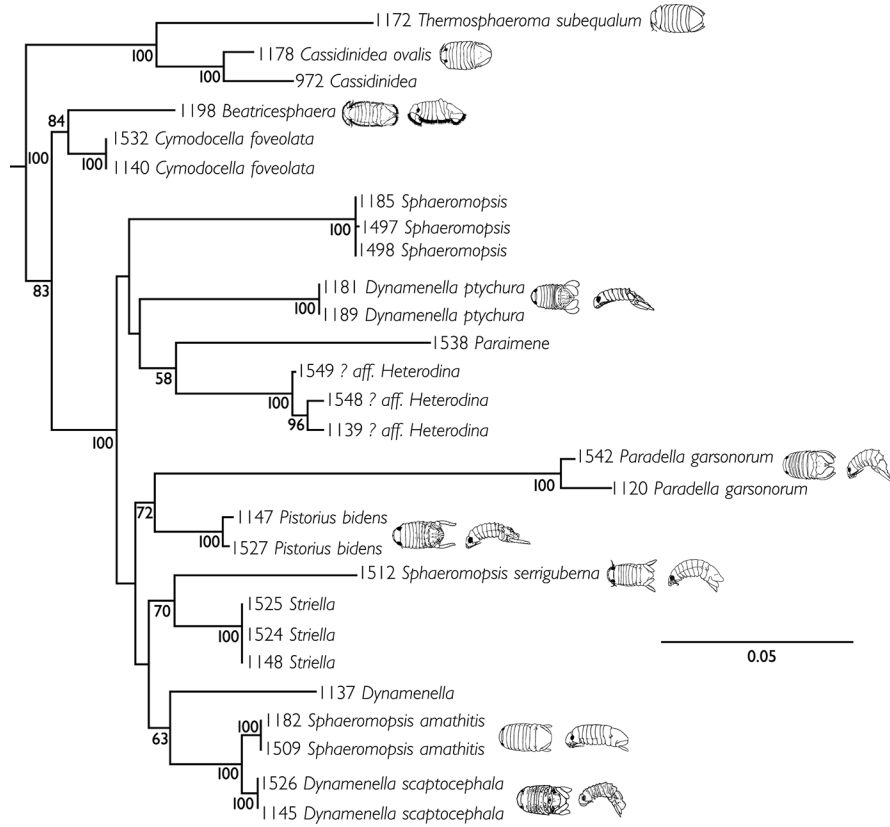
*Thermosphaeroma* with eight species occurs in freshwater springs in the southwest U.S. and northern and central Mexico. It is endemic to thermal springs in Texas and New Mexico, as well as in Chihuahua, Durango, Coahuila and Aguascalientes, Mexico. The genus has interesting North American post-Cretaceous 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.

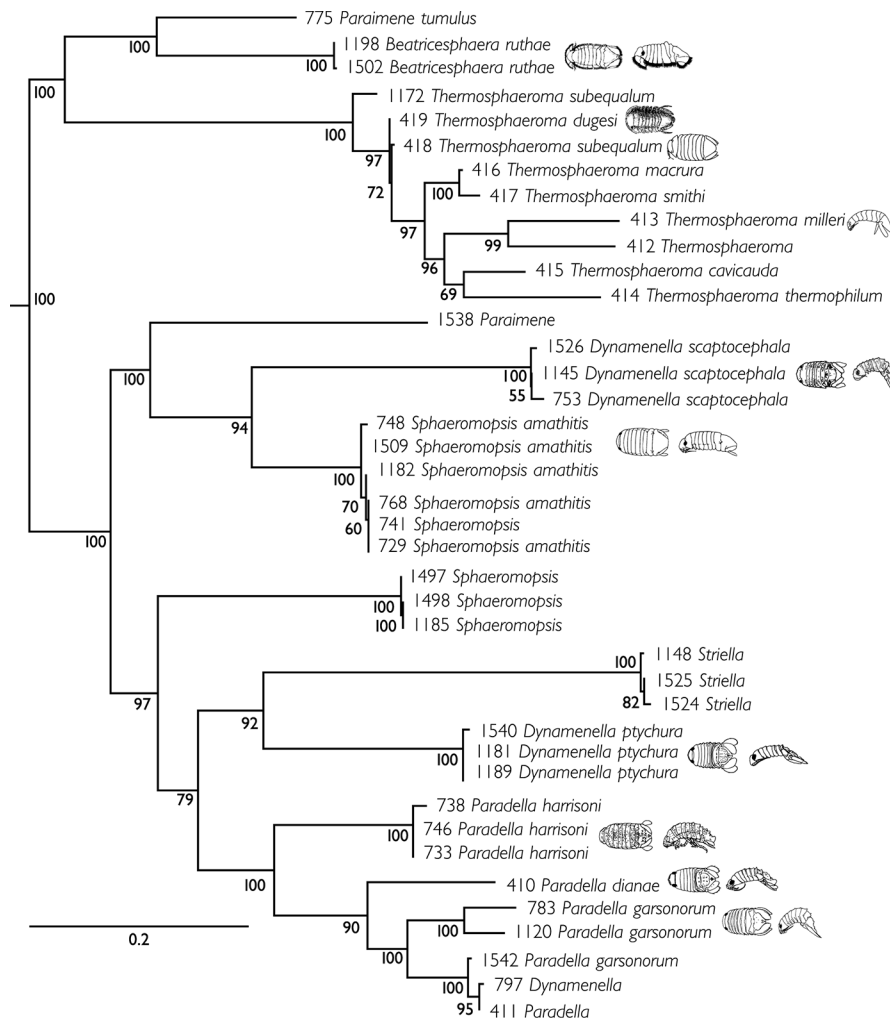
In our 16S rDNA analyses *Cassidinidea ovalis* pairs with *I. huttoni* (Canal Darwin, Chile) in the *Ischyromene* clade rather than as expected within the *Dynamenella* clade. Here again we believe the resolution of the 16S rDNA marker may be misleading and inaccurate at this taxonomic level. Based on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

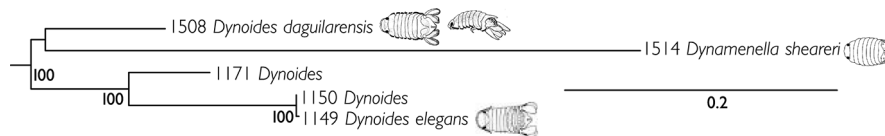


A



B





**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. shearerii* – specimens identified as *Dynamenella sheareii* (San Juan Island, Washington, USA). The later with a long branch. Based on these analyses 1514 *D. shearerii* 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*, *Cassinidea*, *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. *Cassinidea* Hansen, 1905. *Cliamenella* Kussakin & Malyutina, 1987. \**Dynamenella* Hansen, 1905. *Dynoides* Barnard, 1914. \**Heterodina* Schotte & Kensley, 2005. \**Makarasphaera* Bruce, 2005. \**Paradella* Harrison & Holdich, 1982a. \**Paramene* 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 characteristics 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.

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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, *Cassinina* 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  
9 *Ceratocephalus* Woodward, 1877  
10 *Cercosphaera* Bruce, 1994  
11 \**Cilicæa* Leach, 1818  
12 \**Cilicæopsis* 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 \**Paracilicæa* 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 *Cassinidopsis* 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 \**Cassinidias* Richardson 1906  
48 \**Cerceis* Milne Edwards, 1840  
49 *Discerceis* Richardson, 1905  
50 \**Dynamene* Leach, 1814  
51 \**Dynamenoides* Hurley & Jansen, 1977  
52 *Eterocerceis* Messina, 1990  
53 *Exocerceis* Baker, 1926  
54 *Geocerceis* Menzies & Glynn, 1968  
55 \**Haswellia* Miers, 1884  
56 *Holotelson* Richardson, 1909  
57 \**Neonaesa* Harrison & Holdich, 1982  
58 \**Paracassinidopsis* 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 \**Cassinididea* 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 scheme 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 morphologically reasonably well described and their placement is hypothesized. Bold-faced genera lack unambiguous 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 lato, 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.

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## 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.

Appendix Electronic Supplement File 1. Sequences from GenBank and new sequences generated by this project and used in analyses. Taxa denoted with "\*" are the type species for genus.

	18S GenBank No.	16S GenBank No.	Locality/Sequence Source	RW No.
<b>Ancinidae</b>				
<i>Ancinus</i>	JF699514	KU248307	Pacific Panama, Naos Island, Flamenco Beach, beach sand, fixed and preserved in 95% ethanol. 23 Mar 2005. Coll. P.Glynn, I.Bethancourt, G.Hockensmith, T.Smith, A.Romanski. RW05.010	1475
<i>Ancinus</i>	JF699515	KU248308	Pacific Panama, Naos Island, Flamenco Beach, beach sand, fixed and preserved in 95% ethanol. 23 Mar 2005. Coll. P.Glynn, I.Bethancourt, G.Hockensmith, T.Smith, A.Romanski. RW05.010	1476
<b>Valvifera</b>				
<i>Antarcturus</i>		AF268208	C. Held	980
<i>Antarcturus hempeli</i>		AF268205	C. Held	977
<i>Antarcturus hodgsoni</i>		AF268209	C. Held	981
<i>Antarcturus hodgsoni</i>		AF268210	C. Held	982
<i>Antarcturus polaris</i>		AF268207	C. Held	979
<i>Antarcturus spinacoronatus</i>		AF268206	C. Held	978
<i>Antarcturus spinacoronatus</i>	AF279604		C. Held	993
<i>Chaetarcturus adareanus</i>		AF268214	C. Held	986
<i>Chaetarcturus bovinus</i>		AF268213	C. Held	985
<i>Chaetarcturus longispinosus</i>		AF268215	C. Held	987
<i>Furcarcturus polarsterni</i>		AF268211	C. Held	983
<i>Furcarcturus polarsterni</i>		AF268212	C. Held	984
<i>Glyptonotus antarcticus</i>	AF255696		H.Dreyer and J.W.Wägele	975
<i>Glyptonotus antarcticus</i>		GAN269816	C. Held	1028
<i>Cleantis prismatica</i>	AF255697		H.Dreyer and J.W.Wägele	976
<i>Erichsonella attenuata</i>	AY743948		C.C.Babbitt and N.H.Patel	1109
<i>Glyptoidotea lichtensteini</i>		AF260853	Atlantic, Namibia, south of Lüderitz, near Grossebucht (Big Bay), northern point, 0-5 m depth, ~26.38°S ~10.15°E, fixed and preserved in 95% ethanol. 29 Nov 1995. Coll. R.Brusca (PharmaMar Expedition). RW95.030	180
<i>Glyptoidotea lichtensteini</i>		AF259537	Atlantic, Namibia, south of Lüderitz, near Grossebucht (Big Bay), northern point, 0-5 m depth, ~26.38°S ~10.15°E, fixed and preserved in 95% ethanol. 29 Nov 1995. Coll. R.Brusca (PharmaMar Expedition). RW95.030	394
<i>Idotea</i>		ISC388081	A.Michel-Salzat and D.Bouchon	1046



Appendix Electronic Supplement File 1. Sequences from GenBank and new sequences generated by this project and used in analyses. Taxa denoted with "\*" are the type species for genus.

<i>Idotea balthica</i>	AF279603		H.Dreyer and J.W.Wägele	992
<i>Idotea balthica</i>	IBAJ11390		K.Edman and E.Sjoegren	1010
<i>Idotea chelipes</i>		ICH388080	A.Michel-Salzat and D.Bouchon	1045
<i>Idotea metallica</i>			Received from Woods Marine Biological Laboratory, Department of Resources via T.Spears. Aug 1998. RW98.054	369
<i>Paridotea ungulata</i>		AF259539	Atlantic, Namibia, south of Lüderitz, near Grossebucht (Big Bay), northern point, 0-5 m depth, ~26.38°S ~10.15°E, Fixed and preserved in 95% ethanol. 29 Nov 1995. Coll. R. Brusca (PharmaMar Expedition). RW95.030	215
<i>Pentidotea resecata</i>		AF259538	USA, Pacific, California, Monterey Bay, from kelp off Monterey Municipal Pier, fixed in 95%, preserved in 95% EtOH. 12 Dec 1997. Coll. R. Wetzer. RW97.009	182
<i>Pentidotea resecata</i>		AF260854	USA, Pacific, California, Monterey Bay, from kelp off Monterey Municipal Pier, fixed in 95%, preserved in 95% EtOH. 12 Dec 1997. Coll. R. Wetzer. RW97.009	420
<i>Pentidotea wosnesenskii</i>		AF260855	Pacific, USA, Washington, west side of Whidbey Island, Keystone, rocky intertidal among mussels, fixed in 95%, preserved in 95% EtOH. 25 Jun 1998. Coll. T. J. Hilbish. RW98.032	354
<i>Pentidotea wosnesenskii</i>		AF260856	Pacific, USA, Washington, west side of Whidbey Island, Keystone, rocky intertidal among mussels, fixed in 95%, preserved in 95% EtOH. 25 Jun 1998. Coll. T. J. Hilbish. RW98.032	363
<i>Pentidotea wosnesenskii</i>		AF260857	Pacific, USA, Washington, west side of Whidbey Island, Keystone, rocky intertidal among mussels, fixed in 95%, preserved in 95% EtOH. 25 Jun 1998. Coll. T. J. Hilbish. RW98.032	395
<i>Pentidotea wosnesenskii</i>		IWO388082	A.Michel-Salzat and D.Bouchon	1047
<b>Serolidae</b>				
<i>Acutiserolis bromleyana</i>		ABR269805	C. Held	1017
<i>Acutiserolis bromleyana</i>	ABR269818		C. Held	1030
<i>Ceratoserolis meridionalis</i>		CME269800	C. Held	1012
<i>Ceratoserolis meridionalis</i>	CME269825		C. Held	1037
<i>Ceratoserolis pasternaki</i>		CPA269801	C. Held	1013
<i>Ceratoserolis pasternaki</i>	CPA269826		C. Held	1038
<i>Ceratoserolis trilobitoides</i>		CTR269799	C. Held	1011
<i>Ceratoserolis trilobitoides</i>	CTR269824		C. Held	1036
<i>Cristaserolis gaudichaudii</i>		CGA269813	C. Held	1025
<i>Cristaserolis gaudichaudii</i>	CGA269828		C. Held	1040
<i>Cuspidoserolis johnstoni</i>		CJO26980	C. Held	1015
<i>Cuspidoserolis johnstoni</i>	CJO269817		C. Held	1029
<i>Cuspidoserolis luethjei</i>		CLU269802	C. Held	1014
<i>Cuspidoserolis luethjei</i>	CLU269819		C. Held	1031

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<i>Frontoserolis waegelei</i>		FGL269807	C. Held	1019
<i>Frontoserolis waegelei</i>	FWA269822		C. Held	1034
<i>Leptoserolis bonaerensis</i>		LBO269812	C. Held	1024
<i>Paraserolis polita</i>		PPO269808	C. Held	1020
<i>Paraserolis polita</i>	PPO269823		C. Held	1035
<i>Serolella bouvieri</i>		SBO269804	C. Held	1016
<i>Serolella bouvieri</i>	SBO269820		C. Held	1032
<i>Serolina bakeri</i>		AF260864	Australia, Tasmania, Tasmania Peninsula, Pirates Bay, 3-4 m, fixed in 95%, preserved in 95% ethanol. 11 Jan 1988. Coll. K.Gowlett-Holmes. Received from G.C.B.Poore, 5/98. RW98.021	336
<i>Serolina bakeri</i>		AF259542	Australia, Tasmania, Tasmania Peninsula, Pirates Bay, 3-4 m, fixed in 95%, preserved in 95% ethanol. 11 Jan 1988. Coll. K.Gowlett-Holmes. Received from G.C.B.Poore, 5/98. RW98.021	349
<i>Serolina bakeri</i>		SBA269814	C.Held	1026
<i>Serolis glacialis</i>		SGL269806	C.Held	1018
<i>Serolis glacialis</i>	SGL269821		C.Held	1033
<i>Serolis paradoxa</i>		SPA269811	C.Held	1023
<i>Serolis paradoxa</i>	SPA269827		C.Held	1039
<i>Spinoserolis beddardi</i>		SBE269810	C.Held	1022
<i>Spinoserolis latifrons</i>		SBE269810	C.Held	1021
<b>Sphaeromatidae</b>				
<i>Afrocerceis kenyensis</i> *	KU189317		Indian Ocean, Kenya, Mombasa, ca. 0.5 km S. of Ras Iwetine, outer reef flat, 4.039°S 39.726°E, low intertidal, <i>Sargassum</i> wash, fixed and preserved in 95% ethanol. 2 Jul 2004. #52. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.102	1173
<i>Amphoroidea media</i>		KU248295	New Zealand, North Island, Evans Bay, 41.303°S 174.806°E, sea wall, surface night light, fixed and preserved in 95% ethanol. 18 Nov 2003. Coll. G. Read, NIWA. RW04.329	1129
<i>Amphoroidea typa</i>		KU248273	Pacific, Chile, Coquimbo, ~29.57°S ~71.25°W, <i>Macrocystis pyrifera</i> , fixed and preserved in 95% ethanol. 17 Jun 2004. Coll. M.Thiel (Universidad Católica del Norte, Chile). RW04.207	715
<i>Amphoroidea typa</i>	JF699518	KU248274	Pacific, Chile, Coquimbo, ~29.57°S ~71.25°W, <i>Macrocystis pyrifera</i> , fixed and preserved in 95% ethanol. 17 Jun 2004. Coll. M.Thiel (Universidad Católica del Norte, Chile). RW04.207	1543
<i>Beatricesphaera ruthae</i> *	JF699519	KU248279	Costa Rica, Limon Province, Parque Nacional Cahuita, Punta Cahuita Reef, inner reef lagoon, 9.736°N 82.812°W, algae, coral rubble and rock wash, 2-7 m, 31 Oct 1986. LACM 86-205. Coll. R.C.Brusca and P.M.Delaney. RW04.247	1198

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<i>Beatricesphaera ruthae</i> *		KU248280	Atlantic, Costa Rica, Limon Province, Puerto Vargas, Punta Cahuita on and shorewood of inner reef crest, 9.736°N 82.81°W, algae, 1-3 m, 20 May 1987. LACM 87-44. Coll. G.Hendler and R.L.Peck. RW04.250	1502
<i>Campecopea hirsuta</i> *	AF279601		H.Dreyer and J.W. Wägele	990
<i>Campecopea hirsuta</i>		CHI388076	A. Michel-Salzat and D.Bouchon	1044
<i>Campecopea hirsuta</i> *	JF699520	KU248169	Atlantic, Canary Islands, Lanzarote, ~29°N ~13.38°W, empty barnacle shells from the upper shore, fixed in 95%, preserved in 95% ethanol. Received from D. M. Holdich, June 2002. RW02.038	1170
<i>Campecopea lusitanica</i>	AF279602		sequence contributor H. Dreyer and J.W. Wägele	991
<i>Cassidias</i>	JF699521	KU248203	Singapore, Kusu Island (Pulau Tembakul), 1.231°N 103.861°E, mixed rubble and sponges, SCUBA, retained on 240µm mesh net, 4.27 m. Fixed and preserved in 95% ethanol. 28 Oct 2003. Coll. N.L.Bruce and R.Wetzer. RW03.256	1505
<i>Cassidias</i>		KU248171	Pacific, Palau, Siales Corner, 7.313°N 134.225°E, from <i>Halimeda cylindracea</i> Decaisne (Chlorophyceae: Codiaceae) clumps, 10 m. Fixed and preserved in 95% ethanol. 22 May 2002. Sta. 98. Coll. S.De Grave and C.Burras. RW02.055	1534
<i>Cassidinidea</i>	AF255693		H. Dreyer and J.W. Wägele	972
<i>Cassidinidea ovalis</i> *		KU248194	Atlantic, USA, South Carolina, Combahee River, 32.672°N 80.713°W, rotting wood at low tide line, 0 salinity, 27°C, fixed and preserved in 95% ethanol. 1 Jul 2003. T30030010. Coll. D.Knott, R.King, S.deVictor. RW03.226	811
<i>Cassidinidea ovalis</i> *	JF699522	KU248195	Atlantic, USA, South Carolina, Combahee River, 32.672°N 80.713°W, rotting wood at low tide line, 0 salinity, 27°C, fixed and preserved in 95% ethanol. 1 Jul 2003. T30030010. Coll. D.Knott, R.King, S.deVictor. RW03.226	1178
<i>Cassidinopsis admirabilis</i>		KU248299	New Zealand, North Island, Wellington, Island Bay, 41.345°S 174.776°E, fixed and preserved in 95% ethanol. 2 Oct 2003. Coll. N.L.Bruce and A.-N.Loerz. RW04.345	1533
<i>Cerceis</i>		KU248238	Indian Ocean, Kenya, Mombasa, ca. 0.5 km S. of Ras Iwetine, outer reef flat, 4.039°S 39.726°E, low intertidal, Sargassum wash, fixed and preserved in 95% ethanol. 2 Jul 2004. #52. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.102	754
<i>Cerceis</i>	JF699523	KU248186	Pacific, Australia, Queensland, Port Douglas, south end of "4 Mile Beach", 16.521°S 145.477°E, muddy sand flat, mid-intertidal, ~200m seaward from high tide line, fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 29 Apr 2003. Sample #78. Coll. R.Wetzer and N.D.Pentcheff. RW03.187	1539
<i>Cerceis aspericaudata</i>		KU248183	Pacific, Australia, Queensland, Port Douglas, Mirage Marina, 16.486°S 145.459°E, floating dock, Sargassum, fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 26 Apr 2003. Sample #76. Coll. R.Wetzer and N.D.Pentcheff. RW03.185	831
<i>Cerceis aspericaudata</i>		KU248181	Pacific, Australia, Queensland, Lizard Island, Granite Bluff, northwest side of island, 14.651°S 145.45°E, SCUBA, 6.1 m. fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 22 Apr 2003. Sample #75. Coll. R.Wetzer and N.D.Pentcheff. RW03.184	832

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<i>Cerceis pravipalma</i>		KU248200	Singapore, southside of island, Labrador Park, 1.268°N 103.799°E, mid to low rocky intertidal, Sargassum fronds, retained on 240µm mesh net, fixed and preserved in 95% ethanol. 25 Oct 2003. Coll. N.L.Bruce and R.Wetzer. RW03.250	1179
<i>Cilicaea</i>		KU248288	Australia, New South Wales, north west side of Brush Island, north of Bateman's Bay, 35.528°S 150.416°E, <i>Zonaria diesingiana</i> (alga), hand collected on scuba, 16.2 m. Fixed in 95% ethanol. 9 Feb 2003. P 65861, Project: Biodiversity of algal substrates. Coll. G.Wilson and P.Berents, NSW 2029. RW04.274	1132
<i>Cilicaea crassicaudata</i>	JF699524	KU248202	Singapore, Beting Bronok, Tekong Besar patch reef (northeast of Singapore), 1.433°N 104.022°E, mud, gravel and patch reef exposed at 0 ft. tide, assorted rock and sponge washes, retained on 240µm mesh net, fixed and preserved in 95% ethanol. 27 Oct 2003. Coll. N.L.Bruce and R.Wetzer. RW03.254	1196
<i>Cilicaea latreilli*</i>		KU248196	Singapore, Gudang Industrial Estate, north east side of island, fish farm just west of Pulau Ubin (Island), 1.398°N 103.963°E, from floating fish docks fouling organisms (green mussels, algae, hydroids, and bryozoans) on floats and rope, retained on 240µm mesh net, fixed and preserved in 95% ethanol. 21 Oct 2003. Coll. R.Wetzer and N.L.Bruce. RW03.231	809
<i>Cilicaea latreilli*</i>		KU248197	Singapore, Gudang Industrial Estate, north east side of island, fish farm just west of Pulau Ubin (Island), 1.398°N 103.963°E, from floating fish docks fouling organisms (green mussels, algae, hydroids, and bryozoans) on floats and rope, retained on 240µm mesh net, fixed and preserved in 95% ethanol. 21 Oct 2003. Coll. R.Wetzer and N.L.Bruce. RW03.231	810
<i>Cilicaeopsis whiteleggei</i>		KU248223	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.182°S 39.123°E, dead coral and hydrocoral, SCUBA, 4.57 m. Fixed in 100%, preserved in 95% ethanol. 24 Jun 2004. #12. Coll. N.D. Pentcheff and R.Wetzer. RW04.057	764
<i>Cilicaeopsis whiteleggei</i>	JF699525	KU248224	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.182°S 39.123°E, dead coral and hydrocoral, SCUBA, 4.57 m. Fixed in 100%, preserved in 95% ethanol. 24 Jun 2004. #12. Coll. N.D. Pentcheff and R.Wetzer. RW04.057	1144
<i>Cilicaeopsis whiteleggei</i>	JF699526	KU248312	Pacific, Fiji, fixed and preserved in 95% ethanol. NLB Sta. 27. Coll. N.L.Bruce. RW05.307	1481
<i>Cymodoce</i>		KU248265	Indian Ocean, Kenya, Mombasa, Ras Iwetine, 4.018°S 39.731°E, intertidal <i>Ulva</i> , fixed in 100%, preserved in 95% ethanol. 15 Jul 2004. #121. Coll. R.Wetzer. RW04.177	728
<i>Cymodoce</i>		KU248253	Indian Ocean, Kenya, north of Mombasa, Kanamai Beach, 3.922°S 39.793°E, outer reef edge, <i>Sargassum</i> and green stringy algae washes, fixed in 100%, preserved in 95% ethanol. 7 Jul 2004. #94. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW04.147	736
<i>Cymodoce</i>		KU248246	Indian Ocean, Kenya, Mombasa, Bamburi Beach, in front of Giriama Beach Hotel, 4.001°S 39.727°E, sand, fixed in 100%, preserved in 95% ethanol. 6 Jul 2004. #83. Coll. N.L.Bruce. RW04.136	742
<i>Cymodoce</i>		KU248242	Indian Ocean, Kenya, Mombasa, Mama Ngina, inner reef fringe, adjacent to navigation buoy, 4.08°S 39.675°E, <i>Sargassum</i> wash, fixed in 100%, preserved in 95% ethanol. 4 Jul 2004. #69. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.122	749
<i>Cymodoce</i>		KU248236	Indian Ocean, Kenya, Mombasa, Giriama Beach Hotel, tidal flat in front of hotel, 4.009°S 39.73°E, low intertidal, under rock on <i>Gracilaria</i> , fixed and preserved in 95% ethanol. 1 Jul 2004. #45. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.095	755



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<i>Cymodoce</i>		KU248232	Indian Ocean, Tanzania, Zanzibar, Ras Nungwi, northend of island, 5.713°S 39.312°E, coral reef, several species of <i>Halimeda</i> , SCUBA, 10.67 m. Fixed and preserved in 95% ethanol. 27 Jun 2004. #35. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.086	758
<i>Cymodoce aculeata</i>		KU248292	Australia, New South Wales, outer Latitude Rock, Forster, 32.211°S 152.568°E, barnacle chunks, hand collected on SCUBA, 10 m. Preserved in 95% ethanol. 18 Mar 2003. P 66298. Coll. RV Baragula, NSW 2166. RW04.297	1130
<i>Cymodoce tattersalli</i>	AF255695		H.Dreyer and J.W.Wägele	974
<i>Cymodoce tribullis</i>		KU248182	Pacific, Australia, Queensland, Port Douglas, Mirage Marina, 16.486°S 145.459°E, floating dock, <i>Sargassum</i> , fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 26 Apr 2003. Sample #76. Coll. R.Wetzer and N.D.Pentcheff. RW03.185	830
<i>Cymodocella egregia</i>		KU248316	New Zealand, Wellington region, Island Bay, rocky intertidal, coralline red algae, fixed and preserved in 95% ethanol. 15 May 2004. Coll. K.Merrin. RW05.311	1485
<i>Cymodocella egregia</i>		KU248298	New Zealand, North Island, Wellington, Evans Bay, NIWA sea wall, 41.303°S 174.806°E, night light, fixed and preserved in 95% ethanol. 18 Nov 2002. Coll. G.Read. RW04.340	1551
<i>Cymodocella foveolata</i>	JF699527	KU248271	Pacific, Chile, Coquimbo, ~29.57°S ~71.25°W, intertidal, under boulder, fixed and preserved in 95% ethanol. 17 Jun 2004. Coll. M.Thiel (Universidad Católica del Norte, Chile). RW04.205	1140
<i>Cymodopsis</i>	JF699528	KU248261	Indian Ocean, Kenya, north of Mombasa, Mombasa Marine Park, buoy #3, 3.976°S 39.768°E, outer reef, medium mixed rubble on sand, SCUBA, 23.3 m. Fixed in 100%, preserved in 95% ethanol. 14 Jul 2004. #115. Coll. N.L.Bruce and N.D.Pentcheff. RW04.171	1141
<i>Dynamene curalii</i>	JF699529	KU248178	Pacific, Australia, Queensland, Heron Island northern side, seaward reef edge/crest, 23.434°S 151.926°E, "Porolithion" clumps, fixed in 100%, preserved in 95% ethanol. 14 Apr 2003. Sample #40. Coll. N.L.Bruce. RW03.152	1186
<i>Dynamene curalii</i>	JF699530		Pacific, Australia, Queensland, Heron Island northern side, ~50 m back from reef flat outer edge, large boulder covered w. algal turf, 23.435°S 151.926°E, fixed in 100%, preserved in 95% ethanol. 14 Apr 2003. Sample #37. Coll. N.L.Bruce. RW03.149	1544
<i>Dynamenella</i>		KU248201	Singapore, southside of island, Labrador Park, 1.268°N 103.799°E, low rocky intertidal, algal "turf", hand, retained on 240µm mesh net, fixed and preserved in 95% ethanol. 25 Oct 2003. Coll. N. L. Bruce and R. Wetzer. RW03.252	797
<i>Dynamenella</i>	JF699531		Pacific, USA, Washington, northwestside of San Juan Island, mouth of Mitchell Bay, Snug Harbor, 48.572°N 123.171°W, intertidal rocks, fixed and preserved in 95% ethanol. 9 Apr 2004. #10. Coll. R.Wetzer and N.D.Pentcheff. RW04.043	11
<i>Dynamenella ptychura</i>	JF699532	KU248175	Pacific, Australia, Queensland, Heron Island, in front of research lab, 23.444°S 151.916°E, high intertidal beach rock, crevices under slab rock, fixed in 100%, preserved in 95% ethanol. 12 Apr 2003. Sample #17. Coll. N.L.Bruce. RW03.126	1181
<i>Dynamenella ptychura</i>	JF699533	KU248176	Pacific, Australia, Queensland, Heron Island, in front of research lab, 23.444°S 151.916°E, high intertidal beach rock, crevices under slab rock, fixed in 100%, preserved in 95% ethanol. 12 Apr 2003. Sample #17. Coll. N.L.Bruce. RW03.126	1189

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<i>Dynamenella ptychura</i>		KU248174	Pacific, Australia, Queensland, Heron Island, in front of lab, 23.444°S 151.914°E, high intertidal, beach rock above reef flat, below sand cay, turning rocks, fixed in 100%, preserved in 95% ethanol. 9 Apr 2003. Sample #1. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW03.110	1540
<i>Dynamenella scaptocephala</i>		KU248239	Indian Ocean, Kenya, Mombasa, ca. 0.5 km S. of Ras Iwetine, outer reef flat, 4.038°S 39.725°E, high, <i>Padina</i> washings, fixed and preserved in 95% ethanol. 2 Jul 2004. #54. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.104	753
<i>Dynamenella scaptocephala</i>	JF699534	KU248266	Indian Ocean, Kenya, Mombasa, Ras Iwetine, 4.018°S 39.731°E, intertidal <i>Ulva</i> , fixed in 100%, preserved in 95% ethanol. 15 Jul 2004. #121. Coll. R.Wetzer. RW04.177	1145
<i>Dynamenella scaptocephala</i>	JF699535	KU248237	Indian Ocean, Kenya, Mombasa, Giriama Beach Hotel, tidal flat in front of hotel, 4.008°S 39.728°E, mid intertidal, sea grass, fixed and preserved in 95% ethanol. 1 Jul 2004. #51. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.101	1526
<i>Dynamenella sheareri</i>		KU248216	Pacific, USA, Washington, southend of San Juan Island, Cattle Point, 48.451°N 122.967°W, rocky intertidal barnacles from <i>Semibalanus cariosus</i> , fixed and preserved in 95% ethanol. 7 Apr 2004. #3. Coll. R.Wetzer and N.D.Pentcheff. RW04.036	1514
<i>Dynamenoides decima</i>	JF699536	KU248300	New Zealand, North Island, Cape Palliser, 41.612°S 175.274°E, intertidal, mixed algae and under rocks, fixed and preserved in 95% ethanol. 24 Nov 2003. Coll. N.L.Bruce and J.Olesen. RW04.347	1530
<i>Dynamenoides decima</i>	JF699537	KU248301	New Zealand, North Island, Cape Palliser, 41.612°S 175.274°E, intertidal, mixed algae and under rocks, fixed and preserved in 95% ethanol. 24 Nov 2003. Coll. N.L.Bruce and J.Olesen. RW04.347	1531
<i>Dynamenoides vulcanata*</i>		KU248305	New Zealand, North Island, Cape Palliser, 41.612°S 175.274°E, intertidal, mixed algae and under rocks, fixed and preserved in 95% ethanol. 24 Nov 2003. Coll. N.L.Bruce and J.Olesen. RW04.354	1124
<i>Dynamenopsis varicolor</i>	JF699538	KU248315	New Zealand, Wellington region, Island Bay, rocky intertidal, coralline red algae, fixed and preserved in 95% ethanol. 15 May 2004. Coll. K.Merrin. RW05.311	1484
<i>Dynamenopsis varicolor</i>	JF699539	KU248294	New Zealand, North Island, Island Bay, Wellington, 41.345°S 174.776°E, fixed and preserved in 95% ethanol. 2 Oct 2003. Coll. A.-N.Loerz and N.L.Bruce. RW04.327	1516
<i>Dynoides</i>	JF699540	KU248215	Pacific, USA, California, Los Angeles County, Palos Verdes Peninsula, Pt. Fermin, shore at Paseo del Mar, ~0.5 mi. W of Gaffey Street, 33.71°N 118.3°W, mid-low intertidal, chipping overhanging rock with hammer and <i>Phragmatopoma</i> tubes, 1.5 m. Fixed and preserved in 95% ethanol. 27 Mar 2004. Sta. #7. Coll. R.Wetzer, N.D.Pentcheff, and LMU students. RW04.031	1150
<i>Dynoides</i>		KU248172	Mexico, Baja California Sur, Bahia de Concepcion, W. side of bay at the tombolo, east side of island, ~26.656°N ~111.747°W, from white sponge ( <i>Lucetta</i> sp.), 18 Aug 1980. EWI 80-8. Coll. E.W.Iverson. RW02.102	1171
<i>Dynoides daguilaensis</i>		KU248166	Hong Kong, Cape d'Aguilar Marine Reserve, 22.2°N 114.25°E, exposed rocky intertidal associated with black mussel beds ( <i>Septifer virgatus</i> ), fixed in 95%, preserved in 95% ethanol. 10 May 2000. Coll. LiLi. RW00.101	1508

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<i>Dynoides elegans</i>	JF699541	KU248214	Pacific, USA, California, Los Angeles County, Palos Verdes Peninsula, Pt. Fermin, shore at Paseo del Mar, ~0.5 mi. W of Gaffey Street, 33.71°N 118.301°W, mid-low intertidal, chipping overhanging rock with hammer and <i>Phragmatopoma</i> tubes on underside of rock, 0.99 m. fixed and preserved in 95% ethanol. 27 Mar 2004. Sta. #2. Coll. R.Wetzer, N.D.Pentcheff, and LMU students. RW04.030	1149
<i>Exosphaeroma</i>		KU248206	Mexico, Baja California Sur, Gulf of California, Bahía de los Muertos, Boca del Alamo (local signage reads "Boca de Amo"), 23.895°N 109.803°W, from beneath rocks in high intertidal, usually found under those with thin coverage of <i>Ulva</i> , 15:00 hrs., fixed in 95% ethanol, preserved in 95% ethanol. 7 Oct 2003. UC Mexus station 29. Coll. T.A.Haney. RW03.285	782
<i>Exosphaeroma</i>		KU248191	New Zealand, South Island, Kaikoura, South Bay, Shark's Tooth, Atia Point, 42.24°S 173.41°E, off coralline algae, 2.5 m. Fixed in 100%, preserved in 95% ethanol. 19 Apr 2003. Coll. K. Merrin, rcvd. from N.L.Bruce. RW03.208	815
<i>Exosphaeroma</i>		KU248190	New Zealand, South Island, Kaikoura, Seal Reef, 42.24°S 173.41°E, intertidal rocks, fixed in 100%, preserved in 95% ethanol. 20 Apr 2003. Coll. K.Merrin, rcvd. from N.L.Bruce. RW03.204	816
<i>Exosphaeroma</i>	JF699542	KU248344	Australia, Victoria, Pt. Addis, 38.544°S 144.253°E, rocky intertidal, fixed and preserved in 95% ethanol. 26 Sep 1999. VIC108. Coll. R.Wetzer, G.Wilson, S.Keable. RW99.143	1164
<i>Exosphaeroma</i>	JF699543	KU248322	Atlantic, Namibia, south of Lüderitz, near Grossebucht (Big Bay), northern point, 0-5 m depth, ~26.38°S ~10.15°E, fixed and preserved in 95% ethanol. 29 Nov 1995. Coll. R.Brusca (PharmaMar Expedition). RW95.030	1168
<i>Exosphaeroma</i>	JF699544	KU248187	New Zealand, South Island, Kaikoura, Shark's Tooth, Atia Point, 42.24°S 173.41°E, intertidal, 2.5 m. Fixed in 100%, preserved in 95% ethanol. 19 Apr 2003. Coll. K.Merrin, rcvd. from N.L.Bruce. RW03.196	1504
<i>Exosphaeroma</i>	JF699545	KU248345	Australia, Victoria, Pt. Addis, 38.544°S 144.253°E, rocky intertidal, fixed and preserved in 95% ethanol. 26 Sep 1999. VIC108. Coll. R.Wetzer, G.Wilson, S.Keable. RW99.143	1507
<i>Exosphaeroma</i>	JF699546	KU248346	Australia, Victoria, Pt. Addis, 38.544°S 144.253°E, rocky intertidal, fixed and preserved in 95% ethanol. 26 Sep 1999. VIC108. Coll. R.Wetzer, G.Wilson, S.Keable. RW99.143	1511
<i>Exosphaeroma</i>	JF699547	KU248323	Atlantic, Namibia, south of Lüderitz, near Grossebucht (Big Bay), northern point, 0-5 m depth, ~26.38°S ~10.15°E, fixed and preserved in 95% ethanol. 29 Nov 1995. Coll. R.Brusca (PharmaMar Expedition). RW95.030	1521
<i>Exosphaeroma</i>	KU189323		Atlantic, Namibia, south of Lüderitz, near Grossebucht (Big Bay), northern point, 0-5 m depth, ~26.38°S ~10.15°E, fixed and preserved in 95% ethanol. 29 Nov 1995. Coll. R.Brusca (PharmaMar Expedition). RW95.030	1522
<i>Exosphaeroma</i>		KU248309	Pacific, Mexico, Baja California Norte, west of El Rosario, south of Bocana el Rosario, north of Punta Baja, 30.013°N 115.797°W, intertidal, sandy shore with rock outcropping, barnacle scrapplings, fixed and preserved in 95% ethanol. 9 May 2005. Coll. R.Wetzer and N.D.Pentcheff. RW05.106	1121
<i>Exosphaeroma aphrodita</i>		KU248167	Pacific, USA, California, San Diego County, La Jolla, Scripps Institute of Oceanography, beneath seaward end of Scripps Pier, ~32.5°N ~117.16°W, to 8 m, among detritus at base of pilings, water temp. 59 °F, SCUBA, fixed and preserved in 95%. 7 Jan 2001. Coll. T.Haney. RW01.002	1469

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<i>Exosphaeroma bruscai</i>		KU248207	Mexico, Baja California Sur, Gulf of California, Bahía de La Paz, western margin of bay, small embayment between El Saladito and Punta Tarabillas, 24.451°N 110.69°W, from beneath rocks in the high intertidal at northern end of a sandy beach, algal coverage sparse, only subtidal, 34.5 ppt, 10:00 hrs., hand, Fixed in 95% ethanol, preserved in 95% ethanol. 10 Oct 2003. UC Mexus station 43. Coll. T. A. Haney. RW03.286	780
<i>Exosphaeroma inornata</i>		KU248281	Pacific, USA, California, Los Angeles County, Palos Verdes Peninsula, Pt. Fermin, shore at Paseo del Mar, ~0.5 mi. W of Gaffey Street, 33.71°N 118.3°W, intertidal barnacle scrapings, fixed and preserved in 95% ethanol. 18 Sep 2004. Coll. R.Wetzer and D.Striley. RW04.255	1134
<i>Exosphaeroma inornata</i>		KU248212	Pacific, USA, California, Los Angeles County, Palos Verdes Peninsula, San Pedro, Pt. Fermin, shore at Paseo del Mar, ~0.5 mi. W of Gaffey Street, 33.71°N 118.3°W, mostly barnacles, some algal turf, medium to high intertidal, paint scrapper, Fixed and preserved in 95% ethanol. 16 Feb 2004. Coll. R. Wetzer. RW04.002	777
<i>Exosphaeroma obtusum</i>	JF699548	KU248317	New Zealand, Wellington region, Island Bay, rocky intertidal, coralline red algae, fixed and preserved in 95% ethanol. 15 May 2004. Coll. K.Merrin. RW05.311	1486
<i>Exosphaeroma obtusum</i>		KU248189	New Zealand, Wellington, Island Bay, ~41.17°S ~174.47°E, intertidal, rock platform, on <i>Colpomenia</i> , fixed in 100%, preserved in 95% ethanol. 17 Sep 2002. Coll. K. Merrin, rcvd. from N.L.Bruce. RW03.203	1499
<i>Exosphaeroma pentcheffi</i>		KU248282	Pacific, USA, California, Los Angeles County, Palos Verdes Peninsula, Pt. Fermin, shore at Paseo del Mar, ~0.5 mi. W of Gaffey Street, 33.71°N 118.3°W, intertidal barnacle scrapings, fixed and preserved in 95% ethanol. 18 Sep 2004. Coll. R.Wetzer and D.Striley. RW04.255	1470
<i>Exosphaeroma truncatitelson</i>	JF699549	KU248170	Atlantic, South Africa, Betty's Bay, 34.372°S 18.886°E, rocky intertidal, 0 m. fixed in 100%, preserved in 95% ethanol. 24 Jun 2002. Coll. S.R Daniels, N.L.Hoeson, and G.Gouws. RW02.042	1175
<i>Exosphaeroma truncatitelson</i>	JF699550	KU248327	Atlantic, Namibia, south of Lüderitz, Possession Island, inner shore., ~26.38°S ~10.15°E, 1-4 m depth, from dead kelp fronds, fixed and preserved in 95% ethanol. 5 Dec 1995. Coll. R.Wetzer/ R.C.Brusca (PharmaMar Expedition). RW95.040	1177
<i>Exosphaeroma truncatitelson</i>	JF699551	KU248328	Atlantic, Namibia, south of Lüderitz, Possession Island, inner shore., ~26.38°S ~10.15°E, 1-4 m depth, from dead kelp fronds, fixed and preserved in 95% ethanol. 5 Dec 1995. Coll. R.Wetzer/ R.C.Brusca (PharmaMar Expedition). RW95.040	1474
<i>Exosphaeroma varicolor</i>	JF699552	KU248272	Pacific, Chile, Coquimbo, ~29.57°S ~71.25°W, intertidal, under boulder, shell gravel, fixed and preserved in 95% ethanol. 17 Jun 2004. Coll. M.Thiel (Universidad Católica del Norte, Chile). RW04.206	1510
<i>Gnorimosphaeroma</i>	JF699553	KU248165	USA, California, San Mateo County, San Gregorio Creek, lagoon, just W of US Hwy, stream width 30-40m, fixed in 75%, preserved in 75% ethanol. 17 Oct 1999. CCS99-68. Coll. C.Swift, D.Jacobs, T.Haney. RW00.008	1174
<i>Gnorimosphaeroma noblei</i>	JF699554	KU248168	Pacific, California, Marin County, Tomales Bay, head of bay near channel (man-made) adjacent to Hwy. 1, 38.091°N 122.825°W, from under algae and barnacle covered rocks, salinity 20 ppt, fixed in 95%, preserved in 95% ethanol. 4 Jun 2002. Coll. R.Wetzer, S.Boyce, and T.Haney. RW02.021	1541



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<i>Gnorimosphaeroma oregonensis</i> *		AF260866	Pacific, British Columbia, University of British Columbia, nude, rocky intertidal, among mussels, fixed in 95%, preserved in 95% ethanol. 25 Jun 1998. Coll. T.J.Hilbish. RW98.033	324
<i>Gnorimosphaeroma oregonensis</i> *		AF260868	Pacific, USA, Washington, north end of Whidbey Island, Deception Pass, ~48.2°N ~122.4°W, rocky intertidal among mussels, fixed in 95%, preserved in 95% ethanol. 25 Jun 1998. Coll. T.J.Hilbish. RW98.031	391
<i>Gnorimosphaeroma oregonensis</i> *	JF699555	KU248217	Pacific, USA, Washington, westside of San Juan Island, Deadman Bay, 48.513°N 123.008°W, cobble/sand beach washes, fixed and preserved in 95% ethanol. 8 Apr 2004. #5. Coll. R.Wetzer and N.D.Pentcheff. RW04.038	1151
<i>Gnorimosphaeroma oregonensis</i> *	JF699556	KU248330	Pacific, USA, Washington, north end of Whidbey Island, Deception Pass, ~48.2°N ~122.4°W, rocky intertidal among mussels, fixed in 95%, preserved in 95% ethanol. 25 Jun 1998. Coll. T.J.Hilbish. RW98.031	1477
<i>Gnorimosphaeroma oregonensis</i> *	JF699557	KU248218	Pacific, USA, Washington, northeast of San Juan Island, Reuben Tarte County Park, 48.612°N 123.098°W, underside of rocks in intertidal, fixed and preserved in 95% ethanol. 9 Apr 2004. #7. Coll. R.Wetzer and N.D.Pentcheff. RW04.040	1496
<i>Harrieta faxonii</i> *	JF699558	KU248205	USA, Florida, Pensacola Bay, ~30.45°N ~87.217°W, fixed and preserved in 95% ethanol. 9 Mar 2003. Coll. W.Price, donated by M.Bakenhaster. RW03.259	1180
<i>Haswellia</i>	JF699559	KU248287	Australia, New South Wales, west side of North Tollgate Island, Bateman's Bay, 35.747°S 150.258°E, <i>Delisea pulchra</i> (alga), hand collected on scuba, 11 m. Fixed in 95% ethanol. 8 Feb 2003. P 65858, Project: Biodiversity of algal substrates. Coll. G.Wilson and P.Berents, NSW 2021. RW04.272	1193
<i>Haswellia</i>		KU248339	Australia, New South Wales, north west side of Brush Island, north of Bateman's Bay, 35.528°S 150.416°E, <i>Caulerpa flexilis</i> (alga), hand collected on scuba, 16.9 m. Fixed in 95% ethanol. 9 Feb 2003. P 65859, Project: Biodiversity of algal substrates. Coll. G.Wilson and P.Berents, NSW 2027. RW04.273	1415
<i>Haswellia carnea</i> *	KU867648		Australia, New South Wales, north west side of Brush Island, north of Bateman's Bay, 35.528°S 150.416°E, <i>Zonaria diesingiana</i> (alga), hand collected on scuba, 16.2 m. Fixed in 95% ethanol. 9 Feb 2003. P 65853, Project: Biodiversity of algal substrates. Coll. G.Wilson and P.Berents, NSW 2029. RW04.302	1421
<i>Heterodina</i>	JF699560		Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, inner reef lagoon, "Starfish", 3.994°S 39.745°E, rubble from base of bommies, snorkelling on low tide, 1 m. Fixed in 100%, preserved in 95% ethanol. 6 Jul 2004. #86. Coll. R.Wetzer, N.L.Bruce, and N.D.Pentcheff. RW04.139	1139
<i>Heterodina</i>	JF699561		Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, inner reef lagoon, "Starfish", 3.994°S 39.745°E, rubble from base of bommies, snorkelling on low tide, 1 m. Fixed in 100%, preserved in 95% ethanol. 6 Jul 2004. #86. Coll. R.Wetzer, N.L.Bruce, and N.D.Pentcheff. RW04.139	1548
<i>Heterodina</i>	JF699562	KU248251	Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, inner reef lagoon, "Starfish", 3.994°S 39.745°E, small finger rubble and coarse sand, snorkelling on low tide, 1 m. Fixed in 100%, preserved in 95% ethanol. 6 Jul 2004. #87. Coll. R.Wetzer, N.L.Bruce, and N.D.Pentcheff. RW04.140	1549

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<i>Heterodina</i>		KU248249	Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, inner reef lagoon, "Starfish", 3.994°S 39.745°E, small finger rubble and coarse sand, snorkelling on low tide, 1 m. Fixed in 100%, preserved in 95% ethanol. 6 Jul 2004. #87. Coll. R. Wetzer, N. L. Bruce, & N. D. Pentcheff. RW04.140	741
<i>Ischyromene cordiforaminalis</i>	JF699563	KU248296	New Zealand, North Island, Cape Palliser, 41.612°S 175.274°E, intertidal, mixed algae, encrusting algae, vertical rock face, fixed and preserved in 95% ethanol. 24 Nov 2003. Coll. N.L.Bruce and J.Olesen. RW04.335	1128
<i>Ischyromene huttoni</i>	JF699564		New Zealand, North Island, Wellington, Island Bay, 41.345°S 174.776°E, algae, fixed and preserved in 95% ethanol. 2 Oct 2003. Coll. N.L.Bruce and A.-N.Loerz. RW04.346	1492
<i>Ischyromene huttoni</i>	JF699565	KU248267	Pacific, Chile, Canal Darwin, 45.744°S 74.698°W, intertidal kelp holdfast, fixed and preserved in 95% ethanol. 10 Dec 2003. Coll. I.Hinojosa (Universidad Católica del Norte, Chile) rcvd. from M.Thiel July 2004. RW04.199	1517
<i>Ischyromene huttoni</i>	JF699566	KU248268	Pacific, Chile, Canal Darwin, 45.744°S 74.698°W, intertidal kelp holdfast, fixed and preserved in 95% ethanol. 10 Dec 2003. Coll. I.Hinojosa (Universidad Católica del Norte, Chile) rcvd. from M.Thiel July 2004. RW04.199	1518
<i>Ischyromene menziesi</i>	JF699527		Pacific, Chile, Coquimbo, ~29.57°S ~71.25°W, intertidal, under boulder, fixed and preserved in 95% ethanol. 17 Jun 2004. Coll. Martin Thiel (Universidad Católica del Norte, Chile). RW04.205	1140
<i>Ischyromene menziesi</i>	JF699567	KU248270	Pacific, Chile, Coquimbo, ~29.57°S ~71.25°W, intertidal, turf-algae, fixed and preserved in 95% ethanol. 17 Jun 2004. Coll. M.Thiel (Universidad Católica del Norte, Chile). RW04.203	1532
<i>Isocladus armatus*</i>		KU248303	New Zealand, North Island, Wairayaba coast, Castle Point, ~40.54°S ~176.15°E, fixed and preserved in 95% ethanol. 11 Jan 2004. Coll. A.-N.Loerz. RW04.350	663
<i>Isocladus armatus*</i>	JF699568	KU248302	New Zealand, North Island, Northlands, Matai Bay, northern inlet, ~35.5°S ~173.417°E, in sand pool, low tide, fixed and preserved in 95% ethanol. 4 Jan 2004. Coll. K.Merrin. RW04.348	1126
<i>Lekanesphaera hookeri</i>	AF279600		H.Dreyer and J.W.Wägele	989
<i>Lekanesphaera hookeri</i>	JF699569	KU248275	Greece, Patras, Peloponnisos, Araxos, spring in a brackish lake, ~37.833°N ~21.5°E, fixed and preserved in 95% ethanol. 22 Apr 2004. Coll. C.Fiser and R.Verovnik, donated by B.Sket, University Ljubljana. RW04.222	1529
<i>Makarasphaera amnicosa*</i>		KU248304	New Zealand, North Island, Wellington, Mabouie, Ohariu Bay, 41.219°S 174.706°E, fixed and preserved in 95% ethanol. 2 Jan 2004. Coll. N.L.Bruce. RW04.352	1125
<i>Monolistra caeca*</i>		KU248276	Slovenia, Videm-Dobrepoje, Podpec, Podpeska jama, ~45.5°N ~14°E, fixed and preserved in 95% ethanol. 12 May 2002. Coll. B.Sket, University Ljubljana. RW04.226	1183
<i>Monolistra caeca*</i>		KU248277	Slovenia, Videm-Dobrepoje, Podpec, Podpeska jama, ~45.5°N ~14°E, fixed and preserved in 95% ethanol. 12 May 2002. Coll. B.Sket, University Ljubljana. RW04.226	1503
<i>Neonaesa</i>		KU248233	Indian Ocean, Tanzania, Zanzibar, Ras Nungwi, northend of island, 5.713°S 39.312°E, coral reef, <i>Halimeda</i> , SCUBA, 10.67 m. Fixed and preserved in 95% ethanol. 27 Jun 2004. #36. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.087	756

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<i>Neonaesa</i>		KU248234	Indian Ocean, Tanzania, Zanzibar, Ras Nungwi, northend of island, 5.713°S 39.312°E, coral reef, <i>Halimeda</i> , SCUBA, 10.67 m. Fixed and preserved in 95% ethanol. 27 Jun 2004. #36. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.087	757
<i>Neonaesa</i>		KU248181	Pacific, Australia, Queensland, Lizard Island, Granite Bluff, northwest side of island, 14.651°S 145.45°E, SCUBA, 6.1 m. fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 22 Apr 2003. Sample #75. Coll. R. Wetzer and N. D. Pentcheff. RW03.184	832
<i>Neonaesa rugosa</i> *	JF699570	KU248229	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.216°S 39.149°E, coral rubble, SCUBA, 5.5 m. Fixed and preserved in 95% ethanol. 25 Jun 2004. #21. Coll. R.Wetzer, N.D.Pentcheff, N.L.Bruce. RW04.067	1187
<i>Neonaesa rugosa</i> *	JF699571	KU248180	Pacific, Australia, Queensland, Lizard Island, Yonge Reef, inner edge of southern tip, 14.614°S 145.628°E, algae from underside of ledge, SCUBA, 3.05 m. Fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 19 Apr 2003. Sample #62. Coll. R.Wetzer and N.D.Pentcheff. RW03.171	1192
<i>Neonaesa rugosa</i> *	JF699572	KU248311	Pacific, Fiji, fixed and preserved in 95% ethanol. NLB Sta. 19. Coll. N.L.Bruce. RW05.306	1483
<i>Neonaesa rugosa</i> *		KU248179	Pacific, Australia, Queensland, Heron Island northern side, seaward reef edge/crest, 23.434°S 151.926°E, " <i>Porolithion</i> " clumps, fixed in 100%, preserved in 95% ethanol. 14 Apr 2003. Sample #40. Coll. N.L.Bruce. RW03.152	1547
<i>Neonaesa rugosa</i> *	JF699573	KU248177	Pacific, Australia, Queensland, Heron Island, between "Canyons" and "Lost Mooring", 23.458°S 151.925°E, dead <i>Acropora</i> from base of bommie, SCUBA, 13.5 m. Fixed in 100%, preserved in 95% ethanol. 12 Apr 2003. Sample #19. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW03.128	1550
<i>Neosphaeroma laticaudum</i>		KU248289	Australia, New South Wales, Diamond Reef, south east of Hallidays Point, 32.091°S 152.552°E, orange sponge, hand collected on SCUBA, 17 m. Preserved in 95% ethanol. 21 Mar 2003. P 66313. Coll. RV Baragula, NSW 2216. RW04.291	1131
<i>Neosphaeroma laticaudum</i>	JF699574	KU248290	Australia, New South Wales, Diamond Reef, south east of Hallidays Point, 32.091°S 152.552°E, orange sponge, hand collected on SCUBA, 17 m. Preserved in 95% ethanol. 21 Mar 2003. P 66313. Coll. RV Baragula, NSW 2216. RW04.291	1500
<i>Neosphaeroma laticaudum</i>		KU248291	Australia, New South Wales, Diamond Reef, south east of Hallidays Point, 32.091°S 152.552°E, orange sponge, hand collected on SCUBA, 17 m. Preserved in 95% ethanol. 21 Mar 2003. P 66313. Coll. RV Baragula, NSW 2216. RW04.291	1513
<i>Oxinasphaera</i>		KU248259	Indian Ocean, Kenya, north of Mombasa, Mombasa Marine Park, buoy #3, 3.976°S 39.768°E, outer reef, medium mixed rubble on sand, SCUBA, 23.3 m. Fixed in 100%, preserved in 95% ethanol. 14 Jul 2004. #115. Coll. N.L.Bruce and N.D.Pentcheff. RW04.171	730
<i>Oxinasphaera</i>		KU248260	Indian Ocean, Kenya, north of Mombasa, Mombasa Marine Park, buoy #3, 3.976°S 39.768°E, outer reef, medium mixed rubble on sand, SCUBA, 23.3 m. Fixed in 100%, preserved in 95% ethanol. 14 Jul 2004. #115. Coll. N.L.Bruce and N.D.Pentcheff. RW04.171	731
<i>Oxinasphaera</i>		KU248227	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.216°S 39.149°E, brown spikey sponge, SCUBA, 5.5 m. Fixed and preserved in 95% ethanol. 25 Jun 2004. #19. Coll. N.L.Bruce. RW04.064	762

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<i>Oxinasphaera</i>		KU248225	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.216°S 39.149°E, smooth blue tubular sponge, SCUBA, 10.67 m. Fixed and preserved in 95% ethanol. 25 Jun 2004. #17. Coll. R.Wetzer. RW04.062	763
<i>Oxinasphaera lobivia</i>	JF699575	KU248313	Australia, Queensland, Amity Point, fixed and preserved in 95% ethanol. 1 Feb 2004. A804. Coll. A.N.Loerz. RW05.310	1489
<i>Oxinasphaera lobivia</i>	JF699576	KU248314	Australia, Queensland, Amity Point, fixed and preserved in 95% ethanol. 1 Feb 2004. A804. Coll. A.N.Loerz. RW05.310	1490
<i>Oxinasphaera penteumbonata</i>		KU248258	Indian Ocean, Kenya, north of Mombasa, Mombasa Marine Park, buoy #3, 3.976°S 39.768°E, outer reef, orange/red sponge, SCUBA, 17.07 m. Fixed in 100%, preserved in 95% ethanol. 12 Jul 2004. #99. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW04.153	732
<i>Oxinasphaera penteumbonata</i>		KU248231	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.216°S 39.149°E, assorted sponges, SCUBA, 9.14 m. Fixed and preserved in 95% ethanol. 25 Jun 2004. #22. Coll. R.Wetzer, N.D.Pentcheff, N.L.Bruce. RW04.068	760
<i>Oxinasphaera penteumbonata</i>		KU248222	Indian Ocean, Tanzania, Zanzibar, Bawi Island, northend, 6.145°S 39.137°E, sponges ( <i>Callyspongia</i> sp.), SCUBA, 7.62 m. Fixed in 100%, preserved in 95% ethanol. 23 Jun 2004. #10. Coll. N.D. Pentcheff and R.Wetzer. RW04.055	766
<i>Oxinasphaera tetrodon</i>		KU248248	Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, inner reef lagoon, "Starfish", 3.994°S 39.745°E, small finger rubble and coarse sand, snorkelling on low tide, 1 m. Fixed in 100%, preserved in 95% ethanol. 6 Jul 2004. #87. Coll. R. Wetzer, N. L. Bruce, & N. D. Pentcheff. RW04.140	740
<i>Oxinasphaera tetrodon</i>		KU248230	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.216°S 39.149°E, assorted sponges, SCUBA, 9.14 m. Fixed and preserved in 95% ethanol. 25 Jun 2004. #22. Coll. R.Wetzer, N.D.Pentcheff, N.L.Bruce. RW04.068	759
<i>Oxinasphaera tetrodon</i>		KU248226	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.216°S 39.149°E, brown spikey sponge, SCUBA, 5.5 m. Fixed and preserved in 95% ethanol. 25 Jun 2004. #19. Coll. N.L.Bruce. RW04.064	761
<i>Oxinasphaera tetrodon</i>		KU248221	Indian Ocean, Tanzania, Zanzibar, Bawi Island, northend, 6.145°S 39.137°E, sponges ( <i>Callyspongia</i> sp.), SCUBA, 7.62 m. Fixed in 100%, preserved in 95% ethanol. 23 Jun 2004. #10. Coll. N.D. Pentcheff and R.Wetzer. RW04.055	765
<i>Oxinasphaera tetrodon</i>		KU248250	Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, inner reef lagoon, "Starfish", 3.994°S 39.745°E, small finger rubble and coarse sand, snorkelling on low tide, 1 m. Fixed in 100%, preserved in 95% ethanol. 6 Jul 2004. #87. Coll. R.Wetzer, N.L.Bruce, and N.D.Pentcheff. RW04.140	1138
<i>Oxinasphaera tetrodon</i>	JF699577	KU248228	Indian Ocean, Tanzania, Zanzibar, Murogo Island reef, 6.216°S 39.149°E, coral rubble, SCUBA, 5.5 m. Fixed and preserved in 95% ethanol. 25 Jun 2004. #21. Coll. R.Wetzer, N.D.Pentcheff, N.L.Bruce. RW04.067	1142
<i>Paracassidina dama</i>	KU189318		Australia, Queensland, Moreton Bay, 10 m. Fixed and preserved in 95% ethanol. 14 Feb 2005. A802. RW05.309	1377



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<i>Paracassidina dama</i>	KU189322		Australia, Queensland, Moreton Bay, 10 m. Fixed and preserved in 95% ethanol. 14 Feb 2005. A802. RW05.309	1488
<i>Paracassidinopsis perlata</i>		KU248235	Indian Ocean, Tanzania, Zanzibar, Ras Nungwi, northend of island, 5.713°S 39.312°E, coral reef, <i>Halimeda</i> , SCUBA, 10.67 m. Fixed and preserved in 95% ethanol. 27 Jun 2004. #36. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.087	1519
<i>Paracassidinopsis perlata</i>	JF699578	KU248241	Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, outer reef flat, 4.002°S 39.748°E, outer edge of the reef crest, <i>Halimeda</i> wash, fixed in 100%, preserved in 95% ethanol. 3 Jul 2004. #68. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.121	1536
<i>Paracerceis</i>	JF699579	KU248173	Mexico, Baja California Sur, Gulf of California, ~22.9°N ~109.95°W, CAS 25272. RW02.116	1176
<i>Paracerceis glynni</i>	AY743958		Sequence contributed: C.C.Babbit and N.H.Patel	968
<i>Paracerceis sculpta</i>		KU248283	USA, California, Los Angeles County, Marina del Rey, 33.977°N 118.442°W, fouling organisms and sponges on floating dock, 3 m. Fixed and preserved in RNALater. 20 Sep 2004. Coll. R.Wetzer and N.D.Pentcheff. RW04.258	1133
<i>Paracerceis sculpta</i>	JF699580	KU248331	Mexico, Sonora, Guaymas, Punta Colorado, from <i>Lucetta losangelensis</i> at low tide, ~27.95°N ~110.883°W, probably fixed in 95%, preserved in 70% ethanol. 12 Feb 1995, received from S.M.Shuster, Jan. 1999. Coll. C.J.Navarro. RW99.024	1169
<i>Paracilicaea</i>		KU248247	Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, inner reef lagoon, "Starfish", 3.994°S 39.745°E, small finger rubble and coarse sand, snorkelling on low tide, 1 m. Fixed in 100%, preserved in 95% ethanol. 6 Jul 2004. #87. Coll. R.Wetzer, N.L.Bruce, and N.D.Pentcheff. RW04.140	739
<i>Paracilicaea mossambica</i>		KU248257	Indian Ocean, Kenya, north of Mombasa, Kanamai Beach, 3.922°S 39.793°E, outer reef edge, barnacles knocked off rocks, fixed in 100%, preserved in 95% ethanol. 7 Jul 2004. #98. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW04.152	734
<i>Paracilicaea mossambica</i>		KU248254	Indian Ocean, Kenya, north of Mombasa, Kanamai Beach, 3.922°S 39.793°E, outer reef edge, <i>Codium</i> washes, fixed in 100%, preserved in 95% ethanol. 7 Jul 2004. #96. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW04.149	735
<i>Paracilicaea mossambica</i>		KU248240	Indian Ocean, Kenya, Mombasa, N. of Giriama Beach Hotel within Marine Park boundary, outer reef flat, 4.002°S 39.748°E, outer edge of the reef crest, <i>Halimeda</i> wash, fixed in 100%, preserved in 95% ethanol. 3 Jul 2004. #68. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.121	750
<i>Paracilicaea mossambica</i>	JF699581	KU248255	Indian Ocean, Kenya, north of Mombasa, Kanamai Beach, 3.922°S 39.793°E, outer reef edge, <i>Codium</i> washes, fixed in 100%, preserved in 95% ethanol. 7 Jul 2004. #96. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW04.149	1143
<i>Paracilicaea uncinata</i>		KU248245	Indian Ocean, Kenya, Mombasa, Mama Ngina, inner reef fringe, adjacent to navigation buoy, 4.077°S 39.676°E, barnacle wash, fixed in 100%, preserved in 95% ethanol. 4 Jul 2004. #72. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.125	747
<i>Paradella</i>		KU248335	Locality unknown, received from S.Shuster, Jan 1999. RW99.065	411

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<i>Paradella diana</i>		KU248334	Locality unknown, received from S.Shuster, Jan 1999. RW99.064	410
<i>Paradella garsonorum</i>		KU248211	Mexico, Baja California Sur, Gulf of California, Ensenada de los Muertos (aka Bahía de los Suenos), from beach in front of "Giggling Marlin Yacht Club", 23.994°N 109.826°W, from beneath large rocks on/in coarse sand in the mid-intertidal zone, salinity 34ppt, 12:00 hrs., fixed in 95% ethanol, preserved in 95% ethanol. 6 Oct 2003. UC Mexus station 27. Coll. T.A.Haney. RW03.288	783
<i>Paradella garsonorum</i>	JF699582	KU248310	Mexico, Gulf of California, Baja California Sur, Bahia Concepcion, eastside of bay, south of San Ignacio, 26.656°N 111.747°W, rocky intertidal, barnacle covered rocks scrapped and washed, 0 m. Fixed and preserved in 95% ethanol. 12 May 2005. Coll. R.Wetzer. RW05.110	1120
<i>Paradella garsonorum</i>	JF699583	KU248192	Mexico, Sea of Cortez, Baja California Norte, Campo Linares, south of Campo Christina, north of Puertocitos, 30.471°N 114.634°W, intertidal barnacles, fixed and preserved in 95% ethanol. 2 Aug 2003. Coll. R.Wetzer. RW03.223	1542
<i>Paradella harrisoni</i>		KU248256	Indian Ocean, Kenya, north of Mombasa, Kanamai Beach, 3.922°S 39.793°E, outer reef edge, barnacles knocked off rocks, fixed in 100%, preserved in 95% ethanol. 7 Jul 2004. #98. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW04.152	733
<i>Paradella harrisoni</i>		KU248252	Indian Ocean, Kenya, north of Mombasa, Kanamai Beach, 3.922°S 39.793°E, outer reef edge, barnacle, rock, fixed in 100%, preserved in 95% ethanol. 7 Jul 2004. #91. Coll. R.Wetzer, N.L.Bruce, N.D.Pentcheff. RW04.144	738
<i>Paradella harrisoni</i>		KU248244	Indian Ocean, Kenya, Mombasa, Mama Ngina, inner reef fringe, adjacent to navigation buoy, 4.077°S 39.676°E, barnacle wash, fixed in 100%, preserved in 95% ethanol. 4 Jul 2004. #72. Coll. R.Wetzer, N.D.Pentcheff and N.L.Bruce. RW04.125	746
<i>Paraimene</i>	JF699584	KU248264	Indian Ocean, Kenya, Mombasa, Ras Iwetine, 4.018°S 39.731°E, intertidal algal turf scrapings, fixed in 100%, preserved in 95% ethanol. 15 Jul 2004. #119. Coll. R.Wetzer. RW04.175	1538
<i>Paraimene tumulus</i>		KU248213	Atlantic, Costa Rica, Limon Province, Puerto Viejo, near shore in front of "Restaurant Stanford", 9.667°N 82.75°W, algae, intertidal, 1 m. Fixed and preserved in 75% ethanol. 20 Aug 1987. LACM 87-162. Coll. G.Bassey. RW04.025	775
<i>Paraleptosphaeroma brucei</i>	KU867647		Singapore, Beting Bronok, Tekong Besar patch reef (northeast of Singapore), 1.433°N 104.022°E, mud, gravel and patch reef exposed at 0 ft. tide, assorted rock and sponge washes, retained on 240µm mesh net, fixed and preserved in 95% ethanol. 27 Oct 2003. Coll. N.L.Bruce and R.Wetzer. RW03.254	1404
<i>Parisocladius perforatus</i>	JF699585	KU248325	Atlantic, Namibia, Lüderitz Harbor, oyster farm (site #1) and shipwreck (site#2), 0.1-3 m depth, ~26.38°S ~10.15°E, collections made from surface by hauling oyster racks/mussel ropes to surface, fixed and preserved in 95% ethanol. 7 Dec 1995. Coll. R.Wetzer (PharmaMar Expedition). RW95.038	1471
<i>Pistorius bidens*</i>	JF699586		Indian Ocean, Kenya, south shore, Shimoni, in front KWS office, 4.647°S 39.378°E, oyster scrapings from mangrove, fixed in 100%, preserved in 95% ethanol. 16 Jul 2004. #131. Coll. R.Wetzer, N.D.Pentcheff, N.L.Bruce. RW04.188	1147
<i>Pistorius bidens*</i>	KU189320		Pacific, Australia, Queensland, Heron Island, in front of research lab, 23.444°S 151.916°E, high intertidal beach rock, crevices under slab rock, fixed in 100%, preserved in 95% ethanol. 12 Apr 2003. Sample #17. Coll. N.L.Bruce. RW03.126	1478

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<i>Pistorius bidens</i> *	KU189321		Pacific, Australia, Queensland, Heron Island, in front of research lab, 23.444°S 151.916°E, high intertidal beach rock, crevices under slab rock, fixed in 100%, preserved in 95% ethanol. 12 Apr 2003. Sample #17. Coll. N.L.Bruce. RW03.126	1479
<i>Pistorius bidens</i> *	JF699587		Pacific, Australia, Queensland, Heron Island, in front of research lab, 23.444°S 151.916°E, high intertidal beach rock, crevices under slab rock, fixed in 100%, preserved in 95% ethanol. 12 Apr 2003. Sample #17. Coll. N.L.Bruce. RW03.126	1527
<i>Pistorius bidens</i> *	KU867650		Pacific, Australia, Queensland, Heron Island, in front of research lab, 23.444°S 151.916°E, high intertidal beach rock, crevices under slab rock, fixed in 100%, preserved in 95% ethanol. 12 Apr 2003. Sample #17. Coll. N.L.Bruce. RW03.126	1528
<i>Plakarthrium punctatissimum</i>		PPU269815	C.Held	1027
<i>Plakarthrium typicum</i> *	JF699516		New Zealand, North Island, Cape Palliser, 41.612°S 175.274°E, intertidal, mixed algae and under rocks, fixed and preserved in 95% ethanol. 24 Nov 2003. Coll. N.L.Bruce and J.Olesen. RW04.343	1441
<i>Plakarthrium typicum</i> *	JF699517		New Zealand, North Island, Cape Palliser, 41.612°S 175.274°E, intertidal, mixed algae and under rocks, fixed and preserved in 95% ethanol. 24 Nov 2003. Coll. N.L.Bruce and J.Olesen. RW04.343	1523
<i>Platynympha</i>		KU248306	Australia, South Australia, ~34.933°S ~138.667°E, probably fixed and preserved in 95%. Coll. Kirstin Ross via Matthew Yoder, rcvd. 10/2004. RW04.379	1515
<i>Platysphaera</i>		KU248342	Pacific, Australia, Queensland, Lizard Island, southern end of Yonge Reef, 14.62°S 145.62°E, coral head, SCUBA, 7.32 m. Fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 19 Apr 2003. Sample #70. Coll. R.Wetzer and N.D.Pentcheff. RW03.178	1418
<i>Pseudocerceis</i>	JF699588	KU248338	Pacific, Australia, Queensland, Heron Island northern side, mid-reef flat, 23.436°S 151.926°E, <i>Halimeda</i> , fixed in 100%, preserved in 95% ethanol. 14 Apr 2003. Sample #39. Coll. R.Wetzer and N.D.Pentcheff. RW03.151	1414
<i>Pseudocerceis furculata</i> *	KU867649		Pacific, Australia, Queensland, Heron Island northern side, seaward reef edge/crest, 23.434°S 151.927°E, rock wash, fixed in 100%, preserved in 95% ethanol. 14 Apr 2003. Sample #41. Coll. R.Wetzer and N.D.Pentcheff. RW03.153	1545
<i>Pseudosphaeroma campbellense</i> *	JF699589	KU248297	New Zealand, North Island, Evans Bay, 41.303°S 174.805°E, algae on barnacles, fixed and preserved in 95% ethanol. 30 Apr 2004. Coll. N.L.Bruce. RW04.336	1127
<i>Pseudosphaeroma lundae</i>		KU248269	Pacific, Chile, near Concepcion, Chome, ~36.5°S ~73.03°W, intertidal, under boulder, fixed and preserved in 95% ethanol. 14 Mar 2004. Coll. Martin Thiel (Universidad Católica del Norte, Chile). RW04.200	1506
<i>Pseudosphaeroma lundae</i>	JF699590		Pacific, Chile, near Concepcion, Chome, ~36.5°S ~73.03°W, intertidal, under boulder, fixed and preserved in 95% ethanol. 14 Mar 2004. Coll. M.Thiel (Universidad Católica del Norte, Chile). RW04.200	1410
<i>Pseudosphaeroma lundae</i>	JF699591		Pacific, Chile, near Concepcion, Chome, ~36.5°S ~73.03°W, intertidal, under boulder, fixed and preserved in 95% ethanol. 14 Mar 2004. Coll. M.Thiel (Universidad Católica del Norte, Chile). RW04.200	1506

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<i>Scutuloidea</i>	KU189319		New Zealand, Wellington, Island Bay, ~41.17°S ~174.47°E, from intertidal coralline algae, probably fixed in isopropyl and preserved in 95% ethanol. 30 Apr 2002. Coll. K.Merrin and N.L.Bruce. RW03.194	1425
<i>Scutuloidea maculata*</i>	JF699592	KU248293	New Zealand, North Island, Cape Palliser, 41.612°S 175.274°E, intertidal, mixed algae, and under rocks, fixed and preserved in 95% ethanol. 24 Nov 2003. Coll. N.L.Bruce and J.Olesen. RW04.326	1190
<i>Sphaeramene polytylotos*</i>		AF259540	Atlantic, Namibia, south of Lüderitz, near Grossebucht (Big Bay), northern point, 0-5 m depth, ~26.38°S ~10.15°E, fixed and preserved in 95% ethanol. 29 Nov 1995. Coll. R.Brusca (PharmaMar Expedition). RW95.030	183
<i>Sphaeramene polytylotos*</i>		KU248326	Atlantic, Namibia, Lüderitz Harbor, oyster farm (site #1) and shipwreck (site#2), 0.1-3 m depth, ~26.38°S ~10.15°E, collections made from surface by hauling oyster racks/mussel ropes to surface, fixed and preserved in 95% ethanol. 7 Dec 1995. Coll. R.Wetzer (PharmaMar Expedition). RW95.038	1472
<i>Sphaeramene polytylotos*</i>		KU248324	Atlantic, Namibia, south of Lüderitz, near Grossebucht (Big Bay), northern point, 0-5 m depth, ~26.38°S ~10.15°E, fixed and preserved in 95% ethanol. 29 Nov 1995. Coll. R.Brusca (PharmaMar Expedition). RW95.030	1552
<i>Sphaeramene polytylotos*</i>	KU189315		Locality unknown, received from S. Shuster, probably fixed in 95%, preserved in 70% ethanol. 1 Jan 1999. RW99.034	777
<i>Sphaeroma</i>		STE388075	A. Michel-Salzat and D.Bouchon	1043
<i>Sphaeroma</i>	JF699593	KU248329	Atlantic, South Carolina, Pritchard's Island, north end, ~32.417°N ~80.667°W, fixed and preserved in 95% ethanol. 3 Oct 1997. Coll. R.Wetzer. RW97.005	1473
<i>Sphaeroma</i>		EF460860	M.Baratti, M.T.Filippelli, and G.Messana	1601
<i>Sphaeroma</i>		EF460853	M.Baratti, M.T.Filippelli, and G.Messana	1608
<i>Sphaeroma</i>		EF460852	M.Baratti, M.T.Filippelli, and G.Messana	1609
<i>Sphaeroma</i>		KU248204	USA, Florida, Pensacola Bay, ~30.45°N ~87.217°W, fixed and preserved in 95% ethanol. 9 Mar 2003. Coll. Wayne Price, donated by Micah Bakenhaster. RW03.259	788
<i>Sphaeroma quadridentatum</i>		KU248332	Locality unknown, received from S.Shuster, Jan 1999, RW99.062	408
<i>Sphaeroma quoyanum</i>		KU248333	Locality unknown, received from S.Shuster, Jan 1999, RW99.063	409
<i>Sphaeroma serratum*</i>	AF255694		H.Dreyer and J.W.Wägele	973
<i>Sphaeroma serratum*</i>		SSE388074	A.Michel-Salzat and D.Bouchon	1042
<i>Sphaeroma serratum*</i>	JF699594	KU248278	Atlantic, Portugal, Algarve, Ferragudo, ~37.07°N ~8.31°W, fixed and preserved in 95% ethanol. 27 Mar 2004. Coll. C.d'Udekem d'Acoz. RW04.229	1135
<i>Sphaeroma terebrans</i>		KU248193	Atlantic, USA, South Carolina, Combahee River, 32.672°N 80.713°W, rotting wood at low tide line, 0 salinity, 27°C, fixed and preserved in 95% ethanol. 1 Jul 2003. T30030010. Coll. D.Knott, R.King, S.deVictor. RW03.225	812
<i>Sphaeroma terebrans</i>		EF460859	M.Baratti, M.T.Filippelli, and G.Messana	1602



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<i>Sphaeroma terebrans</i>		EF460858	M.Baratti, M.T.Filippelli, and G.Messana	1603
<i>Sphaeroma terebrans</i>		EF460857	M.Baratti, M.T.Filippelli, and G.Messana	1604
<i>Sphaeroma terebrans</i>		EF460856	M.Baratti, M.T.Filippelli, and G.Messana	1605
<i>Sphaeroma terebrans</i>		EF460855	M.Baratti, M.T.Filippelli, and G.Messana	1606
<i>Sphaeroma terebrans</i>		EF460854	M.Baratti, M.T.Filippelli, and G.Messana	1607
<i>Sphaeroma terebrans</i>		EF445550	M.Baratti, M.T.Filippelli, and G.Messana	1610
<i>Sphaeroma walkeri</i>		KU248199	Singapore, Marina Bay, ~1.333°N ~104°E, mooring buoy, fixed and preserved in 95% ethanol. 7 Oct 2003. Donated by TMSI Lab. Coll. CYX, TKS, LSC. RW03.236	807
<i>Sphaeroma walkeri</i>		KU248198	Singapore, south side of island, Republic of Singapore Yacht Club, 1.294°N 103.76°E, from floating dock in marina, dead barnacle tests on settlement panels submerged 0.5 m below surface, retained on 240µm mesh net, fixed and preserved in 95% ethanol. 21 Oct 2003. Coll. R.Wetzer and N.L.Bruce. RW03.232	808
<i>Sphaeromopsis</i>	JF699595	KU248285	Pacific, Ecuador, Salinas, ~2.15°S ~80.58°W, sand, fixed and preserved in 100% ethanol. 10 Mar 2004. RC#113. Coll. Donated by L.Dominguez G. rcvd. 9/28/04. RW04.266	1185
<i>Sphaeromopsis</i>	JF699596	KU248284	Pacific, Ecuador, Data, ~2.13°S ~79.54°W, sand, fixed and preserved in 70% ethanol. 4 Feb 2004. RC#113. Coll. Donated by L.Dominguez G. RW04.264	1497
<i>Sphaeromopsis</i>	JF699597	KU248286	Pacific, Ecuador, Salinas, ~2.15°S ~80.58°W, sand, fixed and preserved in 100% ethanol. 10 Mar 2004. RC#113. Coll. Donated by L.Dominguez G. rcvd. 9/28/04. RW04.266	1498
<i>Sphaeromopsis amathitis*</i>		KU248262	Indian Ocean, Kenya, Mombasa, Giriama Beach Hotel, in front of hotel, 4.007°S 39.727°E, high intertidal sand, sieve, fixed in 100%, preserved in 95% ethanol. 15 Jul 2004. #118. Coll. N.L.Bruce. RW04.174	729
<i>Sphaeromopsis amathitis*</i>		KU248243	Indian Ocean, Kenya, Mombasa, Giriama Beach Hotel, 4.007°S 39.727°E, intertidal sand, fixed in 100%, preserved in 95% ethanol. 4 Jul 2004. #70. Coll. N.L.Bruce. RW04.123	748
<i>Sphaeromopsis amathitis*</i>		KU248219	Indian Ocean, Tanzania, Zanzibar, Bawi Island, northend, exposed at low tide, 6.146°S 39.133°E, high intertidal, algal turf scrappings, fixed in 100%, preserved in 95% ethanol. 22 Jun 2004. #2. Coll. R.Wetzer and N.D. Pentcheff. RW04.047	768
<i>Sphaeromopsis amathitis*</i>	JF699598	KU248220	Indian Ocean, Tanzania, Zanzibar, Bawi Island, northend, exposed at low tide, 6.146°S 39.133°E, high intertidal, algal turf scrappings, fixed in 100%, preserved in 95% ethanol. 22 Jun 2004. #2. Coll. R.Wetzer and N.D. Pentcheff. RW04.047	1182
<i>Sphaeromopsis amathitis*</i>	JF699599	KU248263	Indian Ocean, Kenya, Mombasa, Giriama Beach Hotel, in front of hotel, 4.007°S 39.727°E, high intertidal sand, sieve, fixed in 100%, preserved in 95% ethanol. 15 Jul 2004. #118. Coll. N.L.Bruce. RW04.174	1509
<i>Sphaeromopsis serriguberna</i>	KU867646		Pacific, Australia, Queensland, Lizard Island, Trawler Beach, 14.68°S 145.463°E, edge of mangroves, top 1 cm of coarse quartz sand, fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 21 Apr 2003. Sample #73. Coll. R.Wetzer and N.D.Pentcheff. RW03.181	1188

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<i>Sphaeromopsis serriguberna</i>	JF699600		Pacific, Australia, Queensland, Lizard Island, Trawler Beach, 14.68°S 145.463°E, edge of mangroves, top 1 cm of coarse quartz sand, fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 21 Apr 2003. Sample #73. Coll. R.Wetzer and N.D.Pentcheff. RW03.181	1512
<i>Striella</i>	JF699601	KU248208	Mexico, Baja California Sur, Gulf of California, Bahía de La Paz, western margin of bay, small embayment between El Saladito and Punta Tarabillas, 24.451°N 110.69°W, from beneath rocks in the high intertidal at northern end of a sandy beach, algal coverage sparse, only subtidal, 34.5 ppt, 10:00 hrs., fixed in 95% ethanol, preserved in 95% ethanol. 10 Oct 2003. UC Mexus station 43. Coll. T.A.Haney. RW03.286	1148
<i>Striella</i>	JF699602	KU248209	Mexico, Baja California Sur, Gulf of California, Bahía de La Paz, western margin of bay, small embayment between El Saladito and Punta Tarabillas, 24.451°N 110.69°W, from beneath rocks in the high intertidal at northern end of a sandy beach, algal coverage sparse, only subtidal, 34.5 ppt, 10:00 hrs., fixed in 95% ethanol, preserved in 95% ethanol. 10 Oct 2003. UC Mexus station 43. Coll. T.A.Haney. RW03.286	1524
<i>Striella</i>	JF699603	KU248210	Mexico, Baja California Sur, Gulf of California, Bahía de La Paz, western margin of bay, small embayment between El Saladito and Punta Tarabillas, 24.451°N 110.69°W, from beneath rocks in the high intertidal at northern end of a sandy beach, algal coverage sparse, only subtidal, 34.5 ppt, 10:00 hrs., fixed in 95% ethanol, preserved in 95% ethanol. 10 Oct 2003. UC Mexus station 43. Coll. T.A.Haney. RW03.286	1525
<i>Thermosphaeroma</i>		KU248336	Locality unknown, specimen received from S.Shuster, Jan 1999. RW99.066	412
<i>Thermosphaeroma cavacauda</i>		KU248339	Locality unknown, specimen received from S.Shuster, Jan 1999. RW99.069	415
<i>Thermosphaeroma dugesi*</i>		KU248343	Locality unknown, specimen received from S.Shuster, Jan 1999. RW99.073	419
<i>Thermosphaeroma macrura</i>		KU248340	Mexico, Chihuahua, 0.5 km S. of Julimes, received from S.Shuster, Jan 1999. RW99.070	416
<i>Thermosphaeroma milleri</i>		KU248337	Mexico, Chihuahua, Ejido Rancho Nuevo, received from S.Shuster, Jan 1999. RW99.067	413
<i>Thermosphaeroma smithi</i>		KU248341	Mexico, Chihuahua, Balneario San Diego, received from S.Shuster, Jan 1999. RW99.071	417
<i>Thermosphaeroma subequalum</i>		KU248342	USA, Texas, Big Bend National Park, Boquillas Canyon, received from S.Shuster, Jan 1999. RW99.072	418
<i>Thermosphaeroma subequalum</i>	KU189316		USA, Texas, Big Bend National Park, Rio Grande Village #1 pump station, ~29.17°N ~103.17°W, probably fixed in 95%, preserved in 70% ethanol. 2 Sep 1988. Coll. S.M.Shuster. RW99.029	1172
<i>Thermosphaeroma thermophilum</i>		KU248338	USA, New Mexico, Socorro, thermal springs, received from S.Shuster, Jan 1999. RW99.068	414
<i>Zuzara</i>		KU248188	Australia, Victoria, Melbourne, Holloway Bend, N. E. of Green Point, Brighton, ~37.45°S ~144.58°E, fixed in 100%, preserved in 95% ethanol. 1 Jan 2003. Coll. K. Merrin, rcvd. from N.L.Bruce. RW03.200	818
<i>Zuzara</i>	JF699604	KU248347	Australia, South Australia, Ceduna, behind Budget Motel, 32.115°S 133.67°E, under rocks, rock washings, sand sievings, 0 m. Fixed and preserved in 95% ethanol. 18 Sep 1999. Coll. G. Wilson, R.Wetzer, S.Keable. RW99.147	1197

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<i>Zuzara digitata</i>		KU248184	Pacific, Australia, Queensland, north of Mossman, "Rocky Point", 16.387°S 145.419°E, black rock cobble beach, in algae at mid-low tide, fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 29 Apr 2003. Sample #77. Coll. R.Wetzer and N.D.Pentcheff. RW03.186	829
<i>Zuzara digitata</i>	JF699605	KU248185	Pacific, Australia, Queensland, north of Mossman, "Rocky Point", 16.387°S 145.419°E, black rock cobble beach, in algae at mid-low tide, fixed in 95% ethanol containing a trace of methanol, preserved in 95% ethanol. 29 Apr 2003. Sample #77. Coll. R.Wetzer and N.D.Pentcheff. RW03.186	1195

## Electronic Supplement File 2. Available family-group names in the Sphaeromatidae.

1. Campecopini Hansen, 1905 (tribe)
2. Cassidininae Hansen, 1905 (subfamily by IVERSON 1982)
3. Cymodocini Hansen, 1905 (tribe)
4. Dynameninae Bowman, 1981
5. Monolistrini Hansen, 1905 (tribe)
6. Sphaeromatinae Latreille, 1825
7. Ancinidae Dana, 1852 (separate family by BRUCE 1993)
8. Tecticipitidae Iverson, 1982 (separate family by BRUCE 1993)

**Note:** Hansen's names have priority, so depending where the type species fall one or other of those names may take precedence over Dynameninae Bowman, 1982. Equally some of these names may be validated following a phylogenetic review on the Sphaeromatidae (e.g. for well-supported and distinct clades such as *Ischyromene*-group or *Cerceis*-group for example).

Bowman's name is correctly proposed given that within the Eubranchiatae there were no family-level names, the others being under the Hemibranchiatae (= Sphaeromatini) or Platybranchiatae (later using one of the available names, Cassidininae)

But ICZN Art. 35.5 states that a family-group name that is older will not displace a younger higher-level name that is in prevailing usage. Prevailing usage will be hard to demonstrate (and may not be defined in *The Code* as the names are in general little used anyway – except perhaps for Dynameninae).

Dynameninae usage: IVERSON 1982; MESSANA 1988, 1990; HARRISON & ELLIS 1991; BRUCE 1993; POORE & BRANDT 2001 (discussion); so fairly well used, if not by NLB or by sphaeromatid taxonomists.

Cassidininae usage far less, seemingly little after BRUCE 1994.



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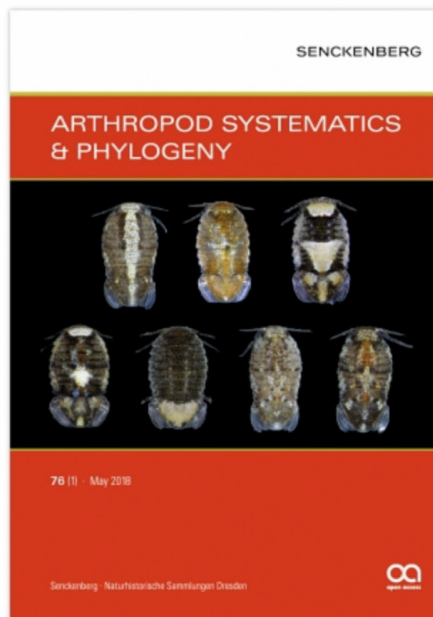
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