A family-level Tree of Life for bivalves based on a Sanger-sequencing approach

David J. Combosch ^a, Timothy M. Collins ^b, Emily A. Glover ^c, Daniel L. Graf ^d, Elizabeth M. Harper ^e, John M. Healy ^f, Gisele Y. Kawauchi ^{a,g}, Sarah Lemer ^a, Erin McIntyre ^a, Ellen E. Strong ^h, John D. Taylor ^c, John D. Zardus ⁱ, Paula M. Mikkelsen ^j, Gonzalo Giribet ^{a,c,j,*}, Rüdiger Bieler ^{j,*}

^a *Museum of Comparative Zoology, Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA*

^b *Department of Biological Sciences, Florida International University, Miami, Florida 33199, USA*

^c *Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*

^d *Biology Department, University of Wisconsin-Stevens Point, 800 Reserve Street, Stevens Point, Wisconsin 54481, USA*

^e *Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, UK*

^f *Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia*

^g *Zoology Department, Universidade Federal de Minas Gerais, Brazil*

^h *Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, PO Box 37012, MRC 163, Washington, DC 20013, USA*

ⁱ *Department of Biology, The Citadel, 171 Moultrie Street, Charleston, South Carolina 29409, USA*

^j *Integrative Research Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA*

* Co-corresponding authors

ABSTRACT

The systematics of the molluscan class Bivalvia are explored using a 5-gene Sanger-based approach including the largest taxon sampling to date, encompassing 219 ingroup species spanning 93 (or 82%) of the 113 currently accepted bivalve families. This study was designed to populate the bivalve Tree of Life at the family level and to place many genera into a clear phylogenetic context, but also pointing to several major clades where taxonomic work is sorely needed. Despite not recovering monophyly of Bivalvia or Protobranchia—as in most previous Sanger-based approaches to bivalve phylogeny—our study provides increased resolution in many higher-level clades, and supports the monophyly of Autobranchia, Pteriomorphia, Heteroconchia, Palaeoheterodonta, Heterodonta, Archiheterodonta, Euheterodonta, Anomalodesmata, Imparidentia, and Neoheterodonte, in addition to many other lower clades. However, deep nodes within some of these clades, especially Pteriomorphia and Imparidentia, could not be resolved with confidence. In addition, many families are not supported, and several are supported as non-monophyletic, including Malletiidae, Nuculanidae, Yoldiidae, Malleidae, Pteriidae, Arcidae, Propeamussiidae, Iridinidae, Carditidae, Myochamidae, Lyonsiidae, Pandoridae, Montacutidae, Galeommatidae, Tellinidae, Semelidae, Psammobiidae, Donacidae, Mactridae, and Cyrenidae; Veneridae is paraphyletic with respect to Chamidae, although this result appears to be an artifact. The denser sampling however allowed testing specific placement of species, showing, for example, that the unusual Australian *Plebidonax deltoides* is not a member of Donacidae and instead nests within Psammobiidae, suggesting that major revision of Tellinoidea may be required. We also showed that *Cleidothaerus* is sister group to the cementing member of Myochamidae, suggesting that Cleidothaeridae may not be a valid family and that cementation in *Cleidothaerus* and *Myochama* may have had a single origin. These results highlight the need for an integrative approach including as many genera as possible, and that the monophyly and relationships of many families require detailed reassessment. NGS approaches may be able to resolve the most recalcitrant nodes in the near future.

1. Introduction

After decades of intense work by anatomists, paleontologists, and molecular biologists (e.g., Newell and Boyd, 1978; Popham, 1979; Steiner and Müller, 1996; Waller, 1998; Carter et al., 2000; Cope, 2000; Giribet and Wheeler, 2002; Giribet and Distel, 2003), the systematics of bivalves is stabilizing and we are beginning to see a resolved 'phylogenetic backbone' for the group, a prerequisite for any meaningful discussion of evolutionary pattern and process (Bieler et al., 2013). Several recent landmark papers on relationships within the class as a whole include large-scale Sanger-based molecular studies (e.g., Sharma et al., 2012), mitogenomic analyses (e.g., Plazzi et al., 2013), and a combination of Sanger-based sequences with an extensive morphological data matrix using an exemplar-based approach (Bieler et al., 2014), as well as the first Illumina-based phylogenomic analysis (González et al., 2015). These studies have resolved key aspects of relationships within bivalves, and virtually all of them converge on the monophyly of Heteroconchia, Pteriomorphia, Heterodonta, Palaeoheterodonta, Archiheterodonta, Euheterodonta, Anomalodesmata, and Imparidentia. This is not the case for many mitogenomic studies (e.g., Doucet-Beaupré et al., 2010; Plazzi et al., 2011), as it has been shown that they fail to recover deep molluscan relationships at many levels (e.g., Bernt et al., 2013; Stöger and Schrödl, 2013; Schrödl and Stöger, 2014). Other issues, including the monophyly of Protobranchia (Sharma et al., 2013), the interrelationships of Pteriomorphia (Lemer et al., 2016), the relative branching of the three main heterodont clades (Palaeoheterodonta, Archiheterodonta, and Euheterodonta), and most notably, the internal relationships of Imparidentia (Taylor et al., 2007), have remained somewhat uncertain (e.g., see Bieler et al., 2014), or have been only recently resolved with strong support by using phylogenomic approaches on transcriptomic data (González et al., 2015; Lemer et al., 2016). In the case of González et al. (2015), however, sampling was limited compared to previous Sanger-based approaches that had analyzed 103 bivalve species, for a group with more than 100 recognized extant families (Bieler et al., 2010).

To maximize taxonomic representation at the family level, we here expand the molecular data set of Bieler et al. (2014), which incorporated 81 of the 108 extant family-level lineages then recognized. Accepting that Sanger-based approaches with traditional markers can provide little additional contribution to the resolution of the deepest nodes of the bivalve tree, this provides the first opportunity to place the vast majority of bivalve families in a phylogenetic context for future studies of the systematics, biogeography, and

ecology of Bivalvia. Our goal was to sample as many of the 113 currently recognized extant bivalve families as possible. Ninety-three of these families are included in the present study, often with more than one representative. Included samples span all 12 families of the Protobranchia, 21 of 23 Pteriomorpha families (missing: Cucullaeidae, Entoliidae); all seven Palaeoheterodonta families; and four of five nominal Archiheterodonta families [but Condyllocardiidae is now considered to be nested within Carditidae after the analysis of Archiheterodonta by González and Giribet (2014), here confirmed, and the only supposed extant member of the otherwise extinct Cardiniidae, *Tellidorella* Berry, 1963, is now recognized as a member of Lucinidae (Taylor et al., 2011)], thus including all of the three currently accepted families. We also sampled 38 of 45 families within the Imparidentia (missing: Basterotiidae, Galatheavalvidae, Sportellidae, Anatinellidae, Cardiliidae, Neoleptonidae, Erodontidae); and eleven of 20 Anomalodesmata families (missing: Penicillidae¹, Pholadomyidae, Parilimyidae, Halonymphidae, Protocrepidariidae, Cetoconchidae, Euciroidae, Lyonsiellidae, Spheniopsidae). We also included samples of Kelliidae and Montacutidae, groups that were subsumed under a broader concept of Lasaeidae by Bieler et al. (2010). Three nominal families that have been added to the extant bivalve fauna most recently could not be analyzed herein: the Parallelodontidae, previously considered extinct, but now accepted by Huber (2015); Cyclochlamydidae (Dijkstra and Maestrati, 2012); and Clistoconchidae (Morton, 2012).

2. Materials and methods

2.1. Species, Samples, Sequences

In total we analyzed 219 ingroup taxa representing 93 bivalve families, and 10 outgroup taxa, including 3 Polyplacophora, 1 Monoplacophora, 1 Scaphopoda, and 5 Gastropoda. All analyzed specimens, including collection and voucher identifiers, GenBank accession numbers, and sampling locations, are listed in Table 1. This analysis is part of a larger study on bivalve evolution and samples were derived from a variety of sources, but here we limit our sampling to the molecular data, as collecting internal anatomical characters has not kept the pace of collecting molecular data (see Bieler et al., 2014).

¹ Penicillidae is invalid because the molluscan name *Penicillus* is a junior homonym. However, the senior name in Polychaeta is not in use and the molluscan name might be salvageable under ICZN (1999) Art. 23.9

Additional collection information can be obtained from the online database of the Museum of Comparative Zoology, MCZbase (<http://mczbase.mcz.harvard.edu>), from the database of the Field Museum of Natural History (<http://emuweb.fieldmuseum.org/iz/invertebrates.php>), and the website of the Bivalve Tree of Life Project (<http://www.bivatol.org>). Authorship and literature information for cited higher taxa can be found at MolluscaBase (<http://www.molluscabase.org>).

2.2. Molecular methods

Total genomic DNA was extracted using the DNeasy tissue kit from QIAGEN (Valencia, CA, USA), from muscle or mantle tissue for large specimens or the entire body of small specimens. Five molecular markers were PCR-amplified, sequenced, and analyzed here, including one nuclear protein-coding gene (histone H3), one mitochondrial protein-coding gene (COI), two nuclear ribosomal genes (complete 18S rRNA and a 2.2kb fragment of 28S rRNA) and one mitochondrial ribosomal gene (16S rRNA), as detailed by Bieler et al. (2014).

Sequence data were visualized and edited in Sequencher 5.1 (Gene Codes Corporation, Ann Arbor, MI, USA) and GENEIOUS Pro 7.1.7 (Biomatters Limited, Auckland, New Zealand). Additional sequences were obtained from RNA-Seq datasets (mostly by González et al., 2015), as indicated in Table 1. Sequences were screened for contamination using BLAST searches (ncbi.nlm.nih.gov) and new sequences were deposited on GenBank under the accession codes listed in Table 1.

2.3. Phylogenetic analyses

Probabilistic analyses were conducted under Bayesian inference and maximum likelihood on the static alignments generated with MUSCLE 3.6 (Edgar, 2004) with default parameters as implemented in GENEIOUS. To remove loci of ambiguous homology, sequence alignments for each amplicon (9 in total; 3 each for 18S and 28S rRNA, and one for each other marker) were individually analyzed with GBlocks 0.91b (Castresana, 2000) under the following conditions: flanking positions present in at least 51% of all sequences (-b2 = 51% instead of 85%), the block size was decreased to 3 (-b4 = 3 instead of 10) and gap positions were removed only if they were present in more than half the sequences (-b = h instead of none). Alignment lengths pre- and post-GBlocks are listed in Table 2. Amplicon

alignments were subsequently concatenated using SeqMatrix 1.7.8 (Vaidya et al., 2011). The best-fit model of sequence evolution was estimated with jModelTest (Darriba et al., 2012) under the Akaike information criterion (AIC). GTR+I+ Γ was selected overall and for each locus except for histone H3 for which the best-fit model was TIM1+I+ Γ .

Maximum likelihood analyses of the individual genes and the concatenated data sets were conducted using RAxML 8.2.8 on XSEDE (Stamatakis, 2014) as implemented on the CIPRES web portal (Miller et al., 2010). A unique GTR model of sequence evolution was specified for each molecular marker with corrections for a discrete gamma distribution (Γ) for site-rate heterogeneity (GTRGAMMA). Nodal support was estimated via the rapid bootstrap algorithm (1000 replicates) using the GTRCAT model (Stamatakis et al., 2008).

Bayesian inference analyses were carried out with MrBayes 3.2 (Ronquist et al., 2012) as implemented on the CIPRES web portal. Analyses were conducted with a unique model applied to each partition with gamma corrections and a proportion of invariable sites (GTR+I+ Γ). Convergence diagnostics were analyzed using Tracer 1.6 (Rambaut et al., 2014). MrBayes analyses started with random trees, default priors and five runs, each with 3 hot and 1 cold Markov chains. The runs were allowed to proceed until the average deviation of split frequencies reached <0.01 (~12M generations). Phylogenetic trees were summarized as a 50% majority-rule consensus tree with a burn-in of 25% removed using sumt as implemented in MrBayes.

In addition, IQtree 1.3.10 (Minh et al., 2013; Nguyen et al., 2015) was used for maximum likelihood analyses including model selection for each partition. Five independent runs were conducted, each with 1000 ultrafast bootstrap replications (Minh et al., 2013), and we present the most likely tree (Fig. S1; Log-likelihood -218588), which is based on the following substitution models (selected according to the Bayesian Information Criterion): 18S: TIM+I+G4; 16S, 28S, COI & H3: GTR+I+G4.

Topology-tests were run constraining the monophyly of Bivalvia and of Protobranchia to assess the strength of evidence for these previously well-resolved nodes (e.g., Sharma et al., 2012; Bieler et al., 2014; González et al., 2015). Log likelihoods of site patterns were generated in RAxML 8.2.8 on XSEDE (Stamatakis, 2014). Resulting suboptimal likelihood trees were then compared to the unconstrained tree ML topology, based on the same dataset, using CONSEL (Shimodaira and Hasegawa, 2001) to conduct the approximately unbiased (au; Shimodaira, 2002), Kishino–Hasegawa (kh), Shimodaira–

Hasegawa (sh), weighted Kishino–Hasegawa (wkh) and weighted Shimodaira–Hasegawa (wsh) tests.

3. Results and discussion

This is the first phylogenetic study of a large molluscan clade (i.e., a class) including comparable dense sampling (i.e., 90 of the 108 families recognized by Bieler et al., 2010), using Sanger sequencing of traditional markers commonly used in bivalve systematics—these same five markers are often referred to as the “work-horses” in previous molluscan literature (Sharma et al., 2012) or as the “usual suspects” in the arachnid literature (Dimitrov et al., 2016). As in virtually all previous phylogenetic analyses of bivalves using standard markers, the monophyly of Bivalvia and of Protobranchia are not supported (Figs. 1–2). We however tested these two specific hypotheses and our analyses are non-significant for rejection of the monophyly of Bivalvia for all five tests that we conducted (Table 3). In contrast, tree topologies that enforce the monophyly of Protobranchia are significantly worse than the unconstrained tree topology in four out of five likelihood-based topology tests (Table 3).

Irrespective of the lack of monophyly, our results (Figs. 1a, 2a) and all densely sampled previous analyses show protobranchs divided into four deep, well-supported clades, Solemyidae, Nucinellidae, Nuculidae, and Nuculanoidea; while Nuculidae and Nuculanoidea are sister groups, Solemyidae often clusters with the outgroups and Nucinellidae appears in different unsupported positions. No analysis finds monophyly of Solemyida (Solemyoidea + Nucinellidae²) (Oliver and Taylor, 2012), as already discussed by Sharma et al. (2013). Taxon sampling, however, allows us to discuss in more detail relationships within each of the four protobranch clades. In Solemyidae, *Acharax* is sister to a monophyletic *Solemya*; in Nuculidae, *Nucula* is paraphyletic with respect to *Acila* and *Ennucula*. Within Nuculanoidea most families represented by more than one specimen, with the exception of Neilonellidae, appear non-monophyletic; however, only Malletiidae appears in the two main nukulanoidean clades, one of which groups the malletiids *Katadesmia* and *Glencharia* with Tindariidae, Sareptidae, and Neilonellidae, while the other

² We follow other authors, e.g., Oliver and Taylor (2012) in separating Nucinellidae and Manzanellidae, and since their sister group relationship (in what would constitute the clade Manzanelloidea [see Bieler et al. 2010]) remains untested, we here refer only to Nucinellidae, the taxon represented molecularly.

malletiid, *Malletia*, clusters with Bathyspinulidae, Nuculanidae, Phaseolidae, Siliculidae, and Yoldiidae (Figs. 1a, 2a).

The unstable position of Nucinellidae as sister group of Pteriomorphia in the Bayesian tree and as sister group of Autobranchia in the ML tree is an unexpected result with the increased taxon sampling of this analysis, as the monophyly of Autobranchia is otherwise uncontroversial (e.g., Waller, 1998; Giribet and Wheeler, 2002; Sharma et al., 2012; Bieler et al., 2014; González et al., 2015). Monophyly of Protobranchia, and more specifically the position of Nucinellidae, should be a focus of future studies using larger data sets, especially since the problematic clade Nucinellidae was not part of prior transcriptome-based phylogenomic analysis able to test Protobranchia monophyly (Smith et al., 2011; González et al., 2015; Kocot et al., 2016; Lemer et al., 2016).

Pteriomorphian monophyly is robustly supported, and, as in most previous analyses, its major clades are well resolved: Mytilidae, Ostreida (as well as its subclades Pinnidae, Ostreoidea, Pterioidea), Arcida, Anomioidea, Limidae, and Pectinoidea. All the analyses find maximum support for a clade composed of Arcida, Limida, and Pectinida, as found in recent densely-sampled phylogenomic analyses (Lemer et al., 2016), but Limidae nests within Pectinida, a result not supported in the same phylogenomic analyses. None of the analyses resolve the position of Mytilidae with high support. The phylogenomic analysis of Pteriomorphia has evaluated these hypotheses and their possible conflict, concluding that Arcida is the most likely sister group of the other Pteriomorphia, while Mytilidae forms the sister group of Ostreida (Lemer et al., 2016). That analysis also shows monophyly of Pectinida (= Anomioidea + Pectinoidea) to the exclusion of Limidae, a result supported by our ML analysis (Figs. 1-3).

Within Ostreida, Pterioidea is well resolved as a clade, but two families, Malleidae and Pteriidae, are not monophyletic: *Malleus* and *Vulsella* do not form a clade, and neither do *Pteria* and *Pinctada*. This is, however, consistent with prior findings about the relationships of Pterioidea (Steiner and Hammer, 2000; Giribet and Distel, 2003; Tëmkin, 2006; 2010; Xue et al., 2012). A phylogenetically sound system for Pterioidea, as in the cases of Nuculanoidea and Arcoida, remains elusive.

Internal relationships of the main pteriomorphian clades resolve between Mytilida + Ostreida and Arcida + Pectinida + Limida, with the limids being nested within Pectinida, as sister group to Pectinoidea. However neither the clade uniting Mytilida + Ostreida or Arcida

with Pectinida–Limida receive sufficient support, again suggesting that these relationships require additional data to be resolved with confidence (Lemer et al., 2016).

With respect to the internal resolution of other pteriomorphian families, Arcidae is not supported as monophyletic, as is often found in other more focused analyses (see Combosch and Giribet, 2016), and neither is Propeamussiidae, as *Cyclopecten* is closer to Pectinidae than to *Propeamussium*, but support for the relationships within Pectinoidea is low (Fig. 1a, 3) and any family-level rearrangements awaits denser taxonomic sampling.

Our analyses provide robust support for the monophyly of Heteroconchia, Palaeoheterodonta, and support, although without significant posterior probability or bootstrap support, Heterodonta, Archiheterodonta, Euheterodonta, Anomalodesmata, and Imparidentia. All of these nodes also received robust support in the phylogenomic analysis of González et al. (2015), illustrating that the work-horse genes used here have signal when analyzed in combination, even though there may not be enough to provide consistently robust support at this level. This also stresses the fact that results based solely on mitochondrial genes are at odds with either the work-horses analyzed together or with the transcriptomic analyses, once more suggesting that mitochondrial genomes may not be sufficient for answering deep evolutionary questions within molluscs or for their relationships with other metazoan clades (Bernt et al., 2013; Stöger and Schrödl, 2013). This is why we do not feel compelled to discuss in any detail results based solely on COI and 16S rRNA in the context of the work conducted here.

Palaeoheterodonts divide into the marine Trigoniida and the freshwater clade Unionida, as in virtually every published bivalve phylogeny. Resolution within Unionida is, however, not well supported, and recent analyses have found alternative resolutions (e.g., Graf and Cummings, 2007; Whelan et al., 2011). For example, our ML tree supports Hyriidae as the sister group to the remaining families, followed by Unionidae and then by Margaritiferidae, which is sister group to a well-supported clade of Iridinidae, Etheriidae, and Mycetopodidae (Figs. 1a, 3), but our Bayesian analysis supports the latter clade as sister group to a monophyletic Hyriidae + Unionidae + Margaritiferidae (Fig. 2a). Resolution within Unionida seems to be highly sensitive to analytical parameters and methodologies (Whelan et al., 2011) as well as taxon sampling (Graf et al., 2015), and again it appears that additional data will be necessary to resolve this enigmatic Triassic radiation of freshwater bivalves (Bieler et al., 2014).

Archiheterodont relationships are well resolved, with two clades, Carditoidea and Crassatelloidea, as shown in an earlier and more densely sampled study (González and Giribet, 2014), and corroborated phylogenomically (González et al., 2015). As in the former study, we find Condyllocardiidae nested within Carditidae, and thus not representing a valid bivalve family. The division of Crassatelloidea in the two families Crassatellidae and Astartidae is well supported. Our results thus corroborate recent findings on the relationships of this clade of primitive heterodonts (González and Giribet, 2014).

Anomalodesmata is well supported as the sister clade to Imparidentia. Anomalodesmatan relationships have received attention both based on molecules and morphology (Harper et al., 2000; Harper et al., 2006; Healy et al., 2008), but little consensus has emerged (Bieler et al., 2014). Here we find good support for a clade including the members of the families Laternulidae, Clavagellidae, Lyonsiidae, and Pandoridae, but the latter two are not monophyletic; this clade corresponds to the 'lyonsiid' lineage of Harper et al. (2006). Clavagellidae is well supported as nested in the Lyonsiidae–Pandoridae clade. Verticordiidae, and Cuspidariidae form a clade of carnivorous bivalves, but it is not well supported, and the other carnivorous family, Poromyidae, does not group with them, and instead appears as the sister group of another well supported clade, composed of the members of the families Periplomatidae, Thraciidae, Cleidothaeridae, and Myochamidae, with *Cleidothaerus* nesting within Myochamidae. While Cleidothaeridae and Myochamidae have been considered separate families, the former consists of two currently recognized extant species (Morton and Harper, 2001), and is highly apomorphic due to the coiling of the shell, as *Cleidothaerus* cements by its robust, coiled, right valve to hard substrata. It is interesting that, although without significant support, *Cleidothaerus* is sister group to the other cementing Myochamidae, *Myochama* (see Harper and Morton, 2000), while the non-cementing *Myadora* constitutes their sister group, indicating that cementation may have originated twice within Anomalodesmata and not three times as previously thought. In addition, *Cleidothaerus* and Myochamidae (i.e., *Myadora* and *Myochama*) are strictly Australasian taxa and both have first appearance data in the Oligocene (Beu and Maxwell, 1990; Beu and Raine, 2009).

The lack of support for the monophyly of the three septibranch families is probably due to the long branches of some of its members, especially *Poromya illevis*, and the clade has been difficult to recover in other Sanger-based analyses (Harper et al., 2006; Bieler et al., 2014). The accelerated evolutionary rates of some anomalodesmatan lineages are

probably responsible for some of the lack of resolution among the deepest nodes, and a major effort should be directed toward generating transcriptomes for this group with many species adapted to highly specialized habitats, including the deep sea.

Relationships within Imparidentia have been difficult to resolve using standard Sanger-based approaches (e.g., Campbell, 2000; Steiner and Hammer, 2000; Giribet and Wheeler, 2002; Giribet and Distel, 2003; Williams et al., 2004; Taylor et al., 2007; Taylor et al., 2009; Sharma et al., 2012; Bieler et al., 2014), and our study corroborates the results of some of these previous studies. Despite increasing the taxon sampling in some poorly represented clades, many deep nodes remain poorly resolved, and new approaches are required to resolve some of the most recalcitrant nodes, such as Gastrochaenidae (see González et al., 2015) and Chamidae.

Our analyses confirm prior hypotheses of a basal position of Thyasiridae, Gastrochaenidae, and Lucinidae within Imparidentia, but relationships between these three families remain poorly supported, limiting the conclusions that may be drawn at present. The Bayesian analysis does add some support to the placement of Thyasiridae as sister group to all other imparidentians and to a clade of Gastrochaenidae + Lucinidae, but this result is contradicted by the phylogenomic analyses of González et al. (2015) which placed Gastrochaenidae as sister group to the non-lucinid imparidentians (that study did not sample Thyasiridae).

Our analyses also recover the clade Adapedonta, consisting of Hiatellidae + Solenoidea (the latter = Solenidae + Pharidae) (e.g., Taylor et al., 2007; Taylor et al., 2009; Bieler et al., 2014), although with low support. Adapedonta appears as the sister group of Galeommatoidea, although again, this relationship is not robustly supported, and while morphological evidence for Adapedonta may exist, no character has been proposed to group Galeommatoidea with Adapedonta, and this clade requires further testing.

Galeommatoidean relationships have received recent phylogenetic attention due to the interesting life habit adaptations of this diverse clade of bivalves (Goto et al., 2012; Li et al., 2016). Our taxon sampling does not overlap well with that of recent analyses, but we find major differences between our study and that of Goto et al. (2012), with Mysellidae being paraphyletic but basal to the other galeommatooids, followed by *Lasaea* (Lasaeidae) and then by a clade of Galeommatidae–Kelliidae.

Cardiidae and Tellinoidea form a clade, as in previous phylogenetic analyses (e.g., Taylor et al., 2007; Taylor et al., 2009; Bieler et al., 2014), although again with marginal support and in clear need for additional evidence supporting this putative clade.

Internal relationships of Cardiidae are well supported, and once more show that *Tridacna* nests within the family, with *Fragum* as the most basal of the sampled species, i.e., the species is sister group to a clade including *Tridacna* and all the other species. However, sampling for Cardiidae is very limited in our study and lacks several basal lineages (see for example Herrera et al., 2015).

Tellinoidea is likewise monophyletic, but none of its families sampled by two or more species are resolved as monophyletic, indicating the need for thorough systematic re-assessment of this commercially important clade. Of special interest is the Australian giant *Plebidonax deltoides*, which does not group with Donacidae, and instead nests within a paraphyletic Psammobiidae. The support for some nodes within this clade, and the current taxon sampling are not sufficient to propose taxonomic changes. Nevertheless, our study points to the urgency of work within this commercially important clade of bivalves.

Neoheterodonte is supported as monophyletic with the same composition as in Taylor et al. (2007); but the position of Chamidae inside or outside the Neoheterodonte requires further assessment (Bieler et al., 2014). Sphaeriidae appears as sister group to all other Neoheterodonte, a clade with few supported interfamilial relationships. One of the well-supported clades includes several members of the former Myoidea: Teredinidae + Pholadidae as sister group to Dreissenidae, Myidae, and Corbiculidae. Mactroidea (Mactridae + Mesodesmatidae) is also well supported, but Mesodesmatidae appears nested within a paraphyletic Mactridae. Ungulinidae + Cyamyoidea (Cyamiidae + Gaimardidae) also form a clade; in this case without significant support in the ML tree (Fig. 1b).

A clade uniting the Glossidae, Trapezidae, Hemidonacidae, Arctidae, Cyrenidae, Cyrenoididae, Glauconomidae, Vesicomidae, Kelliellidae, Veneridae, and Chamidae is found consistently across analyses although it receives marginal support in the ML analysis (68% bootstrap support; BS hereafter) and low posterior probability in the Bayesian analysis (pp = 0.83). However, as a stable clade, it has been recovered by most analyses published to date (e.g., Taylor et al., 2007; Bieler et al., 2014) once more decoupling the notions of stability and support for certain clades (see Giribet, 2003). To evaluate the impact that the long-branched Chamidae may have in the resolution within the Imparidentia, we conducted an analysis with RAxML excluding all Chamidae (Fig. S2). The aforementioned clade was

recovered with 96% BS, suggesting that the likely artefactual placement of Chamidae within Veneridae has widespread impact on the support of this clade and many of the subclades within it.

Glossidae, Trapezidae, Hemidonacidae, and Arctidae cluster together with the fresh-/brackish-water clade of Cyrenidae, Cyrenoididae, and Glauconomidae, but the relationships between this latter clade and the other families is not well supported (Fig. 1b); indeed, in the Bayesian analysis, Glossidae + Trapezidae do not form a clade with Hemidonacidae, Arctidae, Cyrenidae, Cyrenoididae, and Glauconomidae (Fig. 2b). Additional sampling (taxa and genes) may be necessary to resolve this heterogeneous clade of Neoheterodonte.

Vesicomidae and Kelliellidae form a well-supported clade, and appear as sister group to Veneridae, although without significant nodal support in the analyses including Chamidae; but this clade receives 84% BS when Chamidae is excluded. Veneridae appears paraphyletic with respect to the problematic and extremely long-branched Chamidae (see other sections of the discussion). *Chama* aside, the present results confirm the findings of Mikkelsen et al. (2006) who demonstrated that Veneridae divide into two clearly separated subgroups, with one clade including members of Tapetinae, Dosiniinae, Venerinae, and Chioninae, and a second clade spanning Petricolinae, Turtoniinae, and Gemminae (as well as other taxa not reinvestigated herein). The placement of *Clementia*/Clementiinae with the latter is a novel finding, as no representative was available for that earlier study.

The positions of two families, Gastrochaenidae and Chamidae, have been extremely difficult to resolve using Sanger-based approaches (e.g., Sharma et al., 2012; Bieler et al., 2014). Their placements find little support in our analyses and are probably responsible for the low support found in Imparidentia. The position of Gastrochaenidae was, however, well resolved in the phylogenomic analysis of González et al. (2015), appearing as sister group of the non-lucinid imparidentians, but that study did not include Thyasiridae—another key basal imparidentian—or Chamidae.

The phylogenetic position of Chamidae has long been disputed (e.g., Kennedy et al., 1970), among other things for being the only heterodont group in which a few species have distinct calcitic outer shell layers (Taylor and Kennedy, 1969; Harper, 1998), as found in hippuritids. The uncertain affinity of Chamidae based on shell microstructure or sperm ultrastructure has been discussed in detail by Taylor et al. (2007). Future transcriptomic analysis of additional imparidentian families is a promising avenue to resolve the position

of a taxon once considered a surviving lineage of the extinct Mesozoic rudists (Newell, 1965; Yonge, 1967).

4. Conclusions

Through increased taxonomic sampling, we have been able to more densely populate the Bivalvia Tree of Life at the family level and place many species and genera in a broader phylogenetic context, as well as highlighting the need of denser taxon sampling in clades with poorly defined families, especially in Nuculanoidea, Arcoidea, and Tellinoidea. While it is now increasingly evident that Sanger sequencing of a small number of genes will not suffice to robustly resolve the deepest or most recalcitrant nodes, transcriptomic data is starting to be assembled toward this goal (González et al., 2015; Lemer et al., 2016). The application of transcriptomics to other molluscan clades has shown great promise in resolving the interrelationships of the molluscan classes (Kocot et al., 2011; Smith et al., 2011), and those of the megadiverse gastropods (Kocot et al., 2013; Zapata et al., 2014). Yet dense sampling at the species level may still rely on a Sanger approach or on the promising techniques for parallel massive amplicon sequencing (e.g., Faircloth et al., 2012; Lemmon and Lemmon, 2012). As for many other diverse and ancient clades, we thus see the future of bivalve systematics as a tiered approach, combining a well-resolved backbone based on genomic/transcriptomic data, with dense sampling of as many genera and species as possible using gene-target approaches. With this hybrid framework, we shall be positioned to tackle the most challenging evolutionary and ecological questions.

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Figure legends:

Figure 1. Phylogenetic tree of bivalve relationships based on maximum likelihood analysis of five genes with RAxML ($\ln L = -228,263.429012$). Numbers at the nodes indicate bootstrap resampling frequencies; only bootstrap values >50% are reported; asterisks indicate a bootstrap support of 100%. Colors identify higher clades.

Figure 2. Phylogenetic tree of bivalve relationships based on Bayesian inference of five genes. Numbers at the nodes indicate posterior probabilities >0.90; asterisks indicate a posterior probability of 1.0. Colors as in Figure 1.

Figure 3. Summary tree of phylogenetic relationships among bivalve families (based on Fig. 1). Family clades are collapsed (using FigTree v 1.3.1). Filled clades indicate monophyletic families, while unfilled clades indicate non-monophyletic family subclades. Numbers in parentheses indicate the number of species within collapsed clades. Bold numbers attached to family names indicate multiple occurrences of a family. Node support and colors are as in Fig. 1.

Tables:

Table 1. List of samples including family, species identity, sampling locality, voucher accession and gene fragments (including NCBI accession numbers).

Table 2. Alignment data for the analyzed sequences and Modeltest results per partition. GB stands for GBlocks 0.91b (Castresana, 2000). H3 is histone H3; COI is cytochrome *c* oxidase subunit I; 16S is 16S rRNA; 18S is 18S rRNA; and 28S is 28S rRNA.

Locus	Pre-GB	Post-GB	GB removed	Average individual sequence length	Range	Modeltest results
H3	336	325	3%	328	270-330	GTR+I+ Γ
COI	709	631	11%	660	535-710	GTR+I+ Γ
16S	1430	382	73%	480	380-840	GTR+I+ Γ
18S	2722	1668	39%	1780	1700-1990	TIM1+I+ Γ
28S	2900	1894	35%	2100	1830-2300	GTR+I+ Γ
Total	8097	4900	39%			

Table 3. Results of the topology tests conducted with CONSEL.

Ran	Constrain	obs	au	np	bp	pp	kh	sh	wkh	wsh
1	Unconstrained	-	0.89	0.87	0.86		0.87	0.92	0.87	0.94
		20.9	6	0	3	1	5	8	5	2
2	Monophyly Bivalvia	20.9	0.17	0.11	0.12	8.00E-	0.12	0.22	0.12	0.28
			4	4	2	10	5	0	5	0
3	Monophyly Bivalvia & Protobranchia	44.3	0.02	0.00	0.00	6.00E-	0.03	0.03	0.03	0.07
			6	9	9	20	1	1	1	5
4	Monophyly Protobranchia	45.9	0.02	0.00	0.00	1.00E-	0.02	0.02	0.02	0.05
			5	5	6	20	1	2	1	4

obs: observed log-likelihood difference. **au:** p-value of the **approximately unbiased** test calculated from the multiscale bootstrap (main result). **np:** bootstrap probability calculated from the multiscale bootstrap. **bp:** regular bootstrap

probability. **kh**: Kishino-Hasegawa test. **sh**: Shimodaira-Hasegawa test. **wkh**: weighted Kishino-Hasegawa test. **wsh**: weighted Shimodaira-Hasegawa test.

Figure 1a

Figure 1b

Figure 2a

Figure 2b

Figure 3

Table1: List of samples including family, species identity, sampling locality, voucher accession and gene fragments (including NCBI accession numbers).

Family	Species		Locality	Accession	18S	28S	16S	H3	COI
PROTOBRANCHIA									
Solemyidae	<i>Solemya velesiana</i>	Iredale, 1931	Australia, Queensland	BivAToL-73	KC984717	KC984794	KC984674	KC984780	KC984744
Solemyidae	<i>Solemya velum</i>	Say, 1822	USA, Massachusetts	BivAToL-17	AF120524	KC429415	JQ728447	AY070146	U56852
Solemyidae	<i>Solemya elarraichensis</i>	Oliver, Rodrigues & Cunha, 2011	Spain, Gulf of Cádiz	MCZ 379147	KC984719	KC984795	KC984673	KC984779	KC984743
Solemyidae	<i>Acharax gadirae</i>	Oliver, Rodrigues & Cunha, 2011	Spain, Gulf of Cádiz	MCZ 378816	KC984715	KC984793	KC984672	KX713510	–
Nucinellidae	<i>Huxleyia munita</i>	(Dall, 1898)	USA, California	BivAToL-137	KC429323	KC429412–13	–	KC429157	–
Nucinellidae	<i>Nucinella giribeti</i>	Glover & Taylor, 2013	Philippines, Panglao	MCZ 379095	KC429324	KC429414	–	KC429158	KC429089
Nuculidae	<i>Acila castrensis</i>	(Hinds, 1843)	USA, Washington	BivAToL-205	KC429319	KC429408	KC429241	–	KC429087
Nuculidae	<i>Nucula atacellana</i>	Schenck, 1939	Gay Head-Bermuda transect	BivAToL-215	KT757806	KT757852	KC984676	KT757893	KC984742
Nuculidae	<i>Ennucula cumingii</i>	(Hinds, 1843)	Australia, Queensland	BivAToL-153	KC984724	KC984813	KC984683	KC984752	KC984750
Nuculidae	<i>Nucula sulcata</i>	Bronn, 1831	Scotland/Sweden, Tjärnö	BivAToL-189/ AToL T68	AF207642	DQ279960	DQ280029	DQ280001	DQ280017
Nuculidae	<i>Ennucula tenuis</i>	(Montagu, 1808)	Greenland, Disko Island	MCZ 379107	KC984684	KC984826	KC984682	KC984775	KC984747
Sareptidae	<i>Pristigloma nitens</i>	(Jeffreys, 1876)		UMASS EN_10RCa	KC984708	KC984833	KC984670	KC984786	–
Bathyspinulidae	<i>Bathyspinula hilleri</i>	(Allen & Sanders, 1982)		UMASS 3D534.2	KC984712	KC984806	KC993874	KC984773	KC984733
Malletiidae	<i>Clencharia abyssorum</i>	(Verrill & Bush, 1898)	Gay Head-Bermuda transect	BivAToL-217	KC429320	KC429409	–	KC429154	–
Malletiidae	<i>Malletia johnsoni</i>	Clarke, 1961	Gay Head-Bermuda transect	BivAToL-216	KC993879	KC984837	KC993872	KC993888	–
Malletiidae	<i>Katadesmia cuneata</i>	(Jeffreys, 1876)		UMASS Ice142.5	KC984697	KX713391	–	KC984759	–
Neilonellidae	<i>Neilonella whoii</i>	Allen & Sanders, 1996	Gay Head-Bermuda transect	BivAToL-218	KC984695	KC984822	KC984659	KC984756	KC984732
Neilonellidae	<i>Neilonella cf. corpulenta</i>	(Dall, 1881)	Gay Head-Bermuda transect	BivAToL-218X	KX713324	KX713412	–	KX713564	–
Nuculanidae	<i>Ledella ultima</i>	(E.A. Smith, 1885)	Gay Head-Bermuda transect	BivAToL-219	KC984685	KC984820	KC984667	KC984769	KC984740

Nuculanidae	<i>Nuculana pernula</i>	(O.F. Müller, 1779)	Sweden, Tjärnö	BivAToL-147	KC984693	KC984801	–	KC984766	KC984737
Nuculanidae	<i>Scaeoleda caloundra</i>	(Iredale, 1929)	Australia, Queensland	BivAToL-100	KC429321	KC429410	KC429242	KC429155	–
Phaseolidae	<i>Lametila abyssorum</i>	Allen & Sanders, 1973		UMASS EN_10UC1	KC984705	KC984798	KC984661	KC984783	–
Siliculidae	<i>Silicula sp.</i>		Solomon Is.	MCZ 379143	KC984703	KC984840	–	KC984762	KC984734
Tindariidae	<i>Tindaria kennerlyi</i>	(Dall, 1897)		AMNH PRTB011	KC984702	KC984812	–	KC984755	KC984731
Yoldiidae	<i>Yoldia limatula</i>	(Say, 1831)	USA, Massachusetts	BivAToL-19	KC429322	KC429411	–	KC429156	KC429088
Yoldiidae	<i>Yoldiella americana</i>	Allen, Sanders & Hannah, 1995		UMASS 3D8369.2	KC984707	KC984842	KC984662	KC984787	KC984726

PTERIOMORPHIA

Mytilidae	<i>Bathymodiolus brevior</i>	Cosel, Métivier & Hashimoto, 1994	Kilo Moana hydrothermal vent, Lau basin	MCZ 386945	KX713272	KX713360	KX713195	KX713515	–
Mytilidae	<i>Brachidontes exustus</i>	(Linnaeus, 1758)	USA, East Florida	BivAToL-243	KT757791	KT757838	KX713196	–	KX713447
Mytilidae	<i>Dacrydium sp.</i>		Gay Head-Bermuda transect	BivAToL-212	KX713285	KX713372	KX713210	KX713529	KX713456
Mytilidae	<i>Lithophaga antillarum</i>	(d'Orbigny, 1853)	USA, Florida Keys	BivAToL-292	KX713308	KX713397	KX713229	KX713550	–
Mytilidae	<i>Modiolus modiolus</i>	(Linnaeus, 1758)	UK, Wales	BivAToL-197	KX713314	–	KX713235	KX713557	KX713479
Mytilidae	<i>Modiolus rufus</i>	(Fischer von Waldheim, 1807)	Australia, Queensland	BivAToL-154	KC429330	KC429423	KC429248	KC429165	KC429094
Mytilidae	<i>Musculus niger</i>	(J. E. Gray, 1824)	Norway	MCZ 379061	KX713316	KX713404	–	–	KX713481
Mytilidae	<i>Mytilus edulis</i>	Linnaeus, 1758	UK, England	BivAToL-271	KC429331	KC429424	KC429249	KC429166	KC429095
Mytilidae	<i>Mytilisepta virgata</i>	(Wiegmann, 1837)	China, Hong Kong	BivAToL-426	KX713322	KX713410	KX713241	KX713562	–
Mytilidae	<i>Trichomya hirsuta</i>	(Lamarck, 1819)	Australia, Queensland	BivAToL-74	KX713350	KX713436	KX713260	KX713583	KX713503
Arcidae	<i>Anadara trapezia</i>	(Deshayes, 1839)	Australia, Queensland	BivAToL-76	KT757770	KT757817	KX713189	KT757865	KX713443
Arcidae	<i>Arca noae</i>	Linnaeus, 1758	Spain, Catalonia	BivAToL-116	KC429325	KC429416	KX713192	KC429160	KC429090
Arcidae	<i>Barbatia barbata</i>	(Linnaeus, 1758)	Spain, Catalonia	BivAToL-123	KC429326	KC429417–18	KC429244	KC429161	KC429091
Arcidae	<i>Trisidos tortuosa</i>	(Linnaeus, 1758)	Australia, Queensland	BivAToL-91	KT757811	KT757858	KX713263	KT757899	KX713506
Glycymerididae	<i>Glycymeris glycymeris</i>	(Linnaeus, 1758)	France, Atlantic coast	BivAToL-133	KC429328	KC429421	KC429246	KC429163	KC429093

Glycymerididae	<i>Tucetona pectinata</i>	(Gmelin, 1791)	USA, Florida Keys	BivAToL-32	KT757812	KT757859	KX713264	KT757900	KX713507
Noetiidae	<i>Arcopsis adamsi</i>	(Dall, 1886)	USA, Florida Keys	BivAToL-37	KC429327	KC429419–20	KC429245	KC429162	KC429092
Noetiidae	<i>Noetia ponderosa</i>	(Say, 1822)	USA, South Carolina	BivAToL-210	KT757793	KT757840	KX713244	KT757882	KX713487
Noetiidae	<i>Striarca lactea</i>	(Linnaeus, 1758)	Spain, Catalonia	BivAToL-115	AF120531	KT757855	KX713259	KT757897	KX713502
Limopsidae	<i>Limopsis</i> sp. B		Gay Head-Bermuda transect	BivAToL-213	KC429329	KC429422	KC429247	KC429164	–
Philobryidae	<i>Neocardia</i> sp.		South Africa, Port Elizabeth	MCZ 378927	KT757803	KT757849	–	KT757890	KX713486
Philobryidae	<i>Philobrya sublaevis</i>	Pelseneer, 1903	Antartica, Adelaide Island	BivAToL-399	KT757807	KT757853	–	KT757895	–
Pteriidae	<i>Pinctada imbricata</i>	Röding, 1798	USA, Florida Keys	BivAToL-48	KX713333	KX713420	–	KX713569	KX713492
Pteriidae	<i>Pteria hirundo</i>	(Linnaeus, 1758)	Spain, Catalonia	BivAToL-126	KC429332	KC429425	KC429250	KC429167	AF120647
Isognomonidae	<i>Isognomon alatus</i>	(Gmelin, 1791)	USA, Florida Keys	BivAToL-30	KC429333	KC429426	KC429251	KC429168	KC429096
Isognomonidae	<i>Isognomon legumen</i>	(Gmelin, 1791)	China, Hong Kong	BivAToL-425	KT757801	KT757848	–	KT757894	KX713469
Malleidae	<i>Malleus albus</i>	Lamarck, 1819	Australia, Queensland	BivAToL-79	KC429334	KC429427–28	KC429252	KC429169	KC429097
Malleidae	<i>Vulsella vulsella</i>	(Linnaeus, 1758)	Australia, Queensland	BivAToL-102	KX713354	KX713440	–	KX713587	KX713508
Pulvinitidae	<i>Pulvinites exempla</i>	(Hedley, 1914)	Australia, New South Wales	AMS C.129659	AJ414640	AJ307540	–	–	–
Pinnidae	<i>Atrina rigida</i>	(Lightfoot, 1786)	USA, Florida Keys	BivAToL-14	KX713270	KX713359	KX713194	KX713514	KX713446
Pinnidae*	<i>Atrina rigida</i>	Gmelin, 1791	USA, North Carolina	BivAToL-170	KC429337	KC429431–32	KC429255	–	–
Pinnidae*	<i>Pinna carnea</i>	Gmelin, 1791	USA, Florida Keys	BivAToL-15	–	–	–	KC429172	KC429099
Ostreidae	<i>Crassostrea virginica</i>	(Gmelin, 1791)	USA, Florida	BivAToL-276	KC429335	KC429429	KC429253	KC429170	KC429098
Ostreidae	<i>Dendostrea frons</i>	(Linnaeus, 1758)	USA, Florida Keys	BivAToL-54	KX713287	KX713374	KX713212	KX713531	–
Ostreidae	<i>Ostrea edulis</i>	Linnaeus, 1758		BivAToL-174	KX713327	KX713414	KX713245	KX713565	KX713488
Ostreidae	<i>Saccostrea glomerata</i>	(Gould, 1850)	Australia, Queensland	BivAToL-77	KX713341	KX713428	KX713252	KX713576	–
Gryphaeidae	<i>Hyotissa hyotis</i>	(Linnaeus, 1758)	Australia, Queensland	BivAToL-103	KX713300	KX713388	KX713223	KX713544	–
Gryphaeidae	<i>Hyotissa mcgintyi</i>	(Harry, 1985)	USA, Florida Keys	BivAToL-275	KC429336	KC429430	KC429254	KC429171	–
Gryphaeidae	<i>Neopycnodonte cochlear</i>	(Poli, 1795)	Portugal, Açores	MCZ 379087	KX713325	KX713413	–	–	–
Anomiidae	<i>Anomia ephippium</i>	Linnaeus, 1758	Spain, Catalonia	BivAToL-124	KX713269	KX713358	KX713191	KX713513	–
Anomiidae	<i>Monia patelliformis</i>	(Linnaeus, 1767)	UK, Wales	BivAToL-272	KC429342	KC429441	KC429261	KC429179	–

Placunidae	<i>Placuna placenta</i>	(Linnaeus, 1758)	Singapore/Solomon Is.	MCZ 379133	KC429343	KC429442	–	KC429180	KC429104
Dimyidae	<i>Dimya lima</i>	Bartsch, 1913	Philippines	BivAToL-177	KC429344	KX713375	KX713213	KC429181	–
Dimyidae	<i>Dimya sp.</i>		Solomon Is.	MCZ 378956	KX713288	KX713376	–	KX713532	–
Pectinidae	<i>Caribachlamys sentis</i>	(Reeve, 1853)	USA, Florida Keys	BivAToL-13	KX713274	KX713362	KX713199	KX713517	–
Pectinidae	<i>Pecten maximus</i>	(Linnaeus, 1758)	France/UK, England (fish market)	BivAToL-199	AY070112	KC429435–36	KC429258	KC429175	KC429102
Pectinidae	<i>Placopecten magellanicus</i>	(Gmelin, 1791)	USA, Massachusetts	BivAToL-360	KX713335	KX713422	KX713249	KX713571	–
Propeamussiidae	<i>Cyclopecten sp.</i>		North Pacific, Cortes Ridge	BivAToL-138	KX713283	KX713371	KX713208	KX713527	KX713454
Propeamussiidae	<i>Propeamussium watsoni</i>	(E.A. Smith, 1885)	Philippines	BivAToL-179	KC429340	KC429437	KC429259	KC429176	KC429103
Spondylidae	<i>Spondylus ambiguus</i>	Chenu, 1844	USA, Florida Keys	BivAToL-274	KC429341	KC429438–40	KC429260	KC429177	–
Spondylidae	<i>Spondylus gaederopus</i>	Linnaeus, 1758	Spain, Balearic Islands	MCZ 376622	KT757808	KT757854	KX713258	KT757896	KX713501
Plicatulidae	<i>Plicatula sp.</i>		China, Hong Kong	BivAToL-432	KX713337	KX713424	–	KX713573	–
Limidae	<i>Acesta excavata</i>	(Fabricius, 1779)	Norway	BivAToL-201	KX713266	KX713355	KX713188	KX713509	KX713441
Limidae	<i>Ctenoides scaber</i>	(Born, 1778)	USA, Florida Keys	BivAToL-45	KC429338	KC429433	KC429256	KC429173	KC429100
Limidae	<i>Ctenoides mitis</i>	(Lamarck, 1807)	USA, Florida Keys	BivAToL-28	KT757792	KT757839	KX713206	KT757881	KX713451
Limidae	<i>Lima lima</i>	(Linnaeus, 1758)	Spain, Catalonia	BivAToL-114	KC429339	KC429434	KC429257	KC429174	KC429101
Limidae	<i>Limaria pellucida</i>	(C.B. Adams, 1846)	USA, Florida Keys	BivAToL-29	KX713307	KX713396	KX713228	KX713549	KX713474

PALAEOHETERODONTA

Trigoniidae	<i>Neotrigonia margaritacea</i>	(Lamarck, 1804)	Australia, Tasmania	MCZ 379090	KP068219	KP068171	KX713243	KP068290	KP068122
Trigoniidae	<i>Neotrigonia lamarckii</i>	(Gray, 1838)	Australia, Queensland	BivAToL-97	KC429345	KC429443	KC429262	KC429182	KC429105
Etheriidae	<i>Etheria elliptica</i>	Lamarck, 1807	Zambia	BivAToL-404	KX713296	KX713384	KX713219	KX713540	KX713462
Iridinidae	<i>Aspatharia pfeifferiana</i>	(Bernardi, 1860)	Zambia	BivAToL-330	KC429347	KC429445	KC429264	KC429184	KC429107
Iridinidae	<i>Chambardia wahlbergi</i>	(Krauss, 1848)	Zambia	BivAToL-405	KX713277	KX713365	KX713202	KX713520	KX713448
Iridinidae	<i>Mutela harger</i>	(E. A. Smith, 1908)	Zambia	BivAToL-401	KX713317	KX713405	KX713237	KX713559	KX713482
Mycetopodidae	<i>Anodontites elongata</i>	(Swainson, 1823)	Peru	BivAToL-323	KX713268	KX713357	KX713190	KX713512	KX713444

Mycetopodidae	<i>Lamproscapha ensiformis</i>	(Spix, 1827)	Peru	BivAToL-382	KX713304	KX713393	KX713225	KX713546	KX713471
Hyriidae	<i>Hyridella australis</i>	(Lamarck, 1819)	Australia, New South Wales	BivAToL-378	KX713301	KX713389	KX713224	KX713545	KX713467
Hyriidae	<i>Triplodon corrugatus</i>	(Lamarck, 1819)	Peru	BivAToL-380	KX713352	KX713438	KX713262	KX713585	KX713505
Hyriidae	<i>Velesunio ambiguus</i>	(Philippi, 1847)	Australia, New South Wales	BivAToL-379	KC429346	KC429444	KC429263	KC429183	KC429106
Unionidae	<i>Lampsilis cardium</i>	Rafinesque, 1820	USA, Illinois	BivAToL-421	KX713305	KX713394	KX713226	KX713547	KX713472
Unionidae	<i>Scabies crispata</i>	(Gould, 1843)	unknown [UK aquarium trade]	BivAToL-373	KX713342	KX713429	KX713253	KX713577	–
Unionidae	<i>Unio pictorum</i>	(Linnaeus, 1758)	UK, England	BivAToL-204	KC429349	KC429447	KC429266	KC429186	KC429109
Margaritiferidae	<i>Margaritifera margaritifera</i>	(Linnaeus, 1758)	U. K., Northern Ireland (farmed)	BivAToL-299	KC429348	KC429446	KC429265	KC429185	KC429108

ARCHIHETERODONTA

Carditidae	<i>Cardita calyculata</i>	(Linnaeus, 1758)	Spain, Catalonia	BivAToL-119	KC429352	KC429450	–	KC429189	KC429112
Carditidae	<i>Carditamera floridana</i>	Conrad, 1838	USA, Florida Keys	BivAToL-31	KP068196	KP068148	KX713198	KP068269	–
Carditidae	<i>Cardites antiquatus</i>	(Linnaeus, 1758)	Spain, Catalonia	MCZ 379176	KP068197	KP068149	–	KP068270	KP068096
Crassatellidae	<i>Crassinella lunulata</i>	(Conrad, 1834)	Panama, Bocas del Toro	MCZ 379774	KP068213	KP068165	–	KP068284	KP068118
Crassatellidae	<i>Eucrassatella cumingii</i>	(A. Adams, 1854)	Australia, Queensland	BivAToL-83	KC429350	KC429448	KC429267	KC429187	KC429110
Astartidae	<i>Astarte sulcata</i>	(Da Costa, 1778)	Wales, UK	BivAToL-192	KC429351	KC429449	KX713193	KC429188	KC429111
Astartidae	<i>Digitaria digitaria</i>	(Linnaeus, 1758)	Spain, Andalusia	BivAToL-120	KP068174	KP068124	–	KP068247	–
Astartidae	<i>Goodallia triangularis</i>	(Montagu, 1803)	Spain, Andalusia	MCZ 378994	KP068173	KP068123	–	KP068246	–
Condylocardiidae	<i>Carditella capensis</i>	E. A. Smith, 1885	South Africa, Western Cape	MCZ 378903	KP068206	KP068157	–	KP068278	KP068112
Condylocardiidae	<i>Carditopsis rugosa</i>	(Sowerby III, 1892)	South Africa, Eastern Cape	MCZ 378909	KP068209	KP068160	–	KP068281	KP068115

ANOMALODESMATA

Clavagellidae	<i>Bryopa melitensis</i>	(Broderip, 1835)	Italy, Sorrento	MCZ 378923	KX713273	KX713361	KX713197	KX713516	–
Myochamidae	<i>Myadora brevis</i>	(Sowerby I, 1827)	Australia, Queensland	BivAToL-166	KX713318	KX713406	KX713238	KX713560	KX713483
Myochamidae	<i>Myochama anomioides</i>	Stutchbury, 1830	Australia, Queensland	BivAToL-84	KC429357/ KC429358	KC429457	KC429272	KC429195	KC429116

Cleidothaeridae	<i>Cleidothaerus albidus</i>	(Lamarck, 1819)	Australia, New South Wales	BivAToL-361	KC429359	KC429458	KC429273	–	KC429117
Pandoridae	<i>Frenamya aversa</i>	(Hedley, 1913)	Australia, Queensland	BivAToL-162	AM774486	AM779660	–	KC429190	KX713463
Pandoridae	<i>Pandora pinna</i>	(Montagu, 1803)	France, Banyuls sur Mer	MCZ 379116	KX713328	KX713415	GQ166569	KX713566	GQ166588
Thraciidae	<i>Thracia phaseolina</i>	(Lamarck, 1818)	UK, England	BivAToL-266	KC429356	KC429454–56	KC429271	KC429194	KC429115
Thraciidae	<i>Thracia villosiuscula</i>	(MacGillivray, 1827)	Sweden, Tjärno	MCZ 381367	KX713349	KX713435	–	KX713582	–
Laternulidae	<i>Laternula elliptica</i>	(King, 1832)	Antarctica, Adelaide Island	BivAToL-202	KC429354	KC429452	KC429269	KC429192	–
Laternulidae	<i>Laternula gracilis</i>	(Reeve, 1860)	Australia, Queensland	BivAToL-78	KX713306	KX713395	KX713227	KX713548	–
Periplomatidae	<i>Cochlodesma praetenue</i>	(Pulteney, 1799)	UK, England	BivAToL-321	KC429355	KC429453	KC429270	KC429193	KC429114
Cuspidariidae	<i>Bathyneera demistriata</i>	(Allen & Morgan, 1981)	Gay Head-Bermuda transect	BivAToL-214	KC429362	KC429463–64	KC429276	KC429198	KC429118
Cuspidariidae	<i>Cuspidaria latesulcata</i>	(Tennison Woods, 1878)	Australia, Queensland	BivAToL-98	KX713282	KX713370	KX713207	KX713525	–
Cuspidariidae	<i>Cuspidaria cuspidata</i>	(Olivi, 1792)	Sweden	BivAToL-110	KX713281	KX713369	–	KX713524	KX713452
Poromyidae	<i>Poromya illevis</i>	Hedley, 1913	Australia, Queensland	BivAToL-159	KC429361	KC429461–62	KC429275	KC429197	–
Verticordiidae	<i>Haliris tenerrima</i>	(Jaekel & Thiele, 1931)	Mozambique channel	BivAToL-305	KC429360	KC429459–60	KC429274	KC429196	–
Lyonsiidae	<i>Lyonsia floridana</i>	Conrad, 1849	USA, Florida	BivAToL-248	KC429353	KC429451	KC429268	KC429191	AF120654
Lyonsiidae	<i>Mytilimeria nuttalli</i>	Conrad, 1837	USA, San Juan Is.	MCZ 377787	KX713321	KX713409	KX713240	–	–
Lyonsiidae	<i>Entodesma navicula</i>	(Adams & Reeve, 1850)	USA, San Juan Is.	UF	KX713295	KX713383	KX713218	KX713539	–

IMPARIDENTIA

Lucinidae	<i>Cavatidens omissa</i>	Iredale, 1931	Australia, Queensland	BivAToL-71	KC429363	KC429465	KC429277	KC429199	KC429120
Lucinidae	<i>Codakia orbicularis</i>	(Linnaeus, 1758)	USA, Florida Keys	BivAToL-10	KC429364	KC429466	–	–	KC429121/ AF12657
Lucinidae	<i>Lucina pensylvanica</i>	(Linnaeus, 1758)	USA, Florida Keys	BivAToL-50	KC429365	KC429467	KC429278	KX713551	KC429119
Lucinidae	<i>Lucinoma borealis</i>	(Linnaeus, 1767)	UK, England	BivAToL-265	KX713309	KX713398	KX713230	KX713552	–
Lucinidae	<i>Phacoides pectinatus</i>	(Gmelin, 1791)	USA, Florida	BivAToL-278	KX713331	KX713418	KX713247	KX713568	KX713490
Lucinidae	<i>Myrtea spinifera</i>	(Montagu, 1803)	France, Banyuls sur Mer	MCZ 379069	KX713319	KX713407	KX713239	AY070157	AY070139
Thyasiridae	<i>Thyasira equalis</i>	(Verrill & Bush, 1898)	Sweden	BivAToL-374	KC429367	KC429469	–	KC429200	KC429122

Hemidonacidae	<i>Hemidonax pictus</i>	(Tryon, 1870)	Australia, Queensland	BivAToL-95	KC429386	KC429494	KC429297	KC429218	–
Arctiidae	<i>Arctica islandica</i>	(Linnaeus, 1767)	UK, Scotland	BivAToL-191	KC429377	KC429482	KC429288	KC429210	KX713445
Trapezidae	<i>Neotrapezium sublaevigatum</i>	(Lamarck, 1819)	Thailand/China, Hong Kong	BivAToL-395	KC429378	KC429483	KC429289	KC429211	KC429128
Cardiidae	<i>Cerastoderma edule</i>	(Linnaeus, 1758)	UK, England	BivAToL-21	KC429384	KC429492	KC429296	KC429217	KC429134
Cardiidae	<i>Dalloccardia muricata</i>	(Linnaeus, 1758)	USA, South Carolina	BivAToL-207	KX713286	KX713373	KX713211	KX713530	KX713457
Cardiidae	<i>Fragum unedo</i>	(Linnaeus, 1758)	Australia, Queensland	BivAToL-75	KC429385	KC429493	KC429318	KC429239	KC429135
Cardiidae	<i>Laevicardium serratum</i>	(Linnaeus, 1758)	USA, Florida Keys	BivAToL-56	KX713303	KX713392	–	–	KX713470
Cardiidae	<i>Tridacna maxima</i>	(Röding, 1798)	Aquarium specimen	MCZ 381362	KX713351	KX713437	KX713261	KX713584	KX713504
Chamidae	<i>Chama asperella</i>	Lamarck, 1819	China, Hong Kong	BivAToL-434	KX713275	KX713363	KX713200	KX713518	–
Chamidae	<i>Chama gryphoides</i>	Linnaeus, 1758	Spain, Catalonia	BivAToL-117	KX713276	KX713364	KX713201	KX713519	–
Chamidae	<i>Chama macerophylla</i>	Gmelin, 1791	USA, Florida Keys	BivAToL-36	KC429369	KC429471	KC429281	KC429202	–
Cyamiidae	<i>Cyamiomactra laminifera</i>	(Lamy, 1906)	Antarctic Peninsula	BivAToL-398	KC429382	KC429488–89	KC429293	–	KC429131
Cyrenidae	<i>Corbicula fluminea</i>	(O.F. Müller, 1774)	USA, Florida	BivAToL-242	AF120557	KC429490	KC429294	AY070161	KC429132
Cyrenidae	<i>Polymesoda caroliniana</i>	(Bosc, 1801)	USA, Florida	BivAToL-281	KX713338	KX713425	KX713250	–	–
Glauconomidae	<i>Glauconome rugosa</i>	Reeve, 1844	Singapore (fish market)	BivAToL-198	KC429392	KC429500	KC429302	KC429223	KC429140
Cyrenoididae	<i>Cyrenoida floridana</i>	Dall, 1896	USA, Florida Keys	BivAToL-27	KC429368	KC429470	KC429280	KC429201	KC429123
Dreissenidae	<i>Dreissena polymorpha</i>	(Pallas, 1771)	USA, Illinois	BivAToL-300	AF120552	KC429513–14	DQ280038	KC429234	KC429149
Dreissenidae	<i>Mytilopsis leucophaeata</i>	(Conrad, 1831)	USA, Florida Keys	BivAToL-9	KX713323	KX713411	KX713242	KX713563	KX713485
Gaimardiidae	<i>Gaimardia trapesina</i>	(Lamarck, 1819)	Tierra del Fuego	BivAToL-397	KX713297	KX713385	KX713220	KX713541	KX713464
Galeommatidae	<i>Chlamydoconcha orcutti</i>	Dall, 1884	USA, California	BivAToL-440	KX713279	KX713367	KX713204	KX713522	KX713449
Galeommatidae	<i>Divariscintilla octotentaculata</i>	(Mikkelsen & Bieler, 1992)	USA, Florida	BivAToL-253	KX713290	KX713378	KX713215	KX713534	KX713459
Galeommatidae	<i>Galeomma turtoni</i>	Turton, 1825	Spain, Catalonia	BivAToL-127	KX713298	KX713386	KX713221	KX713542	–
Galeommatidae	<i>Varotoga anomala</i>	(Deshayes, 1856)	Australia, Queensland	BivAToL-80	KC429371	KC429473	KC429283	KC429204	–
Lasaeidae	<i>Lasaea adansonii</i>	(Gmelin, 1791)	UK, Wales/England	BivAToL-268	KC429370	KC429472	KC429282	KC429203	KC429124
Montacutidae	<i>Altenaeum charcoti</i>	(Lamy, 1906)	Antarctica, Adelaide Island	BivAToL-203	KC429372	KC429474–75	–	KC429205	–

Montacutidae	<i>Tellimya ferruginosa</i>	(Montagu, 1803)	UK, England	BivAToL-267	KC429476/ KC429477	KC429407	KC429317	KC429240	KC429153
Kelliidae	<i>Bornia sebetia</i>	(Costa, 1829)	Spain, Catalonia	BivAToL-122	KC429373	KC429478	KC429284	KC429206	KC429125
Glossidae	<i>Glossus humanus</i>	(Linnaeus, 1758)	UK, Scotland	BivAToL-200	KC429379	KC429484	KC429290	KC429212	KX713466
Kelliellidae	<i>Kellia</i> sp.		Gay Head-Bermuda transect	BivAToL-211	KC429380	KC429485–86	KC429291	KC429213	KC429129
Vesicomysidae	<i>Calyptogena magnifica</i>	Boss & Turner, 1980	East Pacific Rise	BivAToL-259	KC429381	KC429487	KC429292	KC429214	KC429130
Mactridae	<i>Mactra violacea</i>	Gmelin, 1791	China, Hong Kong	BivAToL-430	KX713310	KX713399	KX713231	KX713553	KX713475
Mactridae	<i>Meropesta nicobarica</i>	(Gmelin, 1791)	China, Hong Kong	BivAToL-429	KX713313	KX713402	KX713234	KX713556	KX713478
Mactridae	<i>Mulinia lateralis</i>	(Say, 1822)	USA, Florida	BivAToL-246	KX713315	KX713403	KX713236	KX713558	KX713480
Mactridae	<i>Rangia cuneata</i>	(Sowerby I, 1831)	USA, Florida	BivAToL-280	KC429401	KC429509	KC429310	KC429232	KC429146
Mactridae	<i>Spisula solida</i>	(Linnaeus, 1758)	UK, England (fish market)	BivAToL-319	KX713347	KX713434	KX713257	KX713581	XXXXXX
Mactridae	<i>Tresus capax</i>	(Gould, 1850)	USA, Oregon (fisheries)	BivAToL-377	KC429402	KC429510	KC429311	–	KC429147
Mesodesmatidae	<i>Donacilla cornea</i>	(Poli, 1795)	Spain, Andalusia	BivAToL-406	KC429403	KC429511–12	KC429312	KC429233	KC429148
Sphaeriidae	<i>Pisidium walkeri</i>	Sterki, 1895	USA, Illinois	BivAToL-303	KX713334	KX713421	KX713248	KX713570	KX713493
Sphaeriidae	<i>Sphaerium nucleus</i>	(Studer, 1820)	UK, England	BivAToL-194	KC429383	KC429491	KC429295	KC429216	KC429133
Tellinidae	<i>Ameritella versicolor</i>	(DeKay, 1843)	USA, Florida	BivAToL-256	KX713267	KX713356	–	KX713511	KX713442
Tellinidae	<i>Macoma balthica</i>	(Linnaeus, 1758)	UK, England	BivAToL-186	KC429393	KC429501	KC429303	KC429224	KC429141
Tellinidae	<i>Scissula similis</i>	(Sowerby I, 1806)	USA, Florida Keys	BivAToL-7	KC429394	KC429502	KC429304	KC429225	KC429142
Donacidae	<i>Donax variegatus</i>	(Gmelin, 1791)	Spain, Catalonia	BivAToL-129	KX713291	KX713379	–	KX713535	KX713460
Donacidae	<i>Plebidonax deltoides</i>	(Lamarck, 1818)	Australia, Queensland	BivAToL-88	KX713336	KX713423	–	KX713572	KX713494
Donacidae	<i>Donax trunculus</i>	Linnaeus, 1758	Spain, Catalonia	BivAToL-132	KC429395	KC429503	–	KC429226	KC429143
Donacidae	<i>Donax veruinus</i>	Hedley, 1913	Australia, Queensland	BivAToL-68	KX713292	KX713380	–	KX713536	–
Psammobiidae	<i>Asaphis deflorata</i>	(Linnaeus, 1758)	USA, Florida Keys	BivAToL-33	KC429396	KC429504	KC429305	KC429227	KC429144
Psammobiidae	<i>Gari maculosa</i>	(Lamarck, 1818)	China, Hong Kong	BivAToL-423	KX713299	KX713387	KX713222	KX713543	KX713465
Semelidae	<i>Abra alba</i>	(Wood, 1802)	UK, Scotland	BivAToL-190	KC429397	KC429505	KC429306	KC429228	–

Semelidae	<i>Scrobicularia plana</i>	(Da Costa, 1778)	UK, Wales	BivAToL-20	KX713343	KX713430	KX713254	KX713578	KX713497
Semelidae	<i>Semele cordiformis</i>	(Holten, 1802)	China, Hong Kong	BivAToL-424	KX713344	KX713431	KX713255	KX713579	KX713498
Semelidae	<i>Semele purpurascens</i>	(Gmelin, 1791)	USA, Florida Keys	BivAToL-55	KX713345	KX713432	–	–	KX713499
Solecurtidae	<i>Tagelus plebeius</i>	(Lightfoot, 1786)	USA, Florida	BivAToL-245	KC429398	KC429506	KC429307	KC429229	–
Ungulinidae	<i>Cycladicama cumingii</i>	(Hanley, 1844)	Singapore	BivAToL-371	KC429366	KC429468	KC429279	KX713526	KX713453
Ungulinidae	<i>Diplodonta sp.</i>		China, Hong Kong	BivAToL-313	KX713289	KX713377	KX713214	KX713533	KX713458
Veneridae	<i>Chamelea striatula</i>	(Da Costa, 1778)	UK, England	BivAToL-270	KX713278	KX713366	KX713203	KX713521	–
Veneridae	<i>Chione elevata</i>	(Say, 1822)	USA, Florida Keys	BivAToL-4	KC429387	KC429495	KC429298	KC429219	KC429136
Veneridae	<i>Clementia papyracea</i>	(Gray, 1825)	Australia, Queensland	BivAToL-228	KX713280	KX713368	KX713205	KX713523	KX713450
Veneridae	<i>Dosinia nedigna</i>	(Iredale, 1930)	Australia, Queensland	BivAToL-156	KX713293	KX713381	KX713216	KX713537	KX713461
Veneridae	<i>Gemma gemma</i>	(Totten, 1834)	USA, Massachusetts	BivAToL-16	KC429388	KC429496	KC429299	KC429220	KC429137
Veneridae	<i>Mercenaria mercenaria</i>	(Linnaeus, 1758)	USA, South Carolina	BivAToL-208	KX713312	KX713401	KX713233	KX713555	KX713477
Veneridae	<i>Mysia undata</i>	(Pennant, 1777)	Sweden	BivAToL-111	KX713320	KX713408	–	KX713561	KX713484
Veneridae	<i>Petricola lapicida</i>	(Gmelin, 1791)	USA, Florida Keys	BivAToL-34	KC429389	KC429497	KC429300	KC429221	KC429138
Veneridae	<i>Irus cumingii</i>	(Deshayes, 1854)	Australia, Queensland	BivAToL-72	KX713302	KX713390	–	–	KX713468
Veneridae	<i>Petricolaria pholadiformis</i>	(Lamarck, 1818)	UK, England	BivAToL-22	KX713330	KX713417	–	KX713567	–
Veneridae	<i>Ruditapes decussatus</i>	(Lamarck, 1818)	UK, England	BivAToL-269	KX713340	KX713427	KX713251	KX713575	KX713496
Veneridae	<i>Turtonia minuta</i>	(Fabricius, 1780)	Iceland	FMNH 302008	KC429390	KC429498	–	DQ184898	DQ184850
Veneridae	<i>Venus verrucosa</i>	Linnaeus, 1758	France, Atlantic (fish market)	BivAToL-176	KC429391	KC429499	KC429301	KC429222	KC429139
Myidae	<i>Mya arenaria</i>	Linnaeus, 1758	USA, Massachusetts	BivAToL-18	AF120560	KC429515	KC429313	AY070164	KC429150
Myidae	<i>Sphenia fragilis</i>	(A. Adams & H. Adams, 1854)	USA, Florida	BivAToL-251	KX713346	KX713433	KX713256	KX713580	–
Corbulidae	<i>Notocorbula tunicata</i>	(Reeve, 1843)	Australia, Queensland	BivAToL-85	KX713326	KC429516	KC429314	KC429236	KC429151
Corbulidae	<i>Varicorbula gibba</i>	(Olivi, 1792)	Sweden, Tjärnö	BivAToL-118	KX713353	KX713439	KX713265	KX713586	–
Pholadidae	<i>Barnea candida</i>	(Linnaeus, 1758)	UK, England	BivAToL-25	KX713271	KC429517	KC429315	KC429237	KC429152
Pholadidae	<i>Martesia striata</i>	(Linnaeus, 1758)	USA, Florida	BivAToL-250	KX713311	KX713400	KX713232	KX713554	KX713476
Pholadidae	<i>Pholas dactylus</i>	Linnaeus, 1758	UK, England	BivAToL-24	KX713332	KX713419	–	–	KX713491

Teredinidae	<i>Teredo clappi</i>	Bartsch, 1923	USA, Florida Keys	BivAToL-59	KX713348	KC429518	KC429316	KC429238	–
Hiatellidae	<i>Cyrtodaria siliqua</i>	(Spengler, 1793)	Canada, Nova Scotia	MCZ 384329	KX713284	–	KX713209	KX713528	KX713455
Hiatellidae	<i>Hiatella arctica</i>	(Linnaeus, 1767)	UK, England	BivAToL-195	KC429375	KC429480	KC429286	KC429208	KC429127
Hiatellidae	<i>Panopea japonica</i>	A. Adams, 1850	Japan, Fukuoka (fish market)	MCZ 379117	KC429374	KC429479	KC429285	KC429207	KC429126
Hiatellidae	<i>Panopea globosa</i>	Dall, 1898	China, Hong Kong (fish market)	BivAToL-431	KX713329	KX713416	KX713246	–	KX713489
Solenidae	<i>Solen vaginoides</i>	Lamarck, 1818	Australia, Queensland	BivAToL-70	KC429399	KC429507	KC429308	KC429230	–
Pharidae	<i>Ensis siliqua</i>	(Linnaeus, 1758)	UK, England	BivAToL-26	KX713294	KX713382	KX713217	KX713538	–
Pharidae	<i>Phaxas pellucidus</i>	(Pennant, 1777)	Sweden, Tjärnö	BivAToL-135	KC429400	KC429508	KC429309	KC429231	KC429145
Gastrochaenidae	<i>Rocellaria dubia</i>	(Pennant, 1777)	Spain, Catalonia	MCZ 378977	KX713339	KX713426	–	KX713574	KX713495
Gastrochaenidae	<i>Lamychaena hians</i>	(Gmelin, 1791)	USA, Florida Keys	BivAToL-289	KC429376	KC429481	KC429287	KC429209	KX713473

OUTGROUPS

Polyplacophora

Leptochitonidae	<i>Leptochiton asellus</i>	(Gmelin, 1791)	Sweden, Tjärnö	Protostome AToL T53	AY145382	AY145414	AY377586	AY377734	FJ461256
Cryptoplacidae	<i>Cryptoplax japonica</i>	Pilsbry, 1901	GenBank	n/a	AY377656	AY145402	AY377611	AY377761	FJ445780
Chaetopleuridae	<i>Chaetopleura apiculata</i>	(Say in Conrad, 1834)	USA, Massachussetts	Protostome AToL000234	AY377636	AY145398	AY377590	AY377741	AY377704

Monoplacophora

Neopilinidae	<i>Laevipilina hyalina</i>	(McLean, 1979)	USA, California	MCZ 378012	FJ445774	FJ449541	FJ449543	FJ445778	FJ445781
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Scaphopoda

Dentaliidae	<i>Antalis entalis</i>	(Linnaeus, 1758)	Sweden, Tjärnö	Protostome AToL T7	DQ279936	AY145388	DQ280027	DQ280000	DQ280016
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Gastropoda

Haliotidae	<i>Haliotis tuberculata</i>	Linnaeus, 1758	Spain, Catalonia	MCZ 378487	GQ160787	–	AY377729	AY377622	AY377775
Haliotidae	<i>Haliotis discus</i>	Reeve, 1846	GenBank	n/a	–	AY145418	–	–	–

Fissurellidae	<i>Diodora graeca</i>	(Linnaeus, 1758)	Spain, Catalonia	MCZ 378383	AF120513	DQ279980	DQ093476	DQ093502	AF120632
Neritidae	<i>Puperita pupa</i>	(Linnaeus, 1767)	Bahamas, Abaco	MCZ 378699	FJ977656	FJ977688	FJ977719	–	FJ977767
Calyptraeidae	<i>Crepidula fornicata</i>	(Linnaeus, 1758)	USA. Massachusetts	Protostome AToL000306	AY377660	AY145406	AY377625	AY377778	AF353154
Siphonariidae	<i>Siphonaria pectinata</i>	(Linnaeus, 1758)	Spain, Andalusia	MCZ 378735	X91973	DQ256744	AY377627	AY377780	AF120638

*Composite terminal, as Pinnidae sp.

MCZ specimens are accessible at <http://mczbase.mcz.harvard.edu/SpecimenSearch.cfm>

BivAToL specimens are vouchered at FMNH; see also <http://www.bivatol.org/>

UF: University of Florida Museum of Natural History

UMASS: University of Massachusetts, Boston.