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Bivalvia – a look at the Branches
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Phylogeny of Veneroidea (Mollusca: Bivalvia) based on morphology and molecules

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The largest Recent family of Bivalvia, the marine Veneridae with approximately 800 species, comprises one of the least understood and most poorly defined molluscan taxa, despite including some of the most economically important and abundant bivalves, for example quahog, Pismo clams, and Manila clams. A review of previous phylogenetic analyses including the superfamily Veneroidea (Veneridae, Petricolidae, Glauconomidae, Turtoniidae, Neoleptonidae) and within the Veneridae shows minimal taxon sampling leading to weak conclusions and few supported synapomorphies. New phylogenetic analyses on 114 taxa tested the monophyly of Veneroidea, Veneridae, and 17 nominal venerid subfamilies, using morphological (conchological, anatomical) data and molecular sequences from mitochondrial (16S, cytochrome oxidase I) and nuclear (28S, histone 3) genes. Morphological analyses using 45 exemplar taxa and 23 traditional characters were highly homoplastic and failed to reconstruct traditional veneroid classification. Full morphological analyses (31 characters) supported the monophyly of Veneroidea and Veneridae but only when certain taxa were excluded, revealing analytical difficulties caused by a suite of characters associated with neotenous or miniaturized morphology. Molecular analyses resulted in substantially higher clade consistency. The combined molecular data set resulted in significant support for a particular topology. The monophyly of Veneridae was supported only when Petricolidae and Turtoniidae were subsumed, and recognized as members with derived or neotenous morphologies, respectively. Morphological character mapping on molecular trees retained a high level of homoplasy, but revealed synapomorphies for major branch points and supported six subfamily groups (Dosiniinae, Gemminae, Samarangiinae, Sunettinae, Tapetinae, combined Chioninae + Venerinae). Glauconomidae and Neoleptonidae are provisionally maintained in Veneroidea pending further study; Petricolinae and Turtoniinae are placed in Veneridae.

ADDITIONAL KEYWORDS: anatomy – conchology – Cooperellidae – Glauconomidae – Neoleptonidae – Petricolidae – systematics – taxonomy – Turtoniidae – Veneridae.

INTRODUCTION

Venerids and their relatives are for the most part shallow-water, infaunal, filter-feeding, marine or estuarine bivalves. The genus *Venus* Linnaeus, 1758 originally included 34 species, 24 of which are still attributable to the modern family Veneridae Rafinesque, 1815 (others represent Lucinidae, Fimbriidae, and Psammobiidae; Dodge, 1952). Linnaeus (1758) himself considered the genus too inclusive and intended to subdivide it in a subsequent edition of *Systema Naturae*, which was never written (Dodge, 1952). In

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the *Treatise on invertebrate paleontology*, Keen (1969) established the most widely used current concept of Veneridae, including 12 well-recognized subfamilies, within the superfamily Veneroidea, along with Petricolidae d'Orbigny, 1840, Cooperellidae Dall, 1900, Glauconomidae J. E. Gray, 1853, and Rzehakiidae Korobkov, 1954 (the last a European Miocene family without extant representatives, which will not be further discussed here). Cooperellidae has been considered a synonym of Petricolidae in recent literature (e.g. Coan, Valentich Scott & Bernard, 2000). Two additional families, Turtoniidae W. Clark, 1855 and Neoleptonidae Thiele, 1934 have also been attributed to Veneroidea, each with some degree of controversy. This paper addresses, through phylogenetic analyses based on morphological and molecular data, the composition and relationships among the 'venus clams' *s.l.* and their presumed relatives in the superfamily Veneroidea.

VENERIDAE

Veneridae is the most diverse Recent bivalve family, comprising over 800 extant, presumably valid, species in approximately 170 genera. William Healy Dall (1902: 336) called venerids 'the culmination of pelecypod evolution' in terms of their morphology, distribution, and bathymetric range. Its members arguably include the most familiar of all bivalves, such as the hardshell clam *Mercenaria* ('quahogs', 'cherrystones'), Pismo clams, littlenecks, butterclams, and Manila clams, which form key components of the world's clam fisheries. They are circumglobally distributed in temperate to tropical waters, and are adapted to a wide range of environments (Kondo, 1998).

Although their numbers and economic relevance have focused attention on certain species, this has not translated into broader systematic studies on Veneridae, nor have the many published single-species studies been placed into phylogenetic context. Venerid classification has been historically unstable in terms of taxon placement and higher-order arrangement. Numerous family-group taxa have been introduced and used in various classification schemes over time (Appendix 1). In his classic systematic compendium, Thiele (1934) declined using venerid subfamilies (then based on hinge teeth), considering them unnatural. The 12 nominal subfamilies in the *Treatise on invertebrate paleontology* (Keen, 1969: N670) were used 'for convenience of arrangement' without 'necessarily reflect[ing] genetic relationships'. Nevertheless, this classification has since become widely accepted. Abbott (1974: 521) summarized that 'classification of the family . . . has been one of continual debate and rearranging for some years', a controversy that originated in the original broad concept of the genus *Venus* (Dodge, 1952). Some alternative subfamilial arrangements have been adopted by a few more recent authors (e.g. Hikida, 1996; Shimamoto, 1996), although without gaining widespread acceptance.

Modern phylogenetic studies on other bivalve groups have shown that morphological traits frequently do not support widely accepted classifications (e.g. Graf, 2000; Lydeard, Minton & Williams, 2000) and are probably influenced by evolutionary convergence (Canapa *et al*., 1996). Wagner (2000: 365) postulated that morphological character states are subject to exhaustion – 'when character [state] change is more likely to yield homoplasy than novelt[y]' – in large deeply rooted families. These tenets also seem to apply to Veneridae, which dates back to the Cretaceous (Skelton & Benton, 1993); there are no recognized synapomorphies for Veneridae or any of its recognized subfamilies. Veneridae is usually distinguished by a single rather generalized hinge character – the presence of three cardinal teeth in each valve – with all other shell characters (of lateral teeth, pallial sinus, lunule, escutcheon, sculpture) varying greatly (Keen, 1969; see below). A good example of the level of morphological variation in venerids relative to the present classification is Harte's (1998b) informal organization of the subfamilies into two groups:

> Weakly ornamented (Clementiinae, Dosiniinae, Meretricinae, Pitarinae, Sunettinae): weak surface ornamentation, smooth margins, well-developed pallial sinuses, well-developed anterior lateral teeth.
> Ornamented (Chioninae, Gemminae, Samarangiinae, Venerinae): strong surface ornamentation, crenulate margins, small or absent pallial sinuses, weak or absent anterior lateral teeth.

Numerous exceptions to this dichotomy are evident, including members of Gemminae with smooth shells, of Sunettinae with crenulate margins, and of Dosiniinae and Clementiinae with weak or absent lateral teeth. Three nominal subfamilies (Cyclininae, Gouldiinae, Tapetinae) exhibit too strong a mixture of features to have been categorized by Harte (1998b) in this scheme. Perhaps most importantly, many of the listed features have been considered as ecophenotypic adaptations against predators: well-developed pallial sinus (= long siphons) for deep infaunal burrowing, strong surface ornamentation for anchorage, and marginal crenulations for tighter closure. Morphological convergence is one potential reason for the difficulty of resolving venerid relationships; paedomorphosis is another. F. R. Bernard (1982) used the degree of reduction of the outer demibranch, the relative length and separation of siphons, and the presence/absence of an adult byssus to develop an evolutionary scenario that grouped small, paedomorphic, brooding venerids together. The resulting taxonomy from this study has

been criticized (Lindberg, 1990) as lacking a phylogenetic framework.

Despite the apparent lack of morphological synapomorphies, higher-order molecular analyses of the Bivalvia using portions of slowly evolving nuclear [18S rRNA, 28S rRNA, histone 3 (H3)] and faster evolving mitochondrial [cytochrome oxidase I (COI)] genes (summarized in the following sections) have supported the monophyly of Veneridae, although none so far has included more than four venerid taxa. Within-group relationships of Veneridae are likewise unresolved. Most molecular studies have focused on single species or genera (e.g. Dillon & Manzi, 1989a, b; Passamonti, Mantovani & Scali, 1997, 1999) rather than relationships within and among subfamilies, and those with wider foci have had limited taxon sampling. Even so, some studies have suggested potential sister relationships between certain subfamilies (see the following sections for summaries of individual studies).

Other Veneroidea

By the mid-19th century, Bivalvia had been classified into an ordinal system. Veneridae were grouped with various other siphon-bearing families in the order Veneracea H. Adams & A. Adams, 1856. The name (now usually modified to Veneroida) and the overall composition of the order changed over time, but key components were retained. In these early classifications (e.g. Adams & Adams, 1857; Chenu, 1862; Gill, 1871; Tryon, 1884; Fischer, 1887), Veneridae was grouped very consistently in direct sequence with two other family-level taxa, Petricolidae and Glauconomidae, whose members showed similarities in shell and/or anatomical characteristics (Appendix 1). With few exceptions, subsequent authors adopted the hypothesis of close relationships among Veneridae, Petricolidae, and Glauconomidae, and these three nominal families became the major constituents of the formal superfamily Veneroidea in the 20th century [e.g. Keen, 1969; Scarlato & Starobogatov, 1979; Boss, 1982; the second also including Vesicomyidae, a group more recently placed in the superfamily Glossoidea; see Allen, 2001]. Hypotheses of relationships and resulting classifications of Veneroidea have differed mostly in the treatment of three smaller families: Turtoniidae, Cooperellidae, and Neoleptonidae.

This study used improved taxon sampling and multiple character sets (including conchology, anatomy, and multiple gene sequences) to examine the phylogenetic composition and status of Veneroidea, Veneridae, and the various proposed venerid subfamilies, and to identify synapomorphies for supported clades.

MATERIAL AND METHODS

Taxa

One of the aims of this analysis was to take advantage of the largest possible assemblage of veneroid taxa, utilizing originally collected material, museum specimens, reliable and adequate published anatomical accounts, and all relevant molecular sequences available on GenBank (GB; http://www.ncbi.nih.gov/Genbank/index.html; through to the end of 2004). Included were representatives of 22 of the 25 available and potentially valid family-level taxa (excluding only synonyms of Glauconomidae and Neoleptonidae; see Systematic summary: ingroup family-level taxa, Appendix 1 and Figure 13), whether currently considered valid or not, and type species of the name-bearing genus for all 17 available venerid subfamilies. For a few groups (e.g. Clementiinae, Cooperellidae, Sunettinae), properly preserved specimens for anatomical and/or molecular data were not available, and coding was restricted to conchological characters. In most cases, the inclusion of at least two subfamily representatives assured minimal testing of monophyly. For Chioninae and Venerinae, representation was reduced in view of ongoing dissertation research by a coauthor (IK). The substantially greater numbers of species in some subfamilies in the analysis (e.g. Pitarinae, Tapetinae) is a reflection of the greater amount of data available for the larger subfamilies. Generic and species-level nomenclature reflects currently employed names in systematic and/or regional literature (with subgenera elevated to genus level), although considerable inconsistency and need for revisionary work are acknowledged. Final taxon lists included 110 species from all veneroid families and venerid subfamilies in the morphological data matrix and 70 species from four of the five veneroid families and 12 of the 17 subfamilies in the molecular data matrix (Appendix 2). Three species, from Arcticidae, Corbiculidae, and Vesicomyidae (the last recently synonymized with Kelliellidae by some authors; e.g. Allen, 2001), were chosen as outgroups based on traditional classification schemes and previous phylogenies (see below). Because of the inconsistent positions of these outgroup species in preliminary analyses, an all-zero outgroup based on the 'larger bivalve outgroup' was added to the morphological data matrix.

Following preliminary morphological analyses, which highlighted the many potential taxonomic problems at the generic level, a restricted taxa data set was chosen in which each family or subfamily in the ingroup was represented by two or three species. For each of the 12 currently recognized venerid subfamilies, these species always included the type species of the name-bearing genus plus in most cases one other species for which we had high confidence of correct

family-level placement; if the former was coded for conchological characters only (i.e. *Pitar tumens* and *Tapes literatus*), we added another member of that genus for which the data set included anatomical data. Sunettinae was the single exception, being represented by two species of the genus *Sunetta*. Nominal subfamilies not currently in widespread use were represented by various combinations: Callistinae as for currently recognized subfamilies, Callocardiinae and Meroinae by a single species each [there was no other species of *Callocardia* available; *Meroe* is currently considered (Keen, 1969) a synonym of *Sunetta*], and Gafrariinae and Lioconchinae by two species of *Gafrarium* and *Lioconcha*, respectively. All outgroups and nonvenerid veneroids used previously were added, bringing the total for this restricted data set to 45 taxa (see Appendix 3, data matrix, boldface). This data set was judged to have the highest potential of reconstructing monophyletic groups for all tested family-level groups.

Cited institutions are: American Museum of Natural History (AMNH), The Natural History Museum [= British Museum (Natural History)], London (BMNH), Florida International University (FIU), Florida Museum of Natural History, Gainesville (FLMNH), Field Museum of Natural History (FMNH), Natural History Museum of Los Angeles County, California (LACM), Museum d'Histoire Naturelle, Geneve (MHNG), Museum National d'Histoire Naturelle, Paris (MNHN), Museu de Zoologia, Universidade de São Paulo (MZUSP), North Carolina State Museum of Natural Sciences, Raleigh (NCSM), Naturhistoriska Riksmuseet, Stockholm (= Swedish Museum of Natural History) (SMNH), and Rosenstiel School of Marine and Atmospheric Sciences, University of Miami (= University of Miami Marine Laboratory), Florida (UMML).

Morphological techniques

Traditional characters were distilled first from taxonomic descriptions in the literature, to allow a test of those shell and anatomical characters historically used to define subfamilies and families; coding was taken from actual specimens or from verifiable literature as necessary (see Appendix 2). This resulted in a data matrix of 23 characters. These characters were then re-evaluated and recoded in light of homology assumptions or other questions raised during this research (see Appendix 3), supplemented by newly identified characters, resulting in an all-morphology data matrix of 31 characters. See Morphological Results and Appendix 3 for a discussion of characters, the full character list with taxon coding, and the data matrices used in these analyses.

Original gross dissections employed an Olympus SZH-10 stereomicroscope equipped with a drawing tube and an ocular micrometer; standard fine dissecting tools and differential tissue stains were used. For the histological examination of small-bodied species, formalin-fixed, ethanol-preserved specimens were soaked in Cal-EX® decalcifier until the shell was completely dissolved. Specimens were dehydrated through a graded ethanol series, followed by clearing in xylene substitute (Hemo-De®) and embedding in paraffin (Paraplast X-tra®). Complete 10 μm serial sections were produced for intact individuals in lateral or anteroposterior orientation, and stained with Alcian Blue/Periodic Acid/Schiff's trichrome stain.

Molecular techniques

DNA extraction

Tissue for molecular work was obtained from recently collected specimens as well as from older material in museum collections. In all instances, tissue had been preserved in 70–100% ethanol or lysis buffer prior to DNA extraction. For older museum material, information regarding the long-term preservation history of these specimens was typically lacking, consequently some specimens might have been initially treated with formalin fixative. Where possible, total genomic DNA was extracted from adductor muscle, foot, or mantle tissue (see Appendix 2 for the taxon-specific tissue used) to increase the likelihood of sampling only maternally transmitted mitochondrial DNA (F-type mtDNA). In some bivalve species, including the venerid *Ruditapes philippinarum* (see Passamonti & Scali, 2001; Passamonti, Boore & Scali, 2003), male specimens are known to harbour not only F-type mtDNA, typically present in their somatic tissues, but also a male-type (M-type) mtDNA transmitted from father to son via the sperm's contribution to the zygote. Although M-type mtDNA is usually restricted to male gonadal tissue, it has been reported at low levels within various organs of adult females and within mesodermally derived adductor muscle tissue of male bivalves (Garrido-Ramos *et al*., 1998), although the latter finding could reflect contamination (see Cao, Kenchington & Zouros, 2004). In particularly small-bodied taxa, such as *Gemma gemma*, *Parastarte triquetra*, and *Turtonia minuta*, a large portion of the bivalve body (minus shell) was used for DNA extraction. However, no evidence of mitochondrial heteroplasmy was detected in subsequent polymerase chain reaction (PCR) amplifications of these taxa.

Two methods of total genomic DNA extraction were used routinely in this study: (1) the standard CTAB and phenol–chloroform extraction protocol for molluscan tissue [see Collins *et al*. (1996) for the detailed DNA extraction procedure followed here], and (2) a sil-

ica-gel membrane DNA-binding protocol, allowing the purification of DNA without organic extraction or ethanol precipitation. The latter method was employed using Qiagen's DNeasy Tissue Kit, following the manufacturer's instructions. Both methods proved equally successful in the DNA extraction and subsequent amplification of target genes.

Target genes for this study included portions of two fast-evolving mitochondrial genes: the mitochondrial large subunit ribosomal RNA gene (16S rRNA; 454–602 bp fragment, primers removed) and the mitochondrial COI protein-encoding gene (658–661 bp fragment, primers removed). The suitability of both the 16S rRNA and COI gene data at this taxonomic level has been shown in numerous other molecular analyses of bivalves (e.g. Canapa *et al*., 1996, 2003; Bogan & Hoeh, 2000; Cooley & Ó Foighil, 2000; Graf & Ó Foighil, 2000; Matsumoto & Hayami, 2000; Park & Ó Foighil, 2000; Carlini, Young & Vecchione, 2001; Roe, Hartfield & Lydeard, 2001; Marko & Moran, 2002; Lee & Ó Foighil, 2003; Matsumoto, 2003; Barucca *et al*., 2004; Therriault *et al*., 2004). For 16S rRNA amplifications, we initially used the primer set 16Sar and 16Sbr of Palumbi (1996), but subsequently redesigned these primers (16Sar-ALT; 16Sbr-ALT) to work more specifically on venerids and our designated outgroups (Table 1). For taxa that failed to amplify with either primer pair, we designed a new primer pair internal to 16Sar/16Sbr and based on known venerid sequences. This primer set (16SH1, 16SL3) amplified a smaller fragment of 303 bp. To amplify the fragment of COI, we employed the primer set LCO1490 and HCO2198 of Folmer *et al*. (1994). Although these primers successfully amplified this gene region for some taxa, they did not work broadly across the Veneridae. Consequently, we redesigned these primers, using COI sequences from venerids in GenBank as well as in our own growing data set, by incorporating degenerate bases at variable positions across taxa (COIF-ALT; COIR-ALT; Table 1). For taxa that failed to amplify with either primer pair, we also designed internal primers to be used in conjunction with end primers that allowed amplification of this gene region in two overlapping pieces (COIMIDF; COIMIDR; Table 1).

For independent nuclear markers, we targeted portions of two nuclear genes: a *c*. 1200 bp region of the 28S rRNA gene and a 328 bp fragment (excluding primers) of the H3 protein-encoding gene. We elected to use the 28S rRNA gene rather than 18S rRNA because, although both genes are evolutionarily very conserved, the faster evolving 28S was more likely to provide informative characters at shallower levels in our phylogeny. Both the 28S and H3 genes have been frequently exploited for higher-level analyses of bivalves and other molluscs (e.g. Colgan, Ponder & Eggler, 2000; Park & Ó Foighil, 2000; Giribet & Wheeler, 2002; Colgan *et al*., 2003; Giribet & Distel, 2003; Passamaneck, Schander & Halanych, 2004; Williams, Taylor & Glover, 2004). Primer sequences used for H3 were those of Colgan *et al*. (2000): H3F and

Table 1. Primer sequences used in this study and the annealing temperature at which successful amplifications were performed

Gene	Primer name	Sequence (5′–3′)	Annealing temperature (°C)	Source
16S	16Sar	CGCCTGTTTATCAAAAACAT	50	Palumbi, 1996
	16Sbr	CCGGTCTGAACTCAGATCACGT	50	Palumbi, 1996
	16Sar-ALT	GCCTGTTTATCAAAAACATSG	48–50	This study
	16Sbr-ALT	CCGGTCTGAACTCAGATCATGT	48–50	This study
	16SL3-Ven	GCAAYGAGAGTTGTRCTAAGGTAGC	58–61	Kappner & Bieler, 2006
	16SH1-Ven	ATAATCCAACATCGAGGTCGCAAA	58–61	Kappner & Bieler, 2006
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	48	Folmer *et al*., 1994
	HC02198	TAAACTTCAGGGTGACCAAAAAATCA	48	Folmer *et al*., 1994
	COIF-ALT	ACAAATCAYAARGAYATYGG	48	This study
	COIR-ALT	TTCAGGRTGNCCRAARAAYCA	48	This study
	COIMIDF	ATRMTNGGNGGDTTYGGNAAYTG	48–50	This study
	COIMIDR	GGRTANABDGTYCANCCNGTNCC	48–50	This study
28S	28SD1F	GGGACTACCCCCTGAATTTAAGCAT	55–60	Park & Ó Foighil, 2000
	28SD6R	CCAGCTATCCTGAGGGAAACTTCG	55–60	Park & Ó Foighil, 2000
	28SD1F-ALT	AACCAGGATTCCCTCAGTAA	55–60	This study
	28SMIDF	CTTGAAACACGGACCAAGG	55	This study
H3	H3F	ATGGCTCGTACCAAGCAGACVGC	50–55	Colgan *et al*., 2000
	H3R	ATATCCTTRGGCATRATRGTGAC	50–55	Colgan *et al*., 2000

COI, cytochrome oxidase I; H3, histone 3.

H3R (Table 1). For 28S rRNA, we employed the primer pair 28SD1F and 28SD6R used by Park & Ó Foighil (2000) (Table 1). For taxa that did not amplify using this primer pair, we designed a new forward primer (28SD1F-ALT) that resulted in a slightly smaller (45 bp shorter) amplification product. Because a large number of taxa did not amplify using either of these two primer pair combinations, presumably because of highly degraded DNA, we attempted to amplify a smaller piece of the 28S rRNA gene (270–280 bp, excluding primers) using the primer pair 28SINTF/28SD6R (Table 1).

Amplification and sequencing

For each amplification, *c*. 10–100 ng of each genomic DNA extraction was used as the template in a 50 µl PCR that consisted of 1.5–2.0 mM $MgCl_2$ buffer, 1× buffer (50 mM KCl, 10 mM Tris-HCl, pH 9.0 at 25 °C, and 0.1% Triton® X-100), 0.5 µM of each primer, 200 µM of each dNTP, and 1–1.5 units of *Taq* DNA polymerase. Under some circumstances, 4% bovine serum albumin (10 mg ml^{-1}) and 0.56 M dimethylsulphoxide were also added to reactions to improve amplifications. PCR were typically performed in one of the following thermal cyclers: an MJ Research PTC-200, a Stratagene Robocycler Gradient 96, or a DNA Engine DYAD Peltier thermal cycler. For the MJ Research PTC-200, we denatured samples for 150 s at 95 °C, followed by 38 denaturation/annealing/extension cycles of 10 s at 94 °C, 45 s at primer-specific annealing temperatures (see Table 1), and 45 s at 72 °C, with a final 10 min extension on the last cycle. For the Robocycler, samples were denatured for 120 s at 94 °C, followed by 38–40 cycles of 32 s at 94 °C, 84 s at primer-specific annealing temperatures (see Table 1), and 90 s at 72 °C, with a final 10 min extension at 72 °C. Cycling conditions for 16S, COI, and H3 genes in the DNA Engine DYAD Peltier thermal cycler were as in Kappner & Bieler (2006) and Table 1. A 5 µl aliquot of each PCR product was run out on a 1.4% agarose gel. When single bands of the appropriate size resulted from these amplifications, the PCR product was prepared for sequencing using Geneclean III. When supernumerary bands were present, the entire PCR product was run out on a 3% Nu-Sieve TAE agarose gel, the band of the correct size was excised under long wavelength ultraviolet light, and purified for sequencing following the protocols in Geneclean III or GELase. Purified PCR products were cycle sequenced using BigDye 3.0/3.1 chemistry and analysed on an ABI 3100 genetic analyser. Both strands were sequenced to ensure accuracy. In a few instances, where there was evidence of intra-individual length variation within a gene region (COI and 28S rRNA), genes were cloned using a TOPO TA cloning kit and the resulting products sequenced.

Sequence alignment and analyses

Multiple sequence alignments of 16S and 28S rRNA genes were performed in CLUSTAL X (Thompson *et al*., 1997) using default pairwise alignment parameters of gap opening and gap extension penalties of 15.00/6.66 and 10/2 for 16S and 28S rRNA genes, respectively, with a transition weighting of 0.5. Alignments of 16S rRNA fragments were subsequently modified by eye within MACCLADE version 4.06 (Maddison & Maddison, 2002) according to secondary structure inferences for molluscan 16S rRNA (Lydeard *et al*., 2000). Regions of poor alignment within the ribosomal RNA genes, typically unpaired loops and bulges of varying sizes bounded by stem regions or highly conserved sites, were excluded from the phylogenetic analyses. The protein-encoding genes, COI and H3, were aligned easily by translating each into its amino acid sequence in MACCLADE; only one indel of one amino acid in length was present within COI and no indels were present within H3. On the basis of these individual alignments, we built a single concatenated data set consisting of all four gene regions; this final alignment is available from the authors upon request.

PHYLOGENETIC ANALYSES

Morphological analyses

Two versions of the morphological data set (Appendix 3) were used: (a) 23 traditional characters (15 binary, eight multistate; marked as 'traditional' in Appendix 3), including 'any anterior lateral tooth' present/absent (character 18), and (b) 31 'all-morphology' characters (24 binary, seven multistate), which expanded the traditional character data set to include additional characters from shell and soft anatomy, but replacing character 18 with characters 15 and 16 (reflecting two probably nonhomologous states of the anterior lateral tooth), and omitting three traditional characters (6, periostracum; 31, siphonal fusion; 32, byssate foot) due to the high probability of artefacts in the material examined (see Discussion).

Morphological analyses used the data management analysis algorithm WINCLADA (Nixon, 2002) to explore character distribution and evolution and as a launch base for the parsimony-based tree-search program NONA version 2.0 (Goloboff, 1993). Within the printed data matrix (Appendix 3), a 'not applicable' character state is coded as 'n' and an unknown character state is coded as 'u'; this system provides the reader with information, although the algorithm treated the two identically. Multistate characters were

treated as non-additive (unordered). Two alternate tree searching strategies were used within WINCLADA/NONA: (1) the parsimony ratchet 'island hopper' (Nixon, 1999) using default settings (200 iterations/replication, holding one tree/iteration and selecting four characters for each, with amb- setting), used in initial explorations of the data sets and (2) more robust heuristic searching (hereafter 'heuristic search') using 1000 replications of random taxon addition, holding up to 100 trees, with up to ten starting trees per replicate, and the branch-swapping option mult*max*. Four replicate runs were completed for each type of search on each data set. Both 'fast' and 'slow' optimization models were used to explore alternative equally parsimonious character distributions on each tree.

The combinations of two taxon lists (all 114 taxa and restricted 45 taxa), two morphological data sets (traditional and all-morphology), and four replicates produced a total of 16 analyses using the more rigorous heuristic search. Strict and majority-rule consensus trees were generated for each analysis, for a total of 32 morphological trees under consideration. The consensus trees of the shortest most-parsimonious trees for each set (all-taxa/traditional, restricted/traditional, all-taxa/all-morphology, restricted/all-morphology) were selected for discussion.

Secondary mapping of morphological characters on molecular trees utilized data generated for the full 114 taxa examined (Appendix 3).

Molecular analyses

Molecular phylogenies were generated using the maximum parsimony (MP) and Bayesian (B/MCMC; Larget & Simon, 1999; Huelsenbeck & Ronquist, 2001) methods of analysis. Because any analytical method, including parsimony, tends to group sequences of similar nucleotide composition together, regardless of evolutionary history (Lockhart *et al*., 1994), a Chi-square test of base frequency homogeneity was run in PAUP* (version 4.0b10; Swofford, 2002) to test for composition bias. The skewness of tree-length distributions as a measure of phylogenetic signal (Hillis & Huelsenbeck, 1992) was estimated by generating 10 000 random trees in PAUP*. Given the presumed age of venerid lineages and divergence from outgroups, saturation as measured by transition and transversion substitution patterns was probable. Consequently, saturation plots were examined for each data set prior to undertaking phylogenetic analyses. Most-parsimonious trees were explored in PAUP* by undertaking 100 random sequence additions, TBR branch swapping, and collapsing branches with minimum length equal to zero. Branch support was typically examined by undertaking 250 bootstrap pseudoreplicates, with a minimum of ten random sequence additions per replicate.

The most appropriate models of molecular evolution to be used in Bayesian analyses for each data set were estimated in MODELTEST 3.06 (Posada & Crandall, 1998), basing model selection on the Akaike information criterion (see Posada & Buckley, 2004) (Table 2). Posterior probabilities (PP) were estimated in MRBAYES 3.0b4 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) by sampling trees using a Markov chain Monte Carlo (MCMC) method. Using this approach, the PP value of each branch indicates the occurrence in trees that were visited during the course of the MCMC analysis. We used default Dirichlet priors for state frequencies (1, 1, 1, 1) and substitution rates (1, 1, 1, 1, 1, 1), a prior for the gamma shape parameter uniformly distributed on the interval (0.50, 50.00), and an invariant sites prior uniformly distributed on the interval (0.00, 1.00). Branch lengths were left unconstrained, with an exponential prior, and all unique tree topologies were assumed to have equal probability. For combined gene analyses, the data set was partitioned such that a specific model of sequence evolution could be applied to each gene, and state frequencies, substitution rates, the gamma distribution shape parameter, and invariant sites parameter were unlinked across partitions. For the two protein-encoding genes, COI and H3, we set up individual partitions for first, second, and third positions within codons to accommodate different patterns of sequence evolution across codon positions. For combined analyses, congruence of the different data sets was tested using a Bayesian approach (Buckley *et al*., 2002). Topologies obtained from separate analyses were compared and examined for conflict across clades supported by PP values $\geq 95\%$. Data sets can be combined if congruent and no conflict is found. If data sets are incongruent, a concatenated analysis could be potentially misleading (Bull *et al*., 1993). We ran analyses for a minimum of 3 000 000 generations, sampling four chains (for heat for different data sets, see Table 2), a sample frequency of 100, and starting with a random starting tree, unless otherwise noted. The software TRACER 1.2 (http://evolve.zoo.ox.ac.uk/software.html?id=tracer) was used to determine how many generations needed to be excluded as 'burn in' of the chain. Of the remaining trees, a majority-rule consensus tree including average branch lengths was calculated using the 'sumt' option of MRBAYES. PP equal to or above 95% were regarded as significant. Phylogenetic trees were visualized using the program TREEVIEW (Page, 1996) or PAUP*. Each analysis was replicated four times to ensure that the MCMC had converged on a stable log likelihood. The replicate with the highest mean estimated likelihood value was chosen for presentation.

Table 2. Selected models for the different mitochrondrial DNA (mtDNA) partitions (by the Akaike Information Criterion), burn-in and heated chain temperature information for different data sets employed in Bayesian analyses

Analysis	Partition	Selected model	Burn-in	Heated chain temperature
mtDNA (69 taxa)	16S	TVM + Γ +I	600	0.2
mtDNA (58 taxa)	COI first position	GTR + Γ +I		
	COI second position	GTR + Γ +I		
	COI third position	TIM + Γ		
	COI	Three partitions	500	0.1
mtDNA (73 taxa)	Combined mtDNA	Four partitions	2000	0.2
28S (36 taxa)	28S	GTR + Γ +I	1000	0.2
Histone 3 (50 taxa)	H3 first position	GTR + I		
	H3 third position	GTR + Γ		
		Two partitions	1000	0.1
mtDNA and 28S (72 taxa)	28S	GTR + Γ +I		
	16S	TVM + Γ +I		
	COI first	GTR + Γ +I		
	COI second	GTR + Γ +I		
	COI third	TIM + Γ		
	Combined	Five partitions	1000	0.2
All 4 genes (56 taxa)	16S	TVM + Γ +I		
	COI first	GTR + Γ +I		
	COI second	TVM + Γ +I		
	COI third	TIM + Γ		
	28S	GTR + Γ +I		
	H3 first	GTR + I		
	H3 third	GTR + Γ		
	Combined	Seven partitions	1000	0.5

COI, cytochrome oxidase I; H3, histone 3.

Hypothesis testing

On the basis of the results from the combined four-gene Bayesian analysis, we tested the traditional systematic arrangements of Veneridae and Veneroidea against our phylogenetic hypothesis by analysing a set of 29 001 suboptimal trees present in our B/MCMC samples. For this analysis, the probability that the null hypothesis (traditional arrangement) is correct is equal to the frequency of trees in the B/MCMC samples that are topologically congruent with this hypothesis. We calculated this by applying constraint-based tree filters in PAUP*, employing the methods of Ihlen & Ekman (2002). Using this approach, we tested the following null hypotheses: (1) that Veneroidea *sensu* Owen (1959), Ockelmann (1964), and Salas & Gofas (1998) [= Veneridae, Petricolidae, Glauconomidae, Turtonidae, and Neoleptonidae (the last, however, not included in this molecular data set)] is monophyletic; (2) that Veneridae *sensu* Keen (1969) is monophyletic; (3) that Petricolidae is a sister taxon to Veneridae; (4) that Turtonidae is a sister taxon to Veneridae; and, following our morphological results (5) that Gemminae does not belong to Veneridae.

Character mapping

Because of the high level of incongruence between the morphological and molecular results, as well as the numerous misleading morphological characters disclosed by these analyses (see below), no attempt at total evidence or partitioned morphological/molecular analyses was made. Instead, and in an attempt to define morphological synapomorphies for supported clades, morphological characters were mapped on the four-gene combined molecular tree (Fig. 12).

SYSTEMATIC SUMMARY

MERCENARIA: AN EXEMPLAR VENEROID

In the absence of undisputed synapomorphies and clear diagnoses of higher-level taxa, a useful means for beginning a discussion of Veneroidea is to examine one of its best understood members, *Mercenaria mercenaria* (Linnaeus, 1758) (Veneridae: Chioninae), the hard-shelled clam or 'quahog', native to eastern North America and introduced to northern Europe, Puerto Rico, and north-western North America. This species has prompted a very large body of published litera-

ture, including that on its morphology and life history (e.g. Kellogg, 1903; Kraeuter & Castagna, 2001), as a result of its role in the commercial hard clam industry of the eastern USA. It has been harvested for food and/or raised in aquaculture for *c*. 300 years in its native range, and was once (as wampum) used as a form of currency among indigenous peoples. *Mercenaria mercenaria* is also appropriate for this role here because it was long treated as the type species of the genus *Venus*; it was designated as such, although invalidly according to ICZN rules, by Lamarck (1799), and many subsequent workers continued to use *Mercenaria mercenaria* as type throughout the 19th century (Dodge, 1952). [The now-accepted type species of *Venus*, *V. verrucosa* Linnaeus, 1758, is comparatively less well known.] This summary description of *Mercenaria mercenaria* will serve to exemplify the morphological characters that have served (or ultimately will serve) to define members of this superfamily and its components.

The shell (Fig. 1) is thick walled, well inflated in the adult, and rounded trigonal in shape, with the umbones more anterior (at approximately one-quarter of the anteroposterior length), resulting in a shorter anterior end and a longer sloping (sometimes rather rostrate) posterior end. The umbones are prosogyrous over a distinctly demarcated, cordiform, and flattened lunule, the latter subequal in each valve and bounded by an incised line. From the anterior aspect, both the shell outline and the lunule are heart-shaped, hinting at the origins of Linnaeus' taxon *Venus* (i.e. the proper name of the Roman goddess of love) and its resultant family name Veneridae. Externally, the shell is sculptured by crowded, coarse commarginal growth lines that are elevated as dense lamellae anteriorly, continuing over the lunule. The ventral surfaces of the lamellae have faint radial riblets. The commarginal lamellae are lowest, often smooth, at the centre of the valve. Posterodorsally, the escutcheon is broad, subequal in each valve, gently sloping towards the ligament, and not bounded by an impressed line or change in sculpture (although slightly heavier on the right side than the left); the shell edge at the posterior end of the right escutcheon overlaps the left. The ligament is external, extending from the lunule to approximately half the distance from the umbo to the posterior corner of the valves. Overall the shell is chalky greyish white, sometimes marked to a variable degree with brown chevrons (forma *notata* Say, 1822), or stained black by anoxic sediments. The periostracum is thin and yellow, but generally inconspicuous, evident in adult shells only as brown threads between the

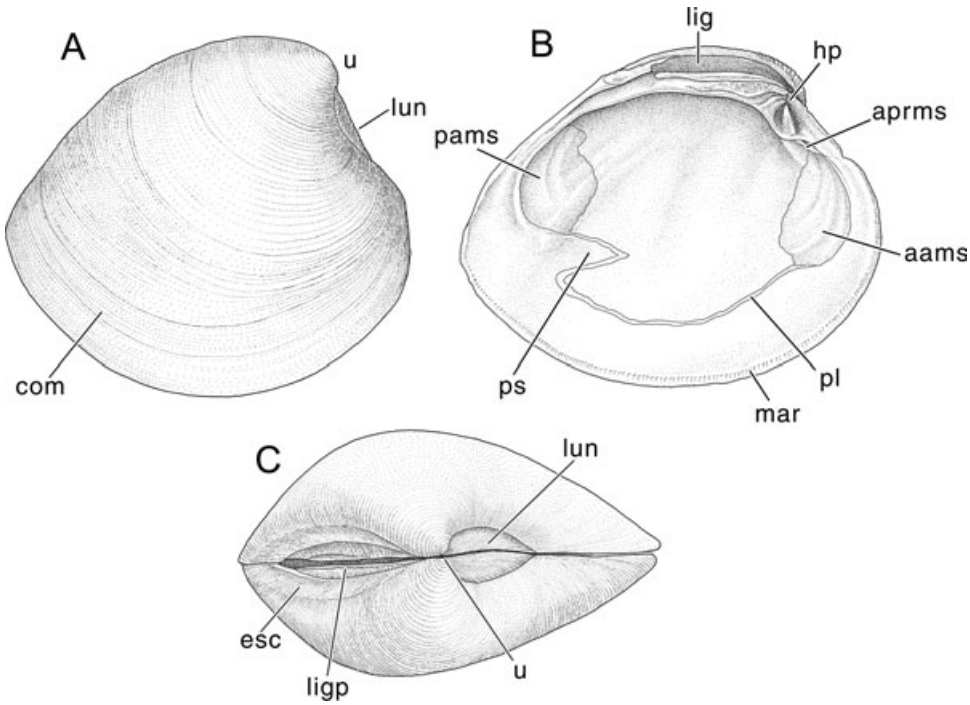


Figure 1. *Mercenaria mercenaria*, showing features of venerid shell morphology coded by this analysis. A, right lateral view of exterior of right valve. B, right lateral view of interior of left valve. C, dorsal view of articulated valves, anterior to the right. aams, anterior adductor muscle scar; aprms, anterior pedal retractor muscle scar; com, commarginal sculpture; esc, escutcheon; hp, hinge plate (with cardinal teeth); lig, ligament; ligp, ligamental pit; lun, lunule; mar, shell margin; pams, posterior adductor muscle scar; pl, pallial line; ps, pallial sinus; u, umbo.

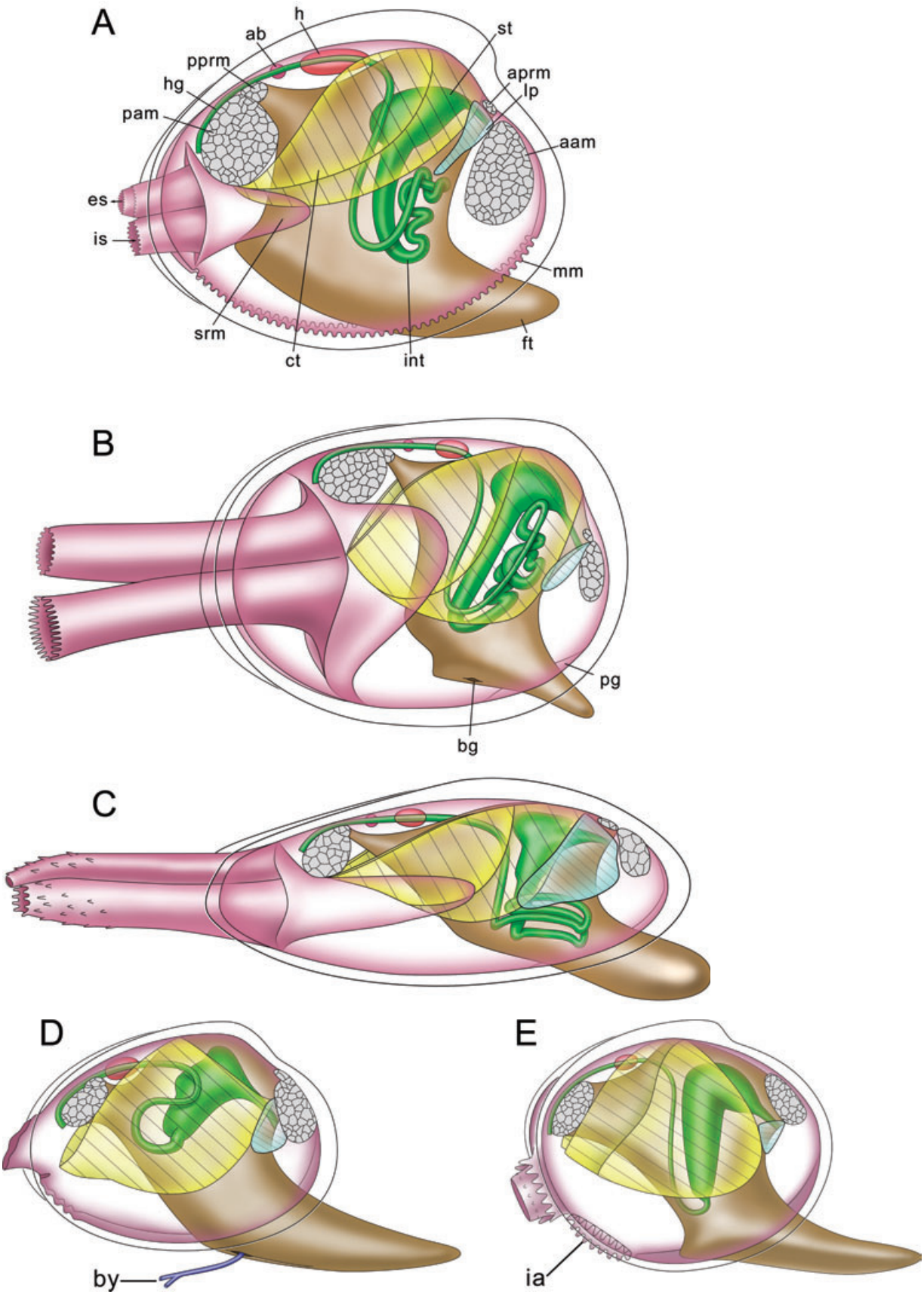
distalmost commarginal ridges. Structurally, the shell is aragonitic and composed of three layers: an outer composite prismatic layer, a middle cross-lamellar layer, and an inner homogenous layer; the inner shell layer has a greater proportion of conchiolin than the outer and middle layers (Jones, 1979).

Internally the shell is porcellaneous white, usually flushed with dark purple. The purple flush is usually located posterodorsally on the hinge plate, anteriorly outside of the anterior adductor muscle (AAM) scar, and especially, posteriorly, covering (to a variable extent) the posterior adductor muscle (PAM) scar, the pallial sinus, and the shell margin outside of the pallial line. The AAM and PAM scars are teardrop-shaped, with the posterior slightly broader than the anterior. The slightly impressed pallial line extends from the posteroventral points of each adductor muscle scar, parallel to the ventral shell margin, and includes a short, triangular, anteriorly directed pallial sinus adjacent to the PAM scar. The anterior pedal retractor muscle scar is impressed, near (but fully separated from) the AAM scar, on the ventral surface of the hinge plate. The posterior pedal retractor muscle scar is confluent with and forms the dorsalmost point of the PAM scar. The outer shell margin is indented at the distal end of the lunule. Across the lunular margin and ventral to the lunule, minute denticulations adorn the margin to the posterior corner of the valves. The margin is smooth from the posterior corner, including the siphonal area, to the distal end of the ligament.

The hinge plate is moderate in strength, and shows no attrition (defined in other bivalves as excavation of the hinge plate so that the hinge teeth effectively extend past the ventral margin). Each valve has three radiating cardinal teeth. In the left valve (LV), the anterior cardinal [2a, numbered following the hinge formula model of Félix Bernard (1895), based on ontogenetic development of the teeth] is strongest and slightly bifid, the middle (2b) is strongly bifid, and the posterior (4b) is blade-like and appressed to an irregularly rugose area between it and the ligamental nymph. In the right valve (RV), the anterior cardinal (3a) is blade-like, and the middle (1) and stronger posterior (3b) cardinals are strongly bifid. An elongated irregularly rugose area exists between the posterior cardinal and the nymph of each valve; these pronounced interlocking rugose areas, diagnostic of the genus *Mercenaria*, possibly function as additional 'teeth' to ensure proper valve occlusion (Dall, 1902; Jones, 1979). No cardinal teeth are united dorsally, as occurs in some other venerid taxa (see below). Both anterior and posterior lateral teeth are absent (although anterior lateral teeth are present in other veneroids, see Appendix 1). The ligament is supported by a nymphal shelf, which terminates abruptly before the posterior end of the ligament or ligamental pit. Posterior to the ligament, the shell edges interlock via an elongated ridge in the LV and a corresponding elongated trough in the RV (also forming the shell overlap seen at the posterior end of the escutcheon).

Internally (Fig. 2A), the *Mercenaria* mantle edges are unfused from the AAM to the ventral point of the siphonal retractor muscle, just behind the heel of the foot. The mantle edge is thickened by muscle fibres and has four folds: (1) the outer (which secretes the shell and periostracum), (2, 3) the middle, divided into two folds (a smaller outer-middle, which is sensory, and a larger inner-middle, which controls water flow), and (4) the inner (which possibly directs foreign particles out of the mantle cavity) (Eble, 2001). Posteriorly, folds 3 and 4 are fused [siphonal fusion type B of Yonge (1957)] to form short (relatively longer in juveniles) incurrent (ventral) and excurrent (dorsal) siphons that are united for their entire length. The incurrent (= branchial) siphon is slightly larger in diameter. The excurrent (= anal) siphon is equipped with a conical valve, more obvious in juveniles. The terminus of each siphon is fringed with simple tentacles. Interiorly, the proximal ends of the siphons have siphonal membranes (to which the tips of the gills attach) and siphonal valves, whose slit-like openings control water flow in both directions. The siphons are retracted by siphonal retractor muscles, which form a triangular muscle mass on the surface of each mantle flap (and whose margins attach to the interior shell surface to produce the pallial sinus). Ciliary waste currents on the inner mantle surfaces pass particles posteriorly to a point at the base of the incurrent siphon; waste is discharged through the incurrent siphon upon contraction of the adductor muscles (rather than

Figure 2. Generalized anatomy of representative Veneroidea, drawn as through a transparent shell and mantle, emphasizing the relative arrangement of major organ systems (reproductive and excretory systems omitted). A, Veneridae, *Mercenaria mercenaria* (from original dissections). B, Petricolidae, *Petricola lapicida* (from original dissections). C, Glauconomidae, *Glauconome rugosa* [from original dissections assisted by the description and figures of Owen (1959)]. D, Turtoniidae, *Turtonia minuta* [interpreted from the description and figures of Oldfield (1955)]. E, Neoleptonidae, *Neolepton sulcatulum* [interpreted from the description and figures of Salas & Gofas (1998)]. aam, anterior adductor muscle; ab, aortic bulb; aprm, anterior pedal retractor muscle; bg, byssal groove; ct, ctenidia; es, excurrent siphon; ft, foot; h, heart; hg, hindgut; int, intestinal coils (= midgut); is, incurrent siphon; lp, labial palp; mm, mantle margin; pam, posterior adductor muscle; pg, pedal gape; pprm, posterior pedal retractor muscle; srm, siphonal retractor muscle; st, stomach.



through the excurrent siphon as one might predict; Kellogg, 1915).

Each adductor muscle is comprised of two parts, a larger, more central, somewhat darker pinkish-to-red portion, composed of 'quick' muscle fibres, flanked on its outer surface by a crescent-shaped whitish portion, comprised of 'catch' fibres. The pink pigment of the adductor muscles has been identified as haemoglobin (Eble, 2001).

The visceral mass is suspended by the anterior and posterior pedal retractor muscles. These originate in the anterior and posterior parts of the foot, respectively, and insert on the shell above the adductor muscles (see pedal retractor muscle scars, above). The foot extends along the entire ventral surface of the visceral mass. It is wedge-shaped, laterally compressed, keeled ventrally, and extended slightly posteriorly (as a 'heel') and greatly anteriorly. Serving as the main tool for burrowing into soft sediment, the foot is composed primarily of muscle fibres. The muscle fibres are irregularly distributed vertically and horizontally, and are interspersed with haemocoelic spaces, which allow expansion when filled. A pedal gland lies in the midline of the foot (Jones, 1979), which produces a byssus in juvenile *Mercenaria*, but which is inactive in adults.

The plicate eulamellibranch ctenidia occupy much of the pallial cavity on either side of the visceral mass. Each consists of an outer and (longer) inner demibranch, extending from between the labial palps, along the ventral edge of the pericardium to the siphonal membrane. A supra-axial extension of the outer demibranch covers the pericardial space (= pericardial coelom) anterior to the PAM. The gill filaments are connected via tissue junctions and the lamellae are connected by interlamellar septa that, together with intervening plicae, define and delimit water tubes. Plicae are of two kinds, major and minor, the latter being secondary folds at the apices of the major plicae (Eble, 2001). Ciliary currents on the gills pass particles on each surface to the food groove at the free edge of each demibranch then forward to the palps (Kellogg, 1915). The anterior ends of the inner demibranchs are inserted into and fused with the distal oral groove [category II of Stasek (1963)]. The labial palps are elongated triangular structures posterior to the AAM on either side of the visceral mass. Each side comprises two palps, the inner surfaces of which are folded to form numerous fine ciliated ridges, which serve to further sort and channel food particles collected by the gills into the mouth opening.

The mouth opening lies between the labial palps just posteroventral to the AAM. It leads to a short oesophagus, lined by dense rugae, which passes posterodorsally to the stomach. The globose stomach lies in the dorsal part of the visceral mass, surrounded anteriorly by lobes of the digestive gland. It comprises a dorsal hood and larger ventral portion, separated by a shelf and possessing a large sorting area. A thin gastric shield covers the roof, most of the left interior wall, and part of the posterior floor of the stomach where it is strengthened by ribs. The ducts to the digestive gland open into the stomach via left and right caeca. Typhlosoles pass in and out of the two caeca [thus corresponding to the type V stomach of Purchon (1960)] and extend into the ventral midgut or intestine (conjoined to the style sack). A crystalline style secreted by the style sack extends well into the stomach in living specimens. The intestine continues ventrally from the distal end of the style sack to create a somewhat variable series of loops in the anteroventral part of the left side of the visceral mass (Jones, 1979), then runs posterodorsally to exit the visceral mass near the posterior end of the heart. The intestine passes through the ventricle of the heart (presumably acting as a stabilizing structure for the contracting ventricle; Eble, 2001) and over the aortic bulb of the posterior aorta, then dorsally over the surface of the PAM to terminate at the anus near the inner opening of the excurrent siphon. The major typhlosole continues into the postmidgut part of the intestine to the point where it turns to ascend posteriorly towards the heart (= ascending intestine). The rectum (Jegla & Greenberg, 1968) is highly muscular with numerous typhlosoles, producing unsculptured oval faeces of uniform composition, a format which has been called derived (vs. sculptured pellets with segregated sediments; Kornicker, 1962).

Gonadal tissue lies within the visceral mass, generally ventral to and surrounding the darker-coloured digestive gland. Gonoducts open into the suprabranchial cavity ventral to the pericardium.

The large pericardium lies at the dorsal midline, posterior to the visceral mass and anterior to the PAM. The heart consists of a single ventricle and two auricles, connected laterally to the ventricle via valved openings. Paired dark brown pericardial glands open into the pericardial space (Eble, 2001). The anterior aorta passes dorsal to the intestine to supply anterior haemocoelic sinuses. The posterior aorta continues posteriorly ventral to the intestine to supply posterior sinuses, interrupted by a muscular, spongy aortic bulb posterior to the pericardium. The haemolymph contains several types of granulocyte capable of phagocytosis (summarized by Eble, 2001). The kidneys lie along the ventral side of the pericardial space, communicating with the auricles and emptying via renopores into the epibranchial chamber.

The nervous system has three main pairs of yellowish ganglia: cerebral (near the anterior pedal retractor muscles; innervating the palps, mantle, visceral mass, pedal retractor muscles, and AAM), vis-

ceral (on the anterior face of the PAM; innervating the mantle, ctenidia, kidneys, heart, and PAM), and the more fully fused pedal (just anteroventral to the distal end of the midgut; innervating the foot). Smaller auxiliary siphonal ganglia communicate via large nerves with the visceral ganglia. The complex system of nerves in *Mercenaria mercenaria* was detailed by Jones (1979).

Mercenaria mercenaria is a protandrous hermaphrodite (although some individuals mature directly into females, whereas others are simultaneous hermaphrodites; Loosanoff, 1937a, b; Jones, 1979) and has 19 pairs of chromosomes (Menzel & Menzel, 1965). Gametes are spawned freely into the water column. Mature spermatozoa have been observed in specimens only 5–7 mm in length (Loosanoff, 1937a). Larval development is planktotrophic, with veligers settling after approximately 12 days; the prodissoconch ranges in size from 170 to 240 μm in length; the plantigrade juvenile (early benthic stage) is byssate, with an unformed incurrent siphon (Carriker, 2001). The growth rate is variable with environmental conditions; growth to a marketable size ('littleneck' or 48 mm shell length) can take 15 months in warm southern waters, but 4 years in cooler northern waters. Shell layers in cross-section reveal annual growth increments through periodic winter growth cessation marks; very large specimens (*c*. 15 cm length) are estimated to be at least 40 years old (Fritz, 2001).

Perhaps because of its commercial status, *Mercenaria mercenaria* is one of the most used veneroids for molecular phylogenetic work. At the time of writing, at least ten independent sequences have been generated for phylogenetic use and either cited or posted on GenBank: 16S (Ó Foighil, Hilbish & Showman, 1996; Canapa *et al*., 2003), 18S (Adamkewicz *et al*., 1997; Campbell, 2000; Giribet & Wheeler, 2002), 28S (Rosenberg *et al*., 1997; Park & Ó Foighil, 2000; Giribet & Wheeler, 2002), and COI (Peek *et al*., 1997; Giribet & Wheeler, 2002) (see below). An additional 18 microsatellite sequences reside on GenBank from an unpublished study by Gjetvaj, King & Lubinski, as does a complete 1628 bp cytochrome P450 30 mRNA sequence (Brown, Clark & Van Beneden, 1998).

Ecologically, *Mercenaria mercenaria* generally inhabits intertidal to shallow subtidal mud, sand or seagrass habitats; the maximum recorded water depth of living specimens is 12 m (Harte, 2001). It is a relatively rapid burrower (Stanley, 1970), and its adult size and shell thickness aid in deterring most predators (e.g. crustaceans, fish; Harte, 2001). The species is tolerant of wide ranges of salinity and temperature, but relies on oceanic conditions for spawning.

INGROUP FAMILY-LEVEL TAXA

Twenty-five family group names are available (and are not deemed invalid due to homonymy or suppression of the name of its type genus[1]) in Veneroidea, listed here within the five currently used family names. Characters currently defining each of the available nominal taxa are summarized in Appendix 1.

Veneridae Rafinesque, 1815, with
- Callistinae Habe & Kosuge, 1967 (alternatively part of Pitarinae)
- Callocardiinae Dall, 1895 (alternatively part of Pitarinae)
- *Chioninae Frizzell, 1936
- *Clementiinae Frizzell, 1936
- *Cyclininae Frizzell, 1936
- *Dosiniinae J. E. Gray, 1853
- Gafrariinae Korobkov, 1954 (alternatively part of Gouldiinae)
- *Gemminae Dall, 1895
- *Gouldiinae Stewart, 1930
- Lioconchinae Habe, 1977 (alternatively part of Pitarinae)
- *Meretricinae J. E. Gray, 1847
- *Pitarinae Stewart, 1930
- *Samarangiinae Keen, 1969
- *Sunettinae Stoliczka, 1870 (= Meroinae Tryon, 1884)
- *Tapetinae J. E. Gray, 1851
- *Venerinae Rafinesque, 1815

Petricolidae d'Orbigny, 1840, with
- Cooperellidae Dall, 1900 (synonymized by Morton, 1995)

Glauconomidae J. E. Gray, 1853 (= Glauconomyidae/Glaucomyidae Carpenter, 1861)

Turtoniidae W. Clark, 1855

Neoleptonidae Thiele, 1934 (= Bernadinidae Keen, 1969)

From this list, the 16 family group names [12 of the venerid subfamilies (marked by an asterisk above), four other veneroid families] that are in widespread use by standard compendia (Keen, 1969; Harte, 1998b; Coan *et al*., 2000) are here diagnosed mainly on the basis of very few, mostly shell, characters (Table 3). Eight of the tabulated characters are

[1]Three additional family-level taxa that are attributable to Veneridae are invalid due to homonymy or suppression. Circinae Dall, 1895, based on *Circe* Schumacher, 1817, has been placed on the Official Index (ICZN, 1981) because of its homonymy with Circinae Sundevall, 1836, based on *Circus* Lacépède, 1799 (Aves). Cythereinae J. E. Gray, 1838, is invalid because its type genus *Cytherea* Lamarck, 1805, is a junior homonym of *Cytherea* Fabricius, 1794 (Diptera). Paphiinae Finley, 1928, based on *Paphia* Röding, 1798, is a junior homonym of Paphiidae J. E. Gray, 1847, based on *Paphia* Lamarck, 1799 (Bivalvia: Mesodesmatidae).

Table 3. Traditional characters in the 16 recognized family group taxa of Veneroidea [data from Keen (1969), Harte (1998b), Coan *et al.* (2000) and supplemented by this study]

	Shell shape	Sculpture	Lunule	Escutcheon	Marginal denticles	Pallial sinus	AII lateral teeth	Cardinal teeth (RV/LV)	Byssus (adult)	Stomach type	Aortic bulb
Veneridae	Triangular	+	+ or –	+ or –	+ or –	+	–	3/3	+ or –	V	+
Chioninae											
Clementiniinae	Oval	+ or –	+	+ or –	–	+	–	3/3	?	V?	+
Cyclininae	Circular	+	+ or –	–	+ or –	+	–	3/3	–	V	+
Dosiniinae	Circular	+	+	+ or –	–	+	+ or –	3/3	–	V?	+
Gemminae	Circular, minute	–	–	–	+	+	–	3/3	+	V	–
Gouldiinae	Circular	+ or –	+	+ or –	+ or –	+ or –	+	3/3	– (± bg)	V?	+
Meretricinae	Oval	+ or –	+	–	–	+	+	3/3	–	V?	+
Pitarinae	Triangular	+ or –	+ or –	+ or –	–	+	+	3/3	+ or –	V	+
Samarranginae	Circular	–	+	+	–	–	+ or –	3/3	–	V?	+
Sunettinae	Oval	+ or –	+	+	+	+	+	3/3	?	V?	?
Tapetinae	Oval	+ or –	+ or –	+ or –	–	+	–	3/3	+ or –	V?	+
Venerinae	Triangular or oval	+	+	+	+	+	+	3/3	– (± bg)	V	+
Petricolidae	Oval or elongate	+ or –	–	–	–	+	–	2/3	– (+ bg)	V	+
Glauconomidae	Elliptical	–	–	–	–	+	–	3/3	–	V?	+
Turtoniidae	Oval, minute	–	+	–	–	–	–	2/3	+	IV	–
Neoleptonidae	Oval, minute	+	–	–	–	–	+	3/2	–	?	–

LV, left valve; RV, right valve; +, present; –, absent; + bg, byssal groove.

scored simply as presence/absence, for a total of 128 scores among the 16 taxa. Of these, 28 (22%) scores are considered as either present or absent within the group. This high degree of apparent homoplasy in relatively decisive characters reflects: (1) the phenetic nature and lack of identified synapomorphies among these nominal taxa; (2) a probable high incidence of character loss or convergence (sources of homoplasy) within the superfamily; and (3) the need for taxonomic revision at generic and suprageneric levels.

ANALYTICAL RESULTS

Previous phylogenies: Veneridae and Veneroidea

There have been 11 notable phylogenetic analyses of higher bivalve relationships that have been in a position to comment on the superfamily Veneroidea. All were primarily, if not exclusively, molecular in character, and all used few representative veneroidean taxa. In most of these studies, the same few veneroid sequences were used in combination with other bivalve representatives, although the methods of analysis often differed among the studies.

1. Rosenberg *et al*. (1997), in a molecular analysis of major clades of Mollusca based on the D6 region of the 28S rRNA gene, used *Mercenaria mercenaria* (Chioninae) and *Venus verrucosa* (Venerinae) to represent Veneroidea. These two taxa formed a monophyletic Veneridae, thus also Veneroidea within the capabilities of that analysis. *Sphaerium nitidum* Westerlund, 1876 (Sphaeriidae) and *Mytilopsis leucophaeata* (Conrad, 1831) (Dreissenidae), two of the few other included components of Heterodonta, were in a sister-group relationship to Veneridae.
2. Adamkewicz *et al*. (1997) used *Mercenaria mercenaria* and *Dosinia discus* (Reeve, 1850) (Dosiniinae) in a molecular-based phylogeny of Bivalvia using partial 18S rRNA sequences. Again Veneridae, and by extension Veneroidea, were concluded as monophyletic. A clade formed by *Corbicula leana* Prime, 1864 (= *C. fluminea*) (Corbiculidae) and *Mulinia lateralis* (Say, 1822) (Mactridae) was in a sister-group position to Veneridae.
3. Canapa *et al*. (1999) used sequences from the 18S rRNA gene in a bivalve phylogeny that included *Venus verrucosa* and *Callista chione* (Pitarinae). Veneridae was monophyletic in a sister relationship to a monophyletic Mactridae; no comment was made about Veneroidea.
4. Steiner & Hammer (2000) presented an 18S rRNA-based molecular phylogeny of Bivalvia, using four venerid taxa, *Mercenaria mercenaria*, *Venus verrucosa*, *Dosinia discus*, and *Callista chione*, the most complete coverage to date within a higher-level analysis. As with the previous analyses, Veneridae and thus Veneroidea were found to be monophyletic. *Arctica islandica* (Arcticidae) and *Corbicula leana* (= *C. fluminea*) were sister groups to Veneridae in this analysis.
5. Campbell (2000) included sequences from three venerids (*Venus verrucosa*, *Mercenaria mercenaria*, *Callista chione*) in a new analysis of the Bivalvia based on the 18S rRNA gene. As in previous studies, Veneridae (and by inference Veneroidea) was monophyletic, and found to be most closely related to *Arctica* in all analyses.
6. Canapa *et al*. (2001) used the same four venerids as employed by Steiner & Hammer (2000) in another 18S rRNA-based phylogeny. Veneridae, representing Veneroidea, was monophyletic and in a sister-group relationship with *Arctica* and *Corbicula*.
7. Giribet & Wheeler (2002) used 18S rRNA, 28S rDNA, and COI sequences combined with morphology in a higher-level phylogeny of Bivalvia. Morphological data were coded largely from the literature, often from family-level descriptions. *Mercenaria mercenaria* and *Callista chione* represented Veneridae and Veneroidea, and formed a monophyletic group in a sister relationship to *Arctica islandica*, *Corbicula fluminea*, and *Calyptogena magnifica* (Vesicomyidae).
8. Matsumoto (2003) included six heterodont taxa, including the two venerids *Macridiscus melanaegis* (as *Gomphina melanegis*) and *Meretrix lusoria*, in a phylogenetic analysis of the subclass Pteriomorphia based on mitochondrial COI sequences. The monophyly of Veneridae (Veneroidea) was supported in this distance-based analysis, as was a sister-group relationship with the representative corbiculid, *Geloina erosa* (Solander, 1786). No representative arcticids, vesicomyids, or glossids were included in this study.
9. Giribet & Distel (2003) furthered investigations of higher-level phylogenetic relationships within the Bivalvia using molecular data from four genes (18S rRNA, 28S rDNA, COI, and H3). Four members of the Veneroidea were represented: *Mercenaria mercenaria* (18S, 28S, COI), *Callista chione* (18S only), and *Venus verrucosa* (18S only) from Veneridae, plus *Petricolaria pholadiformis* (18S and 28S). The monophyly of Veneroidea was not recovered in any parameter set, although the position of *Petricolaria* was highly unstable and sensitive to parameter set variation. Veneridae was found to be monophyletic and formed a general association with Corbiculidae, Arcticidae, and Glossidae.
10. Dreyer, Steiner & Harper (2003) included two venerids (*Venus verrucosa* and *Callista chione*) among many other heterodont taxa, in an extensive phylogenetic analysis of the Anomalodesmata based on 18S rRNA sequences. Veneridae was recovered as a natural group, and most closely related to *Corbicula flu-*

minea. *Arctica* was sister to the clade containing *Venus*, *Callista*, and *Corbicula.*

11. Williams *et al.* (2004) employed two venerids (*Venus verrucosa* and *Mercenaria mercenaria*) in a Bayesian analysis of lucinoid evolution using 18S and 28S rRNA sequences. On the basis of the 18S data set alone, a monophyletic Veneridae was strongly supported, as was a sister-group relationship with *Calyptogena*; sister to this clade was *Arctica islandica*. Only one venerid (*Mercenaria*) was included in the combined gene analysis, which grouped strongly with *Calyptogena*.

All of the above investigations found Veneridae to be monophyletic, and most also considered Veneroidea to be monophyletic, although only one used any nonvenerid Veneroidea representatives in their analyses. Throughout all 11 investigations, only six species of Veneridae, one in each of six subfamilies (Chioninae, Dosiniinae, Meretricinae, Pitarinae, Tapetinae, Venerinae) were utilized. Veneridae was shown to be closest to Arcticidae, Corbulidae, Glossidae, Vesicomyidae, and Mactridae.

Previous phylogenies: venerid subfamilies

The interrelationships of the 12+ venerid subfamilies have remained likewise unresolved, despite a few phylogenetic attempts and considerably more taxon sampling.

1. The first to discuss this problem was Frizzell (1936a, b, c) in a study he called 'phylogenetic', based on the shell characters and stratigraphy of members of 11 subfamilies (used at the family level). This study essentially created the venerid subfamilies, later adopted and expanded by Keen (1969). Although it did not use species-level exemplars and was obviously not phylogenetic in today's sense, the analysis did suggest two groupings, of Dosiniinae + Cyclininae and Meretricinae + Pitarinae.

2. Harte (1998a) examined shell characters of seven species in five subfamilies. Only Tapetinae and Cyclininae were represented by more than one species. Using a member of Lucinidae as an outgroup, she found Veneridae but none of the subfamilies to be monophyletic. Three clades resulted: (a) Dosiniinae, (b) Tapetinae, Clementiinae, Cyclininae (paraphyletic), and (c) Chioninae, Cyclininae (paraphyletic).

3. Adriana Canapa and colleagues investigated Veneridae relationships using molecular sequences in two papers. Canapa *et al*. (1996) used partial 16S rRNA sequences from eight species in five subfamilies; a member of Ostreidae was used as the outgroup. Only Pitarinae and Tapetinae were represented by more than one species; both were found to be monophyletic as was the grouping Chioninae + Venerinae. Canapa *et al*. (2003) again used partial 16S rRNA sequences for additional taxa, 14 species in six subfamilies (four represented by multiple taxa), the best taxon sampling to date. Veneridae was found to be monophyletic (against outgroups in Mactridae and Pharidae). Two subclades were supported, comprising (a) Dosiniinae, Chioninae, Tapetinae, and Venerinae, and (b) Meretricinae and Pitarinae. Veneridae and Tapetinae were found to be monophyletic, as were Meretricinae + Pitarinae and most of Chioninae + Venerinae.

In addition to these results, Roopnarine (1996) investigated the internal structure of the subfamily Chioninae using shell characters in ten Recent and six fossil species, although five of the Recent species were treated as outgroups. Harte (1992) also showed that species of Chioninae grouped together in a radioimmunoassay study.

As a result of these 14 previous works (Table 4), 31 species of Veneridae in nine subfamilies have so far been included in any kind of phylogenetic analysis. None has yet been included from Callocardiinae, Gafrariinae, Gemminae, Gouldiinae *s.s.*, Lioconchinae, Samarangiinae, or Sunettinae/Meroinae, and all morphological characters used to date have been conchological.

Present analysis: morphological

A complete list of the 34 morphological characters used in these analyses appears in Appendix 3. The total data set comprised 24 binary and ten multistate characters, and 28 conchological and six anatomical characters.

All-taxa analyses

Traditional characters: Traditional character analyses using all 114 taxa yielded shortest trees from the heuristic searches of 234 steps [10 000 trees, consistency index (CI) = 0.13, retention index (RI) = 0.74; character length from majority-rule consensus trees]. Both the strict and majority-rule consensus trees (Fig. 3) of these results produced three consistent clades: (A) *Calyptogena* outgroup + Gemminae (*Gemma*, *Parastarte*), supported by anterior lateral tooth absent (nine steps on tree), (B) most of the Tapetinae (with *Petricolaria* from Petricolidae) + *Nutricola* (Pitarinae) + *Corbicula* outgroup, supported by commarginal sculpture present (22 steps) and right middle cardinal tooth bifid (four steps), and (C) all remaining taxa. The node comprising B plus C (above) was supported by pallial sinus present (11 steps) and right posterior cardinal tooth bifid (13 steps). Clade C included the *Arctica* outgroup, *Gomphina* (Tapetinae), and all other nonvenerid veneroids (*Glauconome* spp., *Turtonia*, *Neolepton*,

Table 4. Veneridae species used in previous phylogenetic analyses; species names updated to those in current use

	Callistinae	Chioninae	Clementiinae	Cyclininae	Dosiniinae	Meretricinae	Pitarinae *s.s.*	Tapetinae	Venerinae
VENEROIDEA									
Rosenberg *et al.* (1997; ml)		*Mercenaria mercenaria*							*Venus verrucosa*
Adamkewicz *et al.* (1997; ml)		*Mercenaria mercenaria*			*Dosinia discus*				
Canapa *et al.* (1999; ml)	*Callista chione*								*Venus verrucosa*
Steiner & Hammer (2000; ml)	*Callista chione*	*Mercenaria mercenaria*			*Dosinia discus*				*Venus verrucosa*
Campbell (2000; ml)	*Callista chione*	*Mercenaria mercenaria*							*Venus verrucosa*
Canapa *et al.* (2001; ml)	*Callista chione*	*Mercenaria mercenaria*			*Dosinia discus*				*Venus verrucosa*
Giribet & Wheeler (2002; ml & mp)	*Callista chione*	*Mercenaria mercenaria*							
Matsumoto (2003)						*Meretrix lusoria*		*Macridiscus melanaegis*	
Giribet & Distel (2003; ml)	*Callista chione*	*Mercenaria mercenaria*							*Venus verrucosa*
Dreyer *et al.* (2003)	*Callista chione*								*Venus verrucosa*
Williams *et al.* (2004)		*Mercenaria mercenaria*							*Venus verrucosa*
VENERIDAE									
Canapa *et al.* (1996; ml)	*Callista chione*	*Chamelea gallina*			*Asa lupina*		*Pitar rudis*	*Ruditapes philippinarum, Ruditapes decussatus, Tapes aureus*	*Venus verrucosa*

Table 4. *Continued*

	Callistinae	Chioninae	Clementiinae	Cyclininae	Dosiniinae	Meretricinae	Pitarinae *s.s.*	Tapetinae	Venerinae
Roopnarine (1996; mp; Recent only listed here)		*Anomalocardia auberiana, A. flexuosa, Chione cancellata, C. tumens, Chionista fluctifraga* (G. B. Sowerby II, 1853), *Chionopsis amathusia* (Philippi 1844), *Iliochione subrugosa* (Wood 1828), *Mercenaria mercenaria, Protothaca asperrima* (G. B. Sowerby I, 1835), *Timoclea marica* (Linnaeus, 1758)							
Harte (1998a; mp)		*Austrovenus stutchburii*	*Clementia vitrea* Deshayes, 1853	*Cyclina sinensis, Cyclinella tenuis*	*Dosinia concentrica*			*Ruditapes philippinarum, Tapes literatus*	
Canapa *et al*. (2003; ml)	*Callista chione*	*Chamelea gallina*, *Mercenaria mercenaria*			*Asa lupina*	*Meretrix lyrata*	*Pitar rudis*	*Neotapes undulatus*, *Ruditapes decussatus*, *Ruditapes philippinarum*, *Tapes aureus*, *Tapes rhomboides*, *Venerupis senegalensis*	*Globivenus effossa*, *Venus verrucosa*

ml, molecular; mp, morphological.

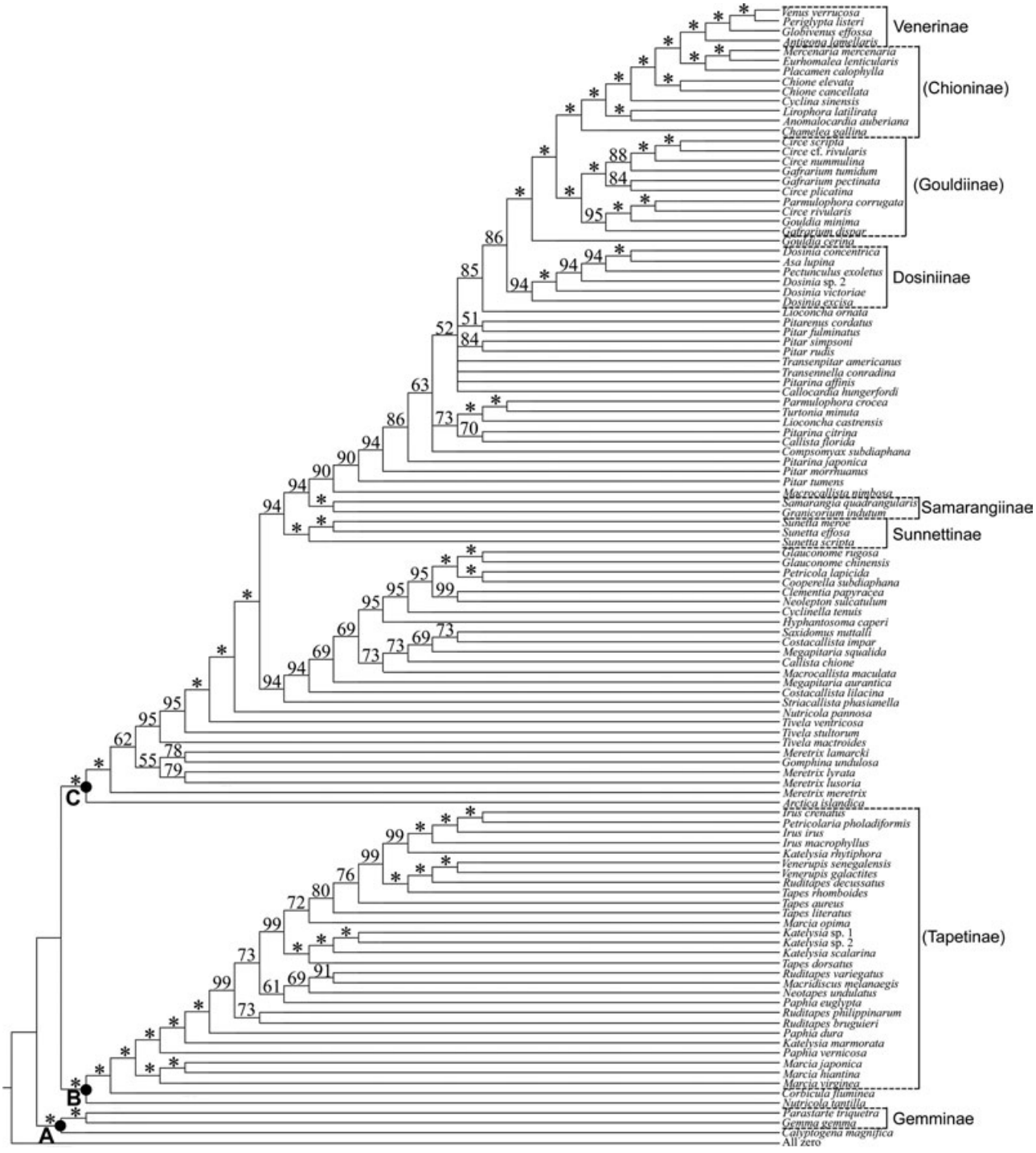


Figure 3. Morphological phylogeny of Veneroidea: an example 50% majority-rule consensus tree (length 234 steps, consistency index = 0.13, retention index = 0.74) based on a maximum parsimony heuristic search of the traditional morphological data set (23 characters) and 114 taxa. See text for a discussion of clades A, B, and C. Subfamily names in parentheses are not monophyletic (see text). *100%.

Cooperella, *Petricola*), and was supported by foot byssate (six steps). Reconstructed as monophyletic within clade C were: Samarangiinae (*Samarangia*, *Granicorium*; 100% majority support), supported by reversals of pallial sinus to small (ten steps) and right anterior/middle cardinals to radiating (six steps), plus the synapomorphy sand-impregnated periostracum (not coded); Sunettinae (*Sunetta* spp., including Meroinae; 100%), supported by the synapomorphy escutcheon sunken (one step) and shell margin denticulate (ten steps); most of Dosiniinae (*Asa*, *Dosinia*, *Pectunculus*, 94%, but excluding *Dosinia excisa* in strict consensus trees), supported by the synapomorphy foot lunate (one step); most of Gouldiinae (100%, including Gafrariinae, but excluding *Gouldia cerina*), supported by one reversal to pallial sinus small (ten steps); and Venerinae (100%), supported by a reversal to anterior lateral tooth present (nine steps), within a paraphyletic Chioninae (also including *Cyclina*), supported by anterior lateral tooth absent (nine steps).

All-morphology: All-morphology character analyses using all 114 taxa all yielded relatively poorly resolved results; the shortest trees from the heuristic searches were of 285 steps (10 000 trees, CI = 0.14, RI = 0.72), but exhibited two slightly different topologies. Strict consensus trees were all largely unresolved 'combs' (Fig. 4A). Most basal on all trees were the three taxa *Neolepton* (Neoleptonidae), *Turtonia* (Turtoniidae) and *Parmulophora* (Gouldiinae), supported by cardinal 2a/b dorsally united (21 steps on tree). Also basal to the main 'comb' were the other outgroups, and either (a) Gemminae (*Gemma*, *Parastarte*), *Cooperella* (Petricolidae), and *Glauconome* spp. (Glauconomidae) or (b) two Pitarinae (*Saxidomus*, *Nutricola*). Consistently supported within the remaining large 'comb' were: Dosiniinae, supported by lunule impressed (12 steps), right anterior cardinal tooth bifid (31 steps, including two reversals in this clade), and the synapomorphy foot lunate (one step); Lioconchinae (*Lioconcha* spp.), supported by cardinal teeth 3a/1 parallel (25 steps) and two reversals of shell to not compressed (34 steps) and pallial sinus to small (29 steps); Sunettinae, supported by the synapomorphy escutcheon sunken (one step), plus lunule impressed (12 steps), shell margin denticulate (22 steps), cardinal teeth 3a/1 parallel (25 steps), and cardinal tooth 4b and nymph appressed (14 steps); and Venerinae, supported by radial sculpture present (18 steps, including one reversal in this clade), shell margin denticulate (22 steps), anterior lateral tooth present and of pseudolateral type (six steps), and two reversals, shell to not elongated (21 steps) and hinge plate not excavated (15 steps).

Majority-rule consensus trees of these results were better resolved but offered little recognizable structure (Fig. 4B). Outgroups remained nested within the ingroup, distal to or grouped with *Neolepton*, *Turtonia*, *Parmulophora*, and Gemminae. The former 'comb' clade now included two main subclades whose members differed in the two topologies. Monophyly was suggested (as in the strict consensus trees) for Dosiniinae, Lioconchinae, Sunettinae, and Venerinae (all at 100% majority support), as well as for Glauconomidae (100%), supported by shell elongated (14 steps) and pallial sinus tapering (12 steps), and, in one of the two topologies (not shown in Figure 4B), Samarangiinae (99%), supported by a reversal of pallial sinus to rounded (12 steps) and periostracum sand-impregnated (not coded). Although *Tivela* and *Meretrix* (Meretricinae) always grouped closely in these analyses, one set of consensus topologies (strict and majority rule of the same heuristic search) produced a monophyletic clade (100% majority support) of these two genera combined (but excluding *Transennella* of Meretricinae) + *Gomphina* (Tapetinae), supported (on the strict consensus tree) by right anterior cardinal excavated (25 steps with two changes within this clade), space between cardinal 4b and nymph with vertical pits/bars (ten steps with one reversal within this clade), plus reversals in commarginal sculpture to absent (33 steps), escutcheon to absent (24 steps), and independent anterior lateral tooth to present (26 steps with one reversal within this clade).

Incongruence among these all-taxa analyses and weak character support were sufficient to suspend further analysis and prompt restricting the data set to a smaller number of taxa. This restriction would increase data set symmetry (fewer taxa vs. the relatively small number of characters) and would reduce the potential influence of 'taxonomic noise' caused by the presence of taxa whose generic and/or subfamilial placement has not been recently revised.

Restricted taxa analyses

Traditional characters: Traditional character analyses with the restricted taxon list produced shortest trees from the heuristic searches of 135 steps (1691–1707 trees, CI = 0.20, RI = 0.63). Three of the four strict consensus trees were 'combs' beyond the all-zero outgroup, supporting only Sunettinae, a combined Chioninae + Venerinae, Tapetinae, and Glauconomidae as monophyletic. The fourth strict consensus tree (Fig. 5A) produced two subclades beyond the outgroups (which were all basal, joined by *Turtonia*): (A) Gemminae, Petricolidae, Glauconomidae, and Tapetinae (the last two monophyletic) and (B) all remaining taxa (mainly in 'comb' formation) with Chioninae + Venerinae and Sunettinae as monophyletic. Cyclininae (*Cyclina*, *Cyclinella*) was split between the two subclades.

Majority-rule consensus trees of these results were closely congruent with the fourth strict consensus result described above, including components of the two subclades, differing from one another only in position and monophyly [weakly (50% majority support) or not] of Callistinae (*Callista*, *Costacallista*). In addition to monophyletic Chioninae + Venerinae (100% majority support) and Sunettinae (100%) in clade B, Dosiniinae (99%) and Gouldiinae *s.s.* (*Gouldia*, *Circe*, 95%; excluding Gafrariinae) were also monophyletic. In clade A, Glauconomidae (100%) and Tapetinae (100%) were again monophyletic, joined by Gemminae (although weakly so, 67–76%).

The best-resolved majority-rule consensus (50% majority rule of 1691 trees) is illustrated in Figure 5B. Clades A and B together essentially capture Veneroidea, including members of Glauconomidae, Petricolidae (both in clade A), and *Neolepton* (in clade B), but excluding *Turtonia*. This Veneroidea clade was supported by pallial sinus moderate (ten steps on tree) and posterior lateral tooth absent (three steps). Clade A was defined by a single character state, anterior lateral tooth absent (seven steps; also shared with basal clade *Turtonia* + *Calyptogena*, see below). Clade B was also defined by a single character state, lunule present (four steps). It should be noted that with the exception of two states (escutcheon sunken; foot lunate), defining Sunettinae and Dosiniinae, respectively, all characters were homoplastic on the tree, some of them strongly so (11 of 23 characters with more than five steps). Glauconomidae and Petricolidae grouped with Tapetinae in clade A based on three characters: pallial sinus large (ten steps, reversed in tapetines); left middle cardinal tooth bifid (seven steps, reversed in *Petricolaria*); and hinge plate excavated (three steps). *Turtonia minuta* grouped with *Calyptogena*, supported by shell elongated (five steps) and anterior lateral tooth absent (seven steps) at the base of the tree, outside of Veneroidea, on the basis of pallial sinus absent, posterior lateral tooth present, right posterior cardinal tooth smooth, and byssus present. *Neolepton* was deeply nested within clade B as a sister taxon to *Clementia*, supported by hinge plate excavated (three steps) and reversal of the lunule to absent (four steps), within a larger clade based on pallial sinus large (ten steps), even though this character is ambiguous for *Neolepton*. Of the Veneridae subfamilies, the following were supported by this topology: Gemminae (*Gemma*, *Parastarte*), supported by shell compressed (12 steps); Tapetinae (*Tapes*, *Ruditapes*), supported by lunule present (four steps), escutcheon present (five steps), pallial sinus moderate (ten steps), and right middle cardinal tooth bifid (five steps); Sunettinae (*Sunetta*, including Meroinae), supported by escutcheon present (five steps) and sunken (one step, synapomorphy), shell compressed (12 steps), shell margin denticulate (three steps) and pallial sinus rounded (nine steps); Callistinae (*Callista*, *Costacallista*), supported by pallial sinus rounded (nine steps); Dosiniinae (*Dosinia*, *Pectunculus*), supported by the synapomorphy foot lunate (one step); Gouldiinae *s.s.* (*Gouldia*, *Circe*, excluding but paraphyletic with Gafrariinae), supported by a reversal of right posterior cardinal tooth to smooth (eight steps); and combined Chioninae + Venerinae (*Chione*, *Mercenaria*, *Venus*, *Antigona*), supported by commarginal sculpture erect (13 steps), pallial sinus moderate (ten steps), and right middle cardinal bifid (five steps, with a reversal in *Chione*). Meretricinae (*Meretrix*, *Tivela*) and Gafrariinae (*Gafrarium*) were paraphyletic; Samarangiinae (*Samarangia*, *Granicorium*) and Lioconchinae (*Lioconcha*) remained unresolved. There was no support for Pitarinae *s.s.* [*Pitar*, *Pitarina*, excluding Callistinae, Lioconchinae, Callocardiinae (represented by only one species)], Clementiinae (*Clementia*, *Compsomyax*), and Cyclininae (*Cyclina*, *Cyclinella*), the last split between clades A and B. This tree differed from the best-resolved strict consensus tree in supporting Gemminae in clade A and Callistinae, Dosiniinae, and Gouldiinae *s.s.* in clade B.

All-morphology: All-morphology analyses with the restricted taxon list produced the shortest trees from the heuristic searches of 162 steps (44–46 trees, CI = 0.23, RI = 0.62). All four replicate strict consensus trees were identical. Compared with the best result of the restricted traditional data set (Fig. 5B): (1) *Neolepton* joined *Turtonia* at the base of the tree, supported by cardinal teeth 2a/b dorsally united (eight steps in tree); (2) clade A for the most part collapsed (except Petricolidae + *Cooperella* + Glauconomidae); and (3) Tapetinae joined clade B, supported by lunule present (three steps). Within clade B, the following were monophyletic: Lioconchinae, supported by three reversals of escutcheon to absent (eight steps), umbones to subcentral (12 steps), and pallial sinus to small (11 steps); Samarangiinae, supported by independent anterior lateral tooth absent (seven steps), periostracum sand-impregnated (not coded), and three reversals of pallial sinus to rounded (12 steps) and small (11 steps), and cardinal teeth 3a/1 to radiating (seven steps); Dosiniinae, supported by lunule impressed (five steps), anterior lateral tooth present and of pseudolateral type (five steps), and the synapomorphy of foot lunate (one step); Tapetinae, supported by shell elongated (seven steps), hinge plate excavated (five steps), and reversals of shell margin to smooth (six steps) and pallial sinus to rounded (nine steps); and Veneridae, supported by anterior lateral tooth present and of pseudolateral type (five steps) and AI/AIII developed (two steps, position of change ambiguous), the last within a paraphyletic Chioninae, the

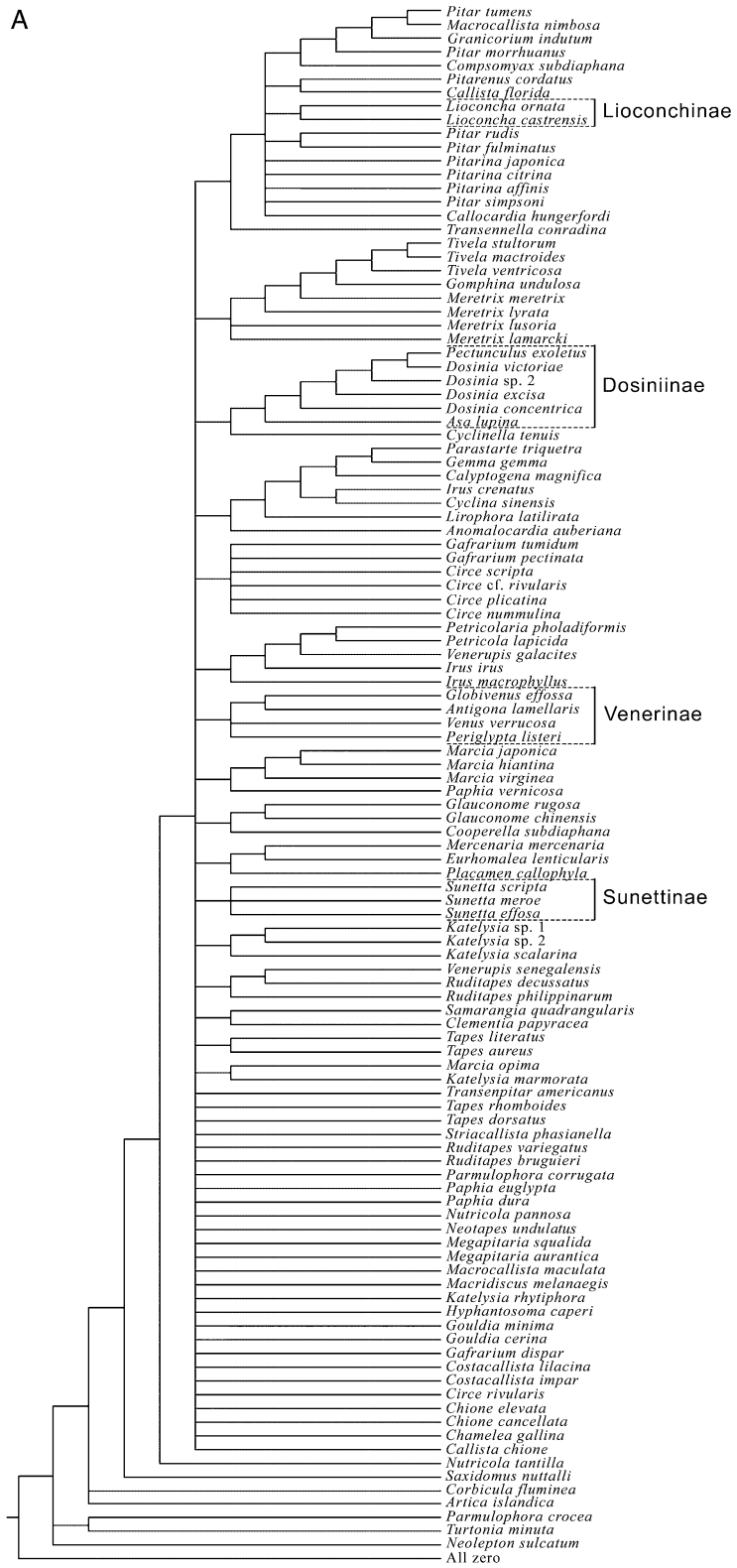


Figure 4. Morphological phylogeny of Veneroidea. A, an example strict consensus tree. B, an example 50% majority-rule tree (length 285 steps, consistency index = 0.14, retention index = 0.72) based on maximum parsimony heuristic searches of the all-morphology data set (31 characters) and 114 taxa. See text for a discussion of supported clades. Subfamily names in parentheses are not monophyletic (see text). *100%.

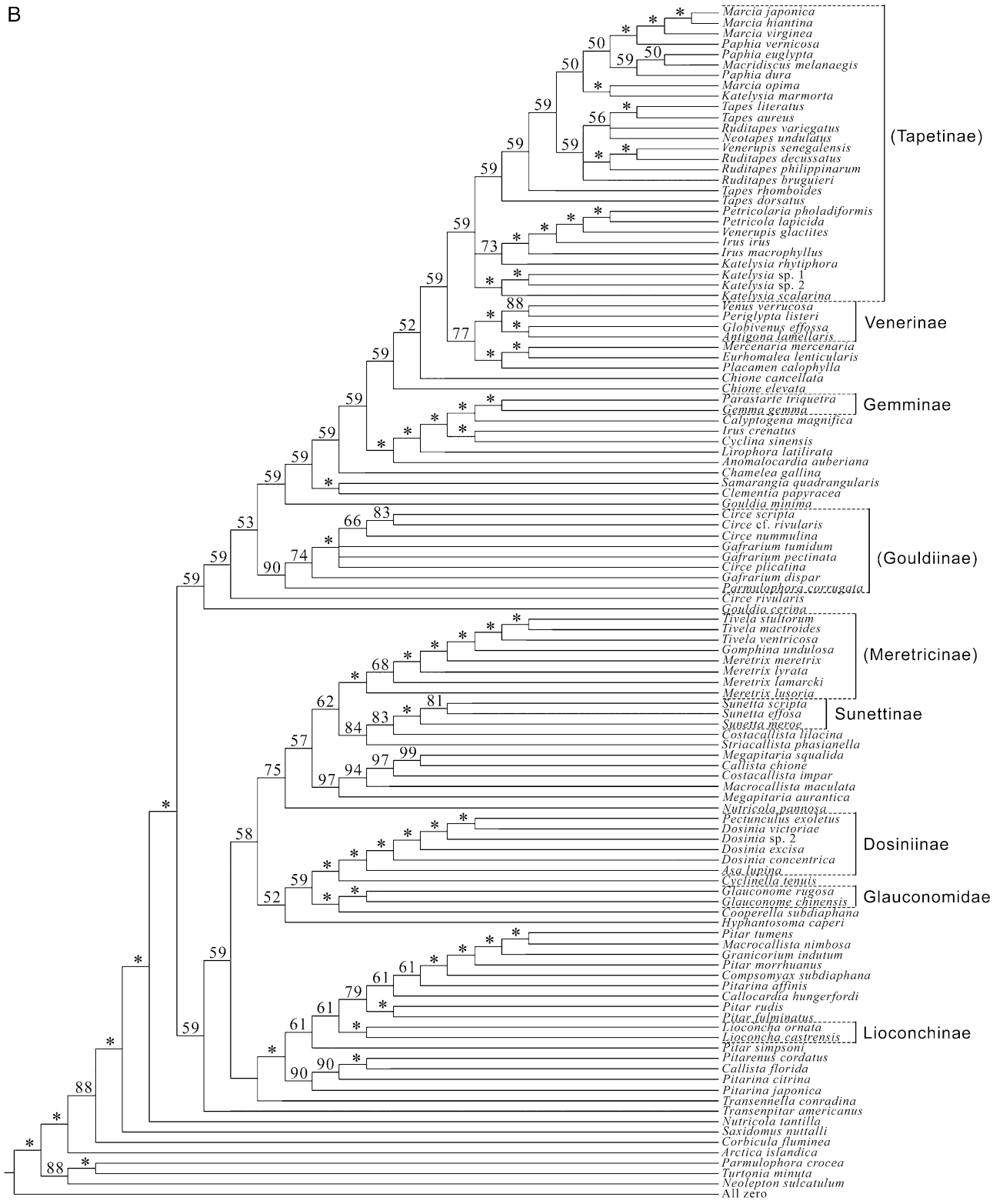


Figure 4. *Continued*

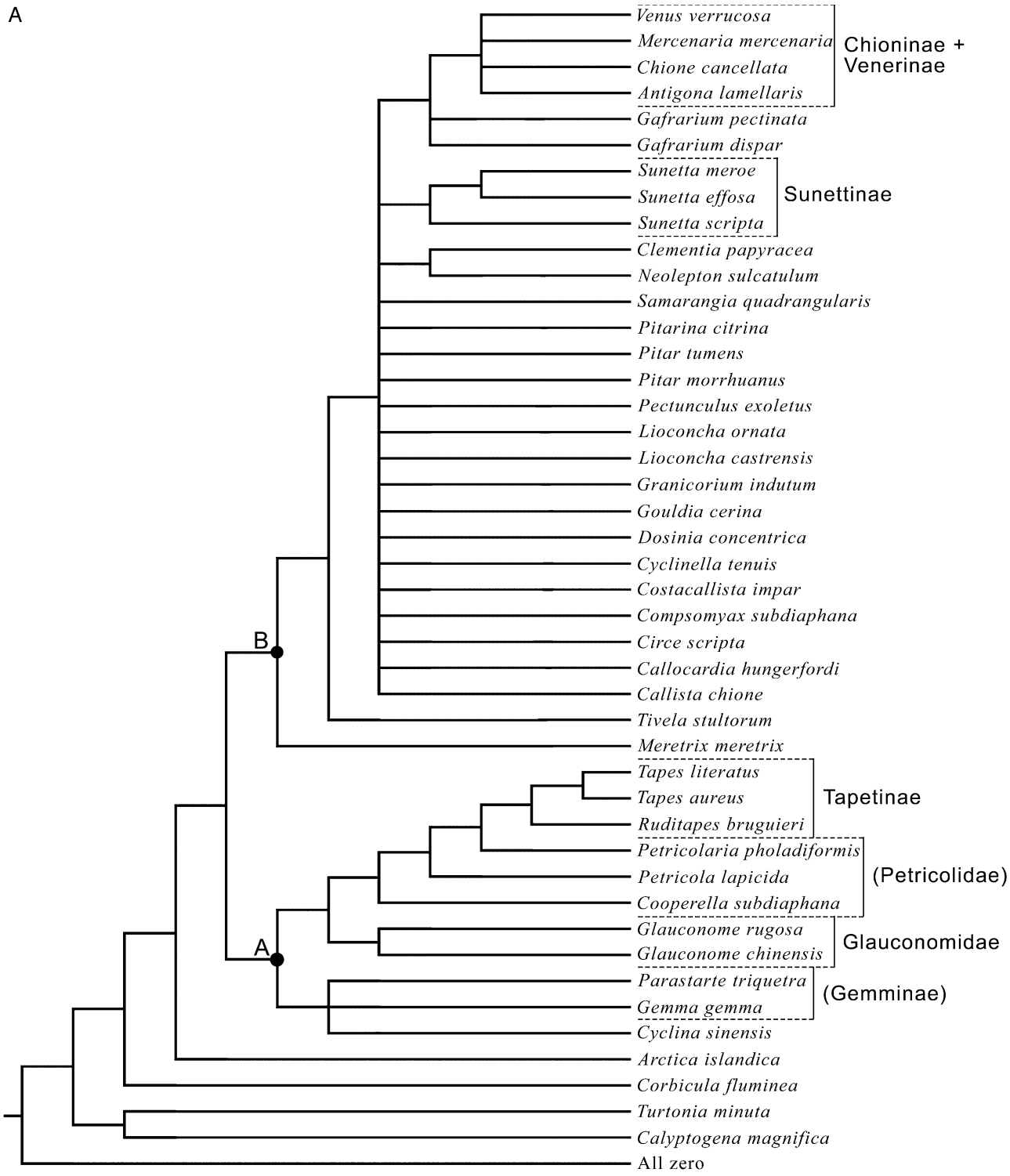


Figure 5. Morphological phylogeny of Veneroidea. A, an example strict consensus tree. B, the best-resolved 50% majority-rule consensus tree (length 135 steps, consistency index = 0.20, retention index = 0.63) based on maximum parsimony heuristic searches of the traditional morphological data set (23 characters) and a restricted set of 45 taxa. See text for a discussion of clades A and B. Subfamily names in parentheses are not monophyletic (see text). *100%.

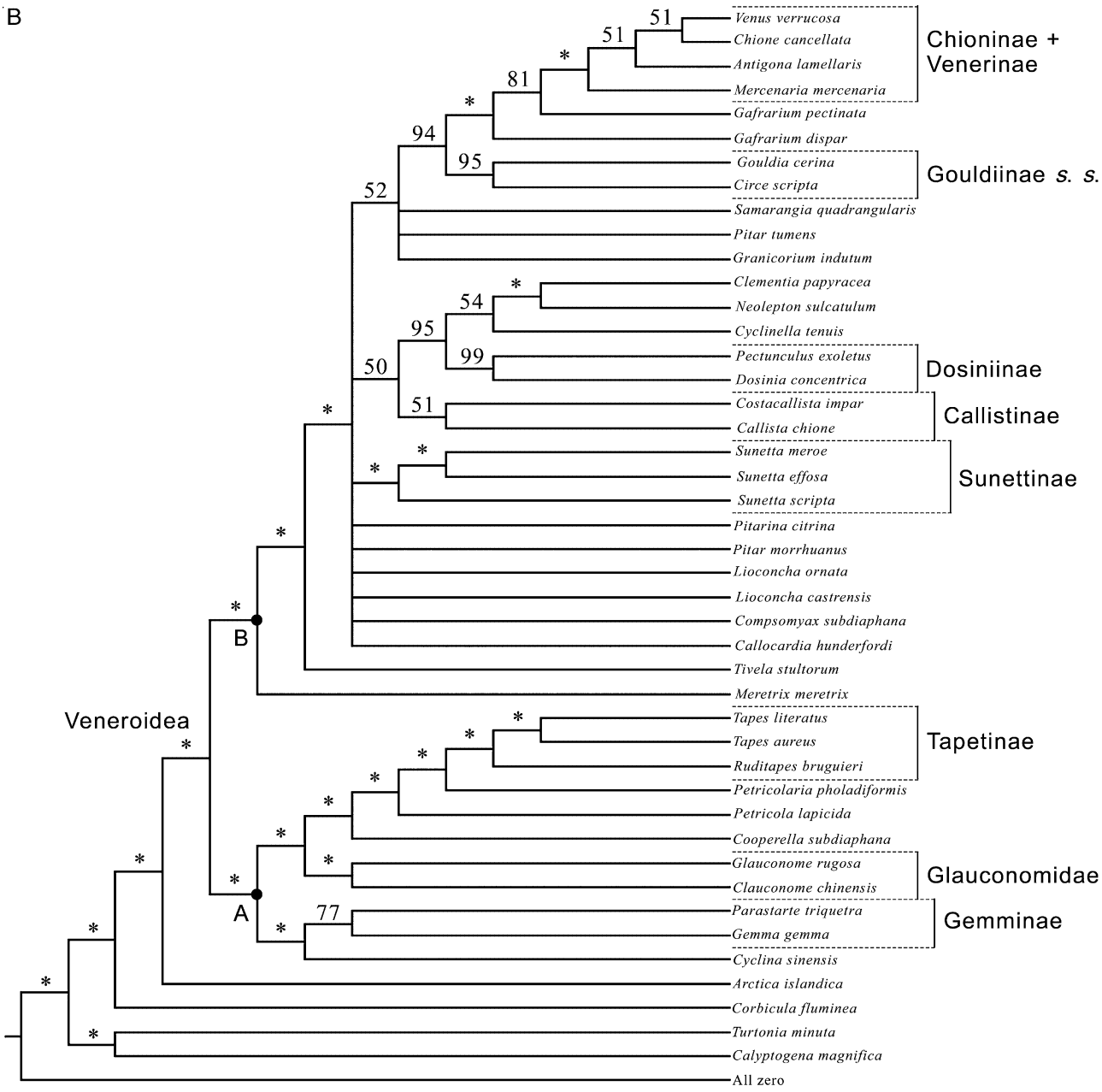


Figure 5. *Continued*

combined clade supported by commarginal sculpture erect (16 steps).

The four majority-rule trees differed only in minor rearrangements within terminal clades. The best-resolved hypothesis (50% majority rule of 46 trees) is illustrated in Figure 6. The base of the tree and former clade A were identical with those of the strict consensus trees. Clade C (combining Petricolidae + *Cooperella* + Glauconomidae) was supported (100% majority support) by pallial sinus large (nine steps) and hinge plate excavated (five steps); the node combining clades B and C could define Veneroidea (with exclusions, see below) based on the nonhomoplastic aortic bulb present (although 12 taxa in this clade were coded ambiguously for this character). In this topology, clade B (= Veneridae, with exclusions, see below) was better resolved than in the traditional character tree (Fig. 5B), but as in the strict consensus tree (above) was supported by lunule present. As in the traditional character tree, two nonhomoplastic states (escutcheon sunken and foot lunate) defined Sunettinae and Dosiniinae, respectively; all other

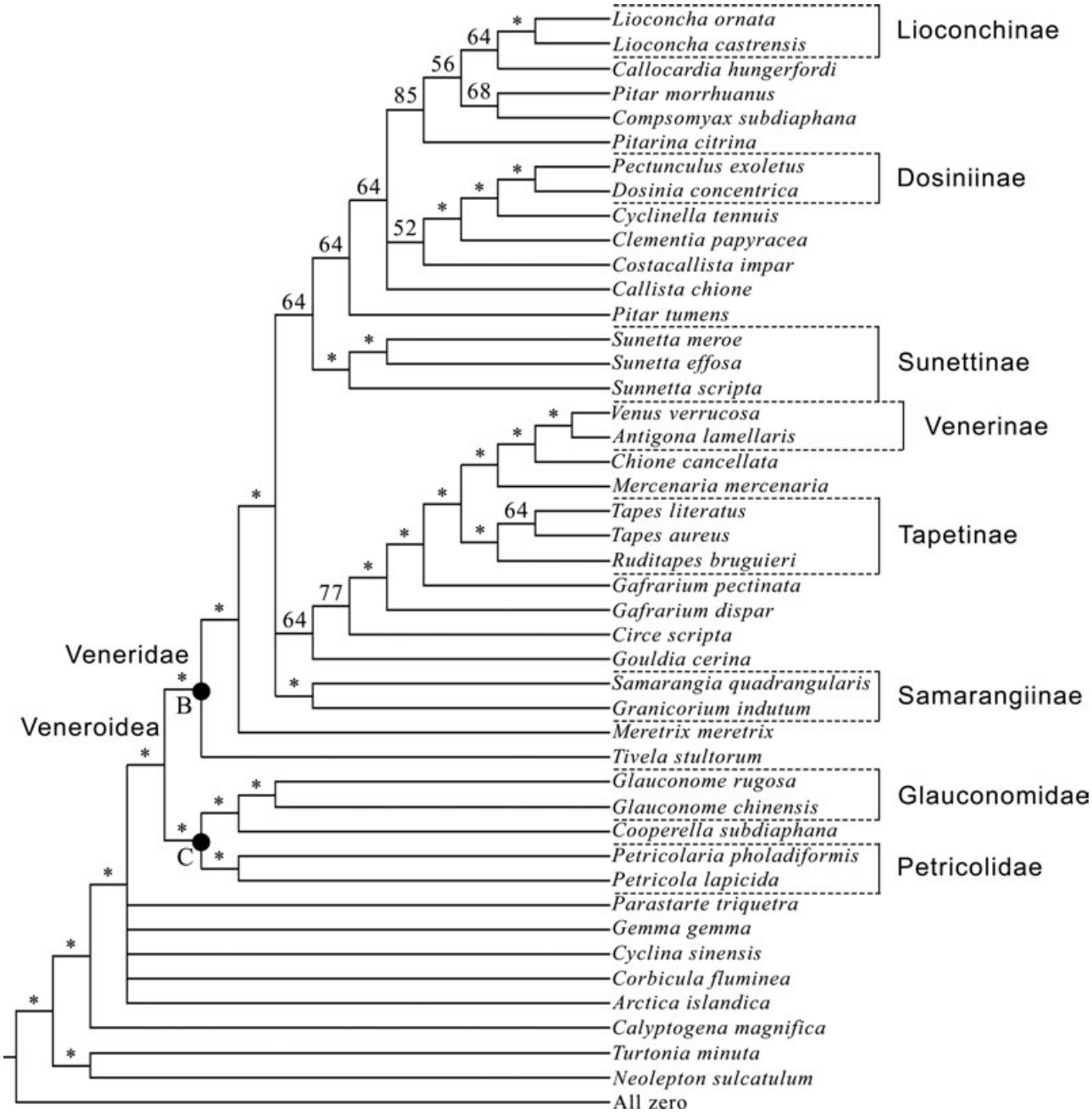


Figure 6. Morphological phylogeny of Veneroidea: a 50% majority-rule consensus tree (46 trees, length 162 steps, consistency index = 0.23, retention index = 0.62) based on a maximum parsimony heuristic search of the all-morphology data set (45 taxa, 31 characters). See text for a discussion of clades B (Veneridae) and 1 (Veneroidea).

characters (apart from these and the aortic bulb at Veneroidea node) were homoplastic, some highly so (13 of 31 characters with more than five steps). Of the Veneridae subfamilies, the following were monophyletic within clade B (all with 100% majority support): Samarangiinae, supported by umbones anterior (nine steps), independent anterior lateral tooth absent (seven steps), periostracum sand-impregnated (not coded), and a reversal of pallial sinus to small (nine steps); Sunettinae (including Meroinae), supported by lunule impressed (five steps), shell margin denticulate (six steps), cardinal tooth 4b and nymph appressed (five steps), and the synapomorphy escutcheon sunken (one step); Lioconchinae, supported by a reversal of pallial sinus to small (nine steps), and Dosiniinae, Tapetinae, and Venerinae supported by the same steps

as in the strict consensus tree (above), the last within a paraphyletic Chioninae, the combined clade supported by commarginal sculpture erect (13 steps). Meretricinae, Gouldiinae *s.s.*, and Gafrariinae were paraphyletic; Callistinae remained unresolved. There was no support for Cyclininae or Pitarinae *s.s.* in this topology.

Five taxa of traditional veneroids were excluded from Veneroidea by this topology. *Neolepton*, formerly part of clade B, appeared as a sister taxon to the likewise small-shelled *Turtonia* (based on cardinal teeth 2a/b dorsal association) at the base of the tree. Likewise in this hypothesis, Gemminae and *Cyclina* were excluded from both Veneroidea and Veneridae. A reexamination of the character states of these five taxa is thus warranted. *Cyclina* can be readily explained by absences; although it does not have a lunule (secondary absence?), it was coded as ambiguous for an aortic bulb (due to the unavailability of preserved specimens), which the algorithm extrapolated as absent. The remaining four excluded species (*Neolepton*, *Turtonia*, *Parastarte*, *Gemma*) all range from 2 to 5 mm adult shell length. Their relocation can be linked with suites of characters associated with small body size (see Discussion).

Although both Veneroidea and Veneridae could be identified on this tree, neither conformed to traditional definitions. Furthermore, only six of the potential 17 venerid subfamilies were reconstructed (Fig. 6). However, it should be noted that these were not the same six recovered in the traditional character tree (cf. Fig. 5B; Callistinae, Gemminae, and Gouldiinae *s.s.* in traditional only; Lioconchinae, Samarangiinae, and Venerinae in all only; Dosiniinae, Sunettinae, and Tapetinae in both analyses). Of the nonvenerid Veneroidea families, Glauconomidae was recovered in both analyses, whereas Petricolidae (excluding *Cooperella*) was monophyletic only in the all-morphology tree. Neoleptonidae (*Neolepton* only) was nested deeply among venerid taxa in the traditional tree (Fig. 5B), whereas it joined Turtoniidae (*Turtonia* only) outside of Veneroidea in the all-morphology tree (Fig. 6).

Present analysis: molecular

Not all taxa could be sampled for each gene region. The largest taxon coverage was for the two mtDNA genes, with 69 taxa represented in the 16S rRNA data set (75 sequences in total; 58 new; 17 GenBank). After the exclusion of poorly aligned regions, this data set consisted of 413 characters, of which 267 were parsimony informative. For COI, 58 taxa were sampled (64 sequences, 53 new; 11 GenBank), with 661 characters in total. Two slightly different COI sequences (8 bp difference) were obtained from the pitarine *Hyphantosoma caperi* during cloning, after initial attempts to sequence this gene from PCR directly proved to be difficult. Both sequences were used in subsequent mtDNA analyses. Of the 423 parsimony-informative characters within the COI data set, 125 were present at first codon positions, 78 at second codon positions, and the majority (220) at third codon positions. The combined data set of concatenated mtDNA genes represented a total of 73 taxa (83 sequences) and a total of 1074 characters (319 constant, 65 variable but parsimony uninformative, 690 parsimony informative). Although only 56 sequences (48 taxa) included coverage of both genes, or portions thereof, we elected to work with the larger data set of 73 taxa for combined mtDNA analyses, because of the apparent advantages of increased taxon sampling, even for incomplete data sets (Hughes & Vogler, 2004).

Our taxon coverage for nuclear genes was less extensive. This resulted in part from fewer available GenBank sequences to complement our sampling [28S rRNA: eight venerid species (*Austrovenus stutchburii* (Wood, 1828), *Mercenaria mercenaria*, *Meretrix meretrix*, *Neotapes undulatus*, *Protothaca jedoensis* (Lischke, 1874), *Ruditapes philippinarum*, *R. variegatus*, *Venus verrucosa*), with sequence lengths varying from 50 bp to > 3 kb; H3: no venerid species]. For the 28S rRNA gene region, however, our reduced sampling also reflected difficulty in amplifying this gene region, probably because of poor DNA quality (e.g. degraded low molecular weight DNA) in older specimens and the presence of protist and fungal contaminants. In other taxa, this difficulty was associated with complications resulting from the amplification of putative paralogous copies of this gene, as reported elsewhere (e.g. chaeotognaths, Telford & Holland, 1997; bivalves, Park & Ó Foighil, 2000).

In total, the 28S rRNA data set comprised 36 taxa with sequences > 700 bp in length (30 new sequences; six GenBank). Slight intra-individual length variation was evident in some taxa (*Glauconome rugosa*, *Paphia vernicosa*), and multiple PCR bands reflecting divergent sequences of putative 28S paralogs were found in some others (e.g. *Compsomyax*, *Chamelea*). When regions of poor alignment were excluded, this data set consisted of 1140 characters, of which 720 were constant and 250 were parsimony informative. Although additional sequences were available in GenBank for *Petricolaria* and *Calyptogena*, these sequences were not included in our analyses because they were shorter in length than our sequences and exhibited little, if any, variation over the shared gene region. We also chose to exclude a GenBank sequence for *Protothaca jedoensis* (Chioninae) because this genus was not represented for other gene regions, and a particularly short sequence for *Venus verrucosa* (224 bp); Chioninae and Venerinae are treated in more detail by another study (Kappner & Bieler,

2006). For an additional 15 taxa, we were successful in amplifying and sequencing a much smaller fragment of the 28S rRNA gene (270–280 bp fragment, excluding primers). This data set of small fragments was aligned to the larger data set and additional analyses undertaken on the combined data set of small and large fragments. Across all taxa, this region comprised 1140 characters, of which 253 were parsimony informative.

The H3 data set consisted of a 328 bp sequence representing 50 taxa. Although the amplification and sequencing of this gene region was routine, there was evidence of strong double peaks in the chromatograms of some species, suggestive of heterozygotes. Although this was not unexpected, the frequency of these polymorphisms at third codon positions was particularly high (up to 19 per sequence) in some taxa (e.g. *Calyptogena*, *Katelysia* sp. 1, *Katelysia* sp. 2, *Paphia vernicosa*, *Periglypta*, *Antigona*), a phenomenon present in sequences generated independently in two of our laboratories (Chicago, Miami). These polymorphic sites were coded as 'uncertainties' in parsimony-based analyses, given that further investigation using cloning techniques is warranted to determine if these sites are truly polymorphic or reflect the amplification of background contaminants within DNA extractions or pseudogenes. Of the 50 sequences generated, variation was confined to first (17/109 variable) and third (100/110 variable) codon positions. Of the 102 parsimony-informative characters, the majority were present at third positions (92/102). There was no variation at the amino acid level in H3 across our sampling of taxa, except for one codon associated with a polymorphic site in *Neotapes undulatus*.

Phylogenetic analyses for all four genes were restricted to a data set of 56 taxa (59 sequences) by pruning those taxa represented by less than 1200 bp of sequence (*Asa lupina*, *Callista chione*, *Chamelea gallina* GB, *Chione elevata* GB, *Cyclina sinensis* GB, *Dosinia excisa*, *Globivenus effossa* GB, *Hyphantosoma caperi*, *Lirophora latilirata*, *Macridiscus melanaegis*, *Macrocallista maculata*, *Mercenaria mercenaria* GB, *Meretrix* spp., *Pitar rudis*, *Placamen calophylla*, *Ruditapes decussatus* GB, *Tapes aureus* GB, *Tapes rhomboides* GB, *Venerupis senegalensis* GB, *Venus verrucosa* GB). This was done to exclude species represented by only one gene region, mainly GenBank sequences, and to minimize the influence of missing data in our combined mitochondrial and nuclear gene analyses. The remaining taxa were represented by an average of 2096 bp (range 1211–2669 bp) over a total alignment length of 2890 bases. The alignment (minus ambiguous regions) of the four-gene data set consisted of 2542 characters, of which 1258 were constant and 1033 parsimony informative.

Mitochondrial genes

16S rRNA: Exploration of the 16S rRNA data set indicated no significant base-compositional heterogeneity across 69 taxa ($\chi^2 = 192.39$, d.f. = 222, $P = 0.925$; 296 variable characters) and a skewed tree length distribution suggestive of phylogenetic signal (g1 = –0.307, $n = 75$ sequences, 267 characters; $P < 0.01$). Saturation plots (number of transitional and tranversional substitutions vs. uncorr-P distances) did not exhibit strong evidence of saturation, with transitional substitutions outnumbering transversional changes even at the highest levels of sequence divergence between taxa (uncorr-P distances up to 0.365; data not shown).

Bayesian and MP methods of analysis inferred similar phylogenetic relationships within the Veneroidea (Fig. 7). Four replicate Bayesian analyses all converged on the same tree topology with similar overall likelihood scores and PP values. The majority-rule consensus tree of 29 401 sampled trees from the analysis with the highest average log-likelihood is shown in Figure 7A, with average branch support illustrated in Figure 7B. Using PP values ≥95% as measures of significantly supported clades, Bayesian analyses of the 16S rRNA data set supported the placement of *Turtonia* and Petricolidae within the Veneroidea (100% PP; clade B) and *Calyptogena* as a closer sister taxon to this group than the traditional veneroid *Glauconome*. Within the Veneroidea, there was strong support (> 99%) for three major clades: (1) clade A (99% PP) including members of the Dosiniinae, Venerinae, Chioninae, and Tapetinae (excluding *Gomphina*); (2) clade B1 (100% PP), including one tapetine (*Gomphina*), Callistinae (*Callista*, *Costacallista*, *Macrocallista*), other Pitarinae *s.l.* (*Megapitaria*, *Nutricola*, *Pitar*, *Pitarina*), Gemminae, Petricolidae, Turtoniidae (*Turtonia* only), plus representatives of Meretricinae and Clementiinae; and (3) clade B2 (100% PP) consisting of the pitarines *Hyphantosoma* and *Lioconcha* (Lioconchinae) and members of Gouldiinae/Gafrariinae (*Circe*, *Gafrarium*). Within clade A, the Dosiniinae (clade A1) was monophyletic and consistently supported by high PP values across four replicates (90–92% PP). Taxa of the subfamilies Venerinae and Chioninae also formed a well-defined combined group (clade A2), albeit with 77% PP and excluding the venerine *Periglypta listeri*, placed as an early offshoot of clade A, and the chionine *Placamen calophylla*, present as a sister taxon to Dosiniinae (clade A1). Independent monophyly for Venerinae or Chioninae was not observed. High support (100% PP) was also evident for a more restricted clade of tapetines (clade A3), with the exclusion of *Irus crenatus* and *Venerupis galactites*, which were positioned at the base of clade A, and *Gomphina undulosa* within clade B1. Despite the sister-group relationship between

clades B1 and B2 (node B, Fig. 7B), PP values supporting clade B were low based on this data set (77–78% across four replicates), although this clade was more strongly supported in the combined analyses (see below).

In parsimony-based analyses, weighting schemes varying from equal weighting to weighting transversional changes (Tv) up to 2.8 times transitions (Ti) converged on similar overall tree topologies, although support (represented as the bootstrap proportion, BP) tended to be higher for some deeper regions within the phylogeny when transversions were weighted more heavily. Overall, however, parsimony analyses corroborated the tree topology of the Bayesian analyses (Fig. 7B), with the same major clades evident (A, B, B1, B2), albeit with weak bootstrap support at deeper regions in the tree (e.g. 56% BP for clade A; 65% BP for clade B, and 61% BP for clade B1).

COI: The COI data set produced a strongly skewed tree distribution ($g1 = -0.653$, $n = 64$ sequences, 423 characters; $P < 0.01$) indicative of phylogenetic signal, but also revealed significant base heterogeneity across the 58 taxa sampled ($\chi^2 = 352.31$, d.f. = 189, $P < 0.001$, 459 variable characters only). When sites were partitioned according to codon position, the source of this base compositional heterogeneity was confined to third positions alone ($\chi^2 = 712.91$, d.f. = 189, $P < 0.001$, 220 variable characters), and when these sites were excluded from the COI data set, no significant base compositional heterogeneity was observed. The difference in base composition at third codon positions was apparent in the wide-ranging AT content across taxa, from a low of 61.3% in *Venerupis galactites* to a high of 87.7–90.0% in *Gemma*, *Parastarte*, and *Turtonia*.

We explored the extent to which base compositional differences might be biasing the placement of taxa in our COI tree by undertaking preliminary analyses in which we excluded third positions (and the associated bias), used distance-based methods that could accommodate base compositional differences across taxa (LogDet), or investigated relationships at the amino acid level (see below). Because the relationships among major clades of ingroup taxa in consensus or neighbour-joining trees remained relatively stable across methods and agreed in large part with the 16S data set (with no base compositional heterogeneity), we elected to continue to include third position sites in subsequent analyses.

Four replicate Bayesian analyses, using an independent partition for each codon position, converged on the tree topology shown in Figure 8. Although this topology was similar in structure to that found for the 16S data set, with high support for the monophyly of the Veneroidea, levels of support were generally weaker for deeper parts of the tree, including support for clades A and B (71 and 67% PP, respectively). Despite this, significant PP values were evident for clades A1, B1, and B2. High PP values also supported the division of clade B1 into two subclades, B1a and B1b, the former including *Cyclina* (Cyclininae), whose problematic/incomplete morphology excluded it from Veneroidea/Veneridae in the all-morphology analyses (Fig. 6). Furthermore, clade B1b represented a sister-group association between Pitarinae *s.s.* (*Pitar*, *Pitarina*) and Petricolidae (*Petricola*, *Petricolaria*), an outcome not seen in the 16S analysis. In parsimony analyses of COI data, although the majority-rule consensus tree revealed a monophyletic Veneroidea and monophyletic A and B clades, saturation of the phylogenetic signal at deeper levels of divergence was reflected in the lack of bootstrap support for this topology; nevertheless, strong support remained for clades B1 and B2. Weighting transversional changes more heavily than transitions (Tv 2.5 : Ti 1.0) recovered clade A, but only with marginal levels of bootstrap support (63% BP).

Considerable variation was evident in the COI data set, even at the amino acid level. Among 220 amino acid characters, 150 were variable across taxa and 129 were parsimony informative. Like the nucleotide sequence analyses, Bayesian and parsimony analyses based on amino acid sequences revealed strong support for clades B1 and B2 (100% PP, BP > 80%), but not for clade A. Likewise, although the MP tree reflected a monophyletic Veneroidea, monophyly was not strongly supported in Bayesian analyses or parsimony bootstrap analyses, with *Calyptogena* nesting within the ingroup. In all analyses, however, Glauconomidae remained strongly associated with the outgroup taxon, *Corbicula fluminea*.

Combined mtDNA genes: Although the COI Bayesian tree (Fig. 8) was considerably less resolved (fewer branches with ≥95% PP) than the 16S rRNA tree (Fig. 7), there were few strongly supported differences between these two tree topologies. The most significant disagreements were confined to clade B1, particularly in the placement of Petricolidae in a clade of meretricines (*Meretrix* spp., *Tivela* spp.) and Pitarinae *s.l.* (*Macrocallista*, *Megapitaria*) in the 16S tree vs. as a sister group to Pitarinae *s.s.* in the COI tree. Given that there appeared to be little strongly supported discordance between data sets, particularly at deeper levels, we chose to explore the advantages of combining the two mtDNA data sets in the hope of drawing out the signal common to both genes.

Both Bayesian and parsimony-based analyses of the combined mtDNA data set (Fig. 9) provided higher support for deeper parts of the phylogeny than either data set alone. Of particular significance were the

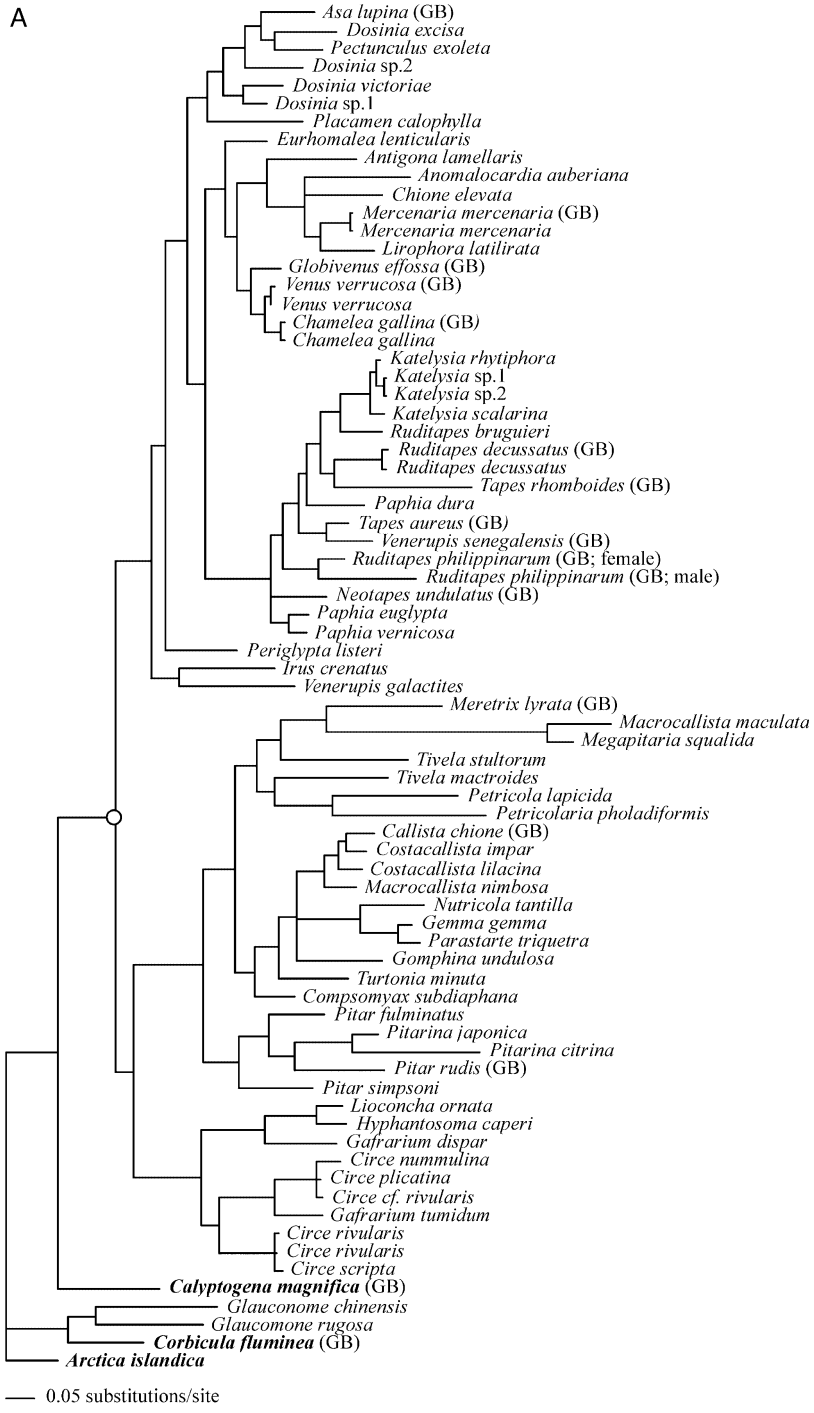


Figure 7. Molecular phylogeny of Veneroidea: a 50% majority-rule consensus tree based on a Bayesian analysis of the 16S rRNA data set and a sampling of 29 401 trees (3 000 000 generations; sample frequency = 100; burn-in = 600; heat = 0.2). Branch lengths are presented in (A) and support indices in (B). Posterior probability values (≥ 90%) are shown above the line; bootstrap proportions (≥ 70%) based on a parsimony analysis (250 replicates, 10 random sequence additions; Tv 2.8 : Ti 1) are shown below the line. Sequences obtained from GenBank are indicated by GB following the species name. Multiple sequences are included for five taxa: *Ruditapes philippinarum* (one from a maternally derived and one from a paternally derived mitochondrial lineage); *Circe rivularis* (sequences from two specimens from different locations); and *Mercenaria mercenaria*, *Venus verrucosa*, and *Chamelea gallina* (one GB sequence, one newly derived sequence). Taxa designated as outgroups are shown in bold. The hollow circle indicates the node supporting a monophyletic Veneroidea = Veneridae (including *Turtonia* and the Petricolidae). Labelled nodes (filled circles) refer to specific clades discussed in the text.

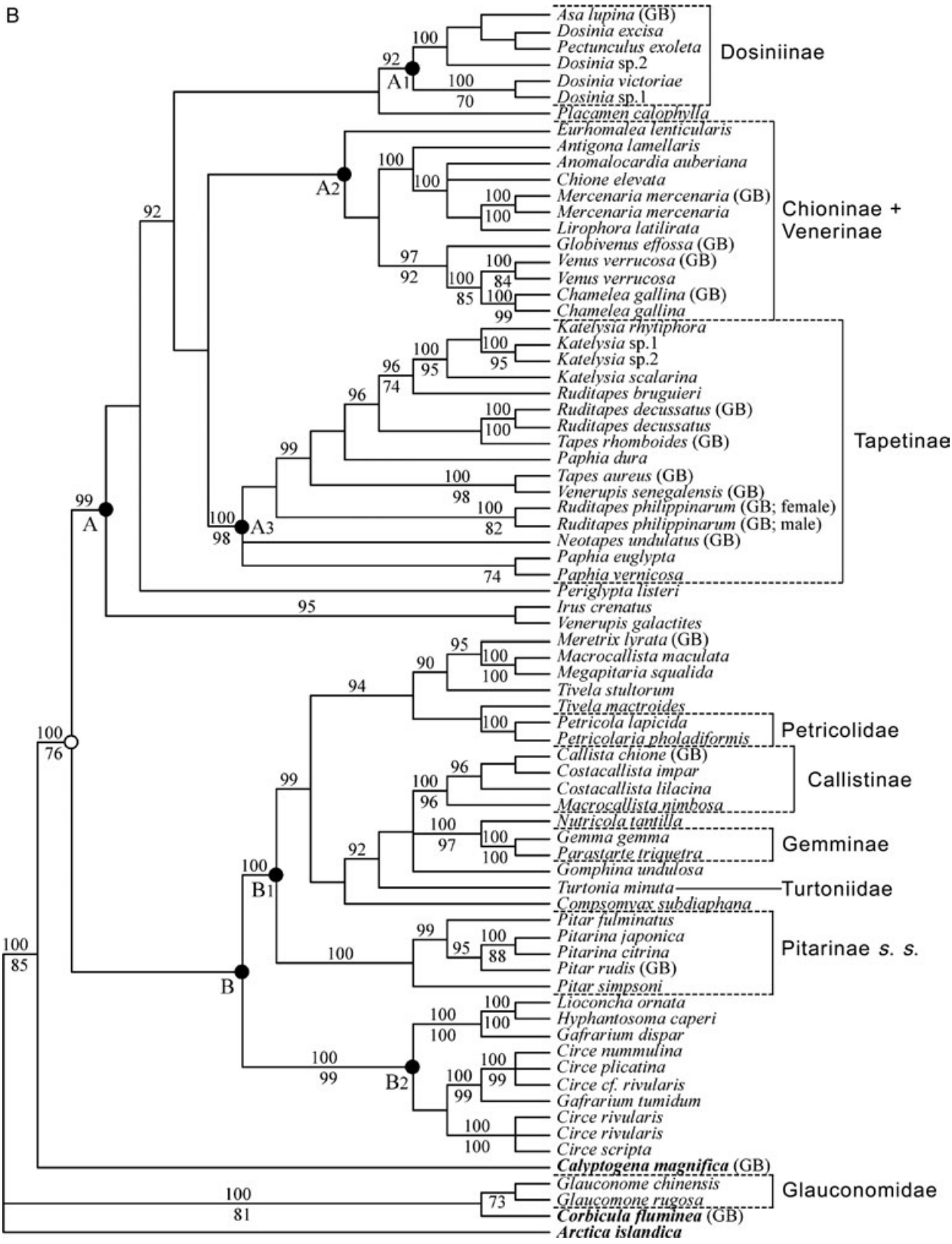


Figure 7. *Continued*

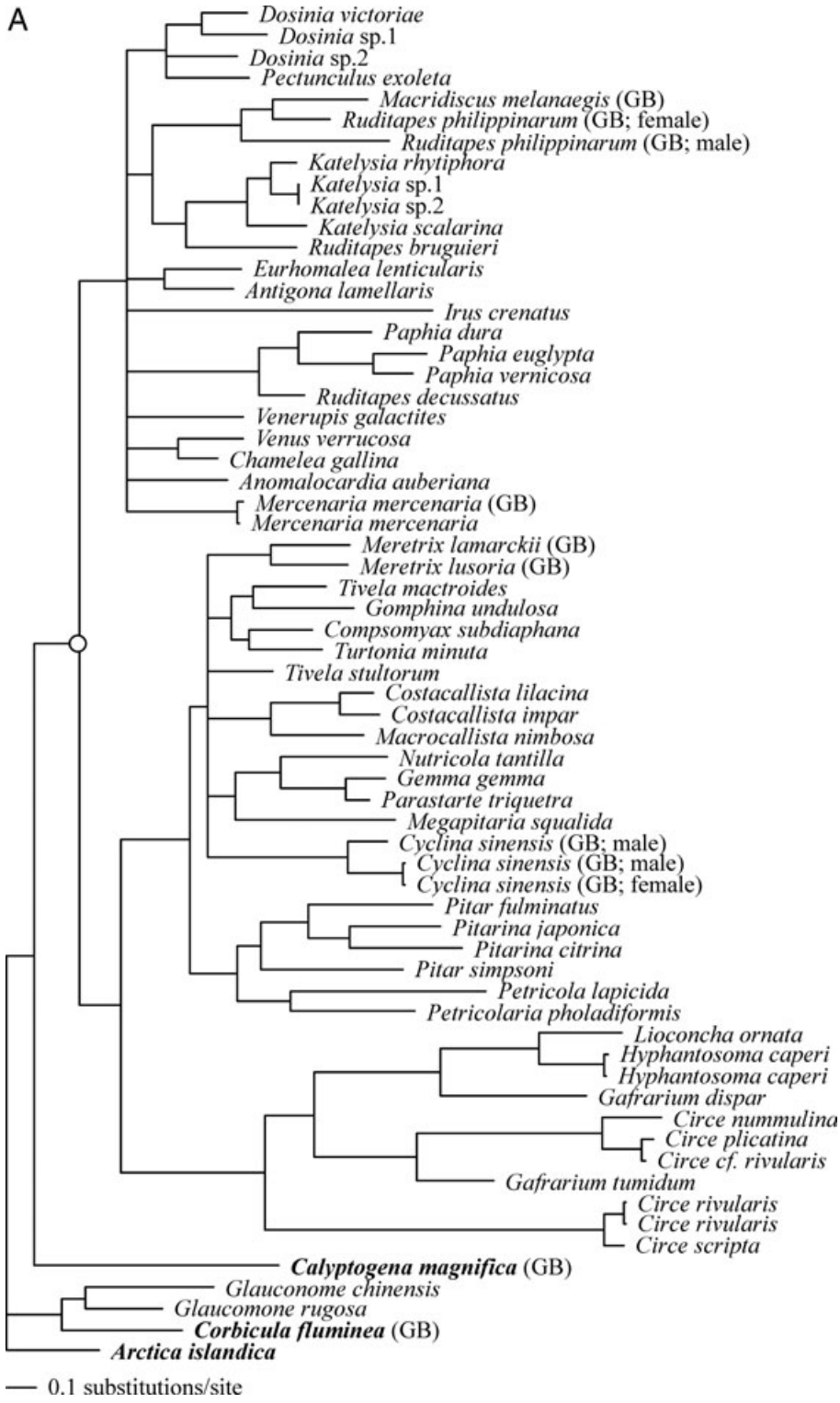


Figure 8. Molecular phylogeny of Veneroidea: a 50% majority-rule consensus tree based on a Bayesian analysis of the cytochrome oxidase I data set and a sampling of 29 501 trees (3 000 000 generations; sample frequency = 100; burn-in = 500; heat = 0.1). Symbols and conventions as in Figure 7; bootstrap proportions (≥ 70%) are based on a parsimony analysis (250 replicates, 10 random sequence additions; Tv 2.5 : Ti 1). The two sequences for *Hyphantosoma caperi* were obtained from the same individual. The three GenBank sequences for *Cyclina sinensis* were obtained from the gonadal tissue of two male specimens and one female specimen.

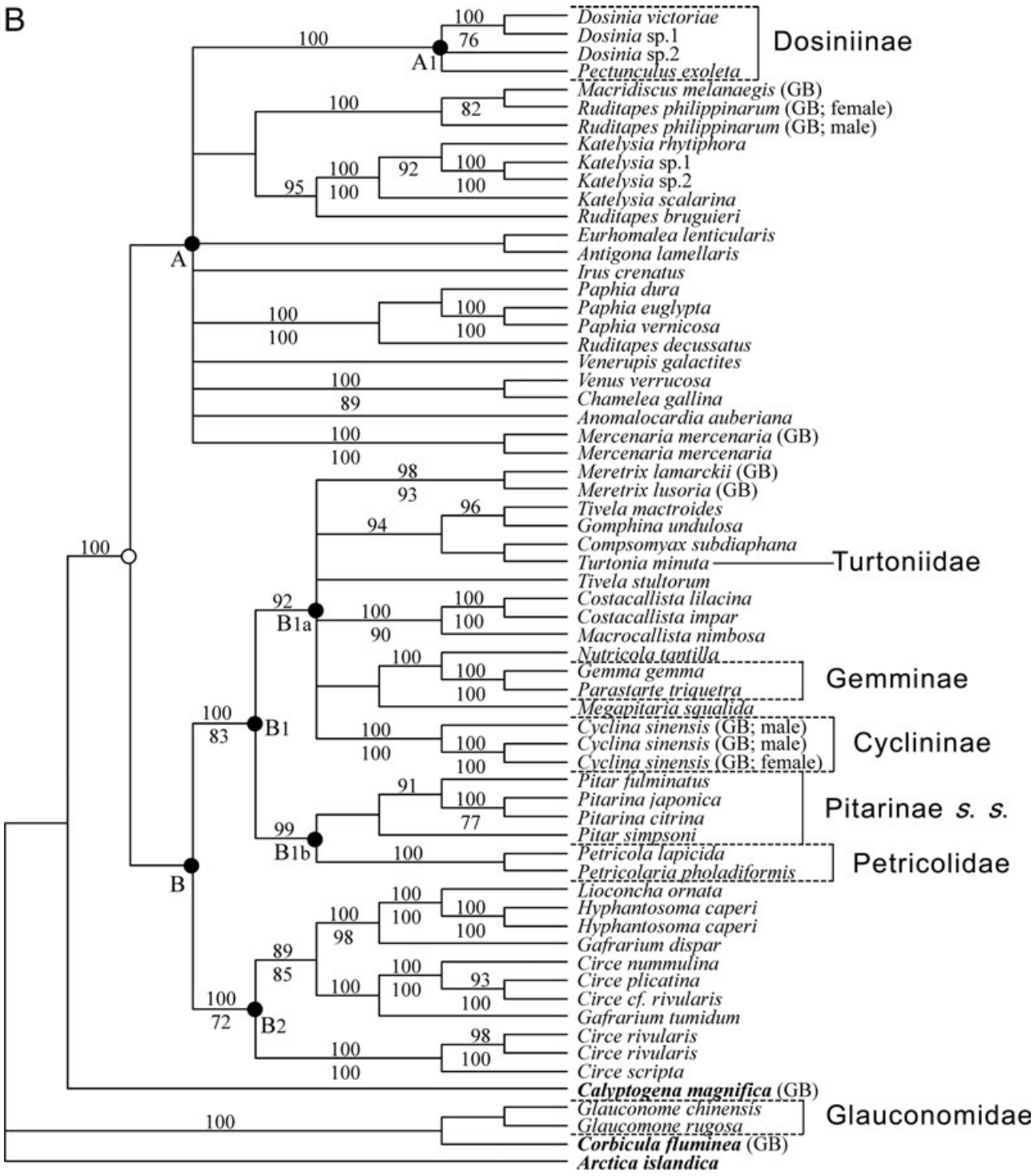


Figure 8. *Continued*

high PP and BP values for the monophyly of clade B, only weakly supported in the separate 16S and COI analyses. Also emerging with significant PP support (99%) in this analysis was the combined Chioninae + Venerinae (clade A2), again excluding *Periglypta listeri* and *Placamen calophylla*. As in the single-gene analyses, two tapetines (*Irus crenatus*, *Venerupis galactites*) were separated from other Tapetinae (clade A3) but grouped at the base of clade A. Combined analyses also reinforced the division of

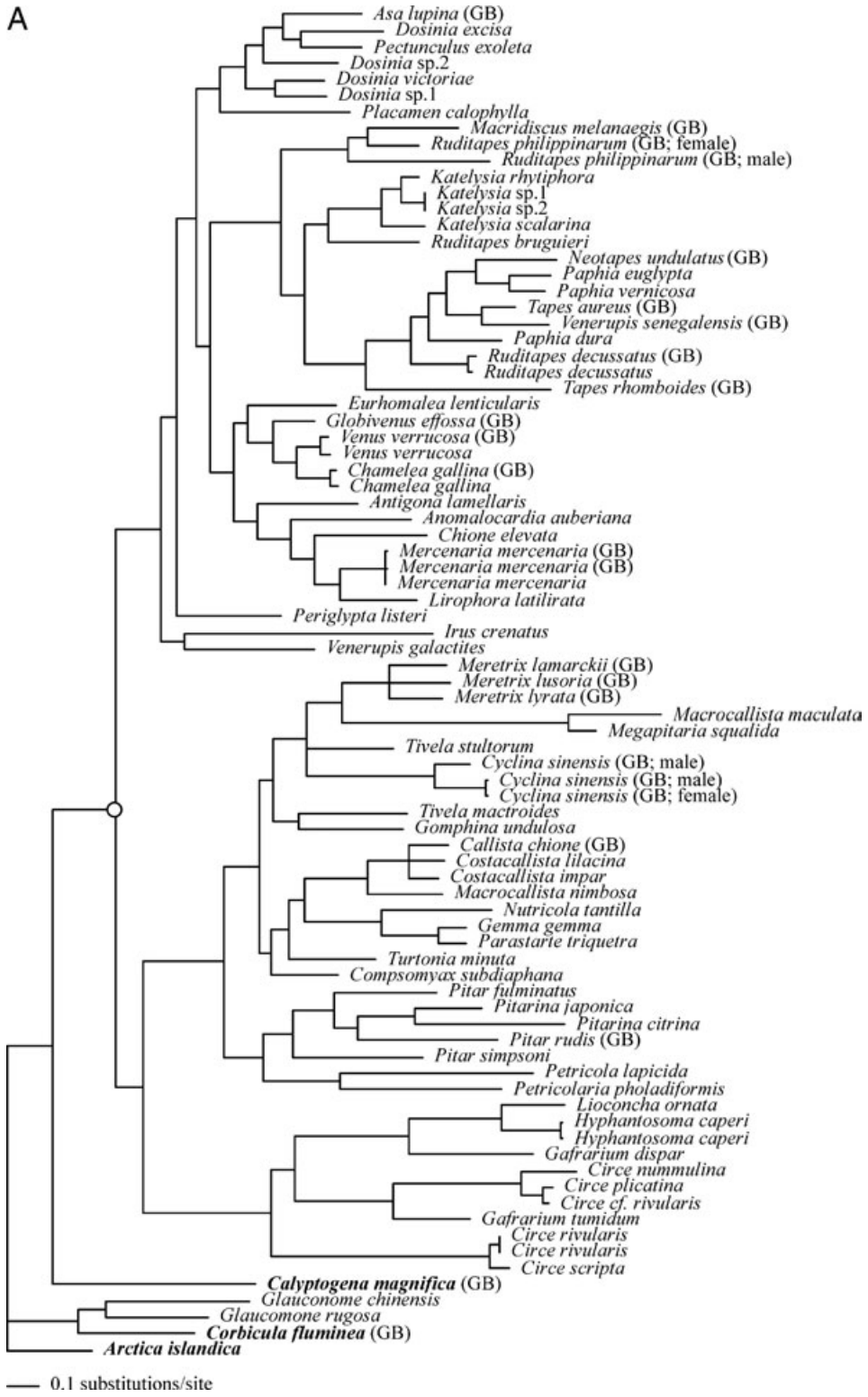


Figure 9. Molecular phylogeny of Veneroidea: a 50% majority-rule consensus tree based on a Bayesian analysis of the combined 16S rRNA and cytochrome oxidase I (COI) data sets and a sampling of 28 001 trees (3 000 000 generations; sample frequency = 100; burn-in = 2000; heat = 0.2). Symbols and conventions as in Figure 7; bootstrap proportions (≥ 70%) are based on a parsimony analysis (250 replicates, 10 random sequence additions; equal weighting). In two cases (*Corbicula fluminea* and *Calyptogena magnifica*), sequences represent the concatenation of independent 16S and COI GenBank submissions.

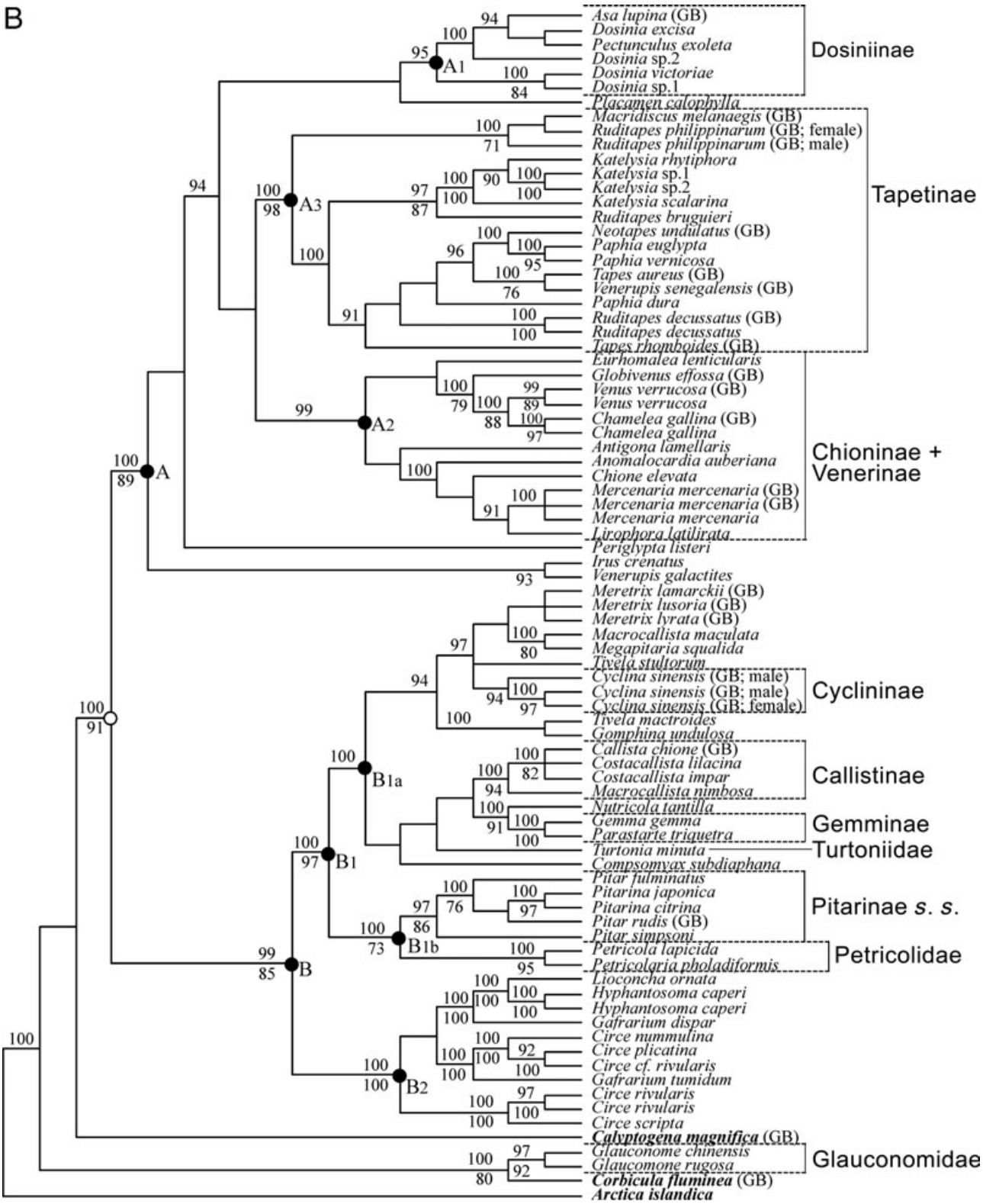


Figure 9. *Continued*

clade B1 into two highly supported subclades, one of which (B1b) included Pitarinae *s.s.* and Petricolidae. The strongly supported placement of *Gomphina undulosa* within subclade B1a also indicated a closer association of this taxon to members of three other venerid subfamilies (Meretricinae, Pitarinae *s.l.*, and Cyclinae) than to its traditional Tapetinae.

Nuclear genes

28S rRNA: Within the 28S rRNA data set, base frequencies were not significantly heterogeneous across 36 sampled taxa ($\chi^2 = 85.61$, d.f. = 105, $P = 0.917$, 420 variable characters) and a skewed tree length distribution suggested the presence of a strong phylogenetic signal (g1 = –0.939, $P < 0.01$, 250 parsimony-informative characters). Plots of numbers of transitions and transversions vs. uncorr-P distances for pairwise comparisons across 36 taxa showed relatively linear relationships for both transitions and transversions, with transitions typically occurring with higher frequency across all comparisons.

Both Bayesian and parsimony-based analyses of the 28S data set strongly supported the placement of Glauconomidae outside Veneroidea, and Petricolidae within (Fig. 10), in agreement with the mtDNA analyses. Weighting transversional changes more heavily than transitional changes in parsimony analyses (e.g. Tv 2 : Ti 1) provided slightly higher bootstrap support for the monophyly of Veneroidea (clades A, B1, and B2), but little difference in topology/support indices for other parts of the tree. Bayesian and parsimony-based analyses of the 28S rRNA data set also provided independent confirmation of the monophyly of clade A and Gouldiinae *s.s.* (clade B2), the latter previously part of clade B, but here a sister group to clade A (with 90% PP in Bayesian analyses; a relationship not strongly supported in the 16S, COI, or combined mtDNA analyses). However, these analyses did not provide significant PP or BP support for the monophyly of clade B1. The clades A1 (Dosiniinae) and A3 (Tapetinae, excluding *Gomphina*) were also recovered in analyses of the 28S rRNA data set, although only A1 was supported by a significant PP value. Bayesian analyses based on the combination of longer and shorter 28S rRNA sequences positioned *Turtonia* within Veneroidea, with weak support for its association with a clade consisting of Petricolidae, *Pitarina*, *Tivela*, Gemminae, *Nutricola*, and *Gomphina*. Overall differences in topology between the mtDNA-based (Fig. 9) and 28S phylogenies (Fig. 10) appeared largely confined to the position of the root of these trees – either between clades A and B in the mtDNA data set or between clades A/B2 and B1 in the 28S data set.

H3: For H3, the composition of nucleotide bases was homogeneous across 50 sampled taxa ($\chi^2 = 80.832$, d.f. = 147, $P = 1.0$, 117 variable characters) and the distribution of tree lengths significantly skewed to the left (g1 = –0.355242, $P < 0.01$, 102 parsimony-informative characters). Despite the apparent phylogenetic information retained within this data set and the utility of H3 at lower taxonomic levels within the Veneridae (Kappner & Bieler, 2006), Bayesian and parsimony-based analyses of this gene provided very little structure at deeper levels within the Veneroidea, and the monophyly of Veneroidea was not supported. When rooted with *Corbicula*, strongly supported clades (> 95% PP) of three or more taxa consisted of: (1) all taxa with the exclusion of *Nutricola*, Gemminae, and *Petricolaria*; (2) *Nutricola* and Gemminae; (3) Tapetinae (*Katelysia* spp., *Ruditapes bruguieri*, *R. decussatus*, *Paphia euglypta*, *P. vernicosa*); and (4) Gouldiinae *s.l.* (*Circe plicatina*, *C.* cf. *rivularis*, *Gafrarium tumidum*). The MP consensus tree (Tv 2 : Ti 1; 100 random sequence additions, 33 MP trees) recovered clade A (Dosiniinae, Tapetinae, Chioninae + Venerinae) in all trees, with two outgroup taxa (*Calyptogena*, *Arctica*) nested within. Other deep clades found in the mtDNA (Fig. 9B, clades B, B1, B2) and 28S rRNA (Fig. 10B, Circinae) analyses were not recovered.

Combined nuclear and mtDNA analyses

Given that similar overall tree topologies were recovered in the mtDNA and 28S rRNA analyses, with areas of disagreement with high PP and BP support limited to those mentioned above, we elected to combine data collected from mtDNA and nuclear genes into a single analysis. This was undertaken with the understanding that the final placement of some taxa in this combined analysis, particularly the sister-group association of Petricolidae with other taxa, should be interpreted cautiously. Because of the low phylogenetic resolution of H3, we undertook two combined mtDNA and nuclear analyses: (1) combining only mtDNA and 28S rRNA (long and short) data sets and (2) combining all four genes, but for a pruned data set of those 56 taxa for which all four gene sequences were available.

MtDNA and 28S: Bayesian analyses of a combined data set of mtDNA and 28S rRNA genes agreed with the previous observations of a monophyletic Veneroidea, including *Turtonia* and Petricolidae, and the grouping of Glauconomidae with *Corbicula* (Fig. 11). Furthermore, the major clades A, B, B1, and B2 were recovered with high PP (> 90%) and BP (> 75%) values. In clade A, significant or near significant PP values supported a monophyletic Dosiniinae (A1)

and Tapetinae (A3; still excluding *Irus*, *Venerupis galactoides*, and *Gomphina*). Although clade A2 (Chioninae + Venerinae) was recovered in this analysis, and for the first time included the venerine *Periglypta*, this clade was not significantly supported (58% PP; BP < 50%). Two clades within A2 were significant, however: one consisting of the venerines *Globivenus*, *Chamelea*, and *Venus*, and a second including the chionines *Anomalocardia*, *Chione*, *Lirophora*, and *Mercenaria*. However, the relationships of these taxa to the chionine *Eurhomalea* and the venerines *Periglypta* and *Antigona* were not resolved, as was that of *Placamen*, which was again positioned as a sister taxon to the Dosiniinae (clade A1). Within clade B, subclade B1a was strongly supported (100% PP), and within this group there was also significant support for the mixed grouping of meretricines (*Tivela*, *Meretrix*), pitarines *s.l.* (*Macrocallista maculata*, *Megapitaria*), and the tapetine *Gomphina*. Both Bayesian and parsimony analyses also recovered subclade B1b with high support.

Four genes: Analyses of combined mtDNA (16S, COI) and nuclear (28S, H3) genes for the 56-taxa pruned data set provided both high PP and BP values for deep and shallow clades in our phylogeny, and confirmed support for the monophyly of the Veneroidea, including *Turtonia* and Petricolidae, as well as the strong association of Glauconomidae with the outgroup taxon *Corbicula* (Fig. 12). Clades A and B received high PP and BP support, as did clades B1 and B2. Within clade A, the monophyly of Dosiniinae (A1), a combined Chioninae + Venerinae (A2), and Tapetinae (A3; excluding *Irus*, *Venerupis galactites*, and *Gomphina*) were supported by PP values > 95%, although there was no significant support for the monophyly of the two separate subfamilies Chioninae and Venerinae. Interestingly, the venerine *Periglypta* was firmly positioned within clade A2 in this combined four-gene analysis, unlike previous analyses of mtDNA alone. Bayesian analyses also suggested a sister-group association between the Dosiniinae (A1) and Chioninae + Venerinae (A2), although this relationship was not significantly supported (79% PP). Subclades B1a and B1b each received high PP values, corroborating the results of single-gene analyses in which Petricolidae nested within clade B1. Although deeper-level relationships within subclade B1a were not well resolved, there was significant PP support for the placement of *Gomphina* and *Turtonia* within this subclade, and significant BP support for the placement of these taxa within the more inclusive clade B1.

Hypothesis testing

Based on the four-gene molecular phylogeny (59 taxa), a constraint analysis was carried out to test the five hypotheses outlined in Material and Methods. All five hypotheses were significantly rejected with probabilities of $p < 1/29001$, indicating that according to our molecular analyses, both Veneroidea and Veneridae in the traditional sense are not monophyletic, Petricolidae and Turtoniidae are not sister taxa to Veneridae, and Gemminae belongs within Veneridae.

Character mapping

When morphological characters were mapped on the four-gene combined molecular tree (Fig. 12), each of the monophyletic groups within Veneroidea (Dosiniinae, Chioninae + Venerinae, Tapetinae, Gemminae, Callistinae, Pitarinae *s.s.*, Petricolidae) had at least two morphological synapomorphies (range two to six) in support. These included various states of shell sculpture, lunule, umbo position, inflation, margin, muscle scars, pallial sinus, hinge plate, AII, cardinal tooth orientation or bifidity, foot, and aortic bulb. However, only one of these was nonhomoplastic on the tree (foot lunate for Dosiniinae; unfortunately Sunettinae, supported by escutcheon deeply sunken, was not represented in the molecular analyses). Veneroidea (clades A + B) was supported by lunule present, although this character was reversed four times on the molecular tree (in *Irus crenatus*, *Cyclina*, *Nutricola* + Gemminae, and Petricolidae). Interestingly, a set of (albeit homoplastic) morphological characters emerged in support of 'crown group' clade A (including Dosiniinae, Chioninae + Venerinae, and Tapetinae): (1) escutcheon present, (2) lunule impressed, (3) pallial sinus moderate to large, (4) anterior lateral tooth (AII), when present, of the 'pseudolateral' type, and (5) right middle cardinal tooth (1) bifid.

DISCUSSION

Although this study has not fully resolved the relationships within Veneroidea or among venerid subfamilies, substantial progress has been made. The morphological analyses have revealed a paucity of character variability within Veneridae, especially with regard to soft anatomical characters. They have failed to reconstruct most units of traditional classification from analyses based on a combination of type species and group-defining traditional characters. They have suggested a number of ways in which features of veneroid morphology are or can be misleading, and have shown considerable levels of homoplasy in resultant trees. The molecular analyses, based on single and combined gene analyses, resulted in substantially higher clade consistency and support. Subsequent morphological character mapping on molecular trees retained a high level of homoplasy, but nevertheless

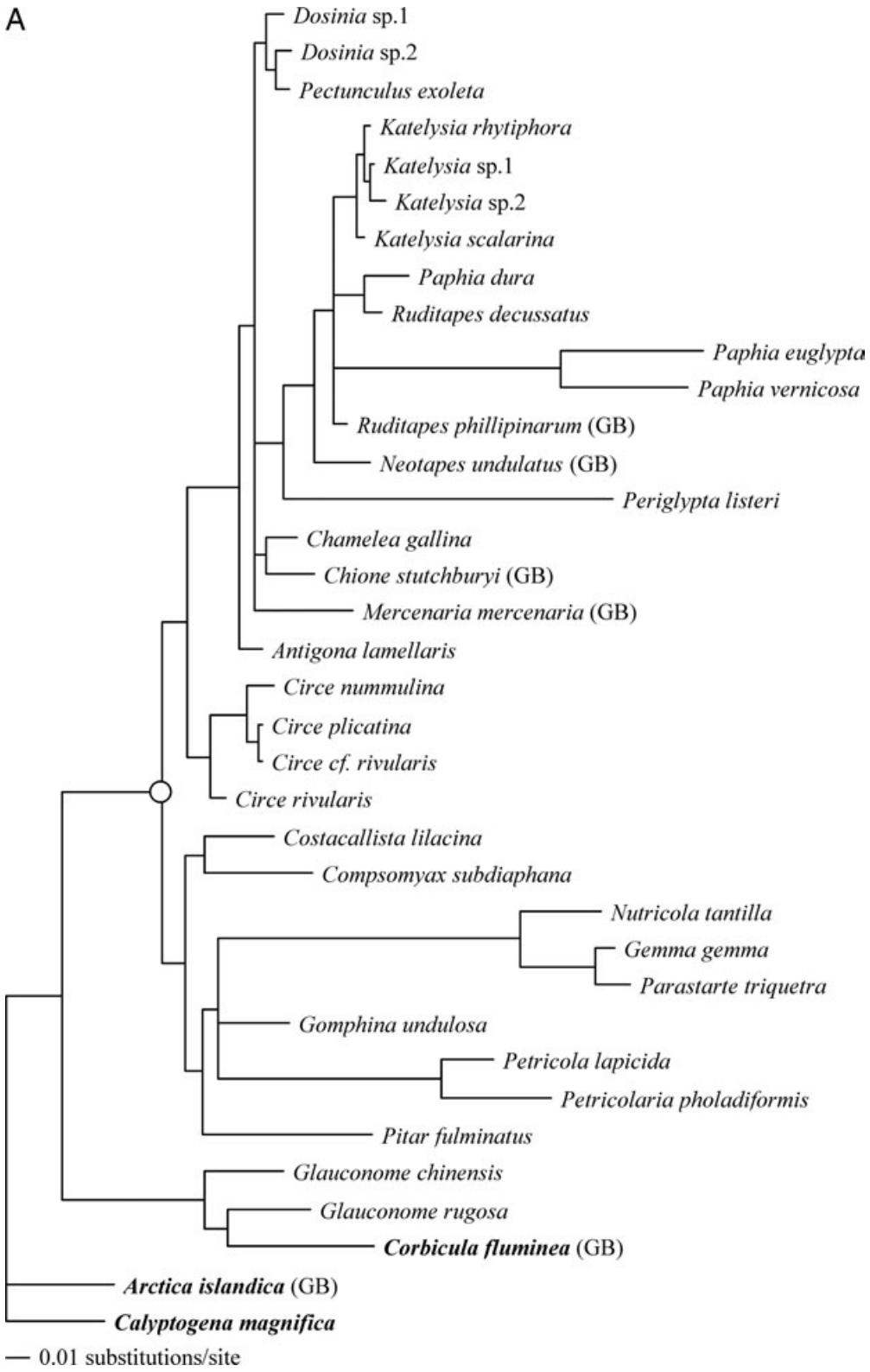


Figure 10. Molecular phylogeny of Veneroidea: a 50% majority-rule consensus tree based on a Bayesian analysis of the long 28S rRNA data set and a sampling of 29 001 trees (3 000 000 generations; sample frequency = 100; burn-in = 1000; heat = 0.2). Symbols and conventions as in Figure 7; bootstrap proportions (≥ 70%) are based on a parsimony analysis (250 replicates, 10 random sequence additions; Tv 2 : Ti 1).

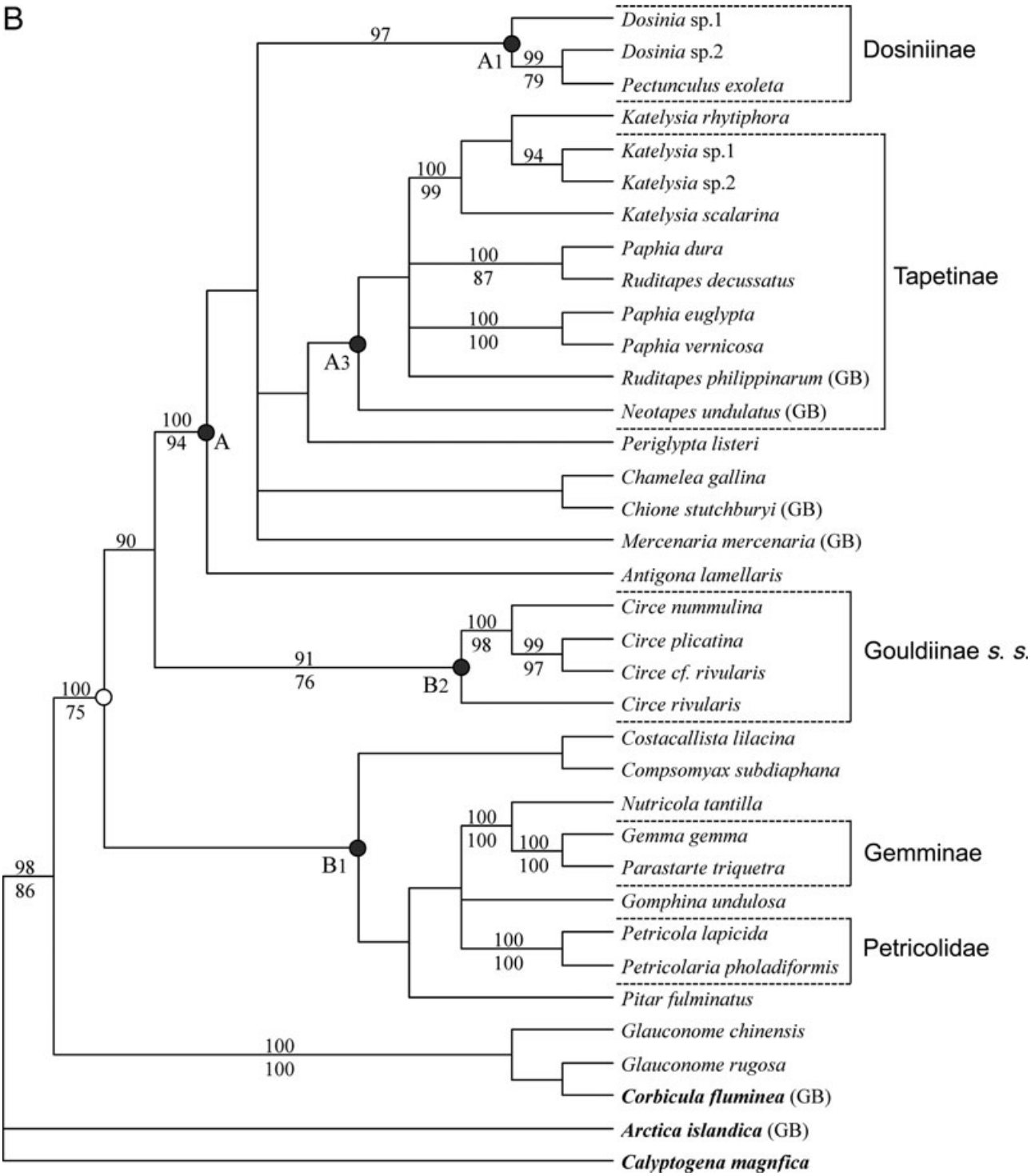


Figure 10. *Continued*

revealed synapomorphies for major branch points and supported family groups, suggesting areas for further morphological refinement. Finally, these analyses have underscored the need for taxonomic revision at generic and subfamilial levels, especially within large nominal subfamilies such as Pitarinae, and for in-depth study of now problematic, yet potentially informative, characters.

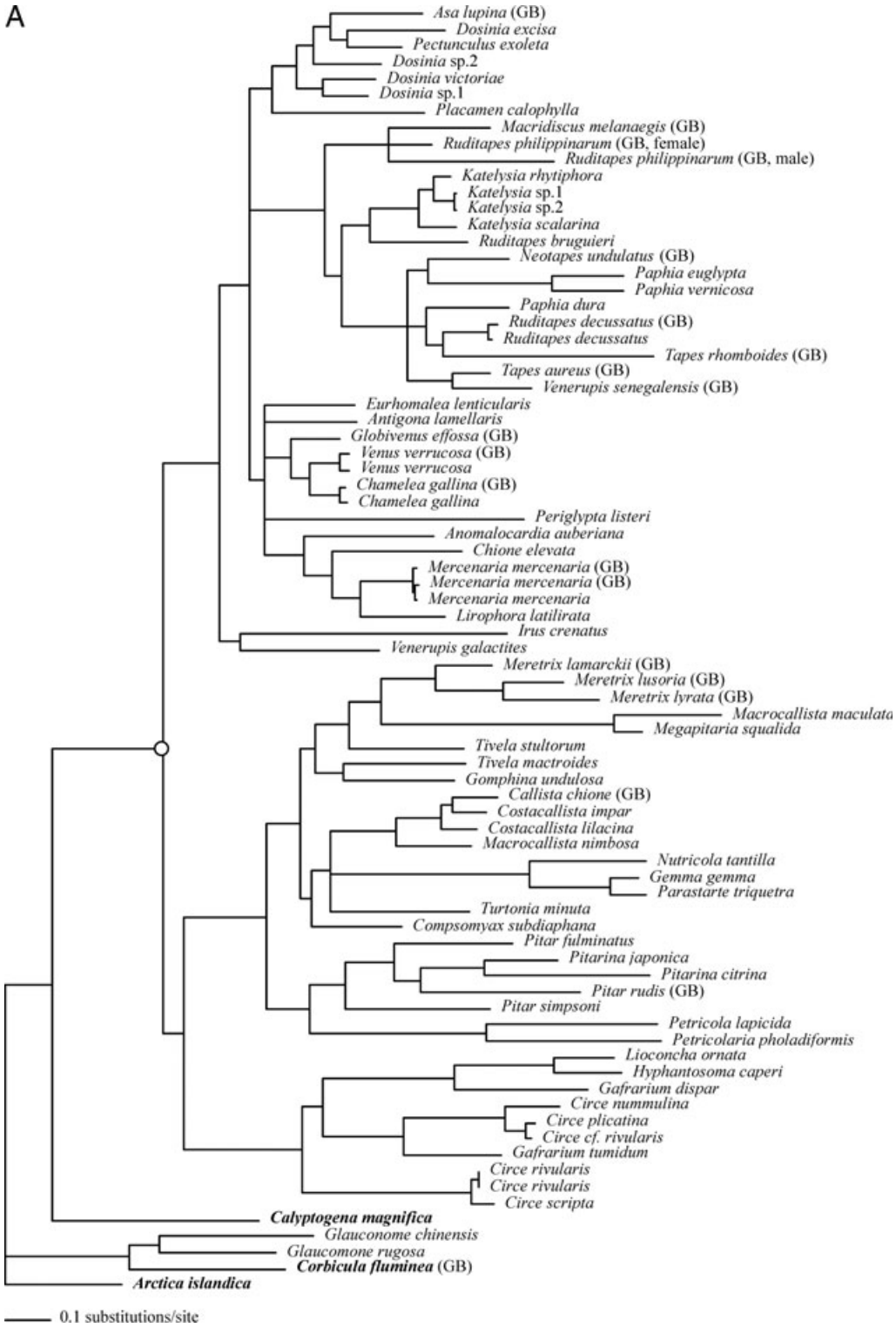


Figure 11. Molecular phylogeny of Veneroidea: a 50% majority-rule consensus tree based on a Bayesian analysis of the 16S rRNA, cytochrome oxidase I (COI), and 28S rRNA (long and short) data sets and a sampling of 29 001 trees (3 000 000 generations; sample frequency = 100; burn-in = 1000; heat = 0.2). Symbols and conventions as in Figure 7; bootstrap proportions (≥ 70%) are based on a parsimony analysis (250 replicates, 10 random sequence additions; equal weighting). The three *Cyclina sinensis* sequences (represented by only a short piece of COI) and a second COI sequence for *Hypantosoma caperi* were removed from the data set prior to undertaking these combined analyses.

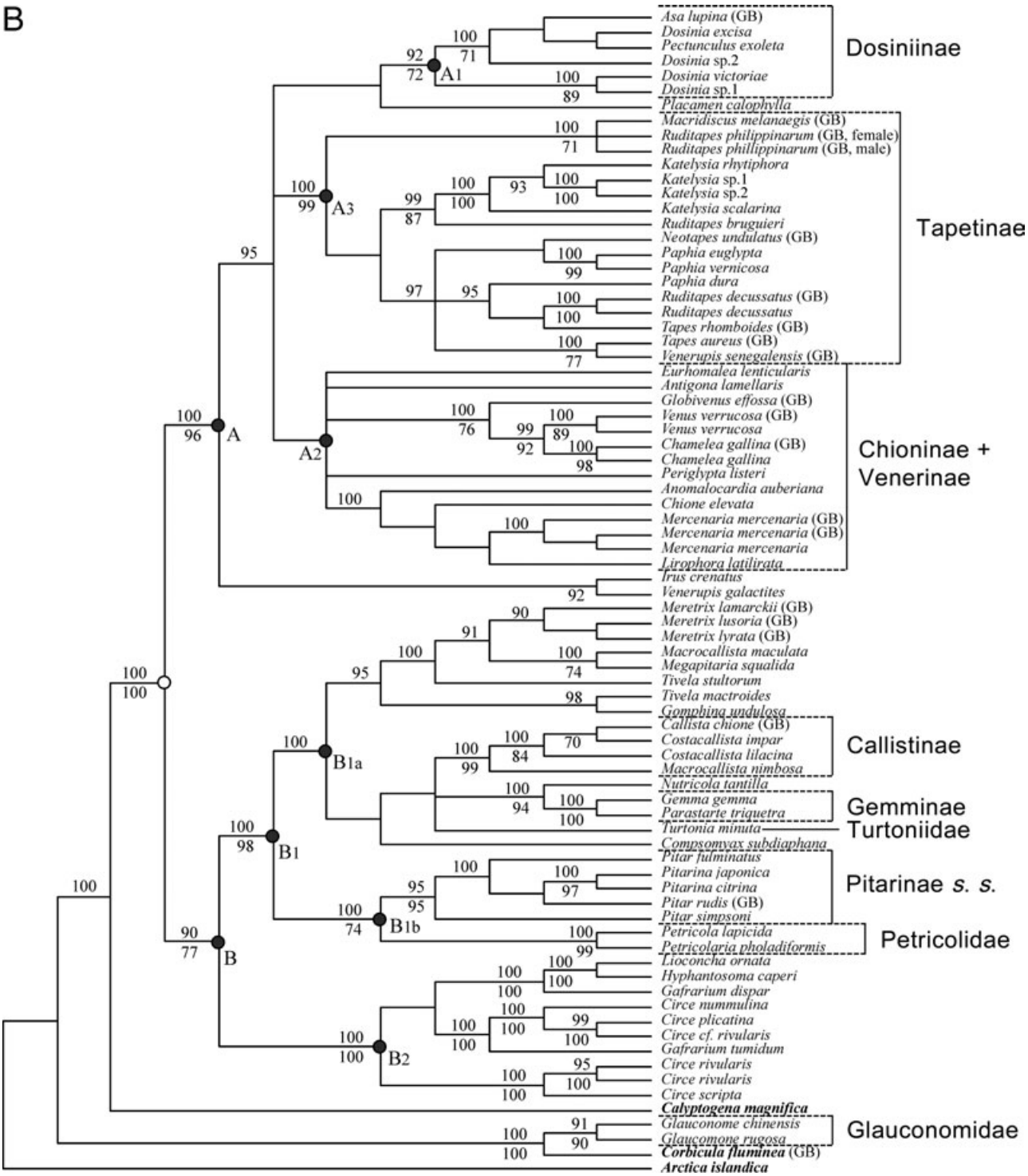


Figure 11. *Continued*

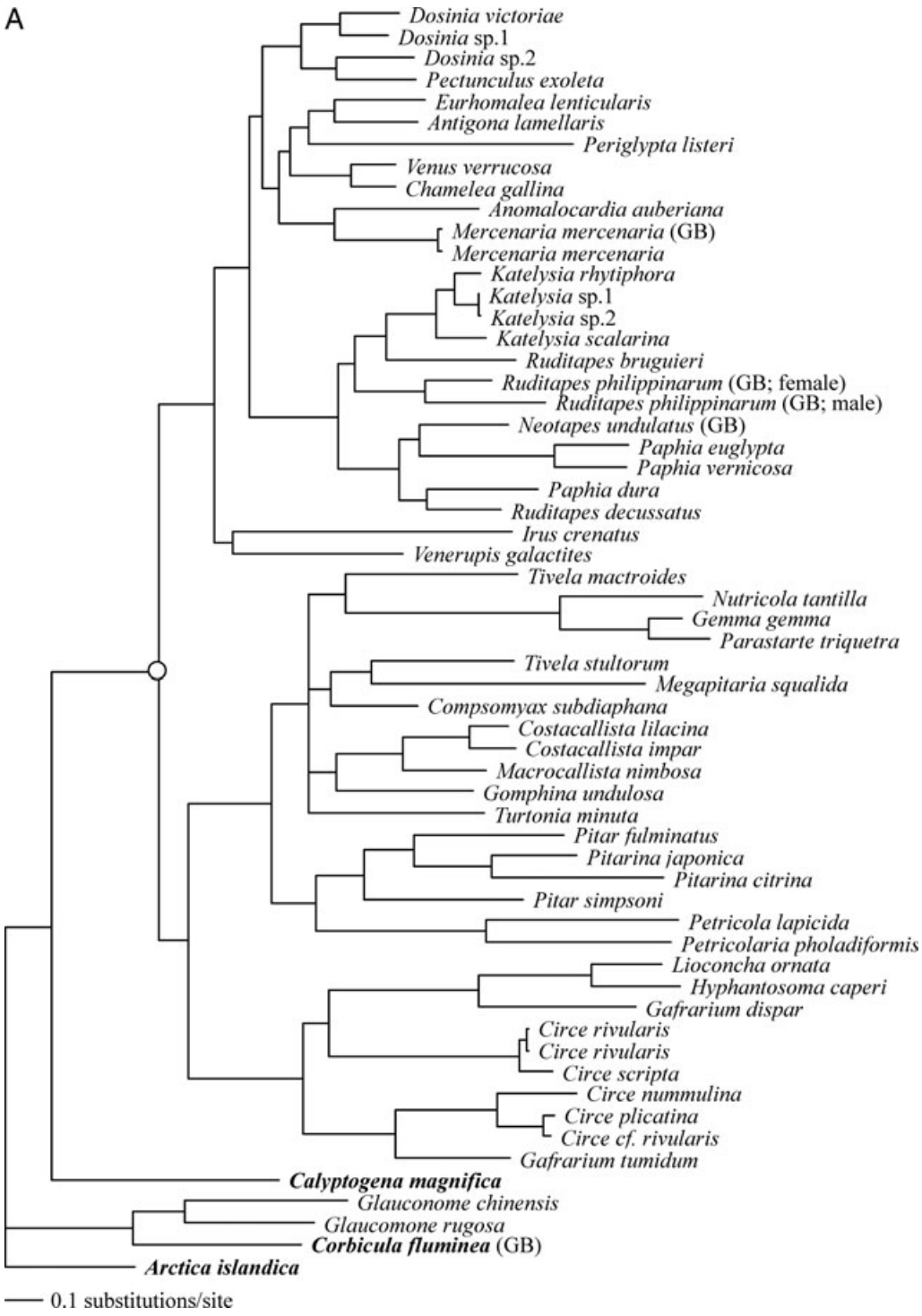


Figure 12. Molecular phylogeny of Veneroidea: a 50% majority-rule consensus tree based on a Bayesian analysis of the 16S rRNA, cytochrome oxidase I, 28S rRNA, and histone 3 data sets for a pruned selection of 56 taxa (59 sequences) with sequences > 1200 bp in length. Branch lengths and posterior probability values based on a sampling of 29 001 trees (3 000 000 generations; sample frequency = 100; burn-in = 1000; heat = 0.5). Symbols and conventions as in Figure 7; bootstrap proportions (≥ 70%) are based on a parsimony analysis (250 replicates, 10 random sequence additions; equal weighting). In *Corbicula*, *Mercenaria*, *Neotapes*, and *Ruditapes philippinarum*, GenBank sequences represent concatenated sequences of independent GenBank submissions for some or all genes. For some other taxa (*Arctica* and *Calyptogena*), sequences represent a mixture of GenBank and newly acquired sequences for the same species.

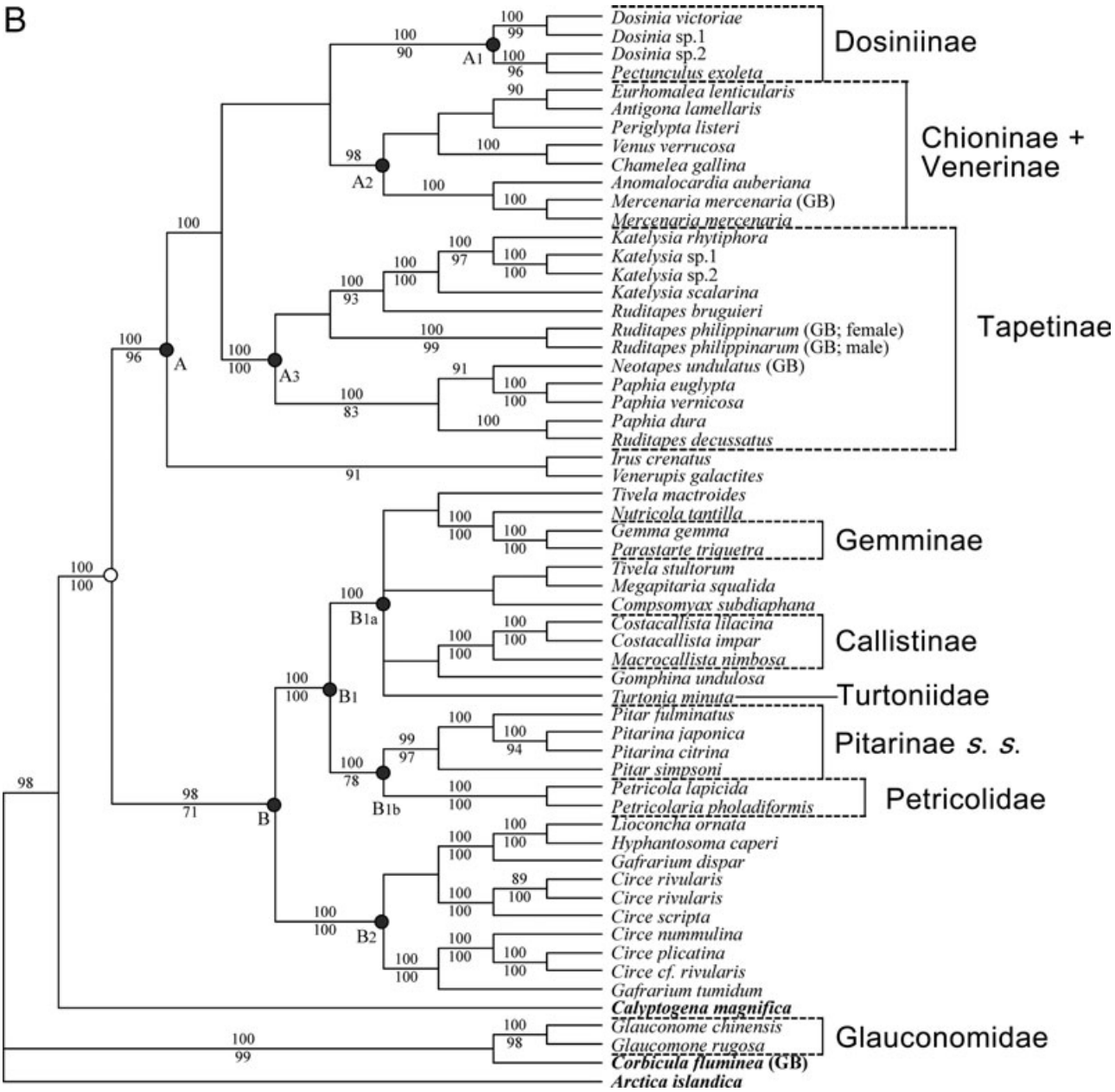


Figure 12. *Continued*

IMPLICATIONS FOR VENEROID CLASSIFICATION

Taken as a whole, the results of these analyses (Figs 3–12) strongly suggest that the following taxonomic groups are monophyletic: Veneroidea, Glauconomidae, Petricolidae *s.s.* (except paraphyletic in traditional morphology; Fig. 5B), Chioninae + Venerinae (except unresolved in COI and 28S results; Figs 8, 10), Dosiniinae, Gemminae (except unresolved in all-morphology results; Fig. 6), Samarangiinae (morphological analyses only, no molecular data available), Sunettinae (morphological analyses only, no molecular data available), and Tapetinae (except unresolved in COI results; Fig. 8). Callistinae, Gouldiinae *s.s.*, Lioconchinae, and Pitarinae *s.s.* each received support in at least one analytical result. No support was found for Clementiinae (polyphyletic in morphological trees, represented by a single taxon in molecular data sets), Cyclininae (polyphyletic in morphological trees, represented by only one taxon and a portion of one gene in molecular data sets), Gafrariinae (paraphyletic in morphological trees, among

Gouldiinae in molecular trees), Meretricinae (paraphyletic in morphological trees, para- or polyphyletic in molecular trees), and Meroinae (within Sunettinae in morphological trees). Callocardiinae, Turtoniidae, and Neoleptonidae were represented by only one taxon each, and their monophyly thus remained untested in these analyses. Cooperellidae was also represented by a single taxon, but morphological analyses (it was not available for molecular work) offered no support for its synonymy with Petricolidae (but see Morton, 1995).

Although Veneroidea was confirmed as monophyletic in all analyses, Veneridae was recognizable as a separate entity only in the all-morphology tree (Fig. 6). What then can we conclude about Veneridae in the remaining analyses? There are two choices, either to split Veneridae into two or more families, or to accept included veneroid families into Veneridae. Given the absence of supporting morphological synapomorphies for the former at present, the latter choice seems more acceptable. If we then hypothesize that Veneroidea = Veneridae in all except the all-morphology tree, we must reconsider the status of the other four veneroid families.

Glauconomidae joined the Veneridae in the traditional morphology tree (Fig. 5B, based on anterior lateral tooth absent, a character later judged to be nonhomologous and recoded), but formed a sister group to the outgroup *Corbicula* in all molecular results. Its relationship to *Corbicula* or Corbiculoidea, however, should not be overinterpreted from this analysis; all we can assure from these results is that Glauconomidae is not a member of Veneridae. Clarification of its relationships to Veneroidea, other superfamilies, and the subclass Heterodonta must await analyses that include better taxon sampling within that larger data set. We therefore provisionally accept it as a member of Veneroidea until such larger analyses can be accomplished.

Neoleptonidae joined the Veneridae in the traditional morphology tree, but fell outside Veneroidea in the all-morphology analyses. Part of the former placement (in a clade with *Clementia*) was due to pallial sinus large, a character coded ambiguously (missing) for *Neolepton*. As previously discussed, the characters pulling it out of Veneroidea in the all-morphology tree were those associated with its small size and probable neoteny. Unfortunately, *Neolepton* was not available for molecular testing. Therefore, we provisionally retain this family as a member of Veneroidea until further material becomes available.

Turtoniidae fell outside of Veneroidea in both morphological analyses, but was a consistent member of Veneridae clade B in all molecular trees. Like *Neolepton*, *Turtonia* is small bodied and probably neotenous (see above), so its exclusion from Veneridae is probably unreliable based on these data. We therefore include it as subfamily Turtoniinae within Veneridae.

Petricolidae *s.s.* joined Veneridae in all except the all-morphology tree (where it formed a monophyletic clade with Glauconomidae and *Cooperella* as nonvenerid Veneroidea). In the molecular trees, Petricolidae was a consistent member of Veneridae clade B, in some cases forming a strongly supported monophyletic clade with Pitarinae *s.s.* (subclade B1b; Figs 8, 9, 11, 12). These results might seem somewhat at odds with those of Giribet & Distel (2003), who did not find a close association between *Petricolaria* and the venerids *Mercenaria*, *Callista*, and *Venus* in a higher-level bivalve analysis based on four gene sequences (of which only one gene –18S rRNA – was sampled across all four taxa). However, the position of *Petricolaria* was highly unstable in their analyses, varying with changes in the parameter sets used (Giribet & Distel, 2003) and probably reflecting the long-branched nature of the *Petricolaria* 18S rRNA sequence relative to those of many other heterodonts. Ecologically, members of Petricolidae are specialized burrowers in soft rock or hard mud (Owen, 1959), and their strongly sculptured, anteriorly skewed, anteroposteriorly elongated shells are testament to this specialized habitat. Members of the unrelated heterodont family Pholadidae (e.g. *Cyrtopleura*, *Barnea*; traditionally placed in the order Myoida), while internally divergent, are superficially similar and the external morphology of petricolids is probably the result of convergent adaptation to a similarly specialized mode of life. Also, in view of the long history of the close association of Veneridae and Petricolidae based on morphology, we do not hesitate to include the latter as subfamily Petricolinae within Veneridae based on both morphological and molecular data analysed herein.

In a recent review, Harte (1998b: 357) noted that '[i]nsufficient research on extant genera still hinders adequate taxonomic treatment' and this is still true. Of the 17 nominal subfamilies of Veneridae, we can definitely acknowledge only five (Dosiniinae, Gemminae, Samarangiinae, Sunettinae, and Tapetinae) as monophyletic groups based on these analyses. The last, however, requires revision with regard to a number of traditionally included taxa that consistently fell outside the subfamily in most molecular analyses: *Gomphina undulosa*, *Irus crenatus*, and *Venerupis galactites*. *Gomphina undulosa* fell farthest afield, consistently within clade B, whereas Tapetinae proper (plus *Irus crenatus* and *Venerupis galactites*) formed parts of the more morphologically derived clade A. It is unlikely that these outliers result from taxonomic misidentifications; specimens of *Gomphina undulosa* (which is the type species of *Gomphina* Mörch, 1853) utilized herein, from Shark Bay, Western Australia, agreed in all aspects with the descriptions presented

in the revisions of Tapetinae by Fischer-Piette & Métevier (1971) and of *Gomphina* by Lutaenko (2001; except for that author's interpretation of anterior and posterior marginal lamellae as lateral teeth). Material from this study of *Irus crenatus* was compared with Lamarck's (1818) type specimens deposited at MNHN. Its relationship and possible synonymy with *I. crebrelamellatus* (Tate, 1886) needs further investigation, as does the overall taxonomy of the *Irus*/*Venerupis* complex. *Irus crenatus* differed from other members of *Irus* studied herein in lacking the escutcheon, having more subcentral umbones, more fully fused siphons, plus differences in four hinge characters; the rock-nestling, byssal-attaching habit of this species is in part responsible for its generic placement, but this should be re-examined in light of possible convergence. *Venerupis galactites* has been recently revised based on living populations in Western Australia (Bieler, Mikkelsen & Prezant, 2005). According to those results and the morphological coding herein, *Venerupis galactites* is a typical tapetine, apart from having an unusually complex byssal structure. Apart from lacking a marginal food groove on the outer demibranch, *Venerupis galactites* was coded nearly identically with *Venerupis senegalensis*; its behaviour in the molecular analyses is perhaps the most confounding of the three outliers.

The union of Chioninae + Venerinae in our analyses is enticing in view of the recent synonymization of the two subfamilies (Coan & Scott, 1997; Coan *et al*., 2000) based on overall similarity and only a single difference (anterior lateral tooth absent in Chioninae, present in Venerinae). This action did little to clarify venerid subfamilial relationships, but rather acknowledged that we understood even less than we had earlier professed. Ongoing work within our research group is investigating this problem by molecular methods (Kappner & Bieler, 2006).

Clade A of the molecular results, consisting of Dosiniinae, Chioninae + Venerinae, and Tapetinae, was consistently supported both within the molecular analyses and by a set of (albeit homoplastic) synapomorphies. It is interesting to note that the earlier 16S results of Canapa *et al*. (2003) also supported this grouping (as well as the union of Meretricinae and Pitarinae, which were two components of our clade B).

Pitarinae could be interpreted as the least supported venerid subfamily. This group seems to be the result of a poorly defined combination of leftover taxa (a 'taxonomic trashcan') evidenced by both morphological and molecular results of this study. The need for in-depth generic revision is indicated by the partial support during this study for its purported subdivisions – Callistinae, Lioconchinae, Callocardiinae, and Pitarinae *s.s.* Meretricinae also warrants in-depth revision, evidenced by its two genera, *Meretrix* and *Tivela*, which often formed clades or paraphyletic grades. At present, both Pitarinae and Meretricinae are provisionally retained as entities within Veneridae. It is interesting to note that these two subfamilies were suggested to be closely related by the early 'phylogenetic' conchological studies of Frizzell (1936a, b, c) and the 16S analyses of Canapa *et al*. (2003).

Gouldiinae/Gafrariinae received little support in the molecular analyses, but this was due in all cases to the inclusion of two supposed pitarines, *Lioconcha ornata* and *Hyphantosoma caperi*. Except for these, Gouldiinae (with Gafrariinae, see below) might have been considered a monophyletic subfamily of Veneridae. Therefore, its provisional status in the revised classification is more a matter of taxonomic uncertainties in Pitarinae than in Gouldiinae itself.

Of the remaining nominal subfamilies, Gafrariinae and Meroinae received no support, joining in these analyses Gouldiinae and Sunettinae, respectively. We see little justification, therefore, in considering them further. The same cannot be said about Clementiinae and Cyclininae, which were insufficiently tested by these analyses for definitive conclusions. We thus provisionally retain them within Veneridae until further material becomes available.

At this point in time, we offer the following revised classification of Veneroidea, subject to revision as our investigations progress:

Veneroidea
- ?Glauconomidae (requires analysis in the context of Heterodonta)
- ?Neoleptonidae (requires additional material for analysis)
- Veneridae
  - Petricolinae + *Cooperella* (the latter requiring molecular data)
  - Turtoniinae
  - Dosiniinae
  - Tapetinae (some members require revision)
  - Gemminae
  - Samarangiinae
  - Sunettinae
  - Chioninae + Venerinae (under analysis; Kappner & Bieler, 2006)
  - Gouldiinae (requires clarification vs. Pitarinae *s.l.*)
  - Pitarinae (requires extensive revision)
  - Meretricinae (requires revision)
  - Clementiinae (requires additional material for analysis)
  - Cyclininae (requires additional material for analysis)

Veneroid molecular issues

Complications associated with patterns of doubly uniparental inheritance (DUI) of mitochondrial genomes could potentially result in misleading phylogenies in cases where the latter are based on a mixture of haplotypes from M- and F-type lineages. The extent to which this could have been a problem for our mtDNA analyses is dependent on: (a) the occurrence of DUI within the Veneroidea; (b) our ability to sample only F-type mitochondrial genomes; and (c) the frequency of masculinization (see Hoeh *et al*., 1997) or the replacement of M-type mtDNA lineages by F-types, a phenomenon that has been reported within some bivalve groups. If masculinization is frequent, gender-specific mtDNA lineages are unlikely to become highly divergent in nucleotide sequence, thus lowering the potential for DUI to result in incorrect phylogenetic inferences in cases where a mixture of mitotypes has been sampled. Although gender-specific mitochondrial lineages are clearly present in some taxa within the Veneroidea (Passamonti & Scali, 2001; Passamonti *et al*., 2003; I. Kappner, pers. observ.), given that we sampled DNA from somatic tissues in nearly all cases (with the exceptions of *Gemma*, *Parastarte*, and *Turtonia*), the likelihood that our mtDNA data set is based on a mixture of M- and F-mitotypes is low. Also, based on a sampling of putative M- and F-type sequences from two taxa in GenBank (*Ruditapes philippinarum*, *Cyclina sinensis*) and unpublished data for other venerids (I. Kappner, pers. observ.), M- and F-type mitochondrial lineages sampled within a species appear to be relatively closely related to one another (Figs 7–9). This suggests that if DUI is indeed an ancestral trait within the Bivalvia, masculinization events might be occurring frequently enough within the Veneroidea that DUI is unlikely to mislead phylogenetic inferences at deeper levels, although it could be more problematic at shallower taxonomic levels. Clearly, this phenomenon needs to be explored in more detail within this group.

Veneroid morphology

As corroborated by the results of this study, veneroid morphology is remarkably uniform, especially from a soft anatomical point of view. Conchological characters, although also quite limited in number, are relatively rich, which favours the inclusion of original descriptions and type specimens (most of which are exclusively conchological) and, ultimately, of extinct taxa from the extensive fossil record of Veneroidea extending back to the Cretaceous (Skelton & Benton, 1993). Nevertheless, the traditional morphological analyses here failed to reconstruct most traditional taxonomic groups, even though they were based on type species of the name-bearing genera (e.g. *Venus verrucosa*, type species of *Venus*, for Venerinae) and on the traditional characters now used to define them in standard monographs (e.g. Keen, 1969; Harte, 1998b; Coan *et al*., 2000).

The most intervening factor in this failure seems to be that of differential coding of many of the characters employed. Three confounding sources of potential artefact have been identified: specimen cleaning, preservation, and ontogeny.

Cleaning

Many mollusc collectors have a regrettable tendency to overclean their specimens. All organic material, interior and exterior, is thereby extracted or dissolved so that the dried shells can be conveniently stored in cabinets. Although so limited, such collections often contain rare or well-documented species records and, upon donation or other means of acquisition, become significant components of major museum collections. Because worldwide studies such as this usually rely in part on museum specimens, we encountered various such cleaned specimens in our research. Among the potentially character-rich features that have been adversely affected by this practice is the periostracum, often considered unsightly by collectors and removed by soaking the shell in sodium hypochlorite (bleach) solution. In this study, the traditional character 'periostracum' was coded simply as present or absent (actually nonpersistent beyond the extreme margin of the shell). The potential artefact is obvious – if material examined is limited to museum specimens that have been cleaned, the periostracum might be falsely recorded as absent. Further potentially informative elaborations of this character complex, such as calcified periostracum present in, for example Pitarinae *s.l.* (Ohno, 1996), were likewise impossible to reliably include in this analysis.

Preservation

A second possible source of coding artefact concerns soft anatomical characters whose interpretation is influenced by the degree of hydrostatic extension or contraction. One such character, used in traditional veneroid descriptions, involves the incurrent–excurrent siphons, which exist in various degrees of longitudinal fusion to one another (i.e. separate from the base to the tip, fused *c.* halfway, fused from the base to the tip). The ability to accurately and consistently code states of this character is highly dependent on the condition of the specimen at the time of recording and on the position of the viewer at that time. Sources of these data can originate in a variety of sources, including (in order of decreasing reliability) freshly collected living specimens, living but semimoribund specimens

from commercial fish markets, preserved specimens, whole-animal photographs, and drawings from the literature. Because the relative expandability of fused vs. unfused portions of siphons is not well studied, even partially contracted siphons could appear fused to a greater or lesser degree than fully expanded siphons.

Ontogeny

Ontogenetic differences in character expression can potentially interfere with the coding of such data in two ways: (1) the stage of life of the specimens examined, and (2) neoteny. A good example of the former is the character byssus present/absent in the adult. It is well established that the majority of bivalves secrete byssal threads as juveniles, to assist in settling and maintaining position during early benthic life. In some species, e.g. *Mercenaria mercenaria*, this ability is lost sometime during early adulthood. Whether (1) a byssal thread can be actually produced, (2) a byssal groove is visible on the foot, and (3) a byssal-producing gland is detectable within the pedal tissues, are thus dependent upon the life stage of the individual(s) examined. Furthermore, byssal retention into adulthood can display intraspecific variability in certain species, such as *Timoclea scabra* (Hanley, 1845) in which the byssal gland remains functional in only some adults (Narchi, 1980; as *Veremolpa*). Although retention of the byssus by the adult is usually interpreted as plesiomorphic retention of a juvenile trait, some adult byssi are undoubtedly derived, for example the monolaterally branched byssal thread of the seagrass-dwelling venerid *Venerupis galactites* (see Bieler *et al.*, 2005).

The more problematic interference of ontogenetic effect is the apparent case of neoteny in *Neolepton* and *Turtonia*, not surprisingly also members of the least understood nominal veneroid families. Ockelmann (1964) considered *Turtonia minuta* as a neotenous veneroid, prompting its inclusion in this data set. He compared *Turtonia* most rigorously with two venerid species, *Venus* (now *Chamalea*) *striatula* Da Costa, 1778 (Chioninae) and *Venerupis pullastra* (= *senegalensis*, Tapetinae), the latter included in this analysis. A comparison was made with both adults and, more importantly, the 'spat' of these two venerids, in the size range of adult *Turtonia* (1–2 mm length); this is well below the typical size of specimens generally available to an analysis such as this, based on field collections and museum material. In this analysis, two sets of characters are evident that assist in interpreting the four small-bodied species (*Neolepton*, *Turtonia*, *Parastarte*, *Gemma*). All four species share four characters that can be associated with small body size in general: lunule absent, aortic bulb absent, intestinal loops lacking extensive coiling, and outer demibranch reduced. Another set of characters distinguish *Neolepton* and *Turtonia* from the gemmines. *Neolepton* and *Turtonia* share an incompletely developed incurrent siphon (thus no siphonal retractor muscles or pallial sinuses), posterior lateral teeth present, and smooth interior shell margins. All of these characters are typical of the juvenile stage ('spat') of, for example *Mercenaria mercenaria* (see Carriker, 2001), and thus can be interpreted as neotenous. In contrast, *Parastarte* and *Gemma* have well-developed incurrent siphons, siphonal retractor muscles and sinuses, posterior lateral teeth absent, and denticulate interior shell margins. These are characters more associated with adult *Mercenaria* than its juvenile form, suggesting that the gemmines are consequences of a miniaturization process from a large-bodied ancestor. The same process has been postulated for members of *Nutricola* (Lindberg, 1990), which were once allocated to Gemminae on the basis of such 'juvenile' characters (Bernard, 1982). Beyond this comparison, additional characters in *Turtonia minuta*, adult *Venerupis senegalensis*, and *Venerupis senegalensis* spat (from Ockelmann, 1964; as *V. pullastra*) further emphasize the ontogenetic changes that occur in Veneroidea: (1) radial sculpture, present in adult *Venerupis senegalensis*, absent in *Turtonia minuta* and in *Venerupis senegalensis* spat (developing at a length of 0.9–1.4 mm); (2) anterior and middle cardinals of LV, dorsally united in *Turtonia minuta* and in *Venerupis senegalensis* spat, separate in mature *Venerupis senegalensis* [Ockelmann (1964: 124) noted 'As growth proceeds, the teeth "radiate" away from their original sites, so that the initial conditions become more or less obscured in the adult']; (3) incurrent siphon, present in mature *Venerupis senegalensis*, absent in *Turtonia minuta* and in *Venerupis senegalensis* spat (the incurrent siphon forms by fusion of the marginal tentacles in *Venerupis senegalensis* after *c.* 1 mm shell length). Stomach structure, which has been the single most contentious feature in the debate over uniting Turtoniidae with Veneroidea, is type IV in *Turtonia* and type V in other veneroids. This argument could collapse in view of Purchon's (1985) suggestion that the type IV stomach is ancestral to those of type V (citing the parallel example of type IV *Donax* as neotenous within typically type V Tellinoidea). Further studies of the early postlarval stages of veneroids are needed to morphologically confirm the placement of Turtoniidae within Veneroidea/Veneridae as these molecular results suggest. Neoleptonidae have been rather consistently placed in Cymioidea since the family's introduction by Thiele; they have only recently and tentatively been moved (e.g. by Coan *et al.*, 2000) to Veneroidea following Salas & Gofas' (1998) rather compelling hinge ontogenetic data for *Neolepton* com-

pared with early stages of *Chamelea*, *Clausinella* (both Chioninae), *Gouldia* (Gouldiinae), and *Pitar* (Pitarinae) spp. Molecular data are especially needed for *Neolepton*, whose phylogenetic position must remain uncertain at this point because of this neotenous morphology. The retention (reversion?) of juvenile character states in *Parastarte* and *Gemma* is similarly problematic from a phylogenetic coding viewpoint; however, the secondary nature of these character states is apparent from the consistent position of Gemminae well within the Veneridae in the molecular analyses.

Much of the problem with this morphological data set thus lies in a suite of problematic characters. Of the 34 morphological characters, four (anterior lateral tooth, periostracum, siphonal fusion, byssus) were either revised for the all-morphology data set or were eliminated pending substantial revision. Two of these characters (anterior lateral tooth, byssus) played key roles in the structure of the (all- and restricted-taxa) traditional character trees, causing substantial topological changes with their revision. An additional five (lunule, pallial sinus, marginal denticles, posterior lateral teeth, aortic bulb) were retained in the all-morphology data set, but are implicated in questions related to neoteny and miniaturization, thus producing a mixture of juvenile and adult character states in the data set. Two of this last list, the lunule and aortic bulb, support Veneroidea in this analysis or traditionally, respectively, yet both are homoplastic and not unique to these taxa among Bivalvia. Strong morphological synapomorphies for most of the higher-level taxa in this analysis thus remain elusive.

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APPENDIX 1

FAMILY-LEVEL TAXA IN VENEROIDEA

Available nominal family-level taxa in Veneroidea, with their traditional defining characters and comments pertinent to these results.

Veneroidea Rafinesque, 1815

According to current descriptions (Keen, 1969; Harte, 1998b; Coan *et al*., 2000), members of this superfamily share shells that are generally ovate, equivalve, inequilateral, and aragonitic in composition, with predominantly commarginal sculpture (also radial in some, and some with spines or erect lamellae, especially near the posterior slope). Umbones are anterior and prosogyrate, and the ligament is external, opisthodetic, and supported by a nymph. A pallial sinus is usually prominent, and the hinge plate is broad, usually with three cardinal hinge teeth in each valve; lateral teeth are present or absent. The animal is dimyarian with subequal adductor muscles, is usually nonbyssate as an adult, has four mantle folds, and usually possesses a type V stomach, with a united midgut and style sac (Purchon, 1985), and an aortic bulb on the posterior aorta (Harte, 1998b). Owen (1959) united Veneridae, Petricolidae, Glauconomidae in Veneroidea on the basis of three cardinal teeth in each valve, a posterior-only fusion layer in the primary ligament, type B mantle fusion and siphons, a pedal protractor muscle lacking, a ctenidial supra-axial extension well developed, a joined style sack and midgut, and the ability to introvert the base of the siphonal process. Ockelmann (1964) and Salas & Gofas (1998) added Turtoniidae and Neoleptonidae, respectively, based on features compared with venerids that suggested neoteny. These analyses suggested the monophyly of Veneroidea, although Glauconomidae and Neoleptonidae remain provisional pending further investigation.

Veneridae Rafinesque, 1815 (Fig. 2A)

Venerids are characterized by thick-walled shells, usually with a well-developed lunule and escutcheon, usually an inconspicuous periostracum (sometimes varnish-like or impregnated with sand), and a pallial sinus that is variable in shape and size. The cardinal teeth are simple or bifid, with middle cardinals commonly more robust than the anterior cardinals. Posterior lateral teeth are almost always absent, but anterior lateral teeth are variably developed or absent (Keen, 1969; Harte, 1998b). The animal is generally equipped with four mantle folds, a wide pedal gape, synaptorhabdic, plicate, heterorhabdic ctenidia, small labial palps, siphons of varying length and degree of fusion, a muscular wedge-shaped foot, and a hindgut passing through the ventricle of the heart (Harte, 1998b; Coan *et al*., 2000). These analyses suggested the monophyly of Veneridae, but only when Turtoniidae and Petricolidae were included.

Various subfamilial classifications have been used within Veneridae. Most commonly recognized are the following 12 subfamilies (in alphabetical order; listed genera not inclusive unless otherwise noted):

Chioninae Frizzell, 1936 (Fig. 13C). Shell ovate–trigonal and inequilateral, sculpture cancellate, lunule usually present, escutcheon bevelled or absent, pallial sinus usually short, triangular and ascending, left anterior and right middle cardinal teeth large, anterior lateral teeth absent, inner margin usually crenulate (Keen, 1969; Harte, 1998b). Includes *Chione*, *Anomalocardia*, *Anomalodiscus*, *Austrovenus*, *Bassina*, *Chamelea*, *Clausinella*, *Eurhomalea*, *Humilaria*, *Irusella*, *Lirophora*, *Mercenaria*, *Placamen*, *Protothaca*, *Tawera*, *Timoclea*. This analysis suggested the monophyly of the combined group Chioninae + Venerinae.

Clementiinae Frizzell, 1936 (Fig. 13D). Shell thin, inflated, and equilateral, oval to subtrigonal, sculpture smooth or weakly commarginal, sometimes overlain with undulating commarginal waves, lunule and escutcheon poorly defined, cardinal teeth thin, fragile, and parallel (not radiating) in right valve, anterior lateral teeth absent, inner margin smooth (Keen, 1969; Harte, 1998b; Coan *et al*., 2000). Includes *Clementia* and *Compsomyax*.

Cyclininae Frizzell, 1936 (Fig. 13E). Shell equivalve, sculpture smooth or commarginal and faintly radial, lunule absent, anterior lateral teeth absent, inner margin smooth or crenulate (Keen, 1969; Harte, 1998b). Includes *Cyclina* and *Cyclinella*. This study showed the presence of a lunule (flush, bounded by a groove) in *Cyclinella tenuis*, although such was absent in *Cyclina sinensis*.

Dosiniinae J. E. Gray, 1853 (Fig. 13F). Shell equivalve, sculpture commarginal, escutcheon present or absent, pallial sinus large, acutely angular and often directed dorsally, cardinal teeth parallel (not radiating) in right valve, anterior lateral tooth present or absent, inner margin smooth (Keen, 1969; Harte, 1998b). Includes *Dosinia*, *Asa*, *Austrodosinia*, *Dosinella*, *Dosinisca*, *Dosinorbis*, *Kereia*, *Pectunculus*, *Phacosoma*. Monophyly was supported by the morphological analyses herein, with the nonhomoplastic synapomorphy of the lunate-shaped foot.

Gemminae Dall, 1895 (Fig. 13H). Shell small and trigonal, sculpture smooth or commarginal, periostracum thin and polished, hinge plate with marginal grooves

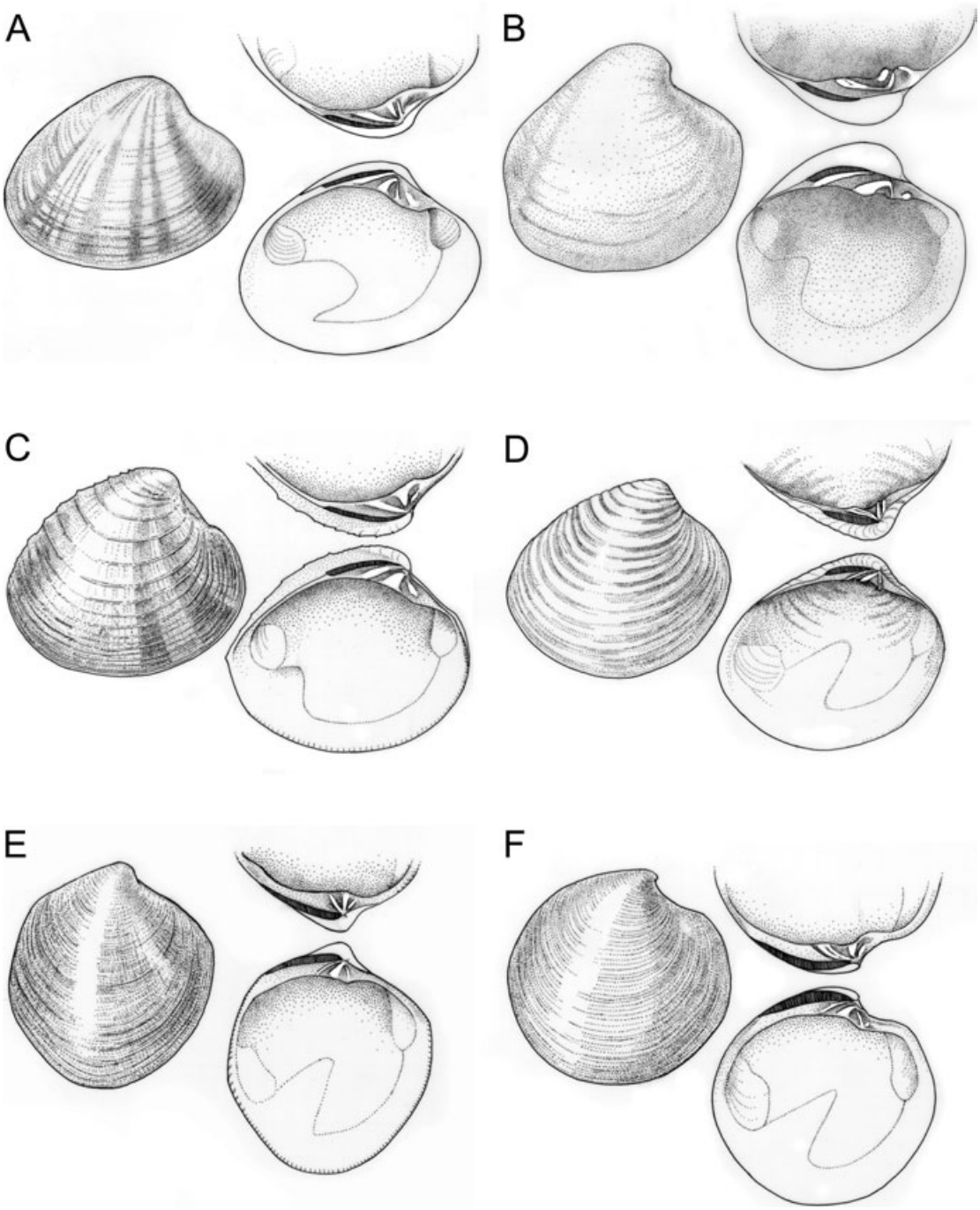

Figure 13. Representatives of the available family-level ingroup taxa investigated by this study, showing external shell, internal shell, and hinge features. In Veneridae: A, Callistinae, *Callista chione* (AMNH 302968); B, Callocardiinae, *Callocardia thorae* (AMNH 302989); C, Chioninae, *Chione cancellata* (AMNH 248270); D, Clementiinae, *Clementia papyracea* (AMNH 51293, 302905); E, Cyclininae, *Cyclina sinensis* (AMNH 32487); F, Dosiniinae, *Dosinia concentrica* (AMNH 190551); G, Gafrariinae, *Gafrarium dispar* (AMNH 303604); H, Gemminae, *Gemma gemma* (AMNH 155236); I, Gouldiinae, *Gouldia cerina* (AMNH 32949); J, Lioconchinae, *Lioconcha castrensis* (AMNH 303127); K, Meretricinae, *Meretrix meretrix* (AMNH 31674); L, Meroinae, *Sunetta* (= *Meroe*) *meroe* (AMNH 32476); M, Pitarinae, *Pitar tumens* (AMNH 303152); N, Samarangiinae, *Samarangia quadrangularis* (AMNH 303507); O, Sunettinae, *Sunetta scripta* (AMNH 303612); P, Tapetinae, *Tapes literatus* (AMNH 303510); Q, Venerinae, *Venus verrucosa* (AMNH 304017). In Veneroidea: R, Petricolidae, *Petricola lapicida* (AMNH 33527, 294770); S, Glauconomidae, *Glauconome rugosa* (NCSM 28970); T, Turtoniidae, *Turtonia minuta* (AMNH 177261); U, Neoleptonidae, *Neolepton sulcatulum* (AMNH 35004).

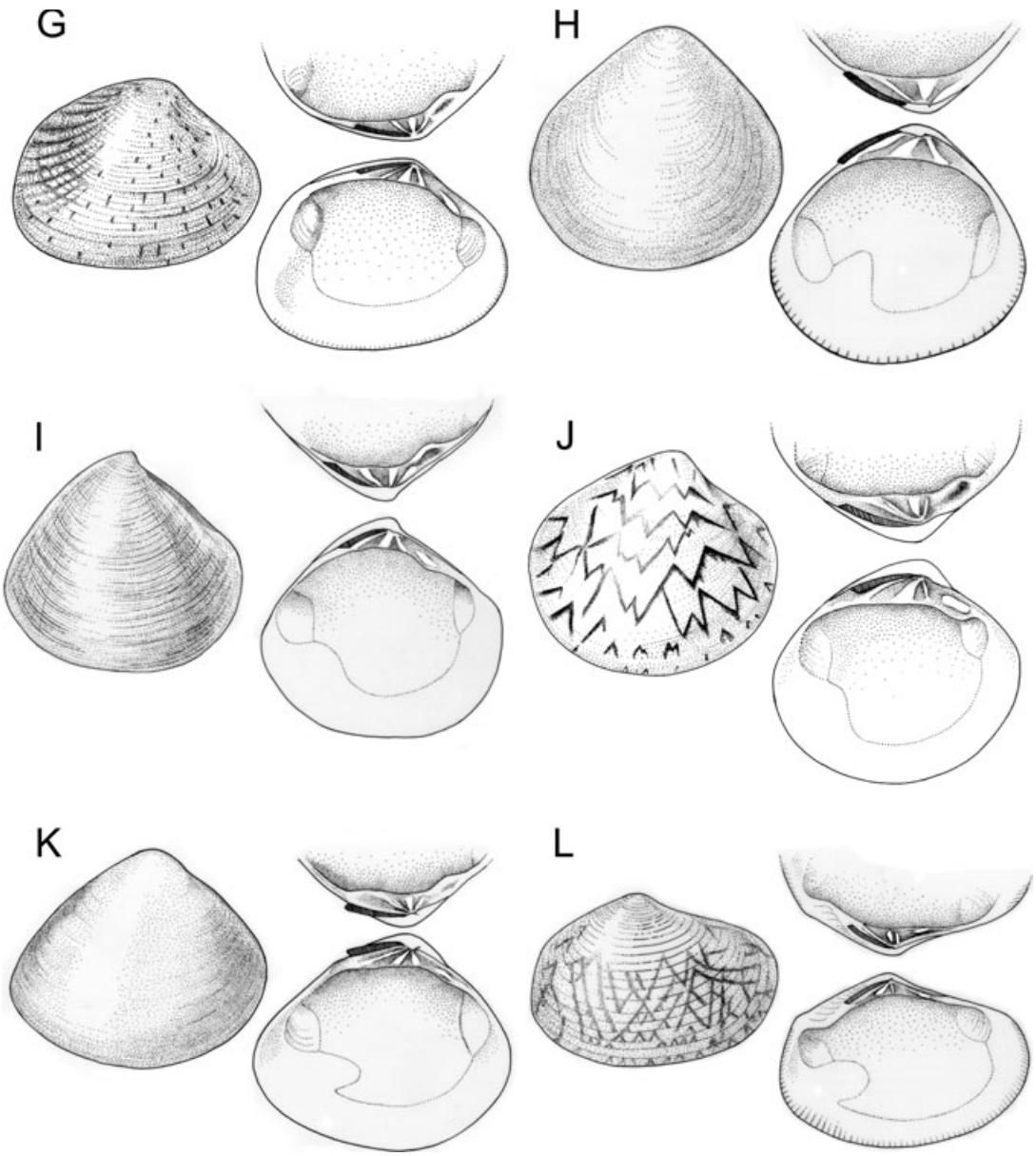

Figure 13. *Continued*

and denticles simulating anterior/posterior lateral teeth (true anterior lateral teeth absent), inner margin crenulate (Keen, 1969; Harte, 1998b; Coan *et al*., 2000). Includes *Gemma* and *Parastarte*. These analyses suggested that these taxa are secondarily small-bodied, derived from a large-bodied ancestor by a process of morphological miniaturization.

Gouldiinae Stewart, 1930 (Fig. 13I). Shell equivalve and subequilateral, sculpture with dichotomous radial ribbing, pallial sinus small or absent, cardinal teeth smooth or faintly grooved, anterior lateral tooth present, inner margin smooth or crenulate (Keen, 1969; Harte, 1998b). Includes *Gouldia*, *Circe*, *Comus*, *Fluctiger*, *Gafrarium*, *Laevicirce*, *Microcirce*, *Privigna*, *Redicirce*. Gafrariinae Korobkov, 1954 (Fig. 13G) is a division or synonym of Gouldiinae, but was not supported by these analyses.

Meretricinae J. E. Gray, 1847 (Fig. 13K). Shell ovate to trigonal, subequilateral, sculpture smooth or weak, 'cardinal teeth tending to radiate' (see below), anterior lateral tooth present, nymphs well developed and sculptured (some into 'pseudocardinal' teeth), inner

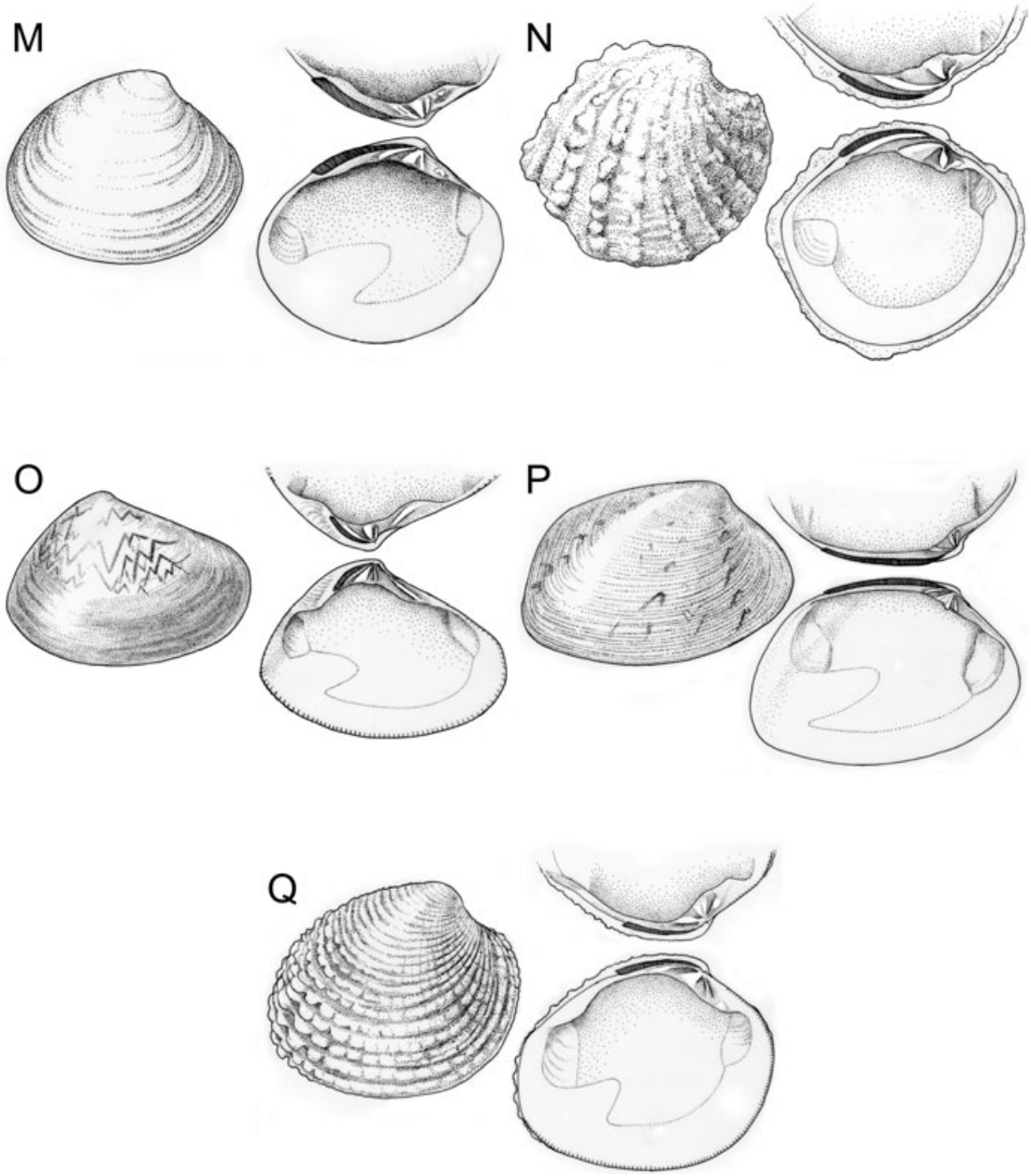

Figure 13. *Continued*

margin smooth (Keen, 1969; Harte, 1998b; Coan *et al*., 2000). Includes *Meretrix* and *Tivela*. Earlier investigations have suggested a close relationship between Meretricinae and Pitarinae, but this was not supported by these analyses, in which Meretricinae was generally paraphyletic.

Pitarinae Stewart, 1930 (Fig. 13M). Shell with smooth or commarginal sculpture, periostracum often smooth and glossy, cardinal teeth parallel (not radiating) in right valve, anterior lateral tooth present, inner margin usually smooth (Keen, 1969; Harte, 1998b; Coan *et al*., 2000). Includes *Pitar*, *Agriopoma*, *Amiantis*, *Callista*, *Callocardia*, *Lepidocardia*, *Lioconcha*, *Macrocallista*, *Megapitaria*, *Notocallista*, *Saxidomus*, *Transennella*, *Transenpitar*. This is the largest venerid subfamily, with approximately 70 valid genera. Callistinae Habe & Kosuge, 1967 (Fig. 13A), Callocardiinae Dall, 1895 (Fig. 13B), and Lioconchinae Habe, 1977 (Fig. 13J) are proposed divisions of Pitarinae *s.l.*; Callistinae and Lioconchinae each received some support in these analyses, as separate from Pitarinae *s.s.*

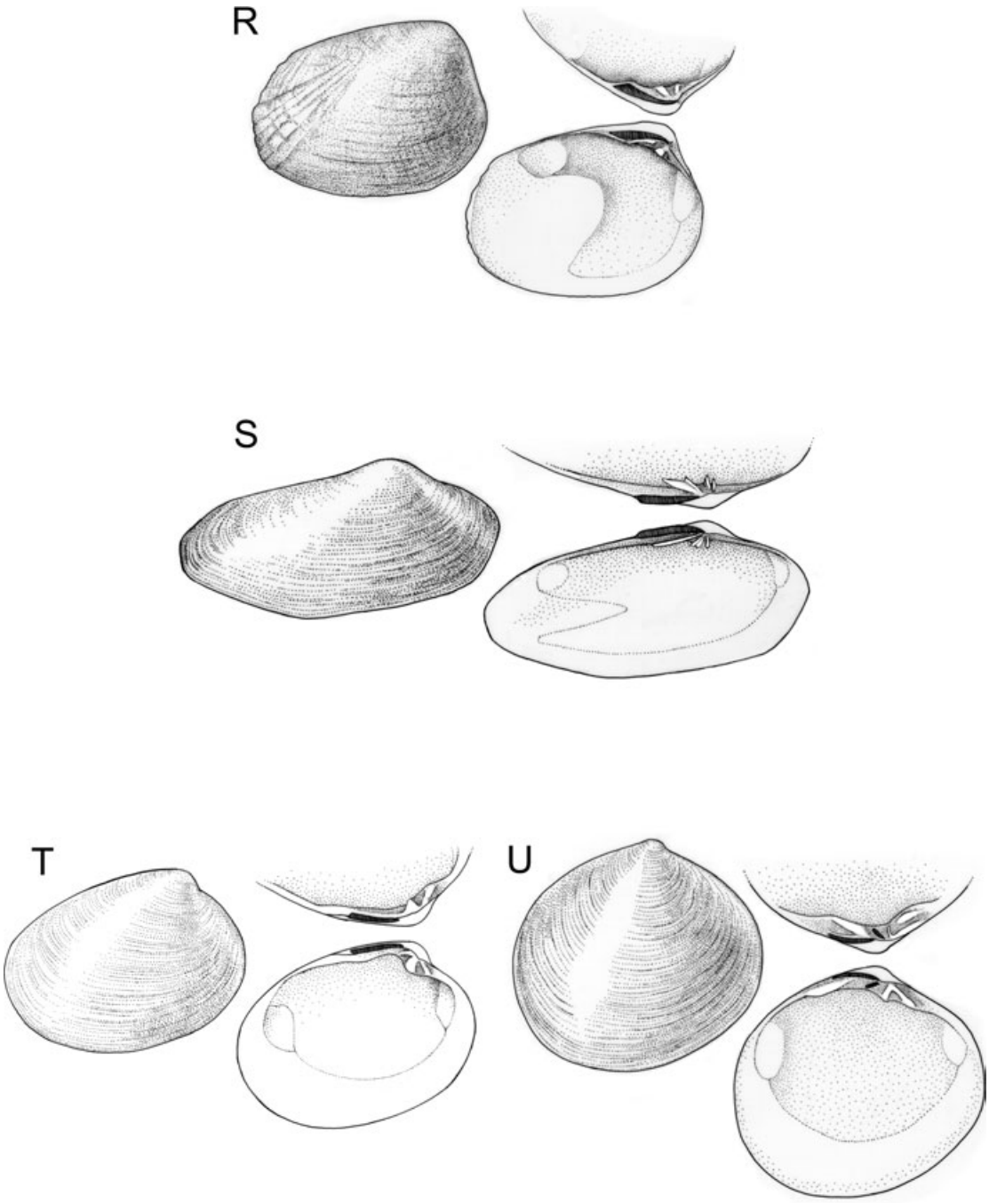

Figure 13. *Continued*

Earlier investigations have suggested a close relationship between Meretricinae and Pitarinae, but this was not supported by these analyses.

Samarangiinae Keen, 1969 (Fig. 13N). Shell inequilateral and quadrate, sculpture smooth, periostracum heavily impregnated with sand, pallial sinus greatly reduced (often called 'absent'), left middle cardinal tooth deeply bifid, anterior lateral tooth pustular (Keen, 1969; Harte, 1998b). Includes *Samarangia* and *Granicorium*. The monophyly of Samarangiinae was supported in the morphological analyses; sand-impregnated periostracum is a synapomorphy.

Sunettinae Stoliczka, 1870 (Fig. 13O). Shell oval to elongate, sculpture smooth or commarginal only, pal-

lial sinus small to medium, ligament sunken into sharply defined escutcheon, anterior lateral tooth elongated, inner margin crenulate (Keen, 1969; Harte, 1998b). Includes *Sunetta*, *Cyclosunetta*, *Sunettina*, *Meroena*. Meroinae Tryon, 1884 (Fig. 13L), based on *Meroe* Schumacher, 1817 (now a recognized synonym of *Sunetta*; Keen, 1969), is a synonym, although still nomenclaturally available. The monophyly of a combined Sunettinae/Meroinae was supported by the morphological analyses herein, with the excavated escutcheon as a nonhomoplastic synapomorphy.

Tapetinae J. E. Gray, 1851 (Fig. 13P). Shell ovate to ellipsoidal, sculpture smooth or commarginal (sometimes radial), hinge plate narrow, often excavated (cardinal teeth overhanging edge), right anterior and posterior cardinal teeth smooth, remaining cardinals usually bifid, anterior lateral teeth absent, inner margin smooth on at least posterior third (Keen, 1969; Harte, 1998b; Coan *et al*., 2000). Includes *Tapes*, *Eumarcia*, *Irus*, *Katelysia*, *Liocyma*, *Marcia*, *Paphia*, *Psephidia*, *Ruditapes*, *Venerupis*. Monophyly (minus a few problematic species) was strongly supported by all analyses herein, although not by nonhomoplastic synapomorphies.

Venerinae Rafinesque, 1815 (Fig. 13Q). Sculpture commarginal or cancellate, pallial sinus short and triangular, anterior lateral tooth pustular, inner margin crenulate (Keen, 1969; Harte, 1998b; Coan *et al*., 2000). Includes *Venus*, *Antigona*, *Circomphalus*, *Globivenus*, *Periglypta*. Coan *et al*. (2000) considered Chioninae to be a synonym of Venerinae. This analysis suggested the monophyly of the combined group Chioninae + Venerinae.

Petricolidae d'Orbigny, 1840 (Figs 2B, 13R)

The petricolid shell is ovate to elongate, and often variable within a species, showing distortion associated with nestling or boring into rock or mud. The umbones are anterior and prosogyrate (subcentral in *Cooperella*), and both the lunule and the escutcheon are absent. The periostracum is thin and adherent, and external sculpture can be smooth or radial or cancellate. The pallial sinus is large. The hinge plate is narrow and excavated. The LV has three cardinal teeth, the middle of which is bifid and the anterior sometimes weak or absent. The RV has two cardinal teeth (the anterior cardinal is absent). Anterior lateral teeth are absent (Keen, 1969; Harte, 1998b; Coan *et al*., 2000). The animal has a small compressed foot with a byssal groove, but adults are nonbyssate; the groove is absent in *Cooperella*. There is a small to extensive pedal opening. The posterior adductor muscle is slightly larger than the anterior one. The siphons are elongated and mostly or completely separate. The ctenidia are synaptorhabdic and heterorhabdic, and the labial palps are small to large. The hindgut passes through the ventricle of the heart, and an aortic bulb is present on the posterior aorta (Purchon, 1955; Harte, 1998b; Coan *et al*., 2000). Includes *Petricola*, *Claudiconcha*, *Cooperella*, *Choristodon*, *Mysia*, *Petricolaria*, *Vellargilla*.

Petricolidae is one of the three original 'veneroid' groups and has been consistently recognized at the family level and closely related to Veneridae. Some authors (e.g. Reeve, 1874a, b) pointed to great similarities between *Petricola s.l.* and the venerid *Venerupis* (then including *Irus* and the petricolid *Rupellaria* = *Choristodon*). Coan (1996: 118) questioned the monophyly of this group: 'The basic family-level characters of the Petricolidae are three cardinal teeth in the LV and two in the RV, as opposed to the Veneridae, which has three teeth in each and sometimes laterals as well. However, it is possible that the loss of a cardinal tooth in the RV has occurred independently at least twice in taxa that have been allocated to the Petricolidae, making it an artificial group.' These analyses prompted the reallocation of Petricolidae as a subfamily within Veneridae. See Cooperellidae.

Cooperellidae Dall, 1900. This nominal family is based on the small genus *Cooperella* Carpenter, 1864, that was subsequently placed in various heterobranch families, including Semelidae, Scrobiculariidae, and Petricolidae. Compendia of the past decades [e.g. those of Scarlato & Starobogatov (1979) and Boss (1982)] recognized Petricolidae and Cooperellidae as distinct families. Morton (1995) discussed the anatomy of the eastern Pacific *Cooperella subdiaphana* and synonymized Cooperellidae with Petricolidae, an action followed by subsequent authors such as Coan (1996), Coan & Scott (1997), and Coan *et al*. (2000). Morphological analyses herein, however, failed to support the synonymy; molecular material for Cooperellidae was regrettably not available.

Glauconomidae J. E. Gray, 1853 (Figs 2C, 13S)

The glauconomid shell is elongate to elliptical, and thin walled, with smooth sculpture and a conspicuous periostracum. Both the lunule and escutcheon are absent. The pallial sinus is large and horizontal. The ligament has a posterior outer extension. There are three cardinal teeth in each valve, and both anterior and posterior lateral teeth are absent (Keen, 1969; Harte, 1998b). The animal has ventrally fused mantle margins, a small anterior pedal gape, a linguiform ungrooved and nonbyssate foot, elongated near-fused siphons that retract partly by introversion, large labial palps, plicate heterorhabdic ctenidia, an aortic bulb, and a united midgut

and style sac (Owen, 1959; Harte, 1998b). Includes *Glauconome* only, specialized for more-or-less permanent lodgement deeply embedded in mud (Owen, 1959).

Traditionally recognized as a family closed aligned with Veneridae and Petricolidae (e.g. Adams & Adams, 1857; Chenu, 1862; Gill, 1871; Tryon, 1884; Fischer, 1887), authors in the early 20th century (e.g. Thiele, 1934) moved the group to Solenoidea. The family was restricted to *Glauconome* and returned to the Veneroidea by Owen (1959; but in agreement with some earlier authors) on the basis of comparative morphology. Molecular analyses herein consistently grouped Glauconomidae with the outgroup *Corbicula fluminea.* However, the validity of that relationship must be tested by an analysis of larger scope; Glauconomidae is here provisionally retained as a member of Veneroidea, outside of Veneridae.

Glauconomyidae and Glaucomyidae Carpenter, 1861 are synonyms. Glauconomeidae is an apparent misspelling.

Turtoniidae W. Clark, 1855 (Figs 2D, 13T)

The turtoniid shell is minute, rounded to subquadrate, with smooth or commarginal sculpture and a thin, polished periostracum. A pallial sinus is absent. The hinge plate is narrow with tubercular cardinal teeth, three in the LV (with the two anterior fused dorsally) and two in the RV (the anterior cardinal is much reduced, essentially absent), and weak posterior lateral teeth (anterior laterals are absent) (Chavan, 1969; Coan *et al*., 2000). The animal has a keeled foot with a byssal groove and adult byssus, a larger posterior adductor muscle, a wide pedal gape, and short excurrent siphon (the incurrent aperture has no siphon). Only the inner demibranchs are present. Labial palps are short, and the stomach is of type IV with a united midgut and style sack, and digestive gland ducts originating on the stomach wall (i.e. lacking right and left caeca typical of type V). The hindgut passes through the ventricle of the heart. An aortic bulb is not present. Adults are dioecious; females produce egg capsules that are attached to byssal threads and hatch nonswimming juveniles (Ockelmann, 1964; Coan *et al*., 2000). Includes *Turtonia* Alder, 1848 only.

The nominal family Turtoniidae Clark, 1855 (introduced as Turtoniadae for *Turtonia* Alder, 1848) was based on the single extant taxon, *T. minuta*. It is a small-shelled (to 3 mm) marine species of circumboreal distribution that lives as a byssally attached suspension feeder among epibiota of rocky shores and tide pools. Originally described in the then-widely defined genus *Venus*, subsequent authors placed it – often with considerable doubt – in various groups within the superfamilies Galeommatoidea or Cyamioidea. Morphological comparisons with the juveniles of several species in Veneridae led Ockelmann (1964: 121) to conclude that this species 'has evolved from a *Venerupis*-like ancestor by a process of neoteny', having 'become sexually mature just before formation of the inhalent siphon and outer demibranchs'. Some subsequent workers thus placed *Turtonia* in Tapetinae (Bowden & Heppell, 1968). Pointing to differences in stomach morphology, Scarlato & Starobogatov (1979) rejected Ockelmann's hypothesis and returned Turtoniidae to the Cyamoidea. Subsequent publications (e.g. Boss, 1982; S. M. Smith & Heppell, 1991; Harte, 1998b; Coan *et al*., 2000) treated *Turtonia* as the representative of a monotypic family Turtoniidae in the Veneroidea, at times hinting at its possible neotenous origin within the Veneridae. Molecular analyses herein prompted the inclusion of Turtoniidae as a subfamily within Veneridae.

Neoleptonidae Thiele, 1934 (Figs 2E, 13U)

The neoleptonid shell is ovate, minute, thin walled, with commarginal sculpture and an inconspicuous periostracum. Both the lunule and the escutcheon are absent. The pallial sinus is absent or very weak. The external ligament is small and an internal ligament is well developed below the umbones, directed obliquely posteriorly. The LV has two cardinal teeth, joined dorsally; the RV has three cardinal teeth (with 3a/3b joined dorsally). Anterior lateral teeth are absent, whereas posterior laterals are present, and the inner shell margin is smooth. The animal has a long finger-like foot without a byssal gland, an incurrent aperture without a siphon, and an excurrent aperture with a short siphonal membrane (Chavan, 1969; Salas & Gofas, 1998; Coan *et al*., 2000). Includes *Neolepton*, *Epilepton*, *Jousseaumiella*, *Pachykellya*, *Puyseguria*, and others.

Neolepton Monterosato, 1875 [type species *Lepton sulcatulum* Jeffreys, 1859 by subsequent designation (Crosse, 1885); originally in Kelliidae (now a family in Galeommatoidea)] has been variously classified throughout its taxonomic history. Thiele (1934) introduced Neoleptonidae for *Neolepton*, *Pachykellya*, and *Puyseguria*, in Cyamioidea, and was followed by Chavan (1969) and a number of subsequent authors [see Salas & Gofas (1998) for details]. Despite the fact that some other authors have 'returned' Neoleptonidae to its original Galeommatoidea [e.g. Tebble (1966) in Leptonidae; Nordsieck (1969) in Leptonidae: Neoleptoninae, introduced as new without recognition of Thiele's (1934) family], its placement in Cymioidea has gained general acceptance. Affinities of Neoleptonidae to Veneroidea were first proposed by Ockelmann (in Bowden & Heppell, 1968),

and recently reinvestigated by Salas & Gofas (1998) who concluded that neoleptonids are neotenous or paedomorphic veneroids, but maintained them separate from Veneridae by the presence of the posterior lateral teeth and an additional internal ligament. These analyses were inconclusive for Neoleptonidae; morphological analyses merely acknowledged its neotenic characteristics, and tissue was unavailable for molecular analyses. It is retained provisionally as a member of Veneroidea, outside of Veneridae.

A synonym of the family name is Bernadinidae Keen, 1969 (Keen's earlier use of this name was nude; Keen, 1963).

APPENDIX 2

DATA SOURCES

Sources for shell, anatomical, and molecular data (synonyms restricted to those pertinent to included source material) [Arc, Arcticidae (outgroup); Cal, Veneridae: Callistinae; Cao, Veneridae: Callocardiinae; Chi, Veneridae: Chioninae; Cle, Veneridae: Clementiinae; Cor, Corbiculidae (outgroup); Cyc, Veneridae: Cyclininae; Dos, Veneridae: Dosiniinae; Gaf, Veneridae: Gafrariinae; Gem, Veneridae: Gemminae; Gla, Glauconomidae; Gou, Veneridae: Gouldiinae; Lio, Veneridae: Lioconchinae; Mer, Veneridae: Meretricinae; Neo, Neoleptonidae; Pet, Petricolidae; Pit, Veneridae: Pitarinae *s.s.*; Sam, Veneridae: Samarangiinae; Sun, Veneridae: Sunettinae; Tap, Veneridae: Tapetinae; Tur, Turtoniidae; Ven, Veneridae: Venerinae; Ves, Vesicomyidae (outgroup)]. Molecular sequences (followed by GenBank registration numbers and tissue extracted, if known) are original data unless otherwise noted.

Anomalocardia auberiana (d'Orbigny, 1842) (Chi)
AMNH 80301, Boca Chica (Monroe County), Florida Keys, B. R. Bales! 1940 (shell); AMNH 312706, FK-279, Key West Salt Ponds, off Bertha Street, Monroe County, Florida Keys, 24°33.16′N, 81°46.64′W, soft mud with sparse *Halodule*, hand dredge, P. M. Mikkelsen & R. Bieler! 7 April 2000 (anatomical); FMNH 305976, Banana River, Brevard County, Florida, northern side of SR 520 along shoreline, clear sand, 0.3 m, M. Krisberg! 13 April 1982, 70% ethanol [sequences 16S DQ184733, COI DQ184834, 28S DQ184785, H3 DQ184885 (mantle)].

Antigona lamellaris Schumacher, 1817 (Ven, type species of *Antigona* Schumacher, 1817)
AMNH 303422, Exmouth Gulf, northern Western Australia, Australia, 1987, Lamprell Collection (shell); FLMNH 281662, near Kata Beach, Phuket, Phuket Province, Thailand, 15–18 m, H. T. Conley! 18 November 1998, 95% ethanol [anatomy; sequences 16S DQ184730, COI DQ184832, 28S DQ184783, H3 DQ184882 (mantle)]; Thorsson, 2002 (anatomy).

Arctica islandica (Linnaeus, 1767) (outgroup, Arc, type species of *Arctica* Schumacher, 1817)
AMNH 31506, Maine, Haines Collection (shell); AMNH 244019, 15 miles east of Asbury Park (Monmouth County), New Jersey, trawled by commercial fishermen, sandy mud, 25.9 m, 1968, Barlow Collection (shell); AMNH 270102, 3 miles off Rockaway Beach, Queens County, New York, 16 June 1982, R/V *Atlantic Twin* (anatomical); AMNH 312707, fish market purchase, Chicago, Illinois (commercially fished, Atlantic Ocean), 9 December 2004 (anatomical); Carrière, 1879 (anatomical); M. E. S. Gray, 1857 (anatomical); Jeffreys, 1863 (anatomical); Morse, 1919 (anatomical); Saleuddin, 1964 (anatomical); Sowerby, 1854 (anatomical); Thiele, 1886 (anatomical); FMNH 305980, fish market purchase, Chicago, Illinois (commercially fished, Atlantic Ocean), May 2003, 100% ethanol [sequences 16S DQ184755, COI DQ184853, H3 DQ184901 (mantle)]; Passamaneck *et al.*, 2004 (sequence 28S AY145390).

Asa lupina (Linnaeus, 1758) (syn. *lincta* Pulteney, 1799) (Dos, type species of *Asa* Basterot, 1825)
AMNH 303190, on beach after storm, near Rome, Italy, Lamprell Collection (shell); Ansell, 1961 (anatomical); M. E. S. Gray, 1857 (anatomical); Jeffreys, 1863 (anatomical); Canapa *et al*., 2003 (sequence 16S AJ548771).

Callista chione (Linnaeus, 1758) (Cal, type species of *Callista* Poli, 1791, name-bearing genus of Callistinae)
AMNH 302968, Vigo Sound, Spain, sand, 0.5 m, Lamprell Collection (shell); MHNG 1/76, Naples, Italy (anatomical); M. E. S. Gray, 1857 (anatomical); Jeffreys, 1863 (anatomical); Sowerby, 1854 (anatomy); Thiele, 1886 (anatomical); Canapa *et al*., 2003 (sequence 16S AJ548772).

Callista florida (Lamarck, 1818) (Cal)
AMNH 303780, Al-Khiran, Kuwait, outermost sand bars at minus tide, Lamprell Collection (shell); M. E. S. Gray, 1857 (anatomical); Fishelson, 2000 (anatomical).

Callocardia hungerfordi (G. B. Sowerby II, 1888) (Cao)
No specimens available; shell characters from Scott (1994) and from the original descriptions of *C. guttata* A. Adams, 1864 (type species of *Callocardia* A. Adams, 1864; name-bearing genus of Callocardiinae) and *C. thorae* Vokes, 1985 and shells of *C. thorae*, AMNH 302989, Cape Moreton, south-eastern Queensland, Australia, 128 m, Lamprell Collection; Morton, 2000 (anatomical).

Calyptogena magnifica Boss & Turner, 1980 (outgroup, Ves)
AMNH 295511, North-east Pacific Rise, 09°50.3′N, 104°17.4′W, 2504 m, R. Lutz! 15–30 May 1999, ALVIN (shell; anatomical); Boss & Turner, 1980 (shell; anatomical); FMNH 307125, North Pacific Ocean, East Pacific Rise, 11°24.91′N, 103°47.20′W, 2492 m, J. Voight! 15 November 2003, ALVIN dive 3934, 95% ethanol [sequences 28S DQ184800, H3 DQ184902 (foot)]; Giribet & Wheeler, 2002 (sequence COI AF120665); Peek *et al.*, 2000 (sequence 16S AF115082).

Chamelea gallina (Linnaeus, 1758) (Chi, type species of *Chamelea* Mörch, 1853)
AMNH 238906, Aegean Sea, Bodrom, Turkey, sand, 3 m (shell); M. E. S. Gray, 1857 (anatomical); Jeffreys, 1863 (anatomical); FMNH 306542, fish market purchase, Las Palmas, Gran Canaria, Canary Islands (commercially fished), 20 February 2004, RNAlater [sequences 16S DQ184735, COI DQ184835, 28S DQ184786, H3 DQ184886 (mantle)]; Canapa *et al.*, 2003 (sequence 16S AJ548762).

Chione cancellata (Linnaeus, 1767) (Chi, type species of *Chione* Megerle von Mühlfeld, 1811, name-bearing genus of Chioninae)
AMNH 248270, Baby Beach, Aruba, Netherlands Antilles, in sand at low tide, J. M. Bijur! May 1970 (shell); FMNH 309250, Bocas del Toro, Atlantic Panama, 09°09.501′N, 81°46.945′W to 09°09.521′N, 81°47.140′W, 50 m, dredge, 1 September 2004, R. Collin! (anatomical); DMNH 229700, sta. KJR04-05, Puerto Rico, west of Parguera, mangrove channels, 30 April 2004, K. Roe! (anatomical); MZSP 32367, Proc. Parcel de Itacolumis, Corumbau, Bahia, Brazil, intertidal, 9 January 2000, Col. P. J. Souza & E. P. Goncalves! (anatomical); Jones, 1979 (anatomical).

Chione elevata (Say, 1822) (Chi)
AMNH 248267, White Marlin Beach, Lower Matecumbe Key (Monroe County), Florida Keys, J. M. Bijur! April 1970 (shell); AMNH 298141, FK-140, West Sister Rock, south of Boot Key, Monroe County, Florida Keys, 24°41.14′N, 81°05.56′W, sand patches between seagrass, 0.3–0.9 m, snorkelling/by hand, R. Bieler and R. Cipriani! R/V *Floridays*, 12 August 1997 (anatomical); Jones, 1979 (as *cancellata*, in part) (anatomical); AMNH 305130, IMBW-FK-629, 'Horseshoe' site, bayside of West Summerland Key (Spanish Harbor Keys), Monroe County, Florida Keys, 24°39.3′N, 81°18.2′W, among rocks along arms of quarry, by hand and snorkelling, to *c*. 1 m, International Marine Bivalve Workshop, P. M. Mikkelsen & R. Bieler *et al*.! 21 and 26 July 2002, RNAlater [sequence 16S DQ184736 (foot)].

Circe nummulina (Lamarck, 1818) (Gou)
AMNH 311610, PMM-1120/RB-1893, Shark Bay Marine Park, Monkey Mia, east coast of Peron Peninsula, Western Australia, Australia, 25°47.025′S, 113°43.293′W, sand, shovel and sieve, 1–1.5 m, P. M. Mikkelsen, R. Bieler *et al*.! 19 July 2004, 100% ethanol (shell); AMNH 311617, PMM-1118/RB-1891, Shark Bay Marine Park, 'big lagoon', north of Denham, west coast of Peron Peninsula, Western Australia, Australia, 25°54.296′W, 113°31.405′W, sand, shovel and sieve, 1–1.5 m, P. M. Mikkelsen, R. Bieler *et al*.! 18 July 2004, 100% ethanol [anatomical; sequences 16S DQ184739, COI DQ184837, 28S DQ184787, H3 DQ184888 (adductor muscle)].

Circe plicatina (Lamarck, 1816) (Gou)
AMNH 311616, PMM-1118/RB-1891, Shark Bay Marine Park, 'big lagoon', north of Denham, west coast of Peron Peninsula, Western Australia, Australia, 25°54.296′W, 113°31.405′W, sand, shovel and sieve, 1–1.5 m, P. M. Mikkelsen, R. Bieler *et al*.! 18 July 2004, 100% ethanol [shell; anatomical; sequences 16S DQ184740, COI DQ184838, 28S DQ184788, H3 DQ184889 (adductor muscle)]; AMNH 312708, PMM-1124/RB-1897, Shark Bay Marine Park, Little Lagoon, north of Denham, west coast of Peron Peninsula, Western Australia, Australia, 25°53.988′S, 113°32.710′E, sand, 1–1.5 m, shovel and sieve, P. M. Mikkelsen, R. Bieler *et al*.! 21 July 2004 (shell).

Circe rivularis (von Born, 1778) (Gou)
FMNH 306198, RB-1850, Bandy Creek Harbour, Esperance, Western Australia, Australia, box dredge, 2–4 m, R. Bieler *et al*.! 17 February 2003, formalin to 70% ethanol (shell; anatomical); FMNH 306153, RB-1858, Esperance Bay, Western Australia, Australia, 34°01.2154′S, 121°59.302′E, box dredge, 34.5 m, R.

Bieler! 19 February 2003, 70% ethanol [sequences 16S DQ184741, COI DQ184839 (foot, Cirriv1)]; FMNH 306214, RB-1850, Bandy Creek Harbour, Esperance, Western Australia, Australia, box dredge, 2–4 m, R. Bieler *et al*.! 17 February 2003, 75% ethanol [sequences 16S DQ184742, COI DQ184840, 28S DQ184789, H3 DQ184890 (foot, Cirriv2)].

Circe cf. rivularis (von Born, 1778) (Gou)
FMNH 306196, RB-1843, Esperance, Western Australia, Australia, under tanker jetty, scuba, 6 m, R. Bieler! 14 February 2003, formalin to 70% ethanol (shell; anatomical); FMNH 306188, RB-1859, Esperance Bay, Western Australia, Australia, 33°56.933′S, 122°01.611′E, box dredge, 33.2 m, R. Bieler! 19 February 2003, 75% ethanol [sequences 16S DQ184743, COI DQ184841, 28S DQ184790, H3 DQ184891 (foot)].

Circe scripta (Linnaeus, 1758) (Gou, type species of *Circe* Schumacher, 1817)
AMNH 250922, Inskip Point, Queensland, Australia, in weeds, Vaught Collection (shell); FMNH 305971, Anse Vata, Noumea, New Caledonia, C. Berthoult! 27 January 2002, 70% ethanol [anatomical; sequences 16S DQ184744, COI DQ184842 (mantle)]; FMNH 306191, Anse Vata, Noumea, New Caledonia, 2–4 m, C. Berthault! 27 January 2002 (anatomical); Pelseneer, 1911 (anatomical).

Clementia papyracea (J. E. Gray, 1825) (Cle, type species of *Clementia* J. E. Gray, 1840, name-bearing genus of Clementiinae)
AMNH 51293, Australia, Constable Collection (shell); AMNH 302905, Broom, northern Western Australia, Australia, Lamprell Collection (shell); Deshayes, 1853 (anatomical).

Compsomyax subdiaphana (Carpenter, 1864) (Cle, type species of *Compsomyax* Stewart, 1930)
AMNH 95624, Satellite Channel, British Columbia, Canada, trawl, November 1958 (shell); LACM 87–124, RFF-87–57, Simoom Inlet, Inland Passage, British Columbia, Canada, 50°50.58′N, 126°28.86′W, 45–60 m, September 1987, R/V *Point Sur* (anatomical); FMNH 305966, San Juan Channel, north of Point Caution (San Juan County), Washington, *c*. 112 m, 23 Alan Kohn! June 2003, 95% ethanol, [sequences 16S DQ184747, COI DQ184845, 28S DQ184792, H3 DQ184893 (mantle)].

Cooperella subdiaphana (Carpenter, 1864) (Pet, type species of *Cooperella* Carpenter, 1864, name-bearing genus of Cooperellidae)
AMNH 257317, Anaheim Bay (Orange County), California, E. P. Chace! (shell); Morton, 1995 (anatomical).

Corbicula fluminea (Müller, 1774) (outgroup, Cor, type species of *Corbicula* Mergele von Muhlfeld, 1811)
AMNH 295779, Pueblo Reservoir, Lake Pueblo State Park, Pueblo County, Colorado, J. R. Cordeiro! November 1996 (shell); AMNH 266397, Lower Connecticut River (Middlesex/New London Counties), Connecticut, Peterson grab, Douglas E. Morgan! 17–18 August 1993 (anatomical); Britton & Morton, 1982 (anatomical); Dudgeon, 1980 (anatomical); Giribet & Distel, 2003 (sequence H3 AY070161); Giribet & Wheeler, 2002 (sequence COI AF120666); Park & Ó Foighil, 2000 (sequence 28S AF131009); Stepien, Hubers & Skidmore, 1999 (sequence 16S AF038999).

Costacallista impar (Lamarck, 1818) (Cal)
AMNH 311623, PMM-1120/RB-1893, Shark Bay Marine Park, Monkey Mia, east coast of Peron Peninsula, Western Australia, Australia, 25°47.025′S, 113°43.293′W, sand, shovel and sieve, 1–1.5 m, P. M. Mikkelsen, R. Bieler *et al*.! 19 July 2004, 100% ethanol [shell; anatomical; sequences 16S DQ184706, COI DQ184808, 28S DQ184762, H3 DQ184861 (adductor muscle)].

Costacallista lilacina (Lamarck, 1818) (Cal)
FMNH 306203, Anse Vata, Noumea, New Caledonia, 2–4 m, C. Berthault! 27 January 2002, 70% ethanol [shell; anatomical; sequences 16S DQ184705, COI DQ184807, 28S DQ184761, H3 DQ184860 (mantle)].

Cyclina sinensis (Gmelin, 1791) (Cyc, type species of *Cyclina* Deshayes, 1850, name-bearing genus of Cyclininae)
AMNH 32487, Fukura Awaji (Akita Prefecture, Honshu), Japan, Weeks Collection (shell); M. Okazaki, unpublished [sequence COI male AB040833 and AB040834, COI female AB040835 (gonadal tissue)].

Cyclinella tenuis (Récluz, 1852) (Cyc, type species of *Cyclinella* Dall, 1902)
AMNH 267023, Lighthouse Point, Sanibel Island, Lee County, Florida, on beach in sand/seaweed after hurricane, B. J. Piech! August 1971 (shell); UMML 30.11737, off Venezuela, 11°34′N, 69°12′W, 10 ft otter

trawl, 27 m, 27 July 1968, R/V *Pillsbury* sta. 756 (anatomical).

Dosinia concentrica (von Born, 1778) (Dos, type species of *Dosinia* Scopoli, 1777, name-bearing genus of Dosiniinae)
AMNH 190551, Niteroi, Rio de Janeiro State, Brazil, in sand, R. Pontes! March 1963, Nowell-Usticke Collection (shell); de Oliveira Castro Gueron & dos Santos Coelho, 1989 (anatomical).

Dosinia excisa (Schroeter, 1788) (Dos)
FMNH 306195 (ex BMNH), near Rottnest Island, Perth, Western Australia, Australia, dredge stations 18 and 31, J. Taylor & E. Glover! 1996, formalin? to 70% ethanol [shell; anatomical; sequence 16S DQ184698 (mantle)].

Dosinia victoriae Gatliff & Gabriel, 1914 (Dos)
AMNH 303552, Port Welshpool, Victoria, Australia, sand flat, J. Austin! 22 June 1995 (shell); LACM 88–62, southern side of Ajer (Gili Air) Islet, north-western side of Lombok, Indonesia, 08°22′S, 116°04′E, coral heads and seagrass, 0–3 m, J. H. McLean! (JHM 88–20), 14 April 1988, 70% ethanol [anatomical; sequences 16S DQ184699, COI DQ184801, 28S DQ184756, H3 DQ184854 (mantle)].

Dosinia sp. 1 (Dos)
FMNH 302202, RB-1849, inshore of Table Island, Duke of Orleans Bay, Western Australia, Australia, 4 m, A. Longbottom! 17 February 2003, 95% ethanol [shell; anatomical; sequences 16S DQ184700, COI DQ184802, 28S DQ184757, H3 DQ184855 (foot)].

Dosinia sp. 2 (Dos)
AMNH 311612, PMM-1120/RB-1893, Shark Bay Marine Park, Monkey Mia, east coast of Peron Peninsula, Western Australia, Australia, 25°47.025′S, 113°43.293′W, sand, shovel and sieve, 1–1.5 m, P. M. Mikkelsen, R. Bieler *et al*.! 19 July 2004, 100% ethanol [shell; anatomical; sequences 16S DQ184701, COI DQ184803, 28S DQ184758, H3 DQ184856 (adductor muscle)].

Eurhomalea lenticularis (G. B. Sowerby I, 1835) [Chi, formerly Tapetinae, moved to Chioninae by Fischer-Piette & Vukadinovic (1977)]
AMNH 31959, Chile, Jay Collection (shell); FMNH 301912, Dakan Island, Chile, Brian Dyer! December 2002, 70% ethanol (unrecorded preservation history) [anatomical; sequences 16S DQ184718, COI DQ184820, 28S DQ184771, H3 DQ184870 (mantle)].

Gafrarium dispar (Holten, 1802) (Gaf)
AMNH 303604, Dingo Beach, northern Queensland, Australia, sand/mud, Lamprell Collection (shell); FMNH 305965, Anse Vata, Noumea, New Caledonia, 2–4 m, C. Berthault! 27 January 2002, 70% ethanol [anatomical; sequences 16S DQ184745, 28S DQ184791, COI DQ184843 (mantle)]; Ridewood, 1903 (anatomical).

Gafrarium pectinata (Linnaeus, 1758) (Gaf, type species of *Gafrarium* Röding, 1798, name-bearing genus of Gafrariinae)
AMNH 302916, New Hebrides, Lamprell Collection (shell); Ridewood, 1903 (anatomical).

Gafrarium tumidum Röding, 1798 (Gaf)
AMNH 302922, Gove, Northern Territory, Australia 1987, Lamprell Collection (shell); FMNH 307858, mouth of Dunbea River, 15 km north of Noumea, New Caledonia, C. Berthault! 13 April 2002, 70% ethanol [anatomical; sequences 16S DQ184746, COI DQ184844, H3 DQ184892 (mantle)].

Gemma gemma (Totten, 1834) (Gem, type species of *Gemma* Deshayes, 1853; name-bearing genus of Gemminae)
AMNH 155236, Crab Meadow Park, Long Island (Suffolk County), New York, in sand in intertidal zone, M. K. Jacobson! 18 July 1952 (shell); AMNH 311615, purchased from Marine Biological Laboratory, Woods Hole, Massachusetts, August 2004, formalin to 70% ethanol, or directly to 100% ethanol [anatomy; sequences 16S DQ184748, COI DQ184846, 28S DQ184793, H3 DQ184894 (whole animal)]; Morse, 1919 (anatomical); Narchi, 1971 (anatomical); Sellmer, 1967 (anatomical).

Glauconome chinensis J. E. Gray, 1828 (Gla, type species of *Glauconome* J. E. Gray, 1828, name-bearing genus of Glauconomidae)
AMNH 311605, PMM-1016/RB-1733, Sanyo-cho, Watashiba, Asa River, Yamaguchi Prefecture, Japan, estuarine, shoreline grass and mud, by hand, intertidal, P. M. Mikkelsen, R. Bieler & H. Fukuda! 5 February 2000, 80% ethanol [shell; anatomical; sequences

16S DQ184753, COI DQ184851, 28S DQ184798, H3 DQ184899 (adductor muscle)].

Glauconome rugosa Reeve, 1844 (Gla)
NCSM 28970, fish market purchase, Ho Chi Minh City, Vietnam (commercially fished), N. T. Hoang! July 2003, 95% ethanol [shell; anatomical; sequences 16S DQ184754, COI DQ184852, 28S DQ184799, H3 DQ184900 (foot)]; Owen, 1955 (anatomical).

Globivenus effossa (Philippi, 1836) (Ven, type species of *Globivenus* Coen, 1934)
AMNH 135535, Spain (shell); Canapa *et al*., 2003 (sequence 16S AJ548768).

Gomphina undulosa (Lamarck, 1818) (Tap, type species of *Gomphina* Mörch, 1853)
AMNH 311621, PMM-1119/RB-1892, Shark Bay Marine Park, 'big lagoon', north of Denham, west coast of Peron Peninsula, Western Australia, Australia, 25°55.207′S, 113°31.093′W, sand with large proportion of shell hash, shovel and sieve, 1.5 m, P. M. Mikkelsen, R. Bieler *et al*.! 18 July 2004, 100% ethanol [shell; anatomical; sequences 16S DQ184717, COI DQ184819, 28S DQ184770, H3 DQ184869 (adductor muscle)].

Gouldia cerina (C. B. Adams, 1845) (Gou, type species of *Gouldia* C. B. Adams, 1847, name-bearing genus of Gouldiinae)
AMNH 32949, Jamaica, Haines Collection (shell); AMNH 299412, M-32-FK-318, off Halfmoon Shoal, Monroe County, Florida Keys, 24°21.35′ to 21.45′N, 82°27.86′ to 28.01′W, 61.6 m, sandy mud, standard ponar grab, P. M. Mikkelsen, R. Bieler *et al*.! R/V *Eugenie Clark*, 5 July 2000 (anatomy).

Gouldia minima (Montagu, 1803) (Gou)
AMNH 260810, off Guernsey, Channel Islands, UK, dredged, Germer Collection (shell); MHNG 1/74, Naples, Italy (anatomical); Ansell, 1961 (anatomical); M. E. S. Gray, 1857 (anatomical); Jeffreys, 1863 (anatomical); Ridewood, 1903 (anatomical); Sowerby, 1854 (anatomical).

Granicorium indutum Hedley, 1906 [Sam, formerly Tapetinae, moved to Samarangiinae by Harte (1998b) and Taylor, Glover & Braithwaite (1999), type species of *Granicorium* Hedley, 1906]
AMNH 303203, Capricorn Channel, central Queensland, Australia, trawled, 128 m, Lamprell Collection (shell); AMNH 303434, Cape Moreton, southern Queensland, Australia, Lamprell Collection (shell); BMNH acc. 2388, reg. no. 20040208, near Rottnest Island, Perth, Western Australia, Australia, J. Taylor & E. Glover! January 1996 (anatomical); Taylor *et al.*, 1999 (anatomical).

Hyphantosoma caperi (Lamprell & Healy, 1997) (Pit)
FMNH 306194, Anse Vata, Noumea, New Caledonia, 2–4 m, C. Berthault! 27 January 2002, 70% ethanol [shell; anatomical; sequences 16S DQ184709, COI DQ184811 (Hypcap1) and DQ184812 (Hypcap2), 28S DQ184765 (mantle)].

Irus crenatus (Lamarck, 1818) (Tap)
AMNH 32415, Australia (shell); FMNH 306208, RB-1841, Bandy Creek Harbour, Esperance, Western Australia, Australia, intertidal sand near boulders, R. Bieler, J. Taylor, E. Glover! 14 February 2003, 0–0.3 m, formalin to 70% ethanol, or directly to 95% ethanol [shell; anatomical; sequences 16S DQ184719, COI DQ184821, 28S DQ184772, H3 DQ184871 (foot)].

Irus irus (Linnaeus, 1758) (Tap, type species of *Irus* Schmidt, 1818)
AMNH 303437, Cape Upstart, northern Queensland, Australia, Lamprell Collection (shell); Morton, 1985 (shell); M. E. S. Gray, 1857 (anatomical); Ridewood, 1903 (anatomical); Sowerby, 1854 (anatomical).

Irus macrophyllus (Deshayes, 1853) (Tap)
AMNH 252292, Okinawa, B. Albert! 5 May 1966 (shell); Morton, 1985 (misidentified as *Irus irus*; anatomical); Pelseneer, 1911 (anatomical).

Katelysia marmorata (Lamarck, 1818) (Tap)
AMNH 31663, Philippines, Haines Collection (shell); Lam, 1980 (anatomical).

Katelysia rhytiphora (Lamy, 1935) (Tap)
AMNH 303676, San Remo, Victoria, Australia, 1988, Lamprell Collection (shell); FMNH 306200, RB-1822, Bandy Creek Harbour, Esperance, Western Australia, Australia, intertidal sand near boulders, sieving, 0–0.3 m, 6/8 February 2003, R. Bieler, J. Taylor, E. Glover! formalin to 70% ethanol (anatomical); Nielsen, 1963 (anatomical); FMNH 302051, RB-1850, Bandy Creek Harbour, Esperance, Western Australia, Australia, box dredge, 2–4 m (five hauls), 17 February 2003, R. Bieler, E. Glover, J. Taylor, J. McDonald! 95% ethanol [sequences 16S DQ184720, COI DQ184822, 28S DQ184773, H3 DQ184872 (foot)].

Katelysia scalarina (Lamarck, 1818) (Tap, type species of *Katelysia* Römer, 1857)
AMNH 303607, Ceduna, South Australia, Australia, 1987, Lamprell Collection (shell); AMNH 311620, PMM-1126/RB-1899, fish market purchase, Fremantle, Western Australia, Australia (commercially fished, Indian Ocean), 23 July 2004, 98% ethanol [shell; anatomical; sequences 16S DQ184721, COI DQ184823, 28S DQ184774, H3 DQ184873 (foot)]; Nielsen, 1963 (anatomical).

Katelysia sp. 1 (Tap)
AMNH 311619, PMM-1126/RB-1899, fish market purchase, Fremantle, Western Australia, Australia (commercially fished, Indian Ocean), 23 July 2004, 98% ethanol [shell; anatomical; sequences 16S DQ184722, COI DQ184824, 28S DQ184775, H3 DQ184874 (foot)].

Katelysia sp. 2 (Tap)
AMNH 311618, PMM-1126/RB-1899, fish market purchase, Fremantle, Western Australia, Australia (commercially fished, Indian Ocean), 23 July 2004, 98% ethanol [shell; anatomical; sequences 16S DQ184723, COI DQ184825, 28S DQ184776, H3 DQ184875 (foot)].

Lioconcha castrensis (Linnaeus, 1758) (Lio, type species of *Lioconcha* Mörch, 1853, name-bearing genus of Lioconchinae)
AMNH 303127, off Palm Island, Queensland, Australia, trawled, 10 m, August 1994, Lamprell Collection (shell); M. E. S. Gray, 1857 (anatomical).

Lioconcha ornata (Lamarck, 1818) (syn. *picta* Lamarck, 1818) (Lio)
AMNH 303282, Little Opolu Reef, northern Queensland, Australia, Lamprell Collection (shell); FMNH 305964, Noumea, Anse Vata, New Caledonia, C. Berthault!, 21 January 2002, 2–4 m, 70% ethanol [anatomical; sequences 16S DQ184707, COI DQ184809, 28S DQ184763 (mantle)]; FMNH 306193, Noumea, Anse Vata, New Caledonia, 2–4 m, C. Berthault! 27 January 2002, 70% ethanol (anatomical); Pelseneer, 1911 (anatomical).

Lirophora latilirata (Conrad, 1841) (Chi, type species of *Lirophora* Conrad, 1862)
AMNH 303002, West Indies, Lamprell Collection (shell); UMML 30.11717, off Palm Beach County, Florida, 27°13′N, 79°54′W, 61 m, 21 May 1968, R/V *Gerda* sta. 1001 (shell; anatomical); UMML 30.11734, off St. Lucie Inlet, Martin County, Florida, 27°19′N, 79°59′W, 41 m, 21 May 1968 (anatomical); UMML 30.11735, off South Carolina, 32°08′N, 79°30′W, 10 ft otter trawl, 46 m, 28 July 1964, R/V *Pillsbury* sta. 111, dry [shell; anatomical; sequences 16S DQ184738 (adductor muscle)].

Macridiscus melanaegis (Römer, 1860) (Tap)
AMNH 51154, Japan, Constable Collection (shell); Matsumoto, unpublished (sequence COI AB76948).

Macrocallista maculata (Linnaeus, 1758) (Cal)
AMNH 312709, FK-519, south of Halfmoon Shoal, Monroe County, Florida Keys, 24°30.59′N, 82°28.29′W to 24°30.78′N, 82°28.26′W, 17.1 m, shells, triangle dredge, P. M. Mikkelsen, R. Bieler *et al*.! R/V *Eugenie Clark*, 26 July 2001 (shell); AMNH 147694, 10 miles south of Alligator Point, Franklin County, Florida, bell buoy #26, 21.3 m, J. Rudloe! 6 September 1968 (anatomical); AMNH 267507, Siesta Key, Sarasota County, Florida, G. Dingerkus & L. D. Uhler! 13 January 1977 (anatomical); NCSM 9848/IMS 1892, south-east of New River Inlet, North Carolina, scallop dredge, 29.3–31.1 m, H. J. Porter! 24 March 1967, R/V *Oregon* sta. 6538–6540, 70% ethanol (previously 70% isopropanol, original fixative unrecorded) [sequence 16S DQ184714 (foot)].

Macrocallista nimbosa (Lightfoot, 1786) (Cal, type species of *Macrocallista* Meek, 1876)
AMNH 114684, Bellaire Beach (Pinellas County), Florida, bay area, beach, 30 August 1964 (shell); AMNH 207508, Siesta Key, Sarasota County, Florida, G. Dingerkus & L. D. Uhler! 13 January 1977 (anatomical); AMNH 267443, Casey Key, Sarasota County, Florida, D. Germer! (anatomical); FMNH 301910, purchased from Gulf Specimen Marine Laboratory, Panacea, Florida, 14 August 2002 (anatomical); FMNH 306613, Ten Thousand Islands, off south-western Florida, T. A. Rawlings! 70% ethanol [sequences 16S DQ184715, COI DQ184817, 28S DQ184768, H3 DQ184867 (foot)].

Marcia hiantina (Lamarck, 1818) (Tap)
AMNH 303628, Dingo Beach, central Queensland, Australia, Lamprell Collection (shell); Lam, 1980 (anatomical).

Marcia japonica (Gmelin, 1791) (Tap)
AMNH 303689, Dumbea River, near Noumea, New Caledonia, Lamprell Collection (shell); Lam, 1980 (anatomical).

Marcia opima (Gmelin, 1791) (Tap, type species of *Marcia* H. & A. Adams, 1857)
AMNH 303413, India, Lamprell Collection (shell).

Marcia virginea (Linnaeus, 1758) (Tap)
AMNH 303691, Turkey Beach, central Queensland, Australia, Lamprell Collection (shell); Jeffreys, 1863 (anatomical); Ridewood, 1903 (anatomical).

Megapitaria aurantica (G. B. Sowerby I, 1831) (Pit, type species of *Megapitaria* Grant & Gale, 1931)
AMNH 243875, off Pedro Gonzales Island, Perlas Islands, Panama, sand bar at low tide, 1966, Barlow Collection (shell); AMNH 303164, La Paz, Baja California Sur, Mexico, Lamprell Collection (shell); LACM 35–106, AHF 465–35, Playa Blanca, Guanacaste Province, Costa Rica, 10°56.8′N, 85°53.5′W, shale, intertidal, 8 February 1935, R/V *Velero III* (anatomical).

Megapitaria squalida (G. B. Sowerby I, 1835) (Pit)
AMNH 186083, Laguna de San Jose, Baja California Norte, Mexico, 28°01′N, 114°08′W, H. DuShane! February 1976 (shell); AMNH 272909, San Carlos Bay, Guaymas, Mexico, mud flats, H. Mac Can! December 1968 (shell); FMNH 305969, Pacific Panama, 09°40.39′N, 78°02.78′W to 09°40.2′N, 78°02.62′W, 19–20.2 m, R. Collin! 8 July 2002, 70% ethanol, ex R. Collin [anatomical; sequences 16S DQ184716, COI DQ184818, 28S DQ184769, H3 DQ184868 (mantle)].

Mercenaria mercenaria (Linnaeus, 1758) (Chi, type species of *Mercenaria* Schumacher, 1817)
AMNH 210056, Waretown (Ocean County), New Jersey, H. Johnstone! 12 February 1950 (shell); AMNH 312710, fish market purchase, Bergen County, New Jersey (commercially fished, Atlantic Ocean), December 2004 (anatomy); Gainey, Walton & Greenberg, 2003 (anatomical); Jones, 1979 (anatomical); Kellogg, 1892, 1903, 1915 (anatomical); Loosanoff, 1937a, b (anatomical); Morse, 1919 (anatomical); Pechenik, 1991 (anatomical); FMNH 306219, fish market purchase, Chicago, Illinois (commercially fished, Atlantic Ocean off Virginia), May 2002, 100% ethanol [sequences 16S DQ184737, COI DQ184836, H3 DQ184887 (mantle)]; Baldwin *et al*., 1996 (sequence COI U47648); Canapa *et al.*, 2003 (sequence 16S AJ528773); Park & Ó Foighil, 2000 (sequence 28S AF131019).

Meretrix lamarckii Deshayes, 1853 (Mer)
AMNH 32010, China, Haines Collection (shell); AMNH 32665, Japan, Constable Collection (shell); Hamaguchi, Sasaki & Higano, unpublished (sequence COI AB059420).

Meretrix lusoria (Röding, 1798) (Mer)
AMNH 303380, Japan, Lamprell Collection (shell); AMNH 303381, Japan, Lamprell Collection (shell); Wu, Liu & Liao, 1993 (anatomical); Matsumoto, unpublished (sequence COI AB076924).

Meretrix lyrata (G. B. Sowerby II, 1851) (Mer)
AMNH 303558, New Guinea, Lamprell Collection (shell); AMNH 303867, New Guinea, Lamprell Collection (shell); Canapa *et al*., 2003 (sequence 16S AJ548769).

Meretrix meretrix (Linnaeus, 1758) (Mer, type species of *Meretrix* Lamarck, 1799, name-bearing genus of Meretricinae)
AMNH 31674, China, Steward Collection (shell); AMNH 179107, Long Hai, Vietnam, R. M. Shenberger! June 1971 (anatomical).

Neolepton sulcatulum (Jeffreys, 1859) (Neo, type species of *Neolepton* Monterosato, 1875, name-bearing genus of Neoleptonidae)
AMNH 35004, [English] Channel, Constable Collection (shell); Salas & Gofas, 1998 (anatomical).

Neotapes undulatus (von Born, 1778) (Tap, type species of *Neotapes* Kuroda & Habe, 1971)
AMNH 303951, Crocker Island, Palm Bay, Northern Territory, Australia, Lamprell Collection (shell); Pelseneer, 1911 (anatomical); Lam, 1980 (anatomical); Canapa *et al*., 2003 (sequence 16S AJ548767); Hosoi *et al.*, 2004 (sequence 28S AB105369).

Nutricola pannosa (G. B. Sowerby I, 1835) [Pit, formerly Meretricinae, moved to Pitarinae by Harte (1998b) and Taylor *et al*. (1999)]
AMNH 32717, Coquimbo (Chile), Constable Collection (shell); LACM 35–26, AHF 387–35, off Isla Middle Chincha, Ica Department, Peru, 13°39.3′S, 76°24.7′W, sand, 9 m, 15 January 1935, R/V *Velero III* (anatomical).

Nutricola tantilla (A. A. Gould, 1853) [Pit, formerly Meretricinae or Gemminae, moved to Tapetinae by Coan *et al*. (2000); type species of *Nutricola* Bernard, 1982]
AMNH 35917, Morro Bay (San Luis Obispo County), California, Oldroyd! (shell); AMNH 257530, near Baywood, Morro Bay (San Luis Obispo County), California, mud flats, 30 June 1961, DuShane Collection (shell); Bernard, 1982 (shell; anatomical); Coan *et al*., 2000 (shell); FMNH 305963, north of Point Caution, San Juan Island, San Juan Channel (San Juan County), Washington, 23 June 2003, 95% ethanol [anatomical; sequences 16S DQ184708, COI DQ184810, 28S DQ184764, H3 DQ184862 (foot)]; Narchi, 1971, 1972 (anatomical); S. Gray, 1982 (anatomical); Hansen, 1953 (anatomical).

Paphia dura (Gmelin, 1791) (Tap)
AMNH 31620, Gaboon, Haines Collection (shell); AMNH 32374, Senegal, Constable Collection (shell); AMNH 303216, Petite Cote, Senegal, Lamprell Collection (shell); AMNH 3241, Lobite, Angola, Lang & Boulton! April 1925 (anatomical); FMNH 305967, IKSE-003, wreck off Dakar, Senegal, sand, I. Kappner & P. DeVoize! 16 September 2003, RNAlater [anatomical; sequences 16S DQ184724, COI DQ184826, 28S DQ184777, H3 DQ184876 (mantle)].

Paphia euglypta (Philippi, 1847) (Tap)
AMNH 150730, Pusan, Korea, Byong um Hur! 5 June 1968 (shell); AMNH 311607, PMM-1010/RB-1727, by-catch of fishing nets, Ueshima Island, off Murozumi, Yamaguchi Prefecture, Japan, 33°53–54′N, 131°56–57′E, mud, commercial fishing trawl, 40–43 m, P. M. Mikkelsen, R. Bieler & H. Fukuda! 3 February 2000, 80% ethanol [shell; anatomical; sequences 16S DQ184725, COI DQ184827, 28S DQ184778, H3 DQ184877 (posterior adductor muscle)].

Paphia vernicosa (A. A. Gould, 1861) (Tap)
AMNH 311608, PMM-1013/RB-1728, by-catch on dock and nets, Iwaishima Island, Yamaguchi Prefecture, Japan, by hand, P. M. Mikkelsen, R. Bieler & H. Fukuda! 4 February 2000, 80% ethanol [shell; anatomical; sequences 16S DQ184726, COI DQ184828, 28S DQ184779, H3 DQ184878 (anterior adductor muscle)].

Parastarte triquetra (Conrad, 1846) (Gem, type species of *Parastarte* Conrad, 1862)
AMNH 248366, Punta Rassa (Lee County), Florida, muddy sand, May 1969, Bijur Collection (shell); AMNH 307905, PMM-1111/RB-1864, Indian River Lagoon, tidal creek east of Round Island, Indian River County, Florida, 27°33.607′N, 80°19.902′W, mud with *Thalassia* and *Halodule* seagrass, petit ponar grab, 1 m, P. M. Mikkelsen, R. Bieler, S. Reed! 15 April 2003, 100% ethanol [anatomical; sequences 16S DQ184749, COI DQ184847, 28S DQ184794, H3 DQ184895 (whole animal (minus shell) in lysis buffer)].

Parmulophora corrugata (Dillwyn, 1817) (Gou, type species of *Parmulophora* Dall, 1905)
AMNH 303254, Eilat, Israel, Lamprell Collection (shell); Fishelson, 2000 (anatomical); Pelseneer, 1911 (anatomical).

Parmulophora crocea (J. E. Gray, 1838) (Gou)
AMNH 303601, Eilat, Israel, Lamprell Collection (shell); Fishelson, 2000 (anatomical).

Pectunculus exoletus (Linnaeus, 1758) (Dos, type species of *Pectunculus* da Costa, 1778)
AMNH 303574, Granville, Bretagne, France, Lamprell Collection (shell); FMNH 305968, IKSE-004, Dakar, Ile de Goree, Senegal, rocks/sand/coral, I. Kappner & P. DeVoize! 16 September 2003, 80% ethanol [anatomical; sequences 16S DQ184702, COI DQ184804, 28S DQ184759, H3 DQ184857 (mantle)]; Ansell, 1961 (anatomical); M. E. S. Gray, 1857 (anatomical); Jeffreys, 1863 (anatomical); Pelseneer, 1897 (anatomical); Ridewood, 1903 (anatomical); Thiele, 1886 (anatomical).

Periglypta listeri (J. E. Gray, 1838) (Ven)
AMNH 269541, Bahia Honda State Park (Monroe County), Florida Keys, 11 July 1973, Germer Collection (shell); AMNH 267424, Crawl Key (Monroe County), Florida Keys, G. Dingerkus & L. D. Uhler! 6 January 1977 (anatomical); Bieler, Kappner & Mikkelsen, 2004 (anatomical); FMNH 296696, FK-273, bayside of West Summerland Key (Spanish Harbor Keys), Monroe County, Florida Keys, at outermost point of western arm of horseshoe, 24°39.35′N, 81°18.22′W, 0.3–1.2 m, snorkelling, by hand, R. Bieler, P. Sierwald & A. Bieler! 19 August 1999, Tris-EDTA buffered ethanol [sequences 16S DQ184731, 28S DQ184784, H3 DQ184883 (mantle)].

Petricola lapicida (Gmelin, 1791) (Pet, type species of *Petricola* Lamarck, 1801, name-bearing genus of Petricolidae)
AMNH 33527, St. Thomas, West Indies, Haines Collection (shell); AMNH 294770, Bonefish Key (Monroe

County), Florida Keys, B. Bales! Eddison Collection (shell); AMNH 298891, FK-047, Channel marker 50A off Ramrod Key, Monroe County, Florida Keys, 24°35.80′N, 81°27.24′W, rubble and patch reef, scuba, 4.6 m, P. M. Mikkelsen & R. Bieler! 21 September 1996 (anatomical); AMNH 299833, FK-244, 'Horseshoe' site, bayside of West Summerland Key (Spanish Harbor Keys), Monroe County, Florida Keys, 24°39′19′N, 81°18′13′W, bayside, rock wall and sand slope, scuba in centre of quarry, 7.0 m maximum, R. Bieler, P. M. Mikkelsen *et al*.! 5 August 1999 (anatomical); Pelseneer, 1911 (anatomical); AMNH 305124, IMBW-FK-629, 'Horseshoe' site, bayside of West Summerland Key (Spanish Harbor Keys), Monroe County, Florida Keys, 24°39.3′N, 81°18.2′W, among rocks along arms of quarry, by hand, snorkelling, to *c*. 1 m, P. M. Mikkelsen, R. Bieler *et al*.! 21 and 26 July 2002, 95% ethanol [sequences 16S DQ184749, COI DQ184848, 28S DQ184795, H3 DQ184896 (adductor muscle)].

Petricolaria pholadiformis (Lamarck, 1818) (Pet, type species of *Petricolaria* Stoliczka, 1870)
AMNH 51629, Staten Island (Richmond County), New York, Constable Collection (shell); AMNH 181376, eastern USA, Haines Collection (anatomical); Ansell, 1961 (anatomical); Morse, 1919 (anatomical); Purchon, 1955 (anatomical); AMNH 311609, vicinity of Woods Hole (Barnstable County), Massachusetts, November 2004, 95% ethanol [sequences 16S DQ184751, COI DQ184849, 28S DQ184796, H3 DQ184897 (posterior adductor muscle)].

Pitar fulminatus (Menke, 1828) (Pit)
AMNH 272920, Flamengo Creek, Ribeira Beach, Ubatuba, São Paulo State, Brazil, C. Ozores! July 1965 (shell); MZUSP 20.806, Baia de Ilha Grande (Rio de Janeiro State), Brazil, 22 July 1966, R/V *Emilia* sta. 206 (anatomical); MZUSP 27004, Barreiro, Ilha Bela, São Paulo State, Brazil (anatomical); AMNH 307917, PMM-1111/RB-1864, Indian River Lagoon, tidal creek east of Round Island, Indian River County, Florida, 27°33.607′N, 80°19.902′W, mud with *Thalassia* and *Halodule* seagrass, petit ponar grab, 1 m, P. M. Mikkelsen, R. Bieler, S. Reed! 15 April 2003, 100% ethanol or lysis buffer [sequences 16S DQ184710, COI DQ184813, 28S DQ184766, H3 DQ184863 (foot)].

Pitar morrhuanus ('Linsley' Dall, 1902) (syn. *convexa* Conrad, 1830) (Pit)
AMNH 303299, Lynn Harbor (Essex County), Massachusetts, Lamprell Collection (shell); AMNH 267268, JJH-74–110, New Jersey, Clam Dredge Survey sta. 24, 14 September 1976 (anatomical); Morse, 1919 (anatomical).

Pitar rudis (Poli, 1795) (Pit)
AMNH 32141, Mediterranean Sea, Jay Collection (shell); AMNH 303387, Black Sea, Fadime (Turkey?), Lamprell Collection (shell); AMNH 181446, Naples, Italy, ex Columbia University Department of Zoology (anatomical); Canapa *et al*., 2003 (sequence 16S AJ548770).

Pitar simpsoni (Dall, 1895) (Pit)
AMNH 248301, around three small islands east of John's Pass, Boca Ciega Bay, St. Petersburg (Pinellas County), Florida, dredged, E. Marcott! 1962 (shell); AMNH 298911, FK-163, Tavernier, Key Largo, Monroe County, Florida Keys, 25°03.61′N, 80°30.00′W to 25°03.53′N, 80°30.21′W, bayside, sandy mud/*Thalassia*/chicken liver sponge/*Dasycladus*, dredge, 1.7 m, P. M. Mikkelsen & R. Bieler! R/V *Floridays*, 12 September 1998 (anatomical); AMNH 298910, FK-172, Cowpens Anchorage, bayside of Plantation Key, Monroe County, Florida Keys, 24°59.13′N, 80°34.45′W, ponar grab and dredge, grey soupy mud/*Thalassia*, 1.8–2.1 m, P. M. Mikkelsen & R. Bieler! R/V *Floridays*, 18 September 1998 (anatomical, including histological slides); FMNH 295722, FK-211, unnamed bay between Shark Key and Big Coppitt Key, Monroe County, Florida Keys, 24°36.38′N, 81°39.18′W, bayside, bottom sample, *Thalassia* seagrass, R. Bieler & P. M. Mikkelsen! R/V *Floridays*, 17 April 1999, 80% ethanol [sequences 16S DQ184712, COI DQ184815, H3 DQ184865 (foot and adductor muscle)].

Pitar tumens (Gmelin, 1791) (Pit, type species of *Pitar* Römer, 1857, name-bearing genus of Pitarinae)
AMNH 303152, Senegal, Lamprell Collection (shell).

Pitarenus cordatus (Schwengel, 1951) (Pit, type species of *Pitarenus* Rehder & Abbott, 1951)
AMNH 303049, off Galveston (Galveston County), Texas, 36.6 m, H. Geis! (shell); AMNH 298909, FK-099, Florida Straits, due south of Dry Tortugas, Monroe County, Florida Keys, 24°24.6′N, 82°53.1′W to 24°24.5′N, 82°54.2′W, dredge, 63–66 m, P. M. Mikkelsen, R. Bieler *et al*.! R/V *Bellows*, 24 April 1997 (anatomical).

Pitarina affinis (Gmelin, 1791) (Pit)
AMNH 303136, Taylor Reef, northern Queensland, Australia, trawled, 10–12 m, December 1995, Lamprell Collection (shell); Pelseneer, 1911 (anatomical).

Pitarina citrina (Lamarck, 1818) (Pit, type species of *Pitarina* Jukes-Brown, 1913)
AMNH 311622, PMM-1120/RB-1893, Shark Bay Marine Park, Monkey Mia, east coast of Peron Peninsula, Western Australia, Australia, 25°47.025′S, 113°43.293′W, sand, shovel and sieve, 1–1.5 m, P. M. Mikkelsen, R. Bieler *et al*.! 19 July 2004 100% ethanol [shell; anatomical; sequences 16S DQ184713, COI DQ184816, 28S DQ184767, H3 DQ184866 (adductor muscle)].

Pitarina japonica (Kuroda & Kawamoto in Kawamoto & Tanabe, 1956) (Pit)
AMNH 303964, sta. 65, Shelburne Bay, northern Queensland, Australia, 12°41.3′N, 140°42.5′E, 60 m, S. Cook! 31 January 1993 (shell); FMNH 305970, mouth of Dunbea River, 15 km north of Noumea, New Caledonia, C. Berthault! 13 April 2002, 70% ethanol (unknown preservation history) [shell; anatomical; sequences 16S DQ184711, COI DQ184814, H3 DQ184864 (foot)].

Placamen calophylla (Philippi, 1836) (Chi)
AMNH 303214, Tree Point, Darwin, Northern Territory, Australia, Lamprell Collection (shell); FMNH 305977 (ex BMNH), Hong Kong, Hong Kong Fisheries! (anatomical); Morton, 1985 (anatomical); Pelseneer, 1911 (anatomical); Ridewood, 1903 (anatomical); FMNH 305977 (ex BMNH), Hong Kong, 70% ethanol (unrecorded preservation history) [sequence 16S DQ184734 (mantle)].

Ruditapes bruguieri (Hanley, 1845) (Tap)
AMNH 311606, PMM-1011/RB-1730, Tanoura, Nagashima, proposed nuclear power plant construction site, Yamaguchi Prefecture, Japan, rocks and tidepools, by hand, shore, P. M. Mikkelsen, R. Bieler & H. Fukuda! 4 February 2000, 80% ethanol [shell; anatomical; sequences 16S DQ184727, COI DQ184829, 28S DQ184780, H3 DQ184879 (anterior adductor muscle)].

Ruditapes decussatus (Linnaeus, 1758) (Tap, type species of *Ruditapes* Chiamenti, 1900)
AMNH 110014, Treueurden, Bretagne, France, Y. Rouget! 1963 (shell); AMNH 181449, Naples, Italy, ex Columbia University Department of Zoology (anatomical); Ansell, 1961 (anatomical); Carrière, 1879 (anatomical); Fishelson, 2000 (anatomical); M. E. S. Gray, 1857 (anatomical); Pelseneer, 1911 (anatomical); Ridewood, 1903 (anatomical); FMNH 306189, fish market purchase, Faro, Portugal (commercially fished), 20 July 2001, 70% ethanol [sequences 16S DQ184728, COI DQ184830, 28S DQ184781, H3 DQ184880 (mantle)]; Canapa *et al*., 2003 (sequence 16S AJ548764).

Ruditapes philippinarum (A. Adams & Reeve, 1850) (Tap)
AMNH 238907, Minabe (Wakayama Prefecture, Honshu), Japan, sand (shell); AMNH 1557, Vladivostok Harbor, Soviet Union, Buxton! 2 June 1900 (anatomical); Lam, 1980 (anatomical); Hashimoto & Matsumoto, unpublished (sequence 28S AB126333); Okazaki & Ueshima, unpublished (sequences 16S male AB065374, 16S female AB065375, COI male AB065374, COI female AB065375).

Ruditapes variegatus (G. B. Sowerby II, 1852) (Tap)
AMNH 303629, Boyne Island, central Queensland, Australia, after storm, 1989, Lamprell Collection (shell); Lam, 1980 (anatomical); Pelseneer, 1911 (anatomical).

Samarangia quadrangularis (A. Adams & Reeve, 1850) (Sam, type species of *Samarangia* Dall, 1902, name-bearing genus of Samarangiinae)
AMNH 303507, Serangapatam (India), 260 miles north of Broome, Western Australia, Australia, in hole in reef, 35 m, Lamprell Collection (shell); Keen, 1969 (shell).

Saxidomus nuttalli Conrad, 1837 (Pit, type species of *Saxidomus* Conrad, 1837)
AMNH 33473, Columbia River (Washington/Oregon), Haines Collection (shell); SBMNH 42709M, Mugu Lagoon, Pt. Mugu (Ventura County), California, sta. 3, below porpoise pool, MacGinitie *et al*.! 27 June 1963 (anatomical); SBMNH 80188, King Harbor, 33°50′45′N, 118°23′56′W, Los Angeles County, California, K. H. Benthic Survey sta. 3–5 #1, July 1975 (anatomical); SBMNH 80189, King Harbor, 33°50′45′N, 118°23′56′W, Los Angeles County, California, K. H. Benthic Survey sta. 1 #3, 17 September 1974 (anatomical); Kellogg, 1915 (anatomical).

Striacallista phasianella (Deshayes, 1854) (Pit)
AMNH 303425, One Arm Point, northern Western Australia, Australia 1987, Lamprell Collection (shell); Pelseneer, 1911 (anatomical).

Sunetta effosa (Hanley, 1843) (Sun)
AMNH 31792, Philippines, Haines Collection (shell).

Sunetta meroe (Linnaeus, 1758) (Sun, type species of *Meroe* Schumacher, 1817, name-bearing genus of Meroinae)
AMNH 32476, Ceylon (shell).

Sunetta scripta (Linnaeus, 1758) (Sun, type species of *Sunetta* Link, 1807, name-bearing genus of Sunettinae)
AMNH 303612, Trincomalee, Sri Lanka, Lamprell Collection (shell).

Tapes aureus (Gmelin, 1791) (Tap)
AMNH 302956, Portland Harbour, Dorset, UK, Lamprell Collection (shell); Ansell, 1961 (shell); Ockelmann, 1964 (anatomical); Ridewood, 1903 (anatomical); Canapa *et al*., 2003 (sequence 16S AJ548766).

Tapes dorsatus (Lamarck, 1818) (Tap)
AMNH 303217, Moreton Bay, southern Queensland, Australia, Lamprell Collection (shell); AMNH 303218, Sams Creek, northern Western Australia, Australia, Lamprell Collection (shell); AMNH 303219, Frenchmans Bay, Botany Bay, New South Wales, Australia, Lamprell Collection (shell); Lam, 1980 (anatomical).

Tapes literatus (Linnaeus, 1758) (Tap, type species of *Tapes* Megerle von Mühlfeld, 1811, name-bearing genus of Tapetinae)
AMNH 303510, King Beach, Dampier, northern Western Australia, Australia 1987, Lamprell Collection (shell).

Tapes rhomboides (Pennant, 1777) (Tap)
AMNH 303102, Le Passous, Bretagne, France, P. van Pel! (shell); Ansell, 1961 (anatomical); Canapa *et al*., 2003 (sequence 16S AJ417848).

Tivela mactroides (von Born, 1778) (Mer)
AMNH 303884, Brazil, Lamprell Collection (shell); AMNH 303885, Venezuela, Lamprell Collection (shell); FMNH 301914, São Paulo State, Brazil, January 2003, ex O. Domaneschi (anatomical); UMML 30.11733, off southern coast of Trinidad, 10°04′N, 61°35′W, *c*. 1.8 m, by hand, sand, R/V *Pillsbury* sta. 701, 70% ethanol (unknown preservation history) [anatomical; sequences 16S DQ184703, COI DQ184805, 28S DQ184760, H3 DQ184858 (adductor muscle)]; Narchi, 1972 (anatomical); Narchi & di Dario, 2002 (anatomical).

Tivela stultorum (Mawe, 1823) (Mer)
AMNH 32727, California, Oldroyd Collection (shell); AMNH 270641, Biological Beach, La Jolla (San Diego County), California, W. S. Teator! January 1922 (shell); Fitch, 1950 (anatomical); Yonge, 1962 (anatomical); FMNH 301909, Santa Claus Lane Beach, Carpinteria (Santa Barbara County), California, J. E. Dugan! 29 November 2002, formalin to 80% ethanol, or directly to 70% ethanol [anatomical; sequences 16S DQ184704, COI DQ184806, H3 DQ184859 (foot)].

Tivela ventricosa (J. E. Gray, 1838) (Mer)
AMNH 303888, La Coronilla Beach, Uruguay, Lamprell Collection (shell); AMNH 303889, La Paloma Rocha, Uruguay, Lamprell Collection (shell); Narchi & di Dario, 2002 (anatomical).

Transennella conradina (Dall, 1884) (Mer, type species of *Transennella* Dall, 1883)
AMNH 294595, Pine Island Sound, Sanibel Island (Lee County), Florida, dredged, shallow water, G. Eddison! August 1962 (shell); Bernard, 1982 (anatomical).

Transenpitar americanus (Doello-Jurado in Carcelles, 1951) (syn. *keenae* Fischer-Piette & Testud, 1967) (Pit, type species of *Transenpitar* Fischer-Piette & Testud, 1967)
AMNH 191889, Cabo Corrientes, Argentina, Nowell-Usticke Collection (shell); HMNS 39597, Mar del Plata, Argentina, dredged, 46 m, Pinto! April 1968 [shell; anatomical (dry)].

Turtonia minuta (O. Fabricius, 1780) (Tur, type species of *Turtonia* Alder, 1848, name-bearing genus of Turtoniidae)
AMNH 177261, Three Entrance Bay, Sitka (Sitka County), Alaska, May 1963 (shell); Ockelmann, 1964 (shell; anatomical); Jeffreys, 1863 (anatomical); Morse, 1919 (anatomical); Oldfield, 1955 (anatomical); FMNH 302008 (ex SMNH 53799), Sandgerdi, southwestern Iceland, among intertidal algae, 95% ethanol [sequences 16S DQ184752, COI DQ184850, 28S DQ184797, H3 DQ184898 (whole animal (minus shell))].

Venerupis galactites (Lamarck, 1818) (Tap)
AMNH 31568, Australia, Haines Collection (shell); AMNH 311150, RB-1823, Esperance Bay Yacht Club, Esperance, Western Australia, Australia, 33°51.9′S, 121°53.65′E, *Posidonia* seagrass, 1–1.5 m, R. Bieler *et al*.! 6–16 February 2003 (shell; anatomical); Bieler *et al*., 2005 (shell; anatomical); FMNH 302019, RB-1823, Esperance Bay Yacht Club, Esperance, Western Australia, Australia, 33°51.9′S, 121°53.65′E, *Posidonia* seagrass, 1–1.5 m, R. Bieler *et al*.! 6–16 February 2003, 95% ethanol [sequences 16S DQ184729, COI DQ184831, 28S DQ184782, H3 DQ184881 (foot)].

Venerupis senegalensis (Gmelin, 1791) (syn. *pullastra* Montagu, 1803) (Tap)
AMNH 31563, England, Haines Collection (shell); Ansell, 1961 (anatomical); Carrière, 1879 (anatomical); M. E. S. Gray, 1857 (anatomical); Jeffreys, 1863 (anatomical); Pelseneer, 1894, 1897, 1911, 1923 (anatomical); Ridewood, 1903 (anatomical); Yonge, 1962 (anatomical); Canapa *et al*., 2003 (sequence 16S AJ417845).

Venus verrucosa Linnaeus, 1758 (Ven, type species of *Venus* Linnaeus, 1758, name-bearing genus of Venerinae)
AMNH 304017, Marmarais, Bay of Marmarais, Turkey, Lamprell Collection (shell); AMNH 181405, Naples, Italy, ex Columbia University Department of Zoology (anatomical); M. E. S. Gray, 1857 (anatomical); Jeffreys, 1863 (anatomical); Pelseneer, 1894, 1897 (anatomical); FMNH 309251, fish market purchase, Paris, France (commercially fished), January 2002, 100% ethanol [sequences 16S DQ184732, COI DQ184833, H3 DQ184884 (mantle)]; Canapa *et al*., 2003 (sequence 16S AJ548763).

APPENDIX 3

MORPHOLOGICAL CHARACTER LIST

Taxon abbreviations: AaCh, *Anomalocardia auberiana* (Chi); AiO, *Arctica islandica* (outgroup, Arc); AlD, *Asa lupina* (Dos); AlV, *Antigona lamellaris* (Ven); CcCh, *Chione cancellata* (Chi); CcPi, *Callista chione* (Cal); CeCh, *Chione elevata* (Chi); CfPi, *Callista florida* (Cal); CfO, *Corbicula fluminea* (outgroup, Cor); CgCh, *Chamelea gallina* (Chi); ChPi, *Callocardia hungerfordi* (Cao); CiPi, *Costacallista impar* (Cal); ClPi, *Costacallista lilacina* (Cal); CmO, *Calyptogena magnifica* (outgroup, Ves); CnGo, *Circe nummulina* (Gou); CpCl, *Clementia papyracea* (Cle); CpGo, *Circe plicatina* (Gou); CrGo, *Circe rivularis* (Gou); CsCl, *Compsomyax subdiaphana* (Cle); CsCy, *Cyclina sinensis* (Cyc); CsGo, *Circe scripta* (Gou); CsPe, *Cooperella subdiaphana* (Pet); CtCy, *Cyclinella tenuis* (Cyc); CxGo, *Circe* cf. *rivularis* (Gou); DcD, *Dosinia concentrica* (Dos); DeD, *Dosinia excisa* (Dos); DvD, *Dosinia victoriae* (Dos); D2D, *Dosinia* sp. 2 (Dos); ElCh, *Eurhomalea lenticularis* (Chi); GcGl, *Glauconome chinensis* (Gla); GcGo, *Gouldia cerina* (Gou); GdGo, *Gafrarium dispar* (Gaf); GeV, *Globivenus effossa* (Ven); GgGe, *Gemma gemma* (Gem); GiSa, *Granicorium indutum* (Sam); GmGo, *Gouldia minima* (Gou); GpGo, *Gafrarium pectinata* (Gaf); GrGl, *Glauconome rugosa* (Gla); GtGo, *Gafrarium tumidum* (Gaf); GuTa, *Gomphina undulosa* (Tap); HcPi, *Hyphantosoma caperi* (Pit); IcTa, *Irus crenatus* (Tap); IiTa, *Irus irus* (Tap); ImTa, *Irus macrophyllus* (Tap); KmTa, *Katelysia marmorata* (Tap); KrTa, *Katelysia rhytiphora* (Tap); KsTa, *Katelysia scalarina* (Tap); K1Ta, *Katelysia* sp. 1 (Tap); K2Ta, *Katelysia* sp. 2 (Tap); LcPi, *Lioconcha castrensis* (Lio); LlCh, *Lirophora latilirata* (Chi); LoPi, *Lioconcha ornata* (Lio); MaPi, *Megapitaria aurantica* (Pit); MhTa, *Marcia hiantina* (Tap); MjTa, *Marcia japonica* (Tap); MlaM, *Meretrix lamarcki* (Mer); MluM, *Meretrix lusoria* (Mer); MlyM, *Meretrix lyrata* (Mer); MmCh, *Mercenaria mercenaria* (Chi); MmM, *Meretrix meretrix* (Mer); MmPi, *Macrocallista maculata* (Cal); MmTa, *Macridiscus melanaegis* (Tap); MnPi, *Macrocallista nimbosa* (Cal); MoTa, *Marcia opima* (Tap); MsPi, *Megapitaria squalida* (Pit); MvTa, *Marcia virginea* (Tap); NpPi, *Nutricola pannosa* (Pit); NsN, *Neolepton sulcatulum* (Neo); NtPi, *Nutricola tantilla* (Pit); NuTa, *Neotapes undulatus* (Tap); PaPi, *Pitarina affinis* (Pit); PcCh, *Placamen calophylla* (Chi); PciPi, *Pitarina citrina* (Pit); PcoGo, *Parmulophora corrugata* (Gou); PcoPi, *Pitarenus cordatus* (Pit); PcrGo, *Parmulophora crocea* (Gou); PdTa, *Paphia dura* (Tap); PeD, *Pectunculus exoletus* (Dos); PeTa, *Paphia euglypta* (Tap); PfPi, *Pitar fulminatus* (Pit); PjPi, *Pitarina japonica* (Pit); PlPe, *Petricola lapicida* (Pet); PlV, *Periglypta listeri* (Ven); PmPi, *Pitar morrhuanus* (Pit); PpPe, *Petricolaria pholadiformis* (Pet); PrPi, *Pitar rudis* (Pit); PsPi, *Pitar simpsoni* (Pit); PtGe, *Parastarte triquetra* (Gem); PtPi, *Pitar tumens* (Pit); PvTa, *Paphia vernicosa* (Tap); RbTa, *Ruditapes bruguieri* (Tap); RdTa, *Ruditapes decussatus* (Tap); RpTa, *Ruditapes philippinarum* (Tap); RvTa, *Ruditapes variegatus* (Tap); SeSu, *Sunetta effosa* (Sun); SmSu, *Sunetta meroe* (Sun); SnPi, *Saxidomus nuttalli* (Pit); SpPi, *Striacallista phasianella* (Pit); SqSa, *Samarangia quadrangularis* (Sam); SsSu, *Sunetta scripta* (Sun); TaPi, *Transenpitar americanus* (Pit); TaTa, *Tapes aureus* (Tap); TcM, *Transennella conradina* (Mer); TdTa, *Tapes dorsatus* (Tap); TlTa, *Tapes literatus* (Tap); TmM, *Tivela mactroides* (Mer); TmTu, *Turtonia minuta* (Tur); TrTa, *Tapes rhomboides* (Tap); TsM, *Tivela stultorum* (Mer); TvM, *Tivela ventricosa* (Mer);

VgTa, *Venerupis galactites* (Tap); VsTa, *Venerupis senegalensis* (Tap); VvV, *Venus verrucosa* (Ven). Family/subfamily abbreviations as in Appendix 2.

EXTERNAL SHELL SCULPTURE

0 External radial sculpture (traditional):
0 = absent (AaCh, AiO, AlD, CcPi, CfO, CfPi, CgCh, ChPi, CiPi, ClPi, CmO, CpCl, CrGo, CsCl, CsGo, CsPe, CtCy, CxGo, DcD, DeD, DvD, ElCh, GcGl, GdGo, GeV, GgGe, GiSa, GmGo, GrGl, GuTa, HcPi, K1Ta, K2Ta, KmTa, KsTa, LcPi, LlCh, LoPi, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MnPi, MoTa, MsPi, MvTa, NpPi, NsN, NtPi, NuTa, PaPi, PciPi, PcoGo, PcoPi, PcrGo, PdTa, PeD, PeTa, PfPi, PjPi, PmPi, PrPi, PsPi, PtGe, PtPi, PvTa, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TcM, TdTa, TmM, TmTu, TrTa, TsM, TvM).
1 = present, at any strength or spacing (AlV, CcCh, CeCh, CnGo, CpGo, CsCy, D2D, GcGo, GpGo, GtGo, IcTa, IiTa, ImTa, KrTa, MmTa, PcCh, PlPe, PlV, PpPe, RbTa, RdTa, RpTa, RvTa, TaTa, TlTa, VgTa, VsTa, VvV).

1 External commarginal (concentric) sculpture (on main body of shell) (traditional):
0 = absent (AiO, CcPi, ChPi, CmO, CsCl, CsPe, CtCy, ElCh, GcGl, GgGe, GiSa, GrGl, GuTa, HcPi, LcPi, MaPi, MlaM, MluM, MlyM, MmM, MmPi, MnPi, MsPi, NpPi, PaPi, PciPi, PcrGo, PjPi, PlPe, PmPi, PsPi, PtGe, RbTa, SpPi, SsSu, TcM, TmM, TmTu, TsM, TvM).
1 = rounded commarginals (AaCh, AlD, CfO, CfPi, CgCh, CiPi, ClPi, CnGo, CpCl, CpGo, CrGo, CsCy, CsGo, CxGo, DcD, DeD, GcGo, GdGo, GeV, GmGo, GpGo, GtGo, IcTa, KmTa, KrTa, LoPi, MhTa, MjTa, MmTa, MoTa, MvTa, NsN, NtPi, NuTa, PcoGo, PcoPi, PdTa, PeTa, PfPi, PrPi, PtPi, PvTa, RdTa, RpTa, RvTa, SeSu, SmSu, SnPi, TaPi, TaTa, TlTa, TrTa, VsTa).
2 = erect commarginals (AlV, CcCh, CeCh, D2D, DvD, IiTa, ImTa, K1Ta, K2Ta, KsTa, LlCh, MmCh, PcCh, PeD, PlV, PpPe, TdTa, VgTa, VvV).
? (SqSa obscured by a sand-covered periostracum, cleaned specimen not available).

OTHER EXTERNAL SHELL FEATURES

2 Lunule (traditional):
0 = absent (AiO, CfO, CmO, CpCl, CsCy, CsPe, GcGl, GgGe, GrGl, IcTa, IiTa, ImTa, NsN, NtPi, PlPe, PpPe, PtGe, SnPi).
1 = present but not bounded by groove (CgCh, MhTa, MjTa, MvTa, PvTa, RdTa, TrTa, VgTa, VsTa).
2 = present and bounded by groove (AaCh, AlD, AlV, CcCh, CcPi, CeCh, CfPi, ChPi based on *C. thorae*, CiPi, ClPi, CnGo, CpGo, CrGo, CsCl, CsGo, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGo, GdGo, GeV, GiSa, GmGo, GpGo, GtGo, GuTa, HcPi, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LlCh, LoPi, MaPi, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MmTa, MnPi, MoTa, MsPi, NpPi, NuTa, PaPi, PcCh, PciPi, PcoGo, PcoPi, PcrGo, PdTa, PeD, PeTa, PfPi, PjPi, PlV, PmPi, PrPi, PsPi, PtPi, RbTa, RpTa, RvTa, SeSu, SmSu, SpPi, SqSa, SsSu, TaPi, TaTa, TcM, TdTa, TlTa, TmM, TmTu, TsM, TvM, VvV).

3 Lunule (inflation):
0 = flush with main body of shell (CcCh, CcPi, CeCh, CfPi, ChPi based on *C. thorae*, CiPi, ClPi, CnGo, CpGo, CrGo, CsCl, CsGo, CtCy, CxGo, GcGo, GdGo, GiSa, GmGo, GpGo, GtGo, GuTa, HcPi, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LoPi, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MnPi, MoTa, MsPi, MvTa, NpPi, NuTa, PaPi, PcCh, PciPi, PcoGo, PcoPi, PcrGo, PfPi, PjPi, PlV, PmPi, PrPi, PsPi, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SpPi, TaPi, TaTa, TcM, TdTa, TmM, TmTu, TrTa, TsM, TvM, VgTa, VsTa, VvV).
1 = impressed below level of main body of shell (AaCh, AlD, AlV, CgCh, D2D, DcD, DeD, DvD, ElCh, GeV, LlCh, MmTa, PdTa, PeD, PeTa, SeSu, SmSu, SqSa, SsSu, TlTa).
n/a = lunule absent (AiO, CfO, CmO, CpCl, CsCy, CsPe, GcGl, GgGe, GrGl, IcTa, IiTa, ImTa, NsN, NtPi, PlPe, PpPe, PtGe, SnPi).

4 Escutcheon (traditional):
0 = absent (AiO, CcPi, CfO, CfPi, ChPi based on *C. thorae*, CiPi, ClPi, CmO, CsCl, CsCy, CsPe, CtCy, D2D, DcD, DeD, GcGl, GgGe, GrGl, GuTa, HcPi, IcTa, LcPi, LoPi, MaPi, MlaM, MluM, MlyM, MmM, MmPi, MmTa, MsPi, NpPi, NsN, NtPi, PaPi, PciPi, PcoPi, PcrGo, PeD, PfPi, PjPi, PlPe, PpPe, PtGe, SnPi, SpPi, TaPi, TcM, TmM, TmTu, TsM, TvM).
1 = present but not bounded by groove (AaCh, AlD, AlV, CcCh, CeCh, CgCh, CnGo, CpCl, CpGo, CrGo, CsGo, CxGo, DvD, ElCh, GcGo, GdGo, GeV, GiSa, GmGo, GpGo, GtGo, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, MhTa, MjTa, MmCh, MnPi, MoTa, MvTa, NuTa, PcCh, PcoGo, PdTa, PeTa, PmPi, PrPi, PsPi, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SeSu, SmSu, SqSa, SsSu, TaTa, TdTa, TlTa, TrTa, VgTa, VsTa, VvV).
2 = present and bounded by groove (PlV).

5 Escutcheon sunken (traditional):
0 = not sunken (AaCh, AlD, AlV, CcCh, CeCh, CgCh, CnGo, CpCl, CpGo, CrGo, CsGo, CxGo, DvD, ElCh, GcGo, GdGo, GeV, GiSa, GmGo, GpGo, GtGo, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, MhTa, MjTa, MmCh, MnPi, MoTa, MvTa, NuTa, PcCh, PcoGo, PdTa, PeTa, PlV, PmPi, PrPi, PsPi, PtPi, PvTa,

RbTa, RdTa, RpTa, RvTa, SqSa, TaTa, TdTa, TlTa, TrTa, VgTa, VsTa, VvV).
1 = greatly sunken (SeSu, SmSu, SsSu).
n/a = escutcheon absent (AiO, CcPi, CfO, CfPi, ChPi based on *C. thorae*, CiPi, ClPi, CmO, CsCl, CsCy, CsPe, CtCy, D2D, DcD, DeD, GcGl, GgGe, GrGl, GuTa, HcPi, IcTa, LcPi, LoPi, MaPi, MlaM, MluM, MlyM, MmM, MmPi, MmTa, MsPi, NpPi, NsN, NtPi, PaPi, PciPi, PcoPi, PcrGo, PeD, PfPi, PjPi, PlPe, PpPe, PtGe, SnPi, SpPi, TaPi, TcM, TmM, TmTu, TsM, TvM).

6 Periostracum (traditional, problematic):
This traditional presence/absence character was omitted from the all-morphology data set due to the potentially high possibility of artefact caused by over-cleaned museum specimens used during the coding process.
0 = present (AiO, AlD, CcPi, CfO, CfPi, ChPi, CiPi, ClPi, CmO, CpCl, CsCl, CsCy, CsGo, CtCy, DcD, GcGl, GgGe, GiSa, GrGl, GuTa, HcPi, K1Ta, K2Ta, KmTa, KsTa, LcPi, LlCh, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmM, MmPi, MnPi, MsPi, NpPi, NtPi, PaPi, PciPi, PcoGo, PcoPi, PdTa, PeD, PeTa, PfPi, PjPi, PmPi, PrPi, PsPi, PtGe, PvTa, RpTa, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TaTa, TcM, TdTa, TmM, TmTu, TsM, TvM).
1 = absent (nonpersistent) (AaCh, AlV, CcCh, CeCh, CgCh, CnGo, CpGo, CrGo, CsPe, CxGo, D2D, DeD, DvD, ElCh, GcGo, GdGo, GeV, GmGo, GpGo, GtGo, IcTa, IiTa, ImTa, KrTa, LoPi, MmCh, MmTa, MoTa, MvTa, NsN, NuTa, PcCh, PcrGo, PlPe, PlV, PpPe, PtPi, RbTa, RdTa, RvTa, TlTa, TrTa, VgTa, VsTa, VvV).

7 Shell length to height ratio (= 'shells getting longer') (traditional):
Divisions of this continuous character were arbitrarily chosen by calculating the mean length to height ratio of the material examined and using that as the breakpoint.
0 = not elongated, less than or equal to mean 1.3 (AiO 1.1, AlD 1.0, AlV 1.2, CcCh 1.2, CcPi 1.3, CeCh 1.2, CfO 1.1, CfPi 1.3, CgCh 1.1, ChPi 1.3, CiPi 1.2, CnGo 1.1, CpCl 1.2, CpGo 1.1, CrGo 1.1, CsCl 1.2, CsCy 1.0, CsGo 1.1, CsPe 1.2, CtCy 1.0, CxGo 1.0, D2D 1.0, DcD 1.0, DeD 1.16, DvD 1.1, ElCh 1.2, GcGo 1.0, GdGo 1.2, GeV 1.1, GgGe 1.1, GiSa 1.1, GmGo 1.1, GpGo 1.3, GtGo 1.2, GuTa 1.2, HcPi 1.2, K1Ta 1.3, K2Ta 1.3, KrTa 1.3, KsTa 1.3, LcPi 1.1, LoPi 1.2, MaPi 1.3, MhTa 1.3, MjTa 1.3, MlaM 1.3, MluM 1.2, MlyM 1.2, MmCh 1.2, MmM 1.2, MmPi 1.3, MmTa 1.3, MsPi 1.3, MvTa 1.3, NpPi 1.2, NsN 1.1, NtPi 1.2, PaPi 1.2, PcCh 1.1, PciPi 1.2, PcoGo 1.0, PcoPi 1.1, PcrGo 1.2, PeD 1.1, PfPi 1.2, PjPi 1.2, PlPe 1.3, PlV 1.1, PmPi 1.1, PrPi 1.1, PsPi 1.1, PtGe 0.8, PtPi 1.2, SnPi 1.3, SpPi 1.3, SqSa 1.2, SsSu 1.3, TaPi 1.2, TmM 1.2, TvM 1.2, VvV 1.2).
1 = elongated, greater than mean 1.3 (AaCh 1.4, ClPi 1.4, CmO 2.5, GcGl 1.71, GrGl 2.1, IcTa 1.6, IiTa 1.5, ImTa 1.4, KmTa 1.5, LlCh 1.4, MnPi 1.9, MoTa 1.4, NuTa 1.7, PdTa 1.5, PeTa 1.6, PpPe 2.9, PvTa 1.6, RbTa 2.1, RdTa 1.4, RpTa 1.4, RvTa 1.4, SeSu 1.4, SmSu 1.4, TaTa 1.4, TcM 1.4, TdTa 1.5, TlTa 1.5, TmTu 1.43, TrTa 1.4, TsM 1.4, VgTa 1.6, VsTa 1.4).

8 Shell inflation to height ratio (= 'shells getting more compressed') (traditional):
Divisions of this continuous character were arbitrarily chosen by calculating the mean inflation to height ratio of the material examined and using that as the breakpoint.
0 = not compressed, greater than or equal to mean 0.7 (AaCh 0.7, AlV 0.7, CcCh 0.8, CcPi 0.7, CeCh 0.7, CfO 0.7, CfPi 0.7, CiPi 0.7, CsCl 0.7, CsCy 0.7, GeV 0.8, GiSa 0.8, GrGl 0.7, GtGo 0.7, IcTa 0.9, IiTa 0.7, ImTa 0.8, KmTa 0.7, KrTa 0.7, LcPi 0.7, LlCh 0.9, LoPi 0.7, MhTa 0.7, MjTa 0.7, MmM 0.7, MsPi 0.7, MvTa 0.7, PaPi 0.7, PcCh 0.7, PciPi 0.7, PcoPi 0.87, PcrGo 0.7, PdTa 0.7, PfPi 0.7, PjPi 0.7, PlPe 0.7, PlV 0.8, PmPi 0.7, PpPe 0.9, PrPi 0.7, PsPi 0.7, PtPi 0.7, PvTa 0.7, RbTa 0.8, RdTa 0.7, RpTa 0.7, SnPi 0.7, TcM 0.7, TdTa 0.7, TmM 0.7, TmTu 0.7, TrTa 0.7, VgTa 0.7, VvV 0.7).
1 = compressed, less than mean 0.7 (AiO 0.6, AlD 0.4, CgCh 0.6, ClPi 0.6, CmO 0.6, CnGo 0.6, CpCl 0.6, CpGo 0.4, CrGo 0.4, CsGo 0.3, CsPe 0.6, CtCy 0.6, CxGo 0.3, D2D 0.5, DcD 0.5, DeD 0.39, DvD 0.6, ElCh 0.6, GcGl 0.6, GcGo 0.6, GdGo 0.6, GgGe 0.5, GmGo 0.5, GpGo 0.6, GuTa 0.6, HcPi 0.6, K1Ta 0.6, K2Ta 0.6, KsTa 0.6, MaPi 0.6, MlaM 0.6, MluM 0.6, MlyM 0.5, MmCh 0.6, MmPi 0.6, MmTa 0.5, MnPi 0.6, MoTa 0.6, NpPi 0.62, NtPi 0.6, NuTa 0.5, PcoGo 0.4, PeD 0.5, PeTa 0.6, PtGe 0.6, RvTa 0.6, SeSu 0.5, SmSu 0.5, SpPi 0.6, SqSa 0.6, SsSu 0.5, TaPi 0.5, TaTa 0.6, TlTa 0.5, TsM 0.6, TvM 0.6, VsTa 0.6).
? = no specimens available, not determinable from literature data (ChPi, NsN).

9 Position of umbo – ratio of distance of umbo from posterior edge to length of lateral line (lower level of adductor muscles) (traditional):
0 = umbones subcentral, ratio less than or equal to 0.70 (AaCh 0.68, AiO 0.67, AlV 0.66, CfO 0.58, ChPi 0.68, ClPi 0.70, CmO 0.68, CnGo 0.66, CpGo 0.69, CrGo 0.67, CsCy 0.62, CsGo 0.67, CsPe 0.58, CxGo 0.63, DeD 0.60, GcGl 0.606, GcGo 0.60, GdGo 0.67, GgGe 0.65, GmGo 0.68, GrGl 0.697, GtGo 0.68, GuTa 0.63, HcPi 0.61, IcTa 0.62, KmTa 0.69, LcPi 0.68, LlCh 0.67, LoPi 0.62, MaPi 0.69, MlaM 0.58, MluM 0.68, MlyM 0.67, MmM 0.62, MmTa 0.55, MvTa 0.66, NpPi 0.67, NsN 0.59, NtPi 0.65, NuTa 0.64, PaPi 0.64, PcoGo 0.62, PdTa 0.65, PeD 0.69, PeTa 0.67, PfPi 0.63,

PrPi 0.64, PsPi 0.66, PtGe 0.64, PvTa 0.63, RbTa 0.66, RdTa 0.65, RpTa 0.67, RvTa 0.68, SeSu 0.53, SmSu 0.52, SnPi 0.70, SpPi 0.69, SsSu 0.52, TaPi 0.62, TcM 0.63, TmM 0.57, TsM 0.50, TvM 0.59).
1 = umbones more anterior, ratio greater than 0.70 (AlD 0.73, CcCh 0.73, CcPi 0.74, CeCh 0.74, CfPi 0.71, CgCh 0.73, CiPi 0.78, CpCl 0.76, CsCl 0.80, CtCy 0.74, D2D 0.71, DcD 0.74, DvD 0.75, ElCh 0.73, GeV 0.72, GiSa 0.83, GpGo 0.70, IiTa 0.75, ImTa 0.79, K1Ta 0.74, K2Ta 0.75, KrTa 0.78, KsTa 0.79, MhTa 0.72, MjTa 0.71, MmCh 0.76, MmPi 0.70, MnPi 0.72, MoTa 0.71, MsPi 0.74, PcCh 0.80, PciPi 0.73, PcoPi 0.82, PcrGo 0.73, PjPi 0.71, PlPe 0.74, PlV 0.75, PmPi 0.73, PpPe 0.79, PtPi 0.73, SqSa 0.84, TaTa 0.72, TdTa 0.74, TlTa 0.73, TmTu 0.73, TrTa 0.70, VgTa 0.79, VsTa 0.75, VvV 0.74).

INTERNAL SHELL FEATURES

10 Internal valve edge (traditional):
Although this character was coded and retained in the all-morphology data set, there is some evidence of homoplasy. Taylor, Kennedy & Hall (1969) found that marginal denticles correspond to radial ribs on the composite prisms in the outer shell layer; this radial structure clearly shows in specimens of *Mercenaria mercenaria* in which the outer shell layers have abraded (e.g. on early growth stages, AMNH 105144; on subfossil shells, AMNH 272045). However, *Austrovenus stutchburii* lacks the radially ribbed outer prismatic layer but has marginal denticles, which are related solely to external sculpture. Also in this data set, obliquely (NtPi, TcM) and commarginally (NpPi) grooved shell margins were coded identically.
0 = smooth (AiO, AlD, CcPi, CfO, CfPi, ChPi based on *C. thorae*, CiPi, ClPi, CmO, CnGo, CpCl, CsCl, CsGo, CsPe, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGl, GcGo, GiSa, GrGl, GuTa, HcPi, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LoPi, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmM, MmPi, MmTa, MnPi, MoTa, MsPi, MvTa, NsN, NuTa, PaPi, PciPi, PdTa, PeD, PeTa, PfPi, PjPi, PlPe, PmPi, PpPe, PrPi, PsPi, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SnPi, SpPi, SqSa, TaPi, TaTa, TdTa, TlTa, TmM, TmTu, TrTa, TsM, TvM, VgTa, VsTa).
1 = denticulate (AaCh, AlV, CcCh, CeCh, CgCh, CpGo, CrGo, CsCy, GdGo, GeV, GgGe, GmGo, GpGo, GtGo, LlCh, MmCh, PcCh, PcoGo, PcoPi, PcrGo, PlV, PtGe, SeSu, SmSu, SsSu, VvV).
2 = grooved (NpPi, NtPi, TcM).

11 Pallial sinus, plus general shape (traditional):
0 = absent, i.e. pallial line attaching at base of posterior adductor muscle scar (coded as present even if tightly or half-appressed to posterior adductor muscle scar) (CmO, NsN, TmTu).
1 = rounded (AiO, CcPi, CfO, CiPi, ClPi, CsPe, GiSa, GuTa, KmTa, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmM, MmPi, MmTa, MnPi, MoTa, MsPi, MvTa, NpPi, NtPi, NuTa, PdTa, PeTa, PlPe, PlV, PpPe, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaTa, TdTa, TlTa, TmM, TrTa, TsM, TvM, VgTa, VsTa).
2 = tapering throughout (AaCh, AlD, AlV, CcCh, CeCh, CfPi, CgCh, ChPi, CnGo, CpCl, CpGo, CrGo, CsCl, CsCy, CsGo, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGl, GcGo, GdGo, GeV, GgGe, GmGo, GpGo, GrGl, GtGo, HcPi, IcTa, IiTa, ImTa, K1Ta, K2Ta, KrTa, KsTa, LcPi, LlCh, LoPi, MmCh, PaPi, PcCh, PciPi, PcoGo, PcoPi, PcrGo, PeD, PfPi, PjPi, PmPi, PrPi, PsPi, PtGe, TaPi, TcM, VvV).

12 Anterior extent (size) of pallial sinus (ratio of anterior extent of sinus over shell length) (traditional):
0 = ratio less than 0.30 (small sinus) (AiO 0.17, CfO 0.23, CnGo 0.23, CsGo 0.22, CpGo 0.25, CrGo 0.26, CxGo 0.21, GdGo 0.23, GiSa 0.18, GmGo 0.23, GpGo 0.23, GtGo 0.23, LcPi 0.23, LoPi 0.29, PcoGo 0.22, PcrGo 0.24, SqSa 0.18).
1 = ratio 0.30–0.50 (AaCh 0.35, AlV 0.32, CcCh 0.37, CeCh 0.32, CfPi 0.50, CgCh 0.30, ChPi 0.47, CsCl 0.45, CsCy 0.49, DeD 0.48, DvD 0.49, GcGo 0.30, ElCh 0.47, GeV 0.34, GgGe 0.37, GuTa 0.32, IcTa 0.45, IiTa 0.42, ImTa 0.44, K1Ta 0.39, K2Ta 0.39, KmTa 0.48, KrTa 0.35, KsTa 0.38, LlCh 0.30, MhTa 0.46, MjTa 0.45, MlaM 0.40, MluM 0.33, MlyM 0.39, MmCh 0.43, MmM 0.42, MmTa 0.44, MnPi 0.46, MoTa 0.46, MvTa 0.50, NpPi 0.49, NtPi 0.44, NuTa 0.41, PaPi 0.45, PcCh 0.34, PciPi 0.39, PcoPi 0.39, PdTa 0.50, PeTa 0.42, PfPi 0.45, PjPi 0.44, PlV 0.41, PmPi 0.41, PrPi 0.39, PsPi 0.47, PtGe 0.42, PtPi 0.50, PvTa 0.40, RbTa 0.36, RpTa 0.50, RvTa 0.45, SeSu 0.42, SmSu 0.45, SpPi 0.46, SsSu 0.40, TaPi 0.48, TaTa 0.50, TcM 0.47, TdTa 0.48, TlTa 0.45, TmM 0.45, TrTa 0.44, TsM 0.47, TvM 0.35, VvV 0.34).
2 = ratio greater than 0.50 (large sinus) (AlD 0.62, CcPi 0.52, CiPi 0.56, ClPi 0.54, CpCl 0.57, CsPe 0.69, CtCy 0.57, D2D 0.59, DcD 0.58, GcGl 0.574, GrGl 0.503, HcPi 0.55, MaPi 0.51, MmPi 0.51, MsPi 0.60, PeD 0.64, PlPe 0.64, PpPe 0.57, RdTa 0.53, SnPi 0.53, VgTa 0.52, VsTa 0.59).
n/a = pallial sinus absent (CmO, NsN, TmTu).

13 Position of greatest anterior extent of pallial sinus relative to lateral line (lower level of adductor muscles):
0 = at or below lateral line (AaCh, AiO, AlV, CcCh, CcPi, CeCh, CfO, CfPi, CgCh, ChPi, CiPi, ClPi, CnGo, CpCl, CpGo, CrGo, CsCl, CsGo, CsPe, CxGo, ElCh,

GcGl, GcGo, GdGo, GeV, GiSa, GmGo, GpGo, GrGl, GtGo, GuTa, HcPi, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LlCh, LoPi, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MmTa, MnPi, MoTa, MsPi, MvTa, NpPi, NtPi, NuTa, PaPi, PcCh, PciPi, PcoGo, PcoPi, PcrGo, PdTa, PfPi, PjPi, PlPe, PlV, PmPi, PpPe, PrPi, PtGe, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TaTa, TcM, TdTa, TlTa, TmM, TrTa, TsM, TvM, VgTa, VsTa, VvV).
1 = above lateral line (AlD, CsCy, CtCy, D2D, DcD, DeD, DvD, GgGe, IcTa, IiTa, PeD, PeTa, PsPi).
n/a = pallial sinus absent (CmO, NsN, TmTu).

14 Anterior pedal retractor muscle scar, relationship with anterior adductor muscle scar:
0 = separated (AlV, CcCh, CmO, CnGo, CpGo, CsGo, CxGo, GdGo, GeV, GgGe, GpGo, GtGo, GuTa, IcTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, MhTa, MjTa, MoTa, MvTa, NuTa, PcoGo, PcrGo, PlV, PvTa, RbTa, RdTa, RpTa, RvTa, TaTa, TdTa, TlTa, TmTu, TrTa, VsTa, VvV).
1 = in partial contact, by narrow to wide band (AaCh, AiO, AlD, CcPi, CeCh, CfO, CfPi, CgCh, CiPi, ClPi, CpCl, CrGo, CsCy, CtCy, DcD, DeD, DvD, ElCh, GcGo, GmGo, HcPi, IiTa, LcPi, LoPi, MaPi, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MmTa, MnPi, MsPi, NpPi, NtPi, PcCh, PciPi, PcoPi, PdTa, PeD, PeTa, PjPi, PpPe, PsPi, PtPi, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TcM, TmM, TsM, TvM, VgTa).
2 = in full contact (ChPi based on *C. thorae*, CsCl, CsPe, D2D, GcGl, GiSa, GrGl, PaPi, PfPi, PmPi, PrPi).
? (NsN not visible, PlPe unclear, PtGe ambiguous, some specimens united, some separate).

HINGE TEETH

15 AII (anterior lateral, left valve), independent of anterior cardinal (2a):
The probability of two forms of anterior lateral teeth in venerids was discussed by Bieler *et al*. (2004). This form is the 'true' anterior lateral, unaligned with the anterior cardinal tooth.
0 = present (AlD, CcPi, CfO, CfPi, ChPi, CiPi, ClPi, CnGo, CpGo, CrGo, CsGo, CxGo, GcGo, GdGo, GpGo, GtGo, HcPi, LcPi, LoPi, MaPi, MlaM, MluM, MlyM, MmM, MmPi, MnPi, MsPi, NpPi, NtPi, PaPi, PciPi, PcoGo, PcoPi, PcrGo, PfPi, PjPi, PmPi, PrPi, PsPi, PtPi, SeSu, SmSu, SnPi, SpPi, SsSu, TaPi, TcM).
1 = absent (AaCh, AiO, AlV, CcCh, CeCh, CgCh, CmO, CpCl, CsCl, CsCy, CsPe, CtCy, D2D, DcD, DeD, DvD, ElCh, GcGl, GeV, GgGe, GiSa, GmGo, GrGl, GuTa, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, MhTa, MjTa, MmCh, MmTa, MoTa, MvTa, NsN, NuTa, PcCh, PdTa, PeD, PeTa, PlPe, PlV, PpPe, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, SqSa, TaTa, TdTa, TlTa, TmM, TmTu, TrTa, TsM, TvM, VgTa, VsTa, VvV).

16 AII (anterior lateral, left valve), novel extension of anterior cardinal (2a):
See character 15. This form is the 'pseudolateral' tooth, aligned with and an apparent extension of the anterior cardinal tooth.
0 = absent (AaCh, AlD, CcCh, CcPi, CeCh, CfO, CfPi, CgCh, ChPi, CiPi, ClPi, CmO, CnGo, CpCl, CpGo, CrGo, CsCl, CsCy, CsGo, CsPe, CtCy, CxGo, ElCh, GcGl, GcGo, GdGo, GgGe, GiSa, GpGo, GrGl, GtGo, GuTa, HcPi, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LlCh, LoPi, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MmTa, MnPi, MoTa, MsPi, MvTa, NpPi, NsN, NtPi, NuTa, PaPi, PcCh, PciPi, PcoGo, PcoPi, PcrGo, PdTa, PeTa, PfPi, PjPi, PlPe, PmPi, PpPe, PrPi, PsPi, PtGe, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SeSu, SmSu, SnPi, SpPi, SsSu, TaPi, TaTa, TcM, TdTa, TlTa, TmTu, TrTa, VgTa, VsTa).
1 = present (AiO, AlV, D2D, DcD, DeD, DvD, GeV, GmGo, PeD, PlV, SqSa, TmM, TsM, TvM, VvV).

17 Margins of AII socket developed into tooth-like structure(s) (AI and/or AIII):
0 = developed to any extent (AiO, AlD, CcPi, CfO, CfPi, ChPi, CiPi, ClPi, CnGo, CpGo, CrGo, CsGo, CxGo, DcD, DeD, DvD, GcGo, GdGo, GmGo, GpGo, GtGo, HcPi, LcPi, LoPi, MaPi, MlaM, MluM, MlyM, MmM, MmPi, MnPi, MsPi, NpPi, NtPi, PaPi, PciPi, PcoGo, PcoPi, PcrGo, PeD, PfPi, PjPi, PmPi, PrPi, PsPi, PtPi, SeSu, SmSu, SnPi, SpPi, SsSu, TaPi, TcM, TmM, TsM, TvM).
1 = not developed (AlV, D2D, GeV, PlV, SqSa, VvV).
n/a = AII absent (AaCh, CcCh, CeCh, CgCh, CmO, CpCl, CsCl, CsCy, CsPe, CtCy, ElCh, GcGl, GgGe, GiSa, GrGl, GuTa, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, MhTa, MjTa, MmCh, MmTa, MoTa, MvTa, NsN, NuTa, PcCh, PdTa, PeTa, PlPe, PpPe, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, TaTa, TdTa, TlTa, TmTu, TrTa, VgTa, VsTa).

18 Any anterior lateral tooth (traditional):
This traditional character was recoded as characters 23 and 24 in the all-morphology data set.
0 = present (AiO, AlD, AlV, CcPi, CfO, CfPi, ChPi, CiPi, ClPi, CnGo, CpGo, CrGo, CsGo, CxGo, D2D, DcD, DeD, DvD, GcGo, GdGo, GeV, GmGo, GpGo, GtGo, HcPi, LcPi, LoPi, MaPi, MlaM, MluM, MlyM, MmM, MmPi, MnPi, MsPi, NpPi, NtPi, PaPi, PciPi, PcoGo, PcoPi, PcrGo, PeD, PfPi, PjPi, PlV, PmPi, PrPi,

PsPi, PtPi, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TcM, TmM, TsM, TvM, VvV).
1 = absent (AaCh, CcCh, CeCh, CgCh, CmO, CpCl, CsCl, CsCy, CsPe, CtCy, ElCh, GcGl, GgGe, GiSa, GrGl, GuTa, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, MhTa, MjTa, MmCh, MmTa, MoTa, MvTa, NsN, NuTa, PcCh, PdTa, PeTa, PlPe, PpPe, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, TaTa, TdTa, TlTa, TmTu, TrTa, VgTa, VsTa).

19 Posterior lateral tooth (traditional):
0 = present (AiO, CfO, NsN, TmTu).
1 = absent (AaCh, AlD, AlV, CcCh, CcPi, CeCh, CfPi, CgCh, ChPi, CiPi, ClPi, CmO, CnGo, CpCl, CpGo, CrGo, CsCl, CsCy, CsGo, CsPe, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGl, GcGo, GdGo, GeV, GgGe, GiSa, GmGo, GpGo, GrGl, GtGo, GuTa, HcPi, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LlCh, LoPi, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MmTa, MnPi, MoTa, MsPi, MvTa, NpPi, NtPi, NuTa, PaPi, PcCh, PciPi, PcoGo, PcoPi, PcrGo, PdTa, PeD, PeTa, PfPi, PjPi, PlPe, PlV, PmPi, PpPe, PrPi, PsPi, PtGe, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TaTa, TcM, TdTa, TlTa, TmM, TrTa, TsM, TvM, VgTa, VsTa, VvV).

20 2b (middle cardinal, left valve) (traditional):
0 = smooth (AaCh, AiO, AlD, CcCh, CcPi, CeCh, CfPi, CgCh, ChPi based on *C. thorae*, CiPi, ClPi, CmO, CnGo, CpCl, CpGo, CrGo, CsCl, CsCy, CsGo, CtCy, CxGo, D2D, DcD, DeD, DvD, GcGo, GgGe, GiSa, GmGo, GtGo, GuTa, HcPi, IcTa, LcPi, LlCh, LoPi, MaPi, MlaM, MluM, MlyM, MmM, MmPi, MnPi, MsPi, NpPi, NsN, NtPi, PaPi, PciPi, PcoGo, PcoPi, PcrGo, PeD, PfPi, PjPi, PmPi, PpPe, PrPi, PsPi, PtPi, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TcM, TmTu).
1 = bifid (AlV, CfO, CsPe, ElCh, GcGl, GdGo, GeV, GpGo, GrGl, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, MhTa, MjTa, MmCh, MmTa, MoTa, MvTa, NuTa, PcCh, PdTa, PeTa, PlPe, PlV, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, TaTa, TdTa, TlTa, TmM, TrTa, TsM, TvM, VgTa, VsTa, VvV).

21 3b (posterior cardinal, right valve) (traditional):
0 = smooth (AaCh, CcCh, CeCh, CmO, CsGo, GcGo, GtGo, IcTa, LlCh, NsN, PcrGo, PlPe, PpPe, PtGe, TmTu).
1 = bifid (AiO, AlD, AlV, CcPi, CfO, CfPi, CgCh, ChPi based on *C. thorae*, CiPi, ClPi, CnGo, CpCl, CpGo, CrGo, CsCl, CsCy, CsPe, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGl, GdGo, GeV, GgGe, GiSa, GmGo, GpGo, GrGl, GuTa, HcPi, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LoPi, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MmTa, MnPi, MoTa, MsPi, MvTa, NpPi, NtPi, NuTa, PaPi, PcCh, PciPi, PcoGo, PcoPi, PdTa, PeD, PeTa, PfPi, PjPi, PlV, PmPi, PrPi, PsPi, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TaTa, TcM, TdTa, TlTa, TrTa, VgTa, VsTa, VvV).
2 = deeply cleft (TmM, TsM, TvM).

22 1 (middle cardinal, right valve) (traditional):
0 = smooth (AaCh, AiO, AlD, CcCh, CcPi, CeCh, CfPi, CgCh, ChPi based on *C. thorae*, CiPi, ClPi, CmO, CnGo, CpCl, CpGo, CrGo, CsCl, CsCy, CsGo, CtCy, CxGo, D2D, DcD, DeD, DvD, GcGl, GcGo, GdGo, GgGe, GiSa, GmGo, GpGo, GrGl, GtGo, GuTa, HcPi, IcTa, LcPi, LlCh, LoPi, MaPi, MlaM, MluM, MlyM, MmM, MmPi, MnPi, MsPi, NpPi, NsN, PaPi, PciPi, PcoGo, PcoPi, PcrGo, PeD, PfPi, PjPi, PlPe, PmPi, PpPe, PrPi, PsPi, PtGe, PtPi, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TcM, TmM, TmTu, TsM, TvM).
1 = bifid (AlV, CfO, CsPe, ElCh, GeV, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, MhTa, MjTa, MmCh, MmTa, MoTa, MvTa, NtPi, NuTa, PcCh, PdTa, PeTa, PlV, PvTa, RbTa, RdTa, RpTa, RvTa, TaTa, TdTa, TlTa, TrTa, VgTa, VsTa, VvV).

23 2a and 2b, dorsal association (traditional):
0 = separate (AiO, CcCh, CeCh, CfO, CgCh, CmO, CnGo, CpGo, CsGo, CsPe, CxGo, GcGl, GeV, GgGe, GpGo, GrGl, GtGo, GuTa, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, MhTa, MjTa, MlaM, MluM, MlyM, MmM, MmTa, MoTa, MvTa, NuTa, PdTa, PeTa, PlPe, PlV, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, TaTa, TdTa, TlTa, TmM, TrTa, TsM, VgTa, VsTa, VvV).
1 = united in an inverted 'V' (AaCh, AlD, AlV, CcPi, CfPi, ChPi, CiPi, ClPi, CpCl, CrGo, CsCl, CsCy, CtCy, D2D, DcD, DeD, DvD, ElCh, GcGo, GdGo, GiSa, GmGo, HcPi, LcPi, LoPi, MaPi, MmCh, MmPi, MnPi, MsPi, NpPi, NsN, NtPi, PaPi, PcCh, PciPi, PcoGo, PcoPi, PcrGo, PeD, PfPi, PjPi, PmPi, PpPe, PrPi, PsPi, PtPi, SeSu, SmSu, SnPi, SpPi, SqSa, SsSu, TaPi, TcM, TmTu, TvM).

24 3a (anterior cardinal, right valve):
0 = sessile (AaCh, AiO, AlV, CcCh, CeCh, CfO, CgCh, CiPi, CnGo, CpCl, CpGo, CsCy, CsGo, CtCy, CxGo, DvD, GcGo, GdGo, GeV, GgGe, GiSa, GmGo, GpGo, GtGo, GuTa, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LlCh, MhTa, MjTa, MmCh, MmM, MoTa, MvTa, NsN, NtPi, NuTa, PcCh, PcoGo, PcrGo, PdTa, PeD, PeTa, PlV, PpPe, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, SeSu, SqSa, TdTa, TlTa, TmM, TrTa, TvM, VgTa, VsTa, VvV).

1 = excavated under 3a, so that sockets for AII (if present) and 2a are confluent (AlD, CcPi, CfPi, ChPi based on *C. thorae*, ClPi, CrGo, CsCl, D2D, DcD, DeD, ElCh, GcGl, GrGl, HcPi, LoPi, MaPi, MlaM, MluM, MlyM, MmPi, MmTa, MnPi, MsPi, NpPi, PaPi, PciPi, PcoPi, PfPi, PjPi, PmPi, PrPi, PsPi, PtPi, SmSu, SnPi, SpPi, SsSu, TaPi, TaTa, TcM, TsM).
n/a = 3a absent (CmO, CsPe, PlPe, TmTu).

25 3a and 1 (anterior and middle cardinals, right valve), orientation to one another (traditional):
The derived state of this character is traditionally diagnostic of Pitarinae, Dosiniinae, and Clementiinae, but was also found during this study in members of Cyclininae, Glauconomidae, Meretricinae, Neoleptonidae, and Sunettinae.
0 = radiating V-shaped (not parallel, 'cardinals tending to radiate') (AaCh, AiO, AlV, CcCh, CeCh, CfO, CgCh, CnGo, CpGo, CrGo, CsCy, CsGo, CxGo, ElCh, GcGl, GcGo, GdGo, GeV, GgGe, GiSa, GmGo, GpGo, GtGo, GuTa, IcTa, IiTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, MhTa, MjTa, MlaM, MluM, MlyM, MmCh, MmM, MmTa, MoTa, MvTa, NtPi, NuTa, PcCh, PcoGo, PcrGo, PdTa, PeTa, PlV, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, SnPi, SqSa, TaTa, TdTa, TlTa, TmM, TrTa, TsM, VgTa, VsTa, VvV).
1 = parallel or nearly so ('cardinals not tending to radiate') (AlD, CcPi, CfPi, ChPi based on *C. thorae*, CiPi, ClPi, CpCl, CsCl, CtCy, D2D, DcD, DeD, DvD, GrGl, HcPi, LcPi, LoPi, MaPi, MmPi, MnPi, MsPi, NpPi, NsN, PaPi, PciPi, PcoPi, PeD, PfPi, PjPi, PmPi, PrPi, PsPi, PtPi, SeSu, SmSu, SpPi, SsSu, TaPi, TcM, TvM).
n/a = 3a absent, unless otherwise noted (CmO, CsPe, PlPe, PpPe 3a/1 'fused', TmTu).

26 4b and nymph, separation:
0 = separated (AaCh, AiO, AlD, AlV, CcCh, CcPi, CeCh, CfO, CfPi, CgCh, ChPi based on *C. thorae*, CmO, CpGo, CrGo, CsCl, CsCy, CsGo, CsPe, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGl, GcGo, GdGo, GeV, GgGe, GiSa, GmGo, GpGo, GrGl, GtGo, HcPi, IiTa, ImTa, KmTa, KrTa, KsTa, LcPi, LlCh, LoPi, MaPi, MhTa, MjTa, MluM, MlyM, MmM, MmPi, MnPi, MoTa, MsPi, MvTa, NpPi, NtPi, NuTa, PaPi, PcCh, PciPi, PcoGo, PcoPi, PdTa, PeD, PeTa, PfPi, PjPi, PlV, PmPi, PpPe, PrPi, PsPi, PtGe, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SnPi, SqSa, TaPi, TaTa, TcM, TdTa, TlTa, TmM, TmTu, TrTa, TsM, TvM, VgTa, VsTa, VvV).
1 = appressed (CiPi, ClPi, CnGo, CpCl half, GuTa, IcTa, K1Ta, K2Ta, MlaM, MmCh, MmTa, PcrGo, PlPe, SeSu, SmSu, SpPi, SsSu).
n/a = 4b absent (NsN).

27 Space between 4b and nymph, sculpture:
0 = smooth (AiO, AlD, AlV, CcCh, CeCh, CfPi, CgCh, ChPi based on *C. thorae*, CmO, CpCl, CpGo, CrGo, CsCl, CsCy, CsGo, CsPe, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGl, GcGo, GdGo, GeV, GgGe, GiSa, GmGo, GpGo, GrGl, GtGo, HcPi, IiTa, ImTa, KrTa, KsTa, LcPi, LlCh, LoPi, MhTa, MjTa, MnPi, MvTa, NpPi, NtPi, NuTa, PaPi, PcCh, PciPi, PcoGo, PcoPi, PdTa, PeD, PeTa, PfPi, PjPi, PlV, PmPi, PpPe, PrPi, PsPi, PtGe, PtPi, PvTa, RbTa, RdTa, RpTa, RvTa, SnPi, SqSa, TaPi, TaTa, TcM, TdTa, TlTa, TmTu, TrTa, VgTa, VsTa, VvV).
1 = irregularly rugose (KmTa, MoTa, TmM, TsM, TvM).
2 = granulose (CcPi, CfO, MaPi, MmPi).
3 = regular vertical pits or bars (AaCh, MluM, MlyM, MmM, MsPi).
n/a = 4b fully appressed to nymph, unless otherwise noted (CiPi, ClPi, CnGo, GuTa, IcTa, K1Ta, K2Ta, MlaM, MmCh, MmTa, NsN 4b absent, PcrGo, PlPe, SeSu, SmSu, SpPi, SsSu).

28 Hinge plate (traditional):
0 = no attrition (not excavated) at ventral edge of cardinal teeth (AaCh, AiO, AlD, AlV, CcCh, CcPi, CeCh, CfO, CfPi, CgCh, ChPi based on *C. thorae*, CiPi, ClPi, CmO, CnGo, CpGo, CrGo, CsCl, CsCy, CsGo, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGo, GdGo, GeV, GgGe, GiSa, GmGo, GpGo, GtGo, GuTa, HcPi, KmTa, LcPi, LlCh, LoPi, MaPi, MhTa, MjTa, MlaM, MluM, MlyM, MmCh, MmM, MmPi, MmTa, MnPi, MoTa, MsPi, MvTa, NpPi, NtPi, PaPi, PcCh, PciPi, PcoGo, PcoPi, PcrGo, PdTa, PeD, PfPi, PjPi, PlV, PmPi, PrPi, PsPi, PtGe, PtPi, PvTa, SeSu, SmSu, SpPi, SsSu, TaPi, TcM, TmM, TmTu, TsM, TvM, VvV).
1 = attrition (excavated between cardinal teeth) (CpCl, CsPe, GcGl, GrGl, IcTa, IiTa, ImTa, K1Ta, K2Ta, KrTa, KsTa, NsN, NuTa, PeTa, PlPe, PpPe, RbTa, RdTa, RpTa, RvTa, SnPi, SqSa, TaTa, TdTa, TlTa, TrTa, VgTa, VsTa).

ANATOMICAL CHARACTERS

Anatomical characters within Veneridae and Veneroidea are remarkably uniform and thus not potentially rich for this type of analysis. Anatomical characters have been taken herein from the siphons, gills, foot, and circulatory system. Unfortunately, the most complex of bivalve structures, the stomach, has so far shown little variation within the family.

29 Gill, outer demibranch (OD), groove:
0 = with marginal food groove (AiO, ElCh, MmCh, PlV, PpPe, RdTa, RpTa, SnPi, TmM, TsM, VsTa).

1 = without marginal food groove (AaCh, AlD, AlV, CcCh, CcPi, CeCh, CfO, ChPi, CiPi, ClPi, CmO, CnGo, CpGo, CrGo, CsCl, CsGo, CsPe, CtCy, CxGo, D2D, DeD, DvD, GcGl, GcGo, GdGo, GiSa, GmGo, GrGl, GtGo, GuTa, HcPi, IcTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, LoPi, MaPi, MhTa, MjTa, MmM, MmPi, MnPi, MsPi, NpPi, NtPi, NuTa, PcCh, PciPi, PcoPi, PdTa, PeD, PfPi, PjPi, PlPe, PmPi, PrPi, PsPi, PvTa, RbTa, RvTa, TaTa, TcM, TdTa, TrTa, TvM, VgTa, VvV).
n/a (GgGe OD single lamella, PtGe OD absent?, TmTu OD absent).
? = no preserved specimens, incomplete literature data only, except as noted (CfPi, CgCh, CpCl, CsCy, DcD, GeV, GpGo, IiTa, LcPi, MlaM, MluM, MlyM, MmTa, MoTa, MvTa, NsN, PaPi, PcoGo, PcrGo, PeTa have posterior half of specimen only, PtPi, SeSu, SmSu, SpPi, SqSa, SsSu, TaPi, TlTa).

30 Gill, inner demibranch, groove:
0 = with marginal food groove (AaCh, AiO, AlD, AlV, CcCh, CcPi, CeCh, CfO, ChPi, CiPi, ClPi, CnGo, CpGo, CsCl, CsGo, CsPe, CtCy, CxGo, D2D, DeD, DvD, ElCh, GcGl, GcGo, GdGo, GgGe, GmGo, GrGl, GtGo, GuTa, HcPi, IcTa, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, LoPi, MaPi, MhTa, MjTa, MluM, MmCh, MmPi, MnPi, MsPi, NpPi, NtPi, NuTa, PcCh, PciPi, PcoPi, PdTa, PeD, PfPi, PjPi, PlPe, PlV, PmPi, PpPe, PrPi, PsPi, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, SnPi, TaTa, TcM, TdTa, TmM, TmTu, TrTa, TsM, TvM, VgTa, VsTa, VvV).
1 = without marginal food groove (CmO, CrGo, MmM).
? = no preserved specimens, incomplete literature data only, except as noted (CfPi, CgCh, CpCl, CsCy, DcD, GeV, GiSa unclear, GpGo, IiTa, LcPi, MlaM, MlyM, MmTa, MoTa, MvTa, NsN, PaPi, PcoGo, PcrGo, PeTa have posterior half of specimen only, PtPi, SeSu, SmSu, SpPi, SqSa, SsSu, TaPi, TlTa).

31 Siphonal fusion (traditional, problematic):
This traditional character was omitted from the all-morphology data set due to the potentially high possibility of artefact caused by variable interpretations from living specimens, preserved specimens, photographs, and gross anatomical drawings in published literature.
0 = not fused (CfO, CmO, CnGo, CsPe, CxGo, GtGo, ImTa, KmTa, MmM, NuTa, PeTa, PlPe, PlV, PtGe, PvTa, RbTa, RvTa, TvM, VvV).
1 = fused approximately mid-length (CfPi, CgCh, GgGe, GuTa, IiTa, K1Ta, K2Ta, LcPi, MhTa, MjTa, MvTa, PciPi, PcoGo, PcrGo, PdTa, PpPe, TaTa, TdTa, TmM, VgTa).
2 = fused near or to tip (AaCh, AiO, AlD, AlV, CcCh, CcPi, CeCh, ChPi, CiPi, ClPi, CpCl, CpGo, CrGo, CsCl, CtCy, D2D, DcD, DeD, DvD, ElCh, GcGl, GdGo, GmGo, GrGl, HcPi, IcTa, LlCh, LoPi, MaPi, MmCh, MmPi, MnPi, MsPi, NpPi, PaPi, PcCh, PcoPi, PeD, PfPi, PjPi, PmPi, PrPi, PsPi, SnPi, SpPi, TaPi, TcM, TsM).
n/a = siphons absent, unless otherwise noted (NsN excurrent siphon only, TmTu excurrent siphon only, GcGo, GiSa).
? = no preserved specimens, incomplete literature data only, unless otherwise noted (CsCy, CsGo conflicting data, GeV, GpGo, KrTa variable, KsTa variable, MlaM, MluM, MlyM, MmTa, MoTa, NtPi conflicting data, PtPi, RdTa conflicting data, RpTa variable, SeSu, SmSu, SqSa, SsSu, TlTa, TrTa, VsTa variable).

32 Foot, byssate (traditional, problematic):
This traditional presence/absence character was omitted from the all-morphology data set due to the potentially high possibility of artefact caused by variable interpretations from juvenile or adult specimens (ontogenetic change), and from extrapolations based on the presence of a pedal groove.
0 = byssate or with byssal groove/gland (CcCh, CfO juvenile byssate, CmO, CpGo, GgGe juvenile byssate, IcTa, IiTa unverified, ImTa, K1Ta, K2Ta, KrTa, KsTa, LcPi, MvTa, NtPi, PdTa, PpPe, PtGe, RbTa, RdTa, RpTa, RvTa, TaTa, TmTu, VgTa, VsTa).
1 = not byssate or without byssal groove/gland (AaCh, AiO, AlV, CcPi, CeCh, CiPi, ClPi, CnGo, CrGo, CsGo, CsPe, CtCy, CxGo, D2D, DeD, DvD, ElCh, GcGl, GcGo, GdGo, GiSa, GmGo, GrGl, GtGo, GuTa, HcPi, LlCh, LoPi, MaPi, MmCh, MmM, MmPi, MnPi, MsPi, NpPi, NsN, PaPi, PcCh, PciPi, PcoPi, PeD, PeTa, PfPi, PjPi, PlPe, PlV, PmPi, PrPi, PsPi, PvTa, SnPi, SpPi, TcM, TmM, TsM, TvM, VvV).
? = no preserved specimens, incomplete literature data only, except as noted (AlD, CfPi, CgCh, ChPi, CpCl, CsCl specimen damaged, CsCy, DcD, GeV, GpGo, KmTa, MhTa, MjTa, MlaM, MluM, MlyM, MmTa, MoTa, NuTa, PcoGo, PcrGo, PtPi, SeSu, SmSu, SqSa, SsSu, TaPi, TdTa, TlTa, TrTa).

33 Foot, shape (traditional):
0 = 'wedge-shaped' or anteriorly pointed (AaCh, AiO, AlV, CcCh, CcPi, CeCh, CfO, CfPi, CgCh, ChPi, CiPi, ClPi, CmO, CnGo, CpCl, CpGo, CrGo, CsGo, CsPe, CtCy, CxGo, ElCh, GcGl, GcGo, GdGo, GgGe, GiSa, GmGo, GrGl, GtGo, GuTa, HcPi, IcTa, IiTa unverified, ImTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LcPi, LlCh, LoPi, MaPi, MluM, MmCh, MmM, MmPi, MnPi, MsPi, MvTa, NpPi, NsN, NtPi, NuTa, PaPi, PcCh, PciPi, PcoPi, PdTa, PeTa, PfPi, PjPi, PlPe, PlV, PmPi, PpPe, PrPi, PsPi, PtGe, PvTa, RbTa, RdTa, RpTa, RvTa, SnPi, TaPi, TcM, TmM, TmTu, TsM, TvM, VgTa, VsTa, VvV).

1 = 'lunate' or quadrangular (AlD, D2D, DcD unconfirmed, DeD, DvD, PeD).
? = no preserved specimens, incomplete literature data only, except as noted (CsCl specimen damaged, CsCy, GeV, GpGo, MhTa, MjTa, MlaM, MlyM, MmTa, MoTa, PcoGo, PcrGo, PtPi, SeSu, SmSu, SpPi, SqSa, SsSu, TaTa, TdTa, TlTa, TrTa).

34 Aortic bulb:
The aortic bulb (= bulbus arteriosus) is a spongy pendulous structure on the ventral side of the posterior aorta and hindgut in the vicinity of the kidney (anterior to the posterior adductor muscle). Its function is to prevent rupture of the heart when the siphons and foot retract suddenly, forcing haemolymph backwards into the posterior aorta; its size can expand by a factor of two to three times its 'empty' size (Eble, 2001), a factor that was noted during dissections in this study. It might also be involved in regulating relative amounts of haemolymph entering the anterior and posterior aortae from the ventricle, or as a neurohaemal site (Deaton, Felgenhauer & Duhon, 2001). As such it is present in a variety of other siphonate bivalves (e.g. Mactridae, Pelseneer, 1906), although it is generally recognized as a characteristic of Veneroidea (e.g. Harte, 1998b). Homologies are uncertain with the posterior aortic bulb of *Fragum* (Cardiidae; Morton, 2000) and of the anterior aortic bulbs of Mytilidae and Ostreidae (Eble, 1996), the latter forming as common origins of major arteries supplying the stomach and posterior visceral mass.
0 = absent (AiO, CfO, CmO, GgGe, ImTa, NsN, TmTu).
1 = present (AaCh unclear, AlV, CcCh, CcPi, CeCh, CgCh, CiPi, ClPi, CnGo, CrGo, CsCl, CsGo, CsPe, CtCy, CxGo, D2D, DcD, DeD, DvD, ElCh, GcGl unclear, GcGo, GdGo, GiSa, GrGl, GtGo, GuTa, HcPi, IcTa, K1Ta, K2Ta, KmTa, KrTa, KsTa, LlCh, LoPi, MaPi, MmCh, MmM, MmPi, MnPi, MsPi, NpPi, NuTa, PaPi, PciPi, PcoPi, PdTa unclear, PfPi, PjPi, PlPe, PlV, PmPi, PpPe, PrPi, PsPi, PvTa, RbTa, RdTa, RpTa, SnPi, SpPi, TcM, TmM, TsM, TvM, VgTa, VvV).
? = no preserved specimens, incomplete literature data only, except as noted (AlD, CfPi, ChPi, CpCl, CpGo specimen damaged, CsCy, GpGo, GeV, GmGo, IiTa, LcPi, MhTa, MjTa, MlaM, MluM, MlyM, MmTa, MoTa, MvTa, NtPi, PcCh, PcoGo, PcrGo, PeD, PeTa specimen damaged, PtGe, PtPi, RvTa, SqSa, SeSu, SmSu, SsSu, TaPi specimen dried, TaTa, TdTa, TlTa, TrTa, VsTa).

Full morphological data matrix (n, not applicable; u, unknown). Bold indicates those taxa that were used in the restricted taxon data set.

Numbers corresponding to list above	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Traditional data set	0	1	2		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
All-morphology data set	0	1	2	3	4	5		6	7	8	9	10	11	12	13	14	15	16		17	18	19	20	21	22	23	24	25	26	27	28			29	30
All zero	**0**	**0**	**0**	**n**	**0**	**n**	**0**	**0**	**0**	**0**	**0**	**0**	**n**	**n**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Arctica islandica	**0**	**0**	**0**	**n**	**0**	**n**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**2**	**1**	**0**	**0**	
Calyptogena magnifica	**0**	**0**	**0**	**n**	**0**	**n**	**0**	**1**	**1**	**0**	**0**	**0**	**n**	**n**	**0**	**1**	**0**	**n**	**1**	**1**	**0**	**0**	**0**	**0**	**n**	**n**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**
Corbicula fluminea	**0**	**1**	**0**	**n**	**0**	**n**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**2**	**0**	**1**	**0**	**0**	**0**	**0**	**0**
Cooperella subdiaphana	**0**	**0**	**0**	**n**	**0**	**n**	**1**	**0**	**1**	**0**	**0**	**1**	**2**	**0**	**2**	**1**	**0**	**n**	**1**	**1**	**1**	**1**	**1**	**0**	**n**	**n**	**0**	**0**	**1**	**1**	**0**	**0**	**1**	**0**	**1**
Glauconome chinensis	**0**	**0**	**0**	**n**	**0**	**n**	**0**	**1**	**1**	**0**	**0**	**2**	**2**	**0**	**2**	**1**	**0**	**n**	**1**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**2**	**1**	**0**	**1**
Glauconome rugosa	**0**	**0**	**0**	**n**	**0**	**n**	**0**	**1**	**0**	**0**	**0**	**2**	**2**	**0**	**2**	**1**	**0**	**n**	**1**	**1**	**1**	**1**	**0**	**0**	**1**	**1**	**0**	**0**	**1**	**1**	**0**	**2**	**1**	**0**	**1**
Neolepton sulcatulum	**0**	**1**	**0**	**n**	**0**	**n**	**1**	**0**	**u**	**0**	**0**	**0**	**n**	**n**	**u**	**1**	**0**	**n**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**n**	**n**	**1**	**u**	**u**	**n**	**1**	**0**	**0**
Petricolaria pholadiformis	**1**	**2**	**0**	**n**	**0**	**n**	**1**	**1**	**0**	**1**	**0**	**1**	**2**	**0**	**1**	**1**	**0**	**n**	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**n**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**1**
Petricola lapicida	**1**	**0**	**0**	**n**	**0**	**n**	**1**	**0**	**0**	**1**	**0**	**1**	**2**	**0**	**u**	**1**	**0**	**n**	**1**	**1**	**1**	**0**	**0**	**0**	**n**	**n**	**1**	**n**	**1**	**1**	**0**	**0**	**1**	**0**	**1**
Turtonia minuta	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**1**	**0**	**1**	**0**	**0**	**n**	**n**	**0**	**1**	**0**	**n**	**1**	**0**	**0**	**0**	**0**	**1**	**n**	**n**	**0**	**0**	**0**	**n**	**0**	**n**	**0**	**0**	**0**
Anomalocardia auberiana	0	1	2	1	1	0	1	1	0	0	1	2	1	0	1	1	0	n	1	1	0	0	0	1	0	0	0	3	0	1	0	2	1	0	1
Antigona lamellaris	**1**	**2**	**2**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**1**	**2**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**1**	**1**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**2**	**1**	**0**	**1**
Asa lupina	0	1	2	1	1	0	0	0	1	1	0	2	2	1	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	u	1	u
Callista chione	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**0**	**0**	**1**	**0**	**1**	**2**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**2**	**0**	**1**	**0**	**2**	**1**	**0**	**1**
Callista florida	0	1	2	0	0	n	0	0	0	1	0	2	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	u	u	1	u	0	u
Callocardia hungerfordi	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**0**	**u**	**0**	**0**	**2**	**1**	**0**	**2**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**2**	**u**	**0**	**u**
Chamelea gallina	0	1	1	1	1	0	1	0	1	1	1	2	1	0	1	1	0	n	1	1	0	1	0	0	0	0	0	0	0	u	u	1	u	0	1
Chione cancellata	**1**	**2**	**2**	**0**	**1**	**0**	**1**	**0**	**0**	**1**	**1**	**2**	**1**	**0**	**0**	**1**	**0**	**n**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**2**	**0**	**0**	**1**
Chione elevata	1	2	2	0	1	0	1	0	0	1	1	2	1	0	1	1	0	n	1	1	0	0	0	0	0	0	0	0	0	1	0	2	1	0	1
Circe nummulina	1	1	2	0	1	0	1	0	1	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	n	0	1	0	0	1	0	1

Continued

Numbers corresponding to list above	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Traditional data set	0	1	2		3	4	5	6	7	8	9	10	11						12	13	14	15	16	17	18	19			20			21	22	23	
All-morphology data set	0	1	2	3	4	5		6	7	8	9	10	11	12	13	14	15	16		17	18	19	20	21	22	23	24	25	26	27	28			29	30
Circe plicatina	1	1	2	0	1	0	1	0	1	0	1	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	2	0	0	u
Circe rivularis	0	1	2	0	1	0	1	0	1	0	1	2	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	0	1	1	2	1	0	1
Circe cf. *rivularis*	0	1	2	0	1	0	1	0	1	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1
Circe scripta	**0**	**1**	**2**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**u**	**1**	**0**	**1**
Clementia papyracea	**0**	**1**	**0**	**n**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**2**	**2**	**0**	**1**	**1**	**0**	**n**	**1**	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**0**	**1**	**u**	**u**	**2**	**u**	**0**	**u**
Compsomyax subdiaphana	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**0**	**0**	**1**	**0**	**2**	**1**	**0**	**2**	**1**	**0**	**n**	**1**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**2**	**u**	**u**	**1**
Costacallista impar	**0**	**1**	**2**	**0**	**0**	**n**	**0**	**0**	**0**	**1**	**0**	**1**	**2**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**n**	**0**	**1**	**0**	**2**	**1**	**0**	**1**
Costacallista lilacina	0	1	2	0	0	n	0	1	1	0	0	1	2	0	1	0	0	0	0	1	0	1	0	1	1	1	1	n	0	1	0	2	1	0	1
Cyclina sinensis	**1**	**1**	**0**	**n**	**0**	**n**	**0**	**0**	**0**	**0**	**1**	**2**	**1**	**1**	**1**	**1**	**0**	**n**	**1**	**1**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**u**	**u**	**u**	**u**	**u**	**u**
Cyclinella tenuis	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**0**	**1**	**1**	**0**	**2**	**2**	**1**	**1**	**1**	**0**	**n**	**1**	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**2**	**1**	**0**	**1**
Dosinia concentrica	**0**	**1**	**2**	**1**	**0**	**n**	**0**	**0**	**1**	**1**	**0**	**2**	**2**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**1**	**0**	**0**	**0**	**u**	**u**	**2**	**u**	**1**	**1**
Dosinia excisa	0	1	2	1	0	n	1	0	1	0	0	2	1	1	1	1	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	1	1
Dosinia victoriae	0	2	2	1	1	0	1	0	1	1	0	2	1	1	1	1	1	0	0	1	0	1	0	1	0	1	0	0	0	1	0	2	1	1	1
Dosinia sp. 2	1	2	2	1	0	n	1	0	1	1	0	2	2	1	2	1	1	1	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	1	1
Eurhomalea lenticularis	0	0	2	1	1	0	1	0	1	1	0	2	1	0	1	1	0	n	1	1	1	1	1	1	1	0	0	0	0	0	0	2	1	0	1
Gafrarium dispar	**0**	**1**	**2**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**u**	**u**	**2**	**u**	**1**	**1**
Gafrarium pectinata	**1**	**1**	**2**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**u**	**u**	**u**	**u**	**u**	**u**
Gafrarium tumidum	1	1	2	0	1	0	1	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1
Gemma gemma	**0**	**0**	**0**	**n**	**0**	**n**	**0**	**0**	**1**	**0**	**1**	**2**	**1**	**1**	**0**	**1**	**0**	**n**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**n**	**0**	**1**	**0**	**0**	**0**
Globivenus effossa	0	1	2	1	1	0	1	0	0	1	1	2	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	u	u	u	u	u	u
Gomphina undulosa	0	0	2	0	0	n	0	0	1	0	0	1	1	0	0	1	0	n	1	1	0	1	0	0	0	0	0	1	n	0	1	0	1	1	0	1
Gouldia cerina	**1**	**1**	**2**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**0**	**2**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**n**	**1**	**0**	**1**
Gouldia minima	0	1	2	0	1	0	1	0	1	0	1	2	0	0	1	1	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0	2	1	0	u
Granicorium indutum	**0**	**0**	**2**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**2**	**1**	**0**	**n**	**1**	**1**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**u**	**n**	**1**	**0**	**1**
Hyphantosoma caperi	0	0	2	0	0	n	0	0	1	0	0	2	2	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1
Irus crenatus	1	1	0	n	0	n	1	1	0	0	0	2	1	1	0	1	0	n	1	1	0	0	0	0	0	0	0	1	n	1	1	0	2	0	0	1
Irus irus	1	2	0	n	1	0	1	1	0	1	0	2	1	1	1	1	0	n	1	1	1	1	1	0	0	0	0	0	1	u	u	1	0	0	0	u
Irus macrophyllus	1	2	0	n	1	0	1	1	0	1	0	2	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0
Katelysia marmorata	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	1	0	1	0	0	u	0	1
Katelysia rhytiphora	1	1	2	0	1	0	1	0	0	1	0	2	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	1	0	u	0	0	1
Katelysia scalarina	0	2	2	0	1	0	0	0	1	1	0	2	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	1	0	u	0	0	1
Katelysia sp. 1	0	2	2	0	1	0	0	0	1	1	0	2	1	0	0	1	0	n	1	1	1	1	1	0	0	0	1	n	1	1	0	1	0	0	1
Katelysia sp. 2	0	2	2	0	1	0	0	0	1	1	0	2	1	0	0	1	0	n	1	1	1	1	1	0	0	0	1	n	1	1	0	1	0	0	1
Lioconcha castrensis	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**0**	**0**	**0**	**0**	**2**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**u**	**u**	**1**	**0**	**0**	**u**
Lioconcha ornata	**0**	**1**	**2**	**0**	**0**	**n**	**1**	**0**	**0**	**0**	**0**	**2**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**2**	**1**	**0**	**1**
Lirophora latilirata	0	2	2	1	1	0	0	1	0	0	1	2	1	0	0	1	0	n	1	1	0	0	0	0	0	0	0	0	0	1	0	2	1	0	1
Macridiscus melanaegis	1	1	2	1	0	n	1	0	1	0	0	1	1	0	1	1	0	n	1	1	1	1	1	0	1	0	1	n	0	u	u	u	u	u	u
Macrocallista maculata	0	0	2	0	0	n	0	0	1	1	0	1	2	0	1	0	0	0	0	1	0	1	0	1	1	1	0	2	0	1	0	2	1	0	1
Macrocallista nimbosa	0	0	2	0	1	0	0	1	1	1	0	1	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1
Marcia hiantina	0	1	1	0	1	0	0	0	0	1	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	0	1	0	1	u	u	u
Marcia japonica	0	1	1	0	1	0	0	0	0	1	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	0	1	0	u	u	u	u
Marcia opima	0	1	2	0	1	0	1	1	1	1	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	0	u	u	u	u	u	u
Marcia virginea	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	0	u	u	1	0	0	u
Megapitaria aurantica	0	0	2	0	0	n	0	0	1	0	0	1	2	0	1	0	0	0	0	1	0	1	0	1	1	1	0	2	0	1	0	2	1	0	1
Megapitaria squalida	0	0	2	0	0	n	0	0	0	1	0	1	2	0	1	0	0	0	0	1	0	1	0	1	1	1	0	3	0	1	0	2	1	0	1
Mercenaria mercenaria	**0**	**2**	**2**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**2**	**1**	**0**	**1**	**1**	**0**	**n**	**1**	**1**	**1**	**1**	**1**	**1**	**0**	**0**	**1**	**n**	**0**	**0**	**0**	**2**	**1**	**0**	**1**
Meretrix lamarcki	0	0	2	0	0	n	0	0	1	0	0	1	1	0	1	0	0	0	0	1	0	1	0	0	1	0	1	n	0	u	u	u	u	u	u
Meretrix lusoria	0	0	2	0	0	n	0	0	1	0	0	1	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	3	0	u	0	u	u	0	u
Meretrix lyrata	0	0	2	0	0	n	0	0	1	0	0	1	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	3	0	u	u	u	u	u	u
Meretrix meretrix	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**3**	**0**	**1**	**1**	**0**	**1**	**0**	**1**
Neotapes undulatus	0	1	2	0	1	0	1	1	1	0	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	1	0	0	u	0	1
Nutricola pannosa	0	0	2	0	0	n	0	0	1	0	2	1	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1
Nutricola tantilla	0	1	0	n	0	n	0	0	1	0	2	1	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	u	0	0	u
Paphia dura	0	1	2	1	1	0	0	1	0	0	0	1	1	0	1	1	0	n	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	1
Paphia euglypta	0	1	2	1	1	0	0	1	1	0	0	1	1	1	1	1	0	n	1	1	1	1	1	0	0	0	0	0	1	u	u	0	1	0	u
Paphia vernicosa	0	1	1	0	1	0	0	1	0	0	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Parastarte triquetra	**0**	**0**	**0**	**n**	**0**	**n**	**0**	**0**	**1**	**0**	**1**	**2**	**1**	**0**	**u**	**1**	**0**	**n**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**n**	**0**	**0**	**0**	**0**	**u**
Parmulophora corrugata	0	1	2	0	1	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	u	u	1	u	u	u
Parmulophora crocea	0	0	2	0	0	n	1	0	0	1	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	n	0	u	u	u	u	u
Pectunculus exoletus	**0**	**2**	**2**	**1**	**0**	**n**	**0**	**0**	**1**	**0**	**0**	**2**	**2**	**1**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**2**	**1**	**1**	**u**
Periglypta listeri	1	2	2	0	2	0	1	0	0	1	1	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1
Pitar fulminatus	0	1	2	0	0	n	0	0	0	0	0	2	1	0	2	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1
Pitar morrhuanus	**0**	**0**	**2**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**2**	**1**	**0**	**2**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**2**	**1**	**0**	**1**
Pitar rudis	0	1	2	0	1	0	0	0	0	0	0	2	1	0	2	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1
Pitar simpsoni	0	0	2	0	1	0	0	0	0	0	0	2	1	1	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1

Continued

Numbers corresponding to list above	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Traditional data set	0	1	2		3	4	5	6	7	8	9	10	11						12	13	14	15	16	17	18	19			20			21	22	23	
All-morphology data set	0	1	2	3	4	5		6	7	8	9	10	11	12	13	14	15	16		17	18	19	20	21	22	23	24	25	26	27	28			29	30
Pitar tumens	**0**	**1**	**2**	**0**	**1**	**0**	**1**	**0**	**0**	**1**	**0**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**u**	**u**	**u**	**u**	**u**	**u**
Pitarina affinis	0	0	2	0	0	n	0	0	0	0	0	2	1	0	2	0	0	0	0	1	0	1	0	1	1	1	0	0	0	u	u	2	1	0	1
Pitarina citrina	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**0**	**0**	**1**	**0**	**2**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**1**	**1**	**0**	**1**
Pitarina japonica	0	0	2	0	0	n	0	0	0	1	0	2	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1
Pitarenus cordatus	0	1	2	0	0	n	0	0	0	1	1	2	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1
Placamen calophylla	1	2	2	0	1	0	1	0	0	1	1	2	1	0	1	1	0	n	1	1	1	1	1	1	0	0	0	0	0	1	0	2	1	0	u
Ruditapes bruguieri	**1**	**0**	**2**	**0**	**1**	**0**	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**1**	**0**	**n**	**1**	**1**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**1**
Ruditapes decussatus	1	1	1	0	1	0	1	1	0	0	0	1	2	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	0	0	u	0	0	1
Ruditapes philippinarum	1	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	0	0	u	0	0	1
Ruditapes variegatus	1	1	2	0	1	0	1	1	1	0	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	u
Samarangia quadrangularis	**0**	**u**	**2**	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**u**	**u**	**u**	**u**	**u**	**u**
Saxidomus nuttalli	0	1	0	n	0	n	0	0	0	0	0	1	2	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	2	1	0	1
Striacallista phasianella	0	0	2	0	0	n	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1	n	0	u	u	2	1	u	1
Sunetta effosa	**0**	**1**	**2**	**1**	**1**	**1**	**0**	**1**	**1**	**0**	**1**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**n**	**0**	**u**	**u**	**u**	**u**	**u**	**u**
Sunetta meroe	**0**	**1**	**2**	**1**	**1**	**1**	**0**	**1**	**1**	**0**	**1**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**1**	**n**	**0**	**u**	**u**	**u**	**u**	**u**	**u**
Sunetta scripta	**0**	**0**	**2**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**1**	**n**	**0**	**u**	**u**	**u**	**u**	**u**	**u**
Tapes aureus	**1**	**1**	**2**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**1**	**1**	**0**	**0**	**1**	**0**	**n**	**1**	**1**	**1**	**1**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**1**	**0**	**u**	**u**
Tapes dorsatus	0	2	2	0	1	0	0	1	0	1	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	0	1	1	0	1	u	u	u
Tapes literatus	**1**	**1**	**2**	**1**	**1**	**0**	**1**	**1**	**1**	**1**	**0**	**1**	**1**	**0**	**0**	**1**	**0**	**n**	**1**	**1**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**u**	**u**	**u**	**u**	**u**	**u**
Tapes rhomboides	0	1	1	0	1	0	1	1	0	1	0	1	1	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	1	0	u	u	u	u
Tivela mactroides	0	0	2	0	0	n	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	2	0	0	0	0	0	1	0	0	0	1	1	0	1
Tivela stultorum	**0**	**0**	**2**	**0**	**0**	**n**	**0**	**1**	**1**	**0**	**0**	**1**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**1**	**1**	**2**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**2**	**1**	**0**	**1**
Tivela ventricosa	0	0	2	0	0	n	0	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	2	0	1	0	1	0	1	0	1	0	0	1	0	1
Transennella conradina	0	0	2	0	0	n	0	1	0	0	2	2	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2	1	0	1
Transenpitar americanus	0	1	2	0	0	n	0	0	1	0	0	2	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	u	u	2	u	0	u
Venerupis galactites	1	2	1	0	1	0	1	1	0	1	0	1	2	0	1	1	0	n	1	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	1
Venerupis senegalensis	1	1	1	0	1	0	1	1	1	1	0	1	2	0	0	1	0	n	1	1	1	1	1	0	0	0	0	0	1	0	0	u	0	0	u
Venus verrucosa	**1**	**2**	**2**	**0**	**1**	**0**	**1**	**0**	**0**	**1**	**1**	**2**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**1**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**1**