

Preliminary phylogenetic analysis of the bivalve family Galeommatidae

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Abstract. A preliminary phylogenetic analysis of species assigned to the ill-defined family Galeommatidae, plus selected others, was attempted in an effort to clarify the relative value of various systematic characters. Aspects of dealing with large numbers of equally parsimonious trees in cladistic analyses and intrinsic problems of analyses based on unordered multistate characters are addressed briefly. The analysis (Hennig86, implicit enumeration) of 18 characters with 46 character states for 20 species yielded 164 equally parsimonious trees (length 52, ci 53, ri 72), displaying five distinctly different branching patterns. Separate consensus trees were produced for the five groups. Of the five topologies, one is considered most likely in an evolutionary context, and is discussed in detail. Three consistent species groups were recognized: 1) *Divariscintilla* group (eight species); 2) *Galeomma-Ehippodonta* group (six species); and 3) *Scintillona-Ceratobornia* group (three species). Two specialized anatomical characters were analyzed for relative systematic value: 1) "hanging" foot morphology, which could have evolved more than once within the Galeommatoidae; 2) flower-like organs, a possible synapomorphy of the *Divariscintilla* species-group. Results also indicated that the monospecific *Phlyctaenachlamys* Popham, 1939, is a junior subjective synonym of *Divariscintilla* Powell, 1932, and suggested that the generic limits of *Galeomma* Sowerby In: Turton, 1825, and *Ehippodonta* Tate, 1889, should be reexamined. Data matrix construction further identified potentially valuable, but currently unusable, characters in need of further investigation: occurrence of flower-like organs; foot morphology including byssus gland(s); homologies of hinge teeth; ligament/resilium apparatus; shell microstructure; reduction/loss of ctenidial interlamellar junctions and outer demibranch; presence/extent of midgut typhlosole, innervation of pallial tentacles, and sperm structure.

"The interchanges of characters and the multiplicity of forms separated by apparently trifling details of structure make this group one of the most perplexing I have ever tried to review."
— William H. Dall, 1899:875.

Galeommatoid bivalves are recognized by a suite of character specializations, character reductions and possible cases of convergence (Boss, 1965; Morton and Scott, 1989). Common traits include a muscular foot modified for snail-like locomotion, a byssus gland present in the adult, species-specific arrangements of sensory papillae and tentacles, anterior-to-posterior water flow through the mantle cavity, and eulamellibranch ctenidia. Trends within the group are toward shell reduction, with corresponding reductions in sculpture, hinge structure and adductor muscles, internalization of the shell by mantle lobes, reduction of the outer demibranch, commensalism, and reproductive specialization, including hermaphroditism, brooding, dwarf males (B. Morton, 1976, 1981; Ó Foighil, 1985a), spermatophores (Ó Foighil, 1985a, b), and mating behavior (Mikkelsen and Bieler, in press).

Five species in the galeommatid genus *Divariscintilla* have been described recently from eastern Florida (Mikkelsen and Bieler, 1989, in press). All five are co-occurring commensals with a single species of burrowing mantis shrimp [*Lysiosquilla scabricauda* (Lamarck)] that inhabits shallow-water sand flats. The only other known member of the genus is the type species, *D. maoria* Powell, 1932, also commensal

in mantis shrimp burrows, in New Zealand.

Anatomical description of the five Floridian species has resulted in redescription of the genus (Mikkelsen and Bieler, 1989), incorporating an interesting suite of complex characters reflective of the clams' specialized nature and habitat. Two of these characters ("hanging" foot morphology, flower-like organs, discussed below), although diagnostic of the genus, are also known from species assigned to other genera, sometimes placed in other nominal families, of Galeommatoidae.

"Hanging" foot morphology involves a bipartite foot with a muscular anterior crawling portion, and an elastic posterior extension. A ciliated ventral groove extends from the primary byssus gland in the antero-ventral part to the terminal, internally-lamellar byssus adhesive gland (see Mikkelsen and Bieler, 1989). This morphology is present in members of the five Floridian *Divariscintilla* species (Mikkelsen and Bieler, 1989: figs. 18, 19, 21, 22; in press), *D. maoria* (see Judd, 1971: 351-352, figs. 1-4; pers. obs.), and *Phlyctaenachlamys lysiosquillina* Popham, 1939 (: 64, figs. 1, 7). It is also known from three members of Lasaeidae (= Erycinidae): *Parabornia squillina* Boss, 1965 (: 4, fig. 3; pers. obs.); *Ceratobornia longipes* (Stimpson, 1855) (Dall, 1899: 889, pl. 88, figs. 10, 11, 13); *C. cema* Narchi, 1966 (: 515, figs. 1, 2, 5).

Flower-like organs are located on the anterior surface of the visceral mass, just ventral to the labial palps. They

are mushroom-shaped, without major nervous supply, with a "head" composed of onion-shaped secretory units emptying into the anterior pallial cavity (Mikkelsen and Bieler, 1989: fig. 23). Their number is species-specific and constant, except in *Divariscintilla yoyo* which has from three to seven organs in a close cluster. Their function is undetermined, but is probably pheromonal, related to intraspecific communication with potential reproductive partners or with free-swimming veliger larvae (Mikkelsen and Bieler, 1989, in press). Flower-like organs are present in members of four of the five Floridian *Divariscintilla* species (Mikkelsen and Bieler, 1989: figs. 26, 27; in press), *D. maoria* (see Judd, 1971: 352, figs. 2, 4, PP; pers. obs.), *Phlyctaenachlamys lysiosquillina* (two in number, pers. obs.), *Vasconiella jeffreysiana* (P. Fischer, 1873) (see Cornet, 1982: fig. 5), and the lasaeid *Parabornia squillina* (single, pers. obs.)

The family Galeommatidae is ill-defined at present. It is differentiated traditionally from other Galeommatoidae mainly by hinge teeth, generally described as irregular, edentulous, or with weak tubercular cardinals (e.g. Chavan *In*: Moore, 1969a; Kay, 1979). This reflects general reduction in the hinge, rather than any defined synapomorphy for the group. In this context, the systematic value of the two specialized characters relative to traditionally employed characters (e.g. hinge teeth, ctenidia) is of interest. In response, a phylogenetic analysis of species assigned to Galeommatidae, plus selected others, was attempted. Characters involving the shell, mantle, mantle cavity, reproduction, and ecology were included, and type species of genera were used whenever possible. The analysis is considered preliminary, in the sense that it is partially based on limited literature data, and as such does not propose to resolve phylogenetic relationships for the family. It has, however, shown the distribution of foot- and flower-like-organ-characters within the group, and perhaps more importantly, identified characters which could not be used at this time due to insufficient data.

MATERIALS AND METHODS

TAXA

Ingroup: Species were selected from as many galeommatid genera as possible, but dependent on those with adequate, available anatomical data. Type species were included whenever possible. Twenty species [18 in Galeommatidae, two in Lasaeidae (= Erycinidae)] were included as members of the ingroup (Appendix 1). Data for most non-Floridian species were based on published literature, but in several cases were supplemented or verified by original observations of specimens (Appendix 1).

Outgroup: Out initial attempts used either or both of the galeommatoidan (but presumably non-galeommatid) species *Montacuta substriata* (Montagu, 1808) and *Lasaea*

rubra (Montagu, 1803) as outgroups. This was abandoned when it became clear that these taxa, with their own specializations (and unresolved taxonomic questions) introduced additional homoplasy complicating the efforts to estimate in-group relationships. Instead, a hypothetical bivalve (all character states = 0) was used as the outgroup. This bivalve, as defined by our character set, approximates closely a generalized member of Lucinoidea, e.g. *Lucina* (see Chavan *In*: Moore, 1969b), except in morphology of the foot which in lucinid species is specialized for burrowing (Yonge and Thompson, 1976).

Abbreviations of repositories are as follows: AMS, Australian Museum, Sydney; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; FSBC, Florida Marine Research Institute, Department of Natural Resources, St. Petersburg; NMP, Natal Museum, Pietermaritzburg, South Africa.

CHARACTERS

Characters used in the analysis were dependent upon those features that could be adequately coded from statements in the literature. Particular attention was paid to those characters which have been employed in genus- and family-level descriptions, e.g. hinge structure. Additional characters were evaluated but could not be used (see Discussion). Eighteen characters were used, involving the shell (ten), anatomy (six), reproduction (one), and life habit (one) (Appendix 2). Commensalism was superimposed upon the completed trees to visualize the taxonomic distribution of commensal versus non-commensal species.

Hinge characters comprised five of the ten shell characters used in this analysis, yet they proved exceedingly difficult to code with regard to the nature and numbers of teeth present (see Discussion). In the absence of data concerning tooth homologies, we coded functional presence/absence states for both cardinal and lateral teeth (characters 5 and 6), i.e. present and interlocking, or present and noninterlocking, or absent. The location of both lateral teeth (character 7), either anterior, posterior or both, was also coded. Thickened ridges along the hinge line (character 8) in several species could not be interpreted as modified lateral teeth with confidence, so they were coded separately as present/absent.

The extent of mantle coverage over the shell (character 10) could not be determined reliably from preserved material nor from published reports based on preserved material alone. Therefore, one question-mark (for *Vasconiella jeffreysiana*) exists in the coding of this character in the final data set. Interpreting the degree of internalization was also a problem. Some species descriptions indicated complete internalization (e.g. *Coleoconcha opalina*, see Barnard, 1964). However in two species with such descriptions (*Chlamydoconcha orcutti*, see B. Morton, 1981; *Phlyctaenachlamys lysiosquillina*, see

Popham, 1939), an umbonal foramen actually exists connecting the external environment and the cavity containing the shell (B. Morton, 1981, and pers. obs., respectively). The mantle tissue with this type of opening is not retractable, even upon preservation. These two cases show a higher degree of mantle fusion than that seen in, e.g. *Divariscintilla troglodytes*, where retraction exposes more than half of the shell. However, in view of the difficulties experienced with *C. orcutti* and *P. lysiosquillina*, all cases of mantle fusion preventing complete retraction, regardless of the degree, were coded identically.

The character "dymantic tentacles" refers to two single dorsal tentacles, one anterior and one posterior, which are used in dymantic, or defensive, display (see B. Morton, 1975). They were coded as present when present morphologically, even when dymantic behavior had not been documented (e.g. for *Galeomma turtoni*, see Popham, 1940). They were coded separately from other, non-dymantic tentacles, which usually exist in lateral pairs.

ANALYSIS

The final data matrix appears in Appendix 3. The Hennig86 program package (version 1.5; Farris, 1988) was used for this analysis on a 486-class IBM-compatible personal computer. Tree generation utilized "implicit enumeration" (ie), an algorithm that guarantees finding all shortest equally parsimonious trees. The terms *consistency index* (ci) and *retention index* (ri) are employed as defined by Kluge and Farris (1969) and Farris (1989), respectively.

No *a priori* assumptions were made regarding

character importance (weighting) or evolutionary direction (ordering of multistate characters). The use of unordered character states avoids bias in tree development. However, the algorithm can find it more parsimonious to interpret the (initially presumed plesiomorphic) state of the outgroup as autapomorphic and the initially presumed synapomorphic state of the ingroup as a symplesiomorphy, shared with the hypothetical ancestor of both ingroup and outgroup. It is therefore necessary to scrutinize every resulting tree for this occurrence [e.g. as discussed further below, all resulting trees assumed some extent of mantle coverage (character 10) for the hypothetical ancestor].

RESULTS

Based on the rigorous ie-algorithm, 164 equally parsimonious trees (length 52, ci 53, ri 72) resulted from the analysis. Each tree was analyzed and most (96%) could be assigned to one of five distinct tree topologies. The remaining trees (4%) were combinations of the five scenarios.

Four of the five topologies (56% of the trees generated) are here considered less likely in an evolutionary context because they are based on assumptions such as complete shell coverage by the mantle in the hypothetical ancestor (character 10 state 3), reversal from lost to interlocking lateral hinge teeth (character 6), a flattened limpet-like ancestor (character 17), or a large number of character state reversals (as opposed to parallel acquisition). The major species groups (discussed below) in these trees were recognizable but often as grades rather than clades.

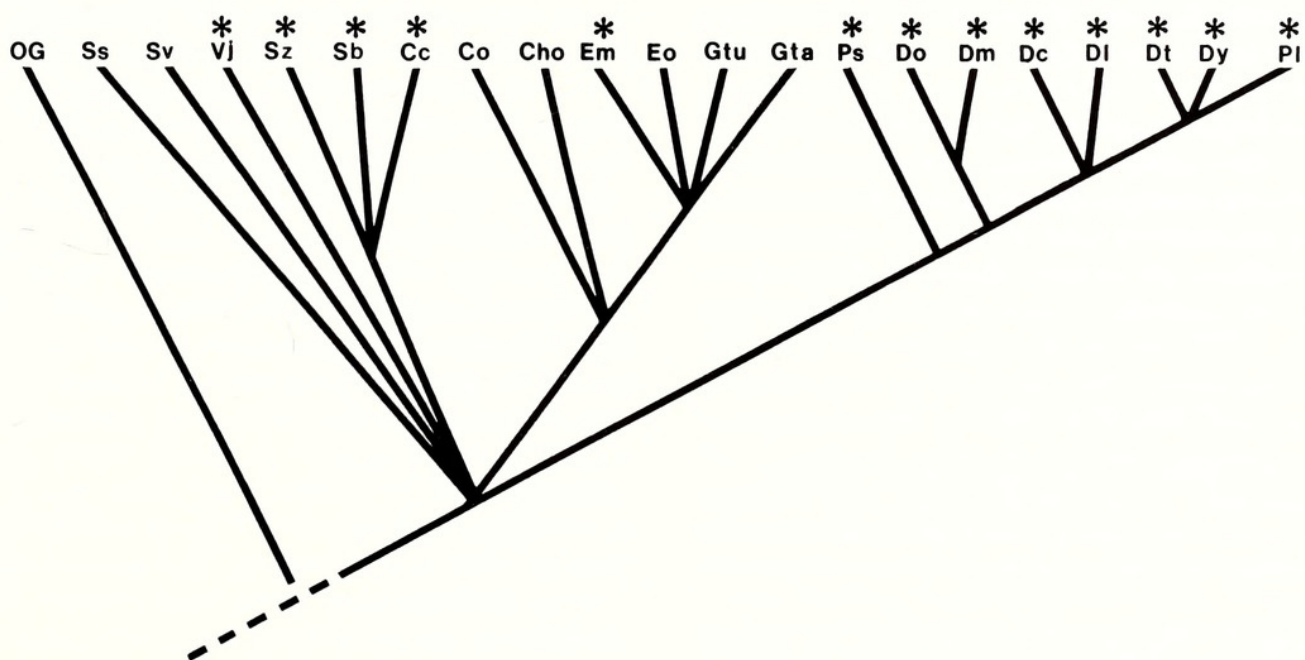


Fig. 1. Nelson (strict) consensus tree of the one of five tree topologies that is here considered most likely in an evolutionary context (based on 44% of all trees generated) [Length = 52, consistency index (ci) = 53, retention index (ri) = 72, * = species known to live commensally with another invertebrate species, OG = hypothetical bivalve outgroup (for other acronyms see Appendix 1)].

The Nelson (strict) consensus tree for the fifth topology, here considered most likely in an evolutionary context (within the limits of the current dataset), is presented in figure 1. Three monophyletic groups were distinct: 1) *Divariscintilla* group (eight species), including *Phlyctaenachlamys lysiosquillina* (Pl), with *Parabornia squillina* (Ps) forming the sister group to *Divariscintilla*; 2) *Galeomma-Ehippodonta* group (six species), including *Coleoconcha opalina* (Co) and *Chlamydoconcha orcutti* (Cho); 3) *Scintillona-Ceratobornia* group (three species), comprising *Scintillona zelandica* (Sz), *S. bellerophon* (Sb), and *Ceratobornia cema* (Cc). *Scintilla stvensoni* (Ss), *S. violescens* (Sv), and *Vasconiella jeffreysiana* (Vj) were not affiliated clearly with any of the three groups, but the two *Scintilla* species (Ss, Sv) appear to be *not* monophyletic. The relationships between the three major branches remain unresolved.

Within the *Divariscintilla*-group, several stable subunits can be recognized. Based on the common character state of anterior shell prolongation (character 2), Dy, Dt and Pl group together. The taxa Do and Dm are linked because of their low degree of shell coverage by the mantle (character 10). Five species (Dc, Dl, Dt, Dy and Pl) fall together because of shell reduction (character 0). *Parabornia squillina* (Ps) joins this clade because of the elongated foot (character 4), absence of lateral hinge teeth (character 7) and presence of a flower-like organ (character 13).

The species of the *Galeomma-Ehippodonta*-group always group together based on the synapomorphies of lateral hinge ridges (character 8), beaded shell sculpture (character 9) and dimantic tentacles (character 12), but with equivocal distinction between the two nominal genera. Two additional taxa (Co and Cho) join the clade based on overall limpet-shape (character 17; Co only), presence of dwarf males (character 16), and a number of character state losses (e.g. cardinal and lateral hinge teeth, characters 5 and 6).

The clade of the *Scintillona-Ceratobornia*-group is determined by the indented hinge plate (character 4), non-interlocking cardinal hinge teeth (character 5), the low degree of shell coverage by the mantle (character 10), and by the specialized foot morphology (character 14, *Scintillona* spp. only).

Two characters in the analysis were interpreted consistently as autapomorphies and not synapomorphies: inequivalve shells and ventral shell notch (characters 1 and 3). The state changes of two other characters (7 and 15; lateral teeth position and adductor muscles) could not positively be placed and could have happened in any of several branches of the trees.

"Hanging" foot morphology (character 14) was not confined to a single group, and may therefore be convergent. It does appear in most members of the *Divariscintilla* group, but also in *Ceratobornia cema* (Cc). Flower-like organs were

primarily confined to members of the *Divariscintilla* group, but are also present in *Vasconiella* (Vj), a taxon of uncertain affiliation at this point. Commensal species (Fig. 1, *) are distributed widely on all trees, confirming a trend toward commensalism in the superfamily, but not defining any taxonomic group.

DISCUSSION

This analysis, that could *not* employ a number of recognizably valuable characters (see below), and that resulted in such a high number of equally parsimonious trees, is obviously a preliminary one. However, without over-interpreting the results, five generalizations can be made. 1) The described *Divariscintilla* species and monotypic *Phlyctaenachlamys* appear to form a monophyletic group. If treated as one genus, *Divariscintilla* Powell, 1932, has priority over *Phlyctaenachlamys* Popham, 1939. 2) The generic allocation of species in *Galeomma* versus *Ehippodonta* needs further study. 3) The postulated close relationship (same genus) of *Scintilla stvensoni* and *S. violescens* is questionable. 4) The relationships between *Ceratobornia cema* and the two studied *Scintillona* species also warrant further investigation. 5) The relationship between *Parabornia squillina* and *Divariscintilla* species, usually placed in different nominal families, needs additional study.

Improvement on the data set using more specimen- (versus literature-) based data is of course indicated before strong taxonomic decisions can be made as a result of phylogenetic analysis of this group. Character states are too often ambiguous in written descriptions, even more so if interpreted from line drawings or photographs. Furthermore, an appreciation of variability of characters within a species (see below) is seldom available in the literature.

We assume that the complex "hanging" foot morphology (with associated glandular structures) and flower-like organs represent synapomorphies within *Galeommatoidea*, but the extent of the groups defined by them presently remains unclear.

Perhaps the most valuable result of this study was the identification of numerous characters that, although potentially valuable, could not be used in the analysis due to lack of data on species not studied by us. These are discussed below as suggestions for needed comparative investigations and/or as useful items to include in future species descriptions.

1. The occurrence of both specialized characters emphasized in this study ("hanging" foot morphology, flower-like organs) requires additional documentation. Examination of additional *Phlyctaenachlamys lysiosquillina* specimens during this study suggested that flower-like organs may vary within a species. These organs were not mentioned or indicated in drawings of anatomy or histological sections in

the excellent original description by Popham (1939). Nor were they present in one of Popham's paratypes (BMNH 1939.5.10.2) examined by us. Therefore, we trust that flower-like organs were not merely overlooked by Popham. Nevertheless, each of three specimens from the Australian Museum (C165143) had two well-defined flower-like organs. Whether this reflects populational, reproductive or seasonal variation is unknown.

In addition to flower-like organs, two other features of *Phlyctaenachlamys lysiosquillina* were clarified during examination of the Australian Museum specimens, and are worthy of mention here: 1) the existence of an umbonal foramen (see above); 2) the presence of ctenidial interlamellar junctions (in inner demibranch, approximately mid-gill) which had been stated as absent by Popham (1939: 72).

2. Hanging foot morphology is complicated. Oldfield (1955, 1961) showed multiple byssus glands in various galeommatoids which compliment our findings in *Divariscintilla*. In *Lasaea rubra*, a "subsidiary byssus gland" empties into the canal of the main byssus gland with its associated byssogenous lamellae in the posterior "heel" of the foot (Oldfield, 1955: 233-234, fig. 4, BG1, BG2, BL). In *Montacuta substriata*, several subsidiary glands "open by long, slender ducts, into the extreme anterior end of the byssus [ventral] groove" (Oldfield, 1961: 270, fig. 7, BG1-3, BL), mirroring the condition seen in Floridian *Divariscintilla* species. In light of these data, as mentioned previously (Mikkelsen and Bieler, 1989), the anteroventral "mucous gland" in the two-part foot of *Ceratobornia cema* should be reevaluated. Behavioral observations and histochemical techniques would be valuable in this area.

3. As was implied above, galeommatoid hinge teeth are difficult to interpret. Problems such as small subumbonal tubercles which may or may not interlock, or lateral ridges which may or may not be true lateral teeth, are not uncommon. Unresolved questions of this kind involving tooth homology prevented rigorous coding of the hinge teeth, and will require ontogenetic studies to resolve with certainty.

Also concerning the hinge, the external ligament and resilium have been described in a variety of ways, e.g. with or without nymph/resilifer/socket, triangular or oblique, subumbonal between teeth or posterior (for examples, see Chavan *In*: Moore, 1969a). Whether these are real differences or mere variation in wording must await reanalysis of hinge structures.

4. Coney (1990) and ourselves (Mikkelsen and Bieler, 1989) have illustrated and described shell microstructure in several galeommatoid species. Additional species should be investigated using more consistent and rigorous methods.

5. Second only to the hinge in traditional taxonomic use in Galeommatoida are the ctenidia. Two potentially useful characters could perhaps be quantified for use in an analysis such as this. 1) Relative size of the outer demibranch

has been subjectively recorded but with implied quantifiable differences, e.g. "much shorter" (*Scintillona zelandica*; J. E. Morton, 1957: 185), "slightly [reduced]" (*Ephippodonta macdougalli*; Woodward, 1893), "longer, dorso-ventrally than the inner" (*Chlamydoconcha orcutti*; B. Morton, 1981). Complete loss of the outer demibranch is characteristic of Montacutidae. 2) Reduction in number or complete loss of interlamellar junctions have been correlated with extensive expansion/contraction of the mantle (Popham, 1939; Narchi, 1966), or with the incubation of larvae in the suprabranchial chamber (B. Morton, 1981). Four of the five Floridian *Divariscintilla* species are known to brood and to have interlamellar junctions. The presence of interlamellar junctions in the type species, *D. maoria*, was also confirmed during this study (from Australian Museum specimens, collected by W. Judd, C165142).

6. The presence and extent of a midgut typhlosole appear to differ among species. For example, it has been reported as absent in *Ceratobornia cema* (see Narchi, 1966), *Phlyctaenachlamys lysiosquillina* (see Popham, 1939), and *Montacuta* spp. (Oldfield, 1961), and as present in *Chlamydoconcha orcutti* (see B. Morton, 1981), *Divariscintilla* spp. (Mikkelsen and Bieler, 1989, in press), and *Galeomma takii* (see B. Morton, 1973).

7. Innervation of the various pallial tentacles could reveal patterns and possible homologies. Many species (e.g. *Ceratobornia cema*, *Scintilla violescens*, *Galeomma turtoni*) show unpaired tentacles along the dorsal midline; in *Divariscintilla yoyo*, these are known to be innervated by branches from both pallial nerves (Mikkelsen and Bieler, 1989: fig. 31). The innervation of "dymantic" tentacles (B. Morton, 1975, 1976) in *Galeomma* and *Ephippodonta* species is especially important to this line of inquiry.

8. Finally, in this group where reproductive complexity is the rule, sperm structure could be a conservative, valuable indicator of phylogenetic relationships. Reported morphologies include elongated curved heads with collared acrosomes [*Divariscintilla* spp., Eckelbarger *et al.*, 1990; *Lasaea australis* (Lamarck, 1818), Ó Foighil, 1988], elongated straight heads with cone-shaped acrosomes [*Mysella tumida* (Carpenter, 1864), Ó Foighil, 1985b], and oval heads (*Chlamydoconcha orcutti*, B. Morton, 1981).

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APPENDIX 1.

Taxa included in the analysis. Reference(s) are sources of literature or original (pers. obs.) data (T = type species of the genus; M = type species of monotypic genus).

	Reference(s)
GALEOMMATIDAE (18)	
M <i>Chlamydoconcha orcutti</i> Dall, 1884 (Cho)	Barnard, 1897; Chavan <i>In</i> : Moore, 1969a; B. Morton, 1981.
M <i>Coleoconcha opalina</i> Barnard, 1964 (Co)	Barnard, 1964; pers. obs. (NMP A1747).
T <i>Divariscintilla maoria</i> Powell, 1932 (Dm)	Powell, 1932, 1979; Judd, 1971; Coney, 1990; pers. obs. (AMS C165142).
<i>D. troglodytes</i> Mikkelsen and Bieler, 1989 (Dt)	Mikkelsen and Bieler, 1989.
<i>D. yoyo</i> Mikkelsen and Bieler, 1989 (Dy)	Mikkelsen and Bieler, 1989.
<i>D. n. sp. "heart-shaped"</i> (Dc)	Mikkelsen and Bieler, in press.
<i>D. n. sp. "yellow"</i> (Dl)	Mikkelsen and Bieler, in press.
<i>D. n. sp. "white"</i> (Do)	Mikkelsen and Bieler, in press.
<i>Ehippodonta macdougalli</i> Tate, 1889 (Em)	Tate, 1889; Woodward, 1893; Chavan <i>In</i> : Moore, 1969a; pers. obs. (CAS 077807).
<i>E. oedipus</i> B. Morton, 1976 (Eo)	B. Morton, 1976.
T <i>Galeomma turtoni</i> Turton, 1825 (Gtu)	Mittre, 1847; Popham, 1940; Tebble, 1966; Chavan <i>In</i> : Moore, 1969a; B. Morton, 1973; Angloy, 1988; pers. obs. (CAS 41198).
<i>G. takii</i> (Kuroda, 1945) (Gta)	Kuroda, 1945; B. Morton, 1973; B. Morton and Scott, 1989.
M <i>Phlyctaenachlamys lysiosquillina</i> Popham, 1939 (Pl)	Popham, 1939; Coney, 1990; pers. obs. (AMS C165143).
<i>Scintilla stevensoni</i> Powell, 1932 (Ss)	Powell, 1932, 1979; Ponder, 1967.
<i>S. violescens</i> Kuroda and Taki, 1961 (Sv)	Arakawa, 1961; Kuroda and Taki, 1961; B. Morton, 1976.
T <i>Scintillona zelandica</i> (Odhner, 1924) (Sz)	Odhner, 1924; J. E. Morton, 1957; Chavan <i>In</i> : Moore, 1969a.
<i>S. bellerophon</i> Ó Foighil and Gibson, 1984 (Sb)	Ó Foighil and Gibson, 1984.
M <i>Vasconiella jeffreysiana</i> (P. Fischer, 1873) (Vj)	Kisch, 1958; Cornet, 1982; Coney, 1990.
LASAEIDAE (2)	
<i>Ceratobornia cema</i> Narchi, 1966 (Cc)	Narchi, 1966.
M <i>Parabornia squillina</i> Boss, 1965 (Ps)	Boss, 1965; pers. obs. (FSBC I6943).

APPENDIX 2.

Characters and character states used in the phylogenetic analysis.

SHELL

0. Size relative to mantle.
0 = subequal, 1 = significantly smaller than mantle.
1. Size of valves relative to each other.
0 = equivalve, 1 = inequivalve.
2. Prolongation.
0 = equilateral, 1 = anteriorly, 2 = posteriorly.
3. Ventral notch.
0 = absent, 1 = notched in one valve, 2 = notched in both valves.
4. Hinge plate.
0 = not indented, 1 = indented.
5. Hinge - cardinal teeth.
0 = interlocking, 1 = present, not interlocking, 2 = absent.
6. Hinge - lateral teeth.
0 = interlocking, 1 = present, not interlocking, 2 = absent.
7. Hinge - lateral teeth (position).
0 = anterior + posterior, 1 = anterior only, 2 = posterior only.
8. Hinge - lateral thickened ridges.
0 = absent, 1 = present.
9. Sculpture.
0 = not reticulate/beaded, 1 = reticulate/beaded.

ANATOMY

10. Extent of mantle coverage.
0 = none, 1 = margins only, 2 = complete, but retractable, 3 = complete, with fusion preventing complete retraction.
11. Elongated tentacles (excluding dymanitic tentacles).
0 = absent, 1 = present.
12. Dymanitic tentacles.
0 = absent, 1 = present.
13. Flower-like organs.
0 = absent, 1 = present.
14. Foot structure.
0 = cylindrical anterior + blunt heel, 1 = cylindrical anterior + elongated heel, 2 = blade-like anterior, without distinct heel.
15. Adductor muscles.
0 = subequal, 1 = posterior reduced, 2 = anterior reduced, 3 = both absent.

OTHER

16. Reproductive - dwarf male.
0 = absent, 1 = present.
17. Life habit.
0 = not flattened limpet-like, 1 = flattened limpet-like.

APPENDIX 3.

Data matrix (? = character state unknown; - = character state not applicable;
OG = hypothetical bivalve outgroup; for other acronyms see Appendix 1).

	CHARACTERS																		
Taxa	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	
OG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Co	0	0	2	0	0	2	2	-	0	0	3	0	0	0	0	3	1	1	
Dm	0	0	2	2	0	1	1	2	0	0	1	1	0	1	1	0	?	0	
Dc	1	0	2	2	0	1	2	-	0	0	2	1	0	1	1	0	0	0	
Dl	1	0	2	0	0	1	2	-	0	0	2	1	0	1	1	0	?	0	
Do	0	0	2	0	0	1	2	-	0	0	1	1	0	0	1	0	0	0	
Dt	1	0	1	0	0	1	2	-	0	0	3	1	0	1	1	0	0	0	
Dy	1	0	1	0	0	1	2	-	0	0	3	1	0	1	1	0	0	0	
Em	0	0	0	0	0	1	2	-	1	1	3	1	?	0	0	1	0	1	
Eo	0	0	0	0	0	2	2	-	1	1	2	0	1	?	?	?	1	1	
Gtu	0	0	2	0	0	2	2	-	1	1	3	0	1	0	0	2	1	1	
Gta	0	0	2	0	0	0	2	-	1	1	3	0	1	0	0	0	?	1	
Pl	1	0	1	0	0	1	0	2	0	0	3	1	0	1	1	1	0	0	
Ss	0	0	0	0	0	0	0	1	0	0	3	0	0	0	1	0	?	1	
Sv	0	0	0	0	0	0	0	1	0	0	2	1	0	?	0	?	?	0	
Sz	0	0	0	0	1	1	0	0	0	0	1	0	0	0	2	0	?	0	
Sb	0	0	0	0	1	1	0	1	0	0	1	1	0	0	2	0	0	0	
Vj	0	1	0	1	0	0	0	2	0	0	?	1	0	1	0	0	?	0	
Ps	0	0	2	0	0	0	2	-	0	0	2	1	0	1	1	0	?	0	
Cho	1	1	1	0	0	2	2	-	0	0	3	0	0	0	0	1	1	0	
Cc	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	?	0	



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