

PHYLOGENETIC RELATIONSHIPS OF THE TROPICAL AMERICAN COLUMBELLID TAXA *CONELLA*, *EURYPYRENE*, AND *PARAMETARIA* (GASTROPODA: NEOGASTROPODA)

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ABSTRACT—*Conella*, *Eurypyrene*, and *Parametaria* are three taxa of columbellid neogastropods native to the Neogene American tropics whose monophyly and relationships have traditionally been confused. The primary objective of this study is to reconstruct the phylogenetic relationships of the tropical American species in these genera, to evaluate their monophyly, and to establish their constituencies. Parsimony-based phylogenetic analysis was used to generate phylogenetic topologies, after which the shortest trees were evaluated to minimize stratigraphic debt using a stratigraphic character added to the data set. The morphologically most parsimonious topologies are well resolved but the main clades are not well supported. Stratocladistic evaluation of the most parsimonious trees resulted in four morphologically and stratigraphically shortest trees. Overall, the resultant trees suggest that *Conella* and *Eurypyrene* are monophyletic with minor changes to their traditional constituency, but the resulting trees do not support monophyly or constituency of *Parametaria*, except in a very restricted sense, or as a paraphyletic group including one or more other traditional genera.

INTRODUCTION

COLUMBELLIDAE, ONE of the families included in the buccinoid neogastropods, comprise one of the most diverse modern gastropod families. The group consists of nearly 400 extant species, an impressive number considering that the fossil record of the group extends only back to the Paleocene (Glibert, 1973). The ecological and anatomical characteristics of columbellids make them interesting and productive subjects for evolutionary studies (deMaintenon, 1999), and columbellids have been used as model taxa for investigating diversification and extinction patterns in the Neogene American tropics (Jackson et al., 1993, 1996). Like many gastropod taxa, however, their evolutionary history and relationships are largely unresolved.

Conella Swainson, 1840, *Eurypyrene* Woodring, 1928, and *Parametaria* Dall, 1916 are three columbellid genera whose members are almost all found in the Neogene American tropics (one species of *Parametaria* is known from the Philippines, see below). The monophyly and relationships of all three genera are unresolved. They are traditionally thought to be closely related, and a previous phylogenetic analysis supports this (deMaintenon, 1999). Species in these taxa have large (10–30 mm long), biconic to coniform shells lacking columellar plaits, and their radular morphologies (where known) are similar; little information is available as to their ecological characteristics. The objectives of this paper are to reconstruct the phylogenetic relationships of the tropical American species included in these taxa and to better understand their history, monophyly, and relationships. Although these are low-diversity groups with limited fossil records, hypotheses of their relationships and those of their included species will contribute to the growing literature describing the changes in marine taxonomic diversity associated with the uplift of the Panamanian Isthmus in the mid-Pliocene.

METHODS

Taxon selection.—Research on the phylogeny of representative columbellid taxa (deMaintenon, 1999) supports the existence of a monophyletic columbellid subgroup composed of the genera *Conella*, *Parametaria*, and *Pyrene* Röding, 1798; synapomorphies of this clade include the shape of the posterior shell sinus, the coniform shell shape, and the presence of spiral ribs on the early teleoconch whorls. *Eurypyrene* was originally named by Woodring (1928) as a subgenus of *Pyrene*, and various authors (i.e., Radwin, 1968, 1978 in his discussion of *Conella*) have since suggested that it is closely related to *Conella*. In this study, all the

Recent and fossil species traditionally placed in *Conella*, *Parametaria*, and *Eurypyrene*, and the type species of *Pyrene*, are subjected to parsimony-based phylogenetic analysis (species listed in Table 1).

All species of *Conella*, *Parametaria*, and *Eurypyrene* are endemic to the American tropics, except for *Parametaria philippinarum* (Reeve, 1859), which is native to the Philippines. It is a common Recent species and also known as a fossil from the Late Miocene and Pliocene Canguina Formation of South Luzon Basin in the Philippines (Popenoe and Kleinpell, 1978). This species may represent an independent coniform lineage, considering its isolation from other members of *Parametaria*, and the paucispiral protoconchs in most species of this group that suggest nonpelagic larval development. The only similar species in the region is *Mitrella oweni* Ladd, 1977 from the Tertiary of Palau; this species is intermediate in form between a coniform and a fusiform shape, and Ladd reported it as resembling both *Columbella bandungensis* Martin, 1880 (= *Parametaria philippinarum*, see Popenoe and Kleinpell, 1978) and *Mitrella yorkensis* (Crosse) (reference not given), a large, fusiform Recent species from Australia.

The type species of *Pyrene* is included in this analysis to evaluate the relationships between this group and the tropical American taxa of interest. *Pyrene* is a tropical west Pacific group, consisting of several large pupiform species with a “uniquely terraced spire configuration” (Radwin, 1978, p. 333) caused by a subsutural spiral cord of varying strength found only in these species. The type species (*Pyrene punctata* Bruguière, 1789) and other *Pyrene* species investigated [*Pyrene obscura* (Sowerby, 1844) and *Pyrene flava* (Bruguière, 1789)] also share some unique anatomical characteristics (deMaintenon, 1999). Other species in the genus are not included here primarily because they are a readily diagnosed group of very similar Recent species and outside the geographic scope of this paper. The fossil record of the group is also poor. Ladd (1977) lists a single fossil specimen of the extant species *Pyrene obtusa* (Sowerby, 1832) found in Holocene sediments of Eniwetok, but no other occurrences have been reported.

Microcithara uncinata (Sowerby, 1832) is included in this study because of its extreme morphological similarity to members of the subgenus *Dominitaria* Jung, 1994. It was originally included in deMaintenon (1999). The species is placed in *Microcithara* Fischer, 1884 because of the strongly angulate labial edge and spoutlike posterior canal, but it differs from the other species of that genus in the sculptural characteristics and its generic placement has been uncertain (Keen, 1971).

TABLE 1—The species currently included in *Conella*, *Parametaria*, and *Eurypyrene* and the outgroup taxa included in phylogenetic analysis, with their geographic and stratigraphic occurrences.

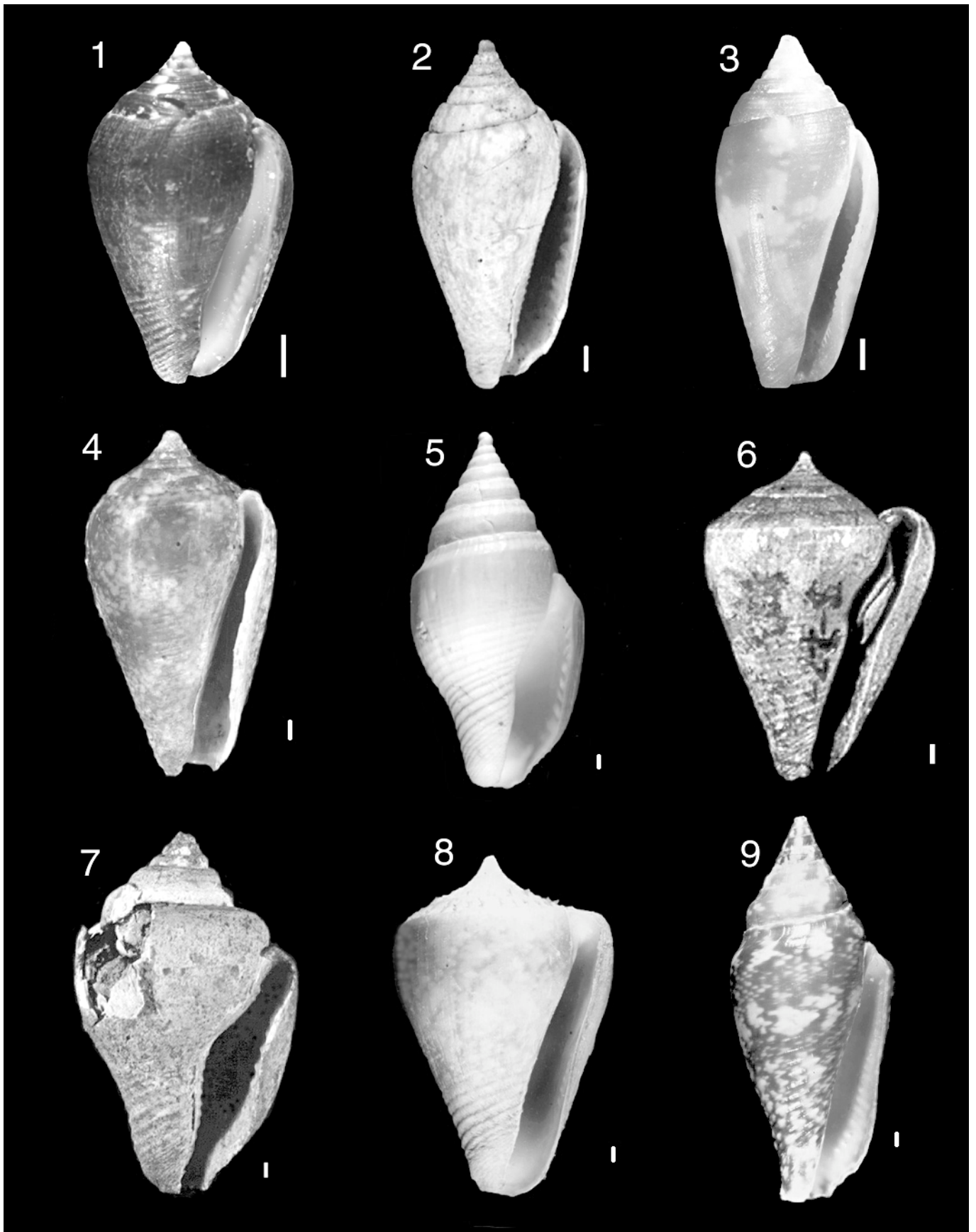
Species	Status
<i>Anachis lyrata</i> (Sowerby, 1832)	outgroup
<i>Glyptanachis atramentaria</i> (Sowerby, 1844)	outgroup
<i>Mitrella ocellata</i> (Gmelin, 1791)	outgroup
<i>Columbella mercatoria</i> (Linnaeus, 1758)	outgroup
<i>Conella ledaluciae</i> (Rios and Tostes, 1981), Fig. 2.3	
• Recent, Brazil	
<i>Conella ovulata</i> (Lamarck, 1822), Fig. 1.1	Type species of <i>Conella</i> Swainson, 1840
• Recent, Caribbean	
<i>Conella ovuloides</i> C.B. Adams, 1850, Fig. 1.3	
• Moín Fm., Costa Rica; Recent, Caribbean	
<i>Conella perplexabilis</i> (Maury, 1917), Fig. 1.2	
• Cercado Fm., Dom. Rep.	
<i>Eurypyrene eurynotum</i> Woodring, 1928, Fig. 2.5	Type species of <i>Eurypyrene</i> Woodring, 1928
• Bowden Fm., Jamaica	
<i>Eurypyrene inflata</i> (Gabb, 1873), Fig. 2.4, 2.6	
• Brasso Fm., Trinidad; Baitoa Fm., Dom. Rep.	
<i>Eurypyrene miccosukee</i> Petuch, 1991, Fig. 2.2	
• Belmont Fm., Florida	
<i>Eurypyrene venezuelana</i> (Weisbord, 1962) = <i>E. occidentalis</i> (Weisbord, 1962)	
• Mare Fm., Venezuela	
<i>Microcithara uncinata</i> (Sowerby, 1832)	
• Recent, Panamic	
<i>Parametaria dupontii</i> (Kiener, 1850), Fig. 1.8, 1.9	Type species of <i>Parametaria</i> Dall, 1916
• Pleistocene, Mexico; Recent, Panamic	
<i>Parametaria bella</i> Schmelz, 1995, Fig. 2.1	
• Chipola Fm., Florida	
<i>Parametaria hertweckorum</i> Petuch, 1991	
• "Pinecrest Beds," Florida	
<i>Parametaria lindae</i> Petuch, 1986, Fig. 1.5	
• "Pinecrest Beds," Florida	
<i>Parametaria macrostoma</i> (Reeve, 1859), Fig. 1.4	
• Recent, Panamic	
<i>Parametaria philippinarum</i> (Reeve, 1859)	
• Canguinsa Fm., Phil.; Recent, Phil.	
<i>Parametaria prototypus</i> (Guppy, 1867), Fig. 1.7	
• Springvale Fm., Trinidad	
<i>Parametaria rutschi</i> Jung, 1969, Fig. 1.6	
• Matura Shell Bed, Talparo Fm., Trinidad	
<i>Parametaria (Dominitaria) islahispaniolae</i> (Maury, 1917)	Type species of <i>Parametaria</i> subgenus <i>Dominitaria</i> Jung, 1994
• Cercado Fm., Dom. Rep.	
<i>Parametaria (Dominitaria) lopezana</i> Jung, 1994	
• Baitoa Fm., Dom. Rep.	
<i>Pyrene punctata</i> (Bruguere, 1789)	Type species of <i>Pyrene</i> Röding, 1798
• Recent, Indo-West Pacific	

Phylogenetic methods.—Characters for analysis of *Conella*, *Parametaria*, and *Eurypyrene* were derived primarily from shell morphology because many species in these groups are extinct and several of the extant species are rarely found alive and are poorly represented in collections. Nonconchological characters were also included where available. Data from soft anatomy are only available for two ingroup species and so are not included. Quantitative characters (characters 1, 7, and 8) were coded using gap coding, where gaps in the measurement ranges (Fig. 3, see Table 2 for species codes) were identified by eye to minimize the number of species overlapping two or more character states. Any species whose range spanned more than one character state was coded as polymorphic. An alternative method that might have minimized

overlap would have been to use statistical multiple comparisons tests, similar to those used by Budd and Klaus (2001), but several species' sample sizes in this case are too small (one or two individuals) to provide accurate statistical estimates.

Recent and fossil specimens were obtained from a number of collections; as many specimens as could be obtained were examined to represent adequately the variation present in each species. Collections acronyms used in the figures include the following: ANSP, Academy of Natural Sciences of Philadelphia; DMNH, Delaware Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard; MORG, Museu Oceanográfico, Rio Grande, Brazil; UF, Florida Museum of Natural History, University of Florida, Gainesville; SBMNH, Santa Barbara

FIGURE 1—Species of the ingroup. Scale bars are 1 mm. 1, *Conella ovulata* (Lamarck, 1822), ANSP 299142, Recent, Great Abaco, Bahamas. 2, *Conella perplexabilis* (Maury, 1917), USNM USGS loc. 8525, Late Miocene Cercado Fm., Rio Mao, Dominican Republic. 3, *Conella ovuloides* (C.B. Adams, 1850), paratype, ANSP 6477, Recent, Turk's Island. 4, *Parametaria macrostoma* (Reeve, 1859), UF 225072, Recent, Islas Perlas, Panama. 5, *Parametaria lindae* Petuch, 1986, holotype, MCZ 29227, Pliocene, Pinecrest Beds, Florida. 6, *Parametaria rutschi* Jung, 1969, UCMP loc. S-177, Pleistocene Matura Shell Bed, Trinidad. 7, *Parametaria prototypus* (Guppy, 1867), UCMP loc. S-7959, early Pliocene, Springvale Fm., Trinidad. 8, 9, *Parametaria dupontii* (Kiener, 1850). 8, Short-spined specimen, SBMNH 345311, Recent, Pulmo Reef, Baja California; 9, Tall-spined specimen, DMNH 151744, Recent, Bahia de Los Angeles, Baja California.



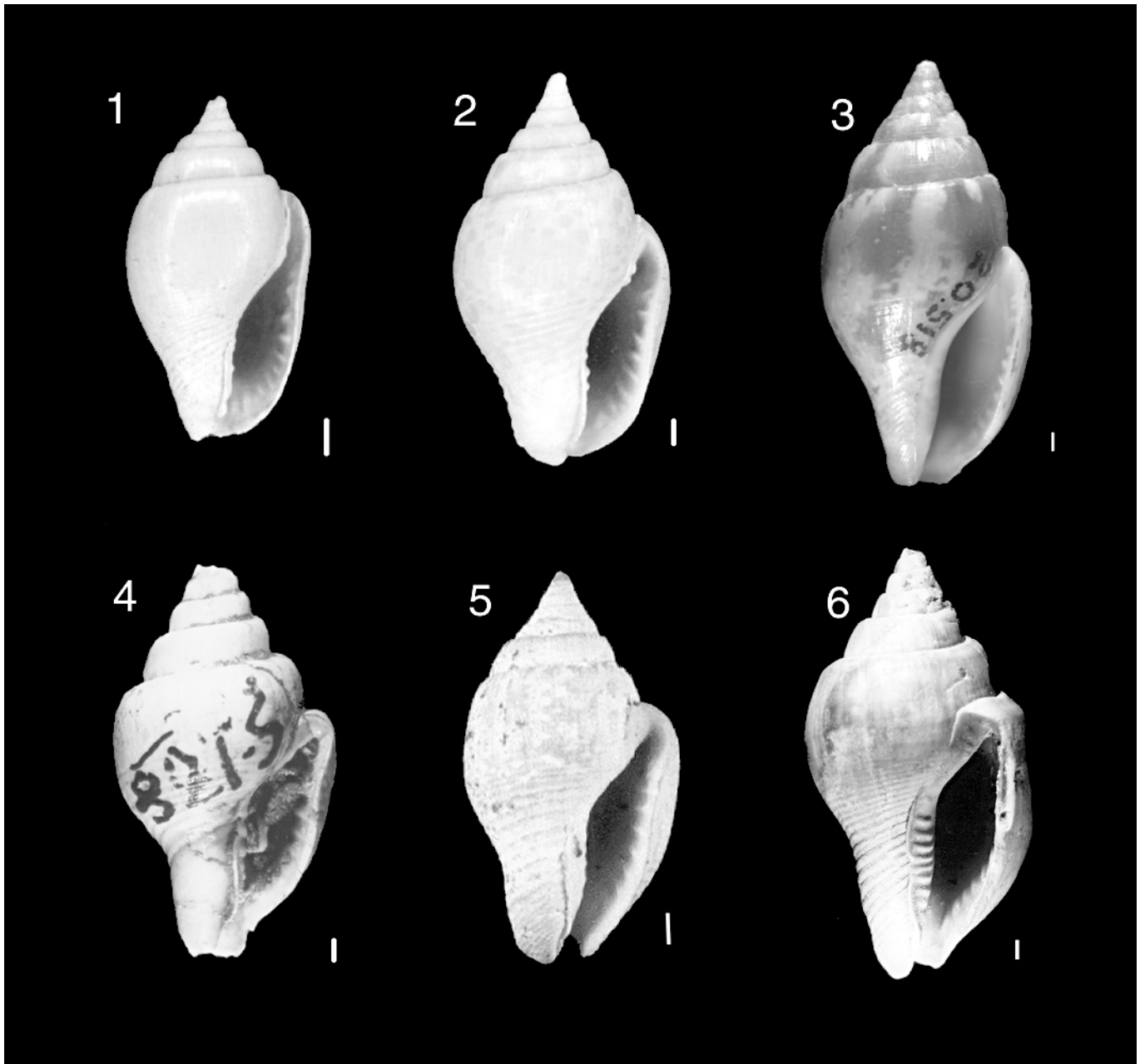


FIGURE 2—Species of the ingroup. Scale bars are 1 mm. 1, *Parametaria bella* Schmelz, 1995, TU-820, early to middle Miocene Chipola Fm., Farley Creek, Florida. 2, *Eurypyrene miccosukee* Petuch, 1991, UF 21696, Pleistocene Bermont Fm., South Bay, Florida. 3, *Conella ledalucia* (Rios and Tostes, 1981) (this species is suggested to belong in *Eurypyrene* Woodring, 1928), holotype, MORG 20.518, Recent, Marica, Rio de Janeiro, Brazil. 4, *Eurypyrene inflata* var. *brassica* (Maury, 1925), UCMP loc. S-178, Early Miocene Brasso Fm., Trinidad. 5, *Eurypyrene eurynotum* Woodring, 1928, holotype, USNM 135512, Bowden Fm., Jamaica. 6, *Eurypyrene inflata* (Gabb, 1873), USNM USGS loc. 26274, Baitoa Fm., Dominican Republic.

Museum of Natural History, Santa Barbara, California; UCMP, University of California Museum of Paleontology; USNM, United States National Museum; and TU, Tulane University.

The character matrix was created using MacClade 4.03 (Maddison and Maddison, 2001) and is given in Table 2. Analyses were carried out on PAUP* 4.0b10 (Swofford, 2003) using the parsimony criterion. Characters were input unordered and equally weighted. Heuristic searches were run using TBR branch swapping, with zero-length branches retained and multistate data treated as polymorphisms. The random addition sequence option of

PAUP was used to increase the probability of finding the most optimal trees; 10 replicate searches were conducted in each case. Outgroups were chosen from closely and more distantly related extant taxa as suggested by a higher-level analysis (deMaintenon, 1999) and are specified in Table 1. The analyses were based on 30 characters, listed below, and 24 species. Tree support was assessed using decay analysis (Bremer, 1994) and heuristic bootstrapping.

To make use of the existing stratigraphic data in phylogeny reconstruction, a stratocladistic approach was used. The fossil

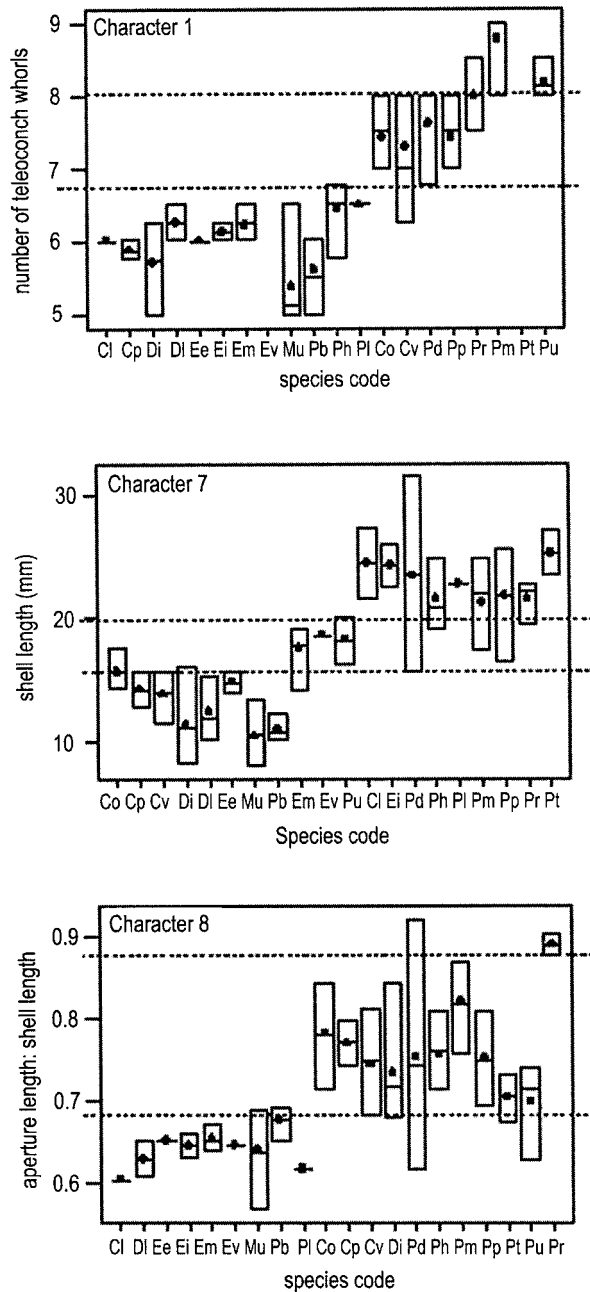


FIGURE 3—Boxplots showing the ranges (box), means (dot), and medians (midline) of measurements for quantitative characters 1, 7, and 8. The dashed lines show the character state breakpoints.

record for most of these species appears very incomplete; many of them are known from fewer than 10 specimens and there are likely to be species missing. Stratigraphy, however, still provides important information on the relative ages of each known species. Age data for formations were obtained from Budd et al. (1994) and other sources as necessary, and a stratigraphic character with six intervals (character 31) was added to the data set. Each age range starting with the oldest was assigned a character state, with species allowed to span more than one character state where necessary. Intervals were based on the ages of the formations in which specimens have been found. Because the ages of some taxa are not precisely resolved, each species was recorded as present

throughout the entire time interval in which it occurs. This character was then used to calculate stratigraphically augmented tree lengths in MacClade 4.0, and the stratigraphically most consistent of the morphologically most parsimonious trees were identified. This approach did not increase the level of parsimony debt, but used temporal range data to minimize stratigraphic debt where morphological data were equivocal. Identification of metataxa as ancestors was also used to optimize stratigraphic fit of the cladogram. Any species lacking autapomorphies (a metataxon) and demonstrably older than its sister species can be hypothesized as an ancestor to its sister species (Archibald, 1993; Smith, 1994). This approach absolves the need for a long stratigraphic range extension where there is no evidence that one exists.

Characters used in phylogenetic analyses.—

1. Adult shell length (quantitative; see Fig. 3): 0. Adult shell length <16 mm; 1. Adult shell length between 16 and 20 mm; 2. Adult shell length >20 mm.
2. Location of widest part of the shell: 0. Central area of shell is widest; 1. Posterior end of shell is widest.
3. Body whorl shape; columbellids tend to be either convex or have a straight-sided coniform shell: 0. Convex; 1. Straight-sided.
4. Funicle constricted; the funicle, between the main portion of the body whorl and the anterior end of the shell, is narrowed in most species: 0. Moderately constricted; 1. Not constricted; 2. Markedly constricted.
5. Shoulder angled or keeled: 0. Shoulder not angled; 1. Shoulder angled.
6. Juvenile shape same as adult shape. In most species, the juvenile shell is similar in shape to the adult, but in some species the juvenile differs by being more or less constricted anteriorly: 0. Juvenile same shape as adult; 1. Juvenile shell more constricted anteriorly; 2. Juvenile shell less constricted anteriorly than adult.
7. Number of adult teleoconch whorls (quantitative; see Fig. 3). Columbellids have determinate growth with the labial edge thickening and developing denticles at adulthood. Adults within a species will have a stereotypic number of whorls when they stop growing, regardless of shell size: 0. Up to 6.75 whorls; 1. 6.75 to eight whorls; 2. More than eight whorls.
8. Aperture length: shell length ratio (quantitative; see Fig. 3): 0. Short aperture; ratio less than 0.68; 1. Moderate aperture length, ratio 0.68 to 0.85; 2. Aperture long, ratio 0.85 or greater.
9. Anterior canal: 0. Anterior canal not recurved; 1. Anterior canal recurved dorsally.
10. Shape of spire: 0. Straight-sided; 1. Concave profile toward apex.
11. Aperture edge profile, from the side: 0. Aperture edge straight or somewhat convex; 1. Aperture edge markedly convex.
12. Aperture edge ascending. The posterior aperture edge in most columbellid species ascends slightly. In some species it deviates markedly so that the posterior edge may overlap the height of the previous whorl: 0. Aperture edge not or slightly ascending; 1. Aperture edge markedly ascending.
13. Posterior sinus: 0. Sinus present as a weak notch on posterior aperture edge (similar to turrid notch); 1. Aperture edge shortened, creating a gap. Some of these species (i.e., *Pyrene punctata*, *Parametaria bella* Schmelz, 1995, Fig. 2.1) occasionally have a spoutlike posterior extension of the suture at the aperture edge as well.
14. Labial denticles: 0. Denticles rounded; 1. Denticles spirally elongated.
15. Spacing of labial denticles: 0. Labial denticles well separated; 1. Labial denticles adjoining, as a raised ridge.

TABLE 2—Character matrix, with species codes for Figure 3. In the matrix, polymorphic characters are coded as follows: a = 0 and 1; b = 1 and 2; c = 0, 1, and 2. The last character is the stratigraphic character.

Species	Characters							
<i>Anachis lyrata</i>	00000	01000	00000	00010	00001	11100	6	
<i>Columbella mercatoria</i>	11000	00000	00001	01121	0?210	02020	6	
<i>Glyptanachis atramentaria</i>	00010	00000	00000	00011	0?101	11000	6	
<i>Mitrella ocellata</i>	00000	00000	00000	00000	00000	00210	6	
<i>Conella ovulata</i> (Co)	a1010	21101	11110	11000	00100	?1210	6	
<i>Conella ovuloides</i> (Cv)	01010	2a101	11110	11000	00100	??210	(56)	
<i>Conella perplexabilis</i> (Cp)	01010	20101	11110	11000	00000	???10	2	
<i>Conella ledaluciae</i> (Cl)	20020	00000	00010	00022	00000	1??20	6	
<i>Eurypyrene eurynotum</i> (Ee)	00020	?0000	00010	00022	00200	???20	3	
<i>Eurypyrene inflata</i> (Ei)	20020	?0000	00010	00022	01000	????0	0	
<i>Eurypyrene miccosukee</i> (Em)	a0020	00000	00110	00022	01000	???20	(45)	
<i>Eurypyrene venezuelana</i> (Ev)	10020	?0000	00010	00022	01200	????0	4	
<i>Microcithara uncinata</i> (Mu)	01000	00001	00001	01130	00010	02000	6	
<i>Parametaria</i> (D.) <i>islahispaniola</i> (Di)	01111	00101	00001	01100	00010	???10	2	
<i>Parametaria</i> (D.) <i>lopezana</i> (DI)	01000	00001	00001	01100	00010	???10	0	
<i>Parametaria bella</i> (Pb)	00000	00a00	01110	00022	20000	???20	0	
<i>Parametaria dupontii</i> (Pd)	ba101	01c0a	a1110	00000	10000	10211	(56)	
<i>Parametaria hertweckorum</i> (Ph)	ba001	00100	11110	00000	11000	???21	(34)	
<i>Parametaria lindae</i> (Pl)	20001	?0000	11110	00000	11000	???2?	(34)	
<i>Parametaria macrostoma</i> (Pm)	b1110	02101	11110	00000	10000	112?0	6	
<i>Parametaria philippinarum</i> (Pp)	b1111	11110	00010	01010	00000	1??10	(23456)	
<i>Parametaria prototypus</i> (Pt)	21000	0?101	00110	00022	10000	???00	3	
<i>Parametaria rutschi</i> (Pr)	21111	?b201	11110	11000	01000	????0	5	
<i>Pyrene punctata</i> (Pu)	11010	12a11	0a110	01021	00000	11200	6	

16. Posterior labial denticles. Some taxa have a few fine denticles in the region of the posterior notch, most have no denticles in that region: 0. No posterior parietal denticles; 1. Few fine denticles present in posterior canal.
17. Labial edge centrally thicker: 0. Labial edge of similar thickness from anterior to posterior; 1. Central part of labial edge thicker than anterior or posterior regions. This may help to make this more accessible part of the shell edge difficult for predators to break.
18. Columellar fold: 0. No fold; 1. One weak fold.
19. Parietal denticles: 0. No denticles; 1. Inconspicuous denticles correspond to funicular grooves; 2. Denticles in a single axial row; 3. Denticles scattered over parietal region.
20. Posterior callus: 0. No callus present; 1. Callus present; 2. Denticulate callus present.
21. Shoulder sculpture: 0. No sculpture between shoulder and suture; 1. Weak, irregularly spaced axial ridges, with tufts of periostracum where still present; 2. Strong, regularly spaced axial ridges.
22. Funicular grooves. These spiral grooves are present on all columbellids, whether or not any other spiral sculptural elements are present. The spiral funicular grooves extend to a varying distance posterior on the body whorl. The distance is not possible to discern on some spirally corded taxa, though funicular grooves tend to be more closely spaced than other spiral sculptural elements: 0. Grooves extend posterior to center of body whorl; 1. Grooves extend posterior farther than the center of the body whorl.
23. Spiral grooves on body whorl (excluding funicular grooves): 0. Absent; 1. Fine incised grooves present; 2. Pronounced grooves present, producing cords between them.
24. Nodules on spire whorls: 0. Absent; 1. Present.
25. Axial sculpture on body/spire whorls: 0. Absent; 1. Present.
26. Opercular shape: 0. Triangular, with the nucleus on the right-side point; 1. Oval, with the nucleus at the base. The muscle scar in both cases is on the left.
27. Shape of median radular plate: 0. Plate less than three times as wide as deep; 1. Plate about three times as wide as deep; 2. Plate about four times as wide as deep.
28. Gap between base and distal cusps of lateral tooth: 0. Gaps

uniformly narrow; 1. No larger gap, but rounded intercuspal gaps; 2. With pronounced gap.

29. Protoconch shape: 0. Multiwhorled conical protoconch, inferred planktotrophic development; 1. Paucispiral conical, peglike, with nuclear whorl not wider than the whorl succeeding it, inferred nonplanktonic development; 2. Paucispiral bulbous, with nucleus wider than the succeeding whorls, inferred nonplanktonic development.
30. Variable spire height: 0. Spire height does not vary; 1. Spire height variable with respect to body whorl size; i.e., *Parametaria dupontii* (Kiener, 1850), Figure 1.8, 1.9.
31. Age (stratigraphic character): 0. Late early to early middle Miocene; 1. Late middle Miocene; 2. Late Miocene; 3. Early Pliocene; 4. Late Pliocene; 5. Pleistocene; 6. Recent.

RESULTS

Parsimony analyses.—A heuristic search of the data in Table 2 (without the stratigraphic character) resulted in 132 most parsimonious trees, 110 steps long (minimum length = 60, maximum length = 226), with consistency indices of 0.545, retention indices of 0.699, rescaled consistency indices of 0.381, and homoplasy index of 0.609. The strict and 50 percent majority rule consensus trees are shown in Figures 4 and 5, respectively. The topology is well resolved, but most branches are not strongly supported. Decay analysis resulted in 5,997 trees 111 steps long, with only one clade, including four species, supported (see Fig. 4); this group collapsed at 112 steps.

The ingroup consists of two clades, the smaller one containing *Columbella mercatoria* (Linnaeus, 1758), *Mitrella ocellata* (Gmelin, 1791), *Microcithara uncinata*, *Parametaria islahispaniola* (Maury, 1917), and *Parametaria lopezana* (Jung, 1994). The larger ingroup clade consists of the remaining species of *Conella*, *Eurypyrene*, and *Parametaria*, and also *Pyrene punctata*. The former group is better supported than the latter. Characters supporting the first group include the presence of columellar folds, nodules on the spire whorls, and close spacing of the labial denticles, as well as two other characters that show greater levels of homoplasy (Fig. 6). The second group is supported by one character,

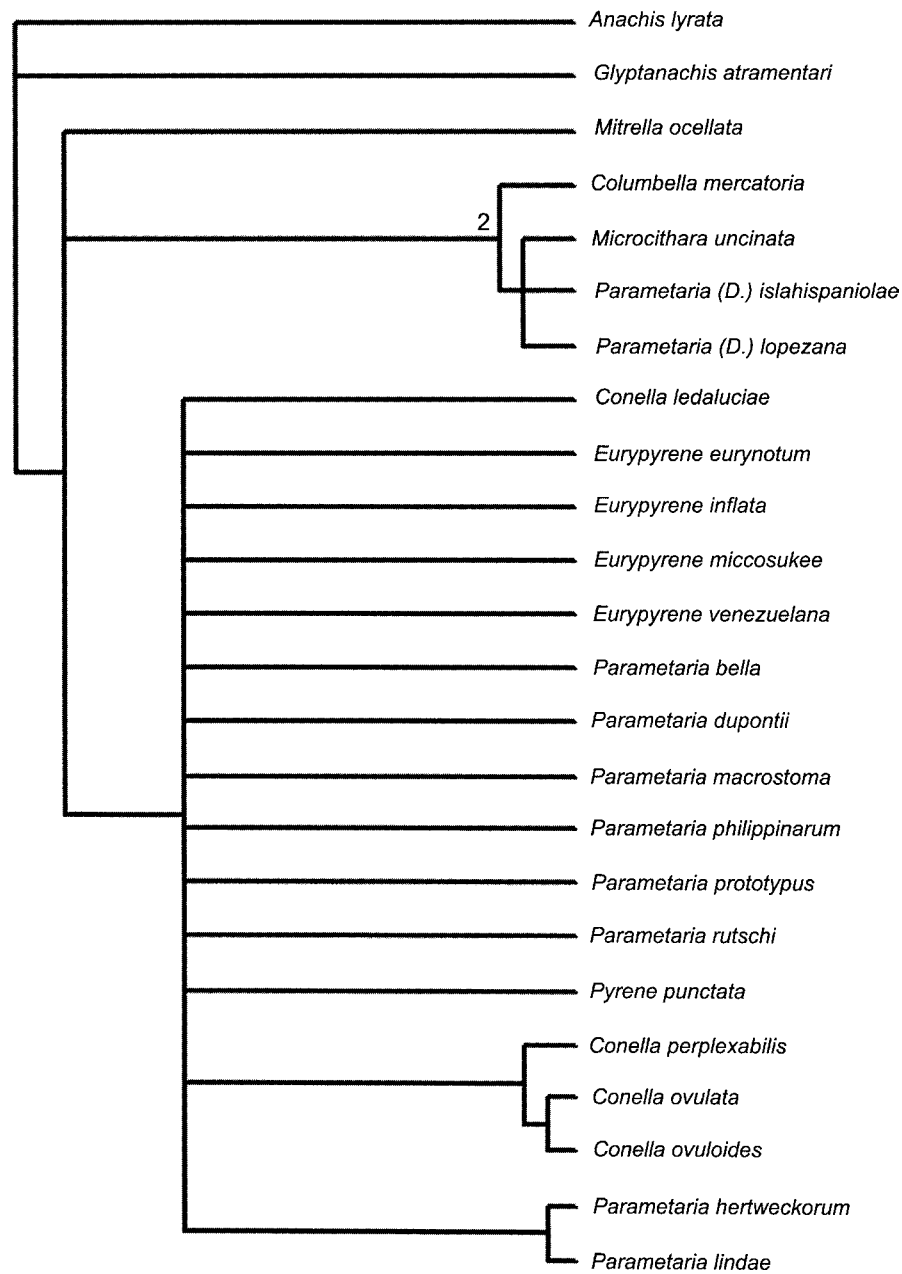


FIGURE 4—Strict consensus of the 132 most morphologically parsimonious trees. The Bremer support values are given in bold above the branch nodes (there is only one).

the elongate shape of the labial denticles, which is not typically seen in columbellids.

Three clades present in the MR consensus tree (Fig. 5) correspond to the constituencies of *Conella*, *Eurypyrene*, and *Parametaria*, but none are strongly supported. There is low to moderate bootstrap support for a *Conella* clade consisting of *Conella ovulata* (Lamarck, 1822), *C. ovuloides* (C.B. Adams, 1850), and *C. perplexabilis* (Maury, 1917); a *Parametaria* clade consisting of *Parametaria dupontii*, *P. hertweckorum* Petuch, 1991, and *P. lindae* Petuch, 1986; and a *Eurypyrene* clade consisting of *E. eurynotum* Woodring, 1928, *Conella ledaluciae* (Rios and Tostes, 1981), *E. inflata* (Gabb, 1873), *E. miccosukee* Petuch, 1991, and *E. venezuelana* (Weisbord, 1962). Terminal clades including *Conella* and *Parametaria* are suggested by the results of this analysis

to be sister taxa, with *Eurypyrene* more basal. Some of the in-group species do not group with any of the three genera, because they have intermediate combinations of character states. *Pyrene punctata* and *Parametaria philippinarum* group together, and tend to fall between *Eurypyrene* and the terminal two genera.

Stratocladistic augmentation.—The 132 morphologically most parsimonious trees had stratigraphically augmented lengths ranging from 171 to 179 steps, with four trees 171 steps in length. The tree lengths on these four trees are thus composed of the minimal length of 60 steps, 50 steps morphological parsimony debt, and 61 steps stratigraphic debt for a total of 171. The four trees differed solely in the placement of two species, *Mitrella ocellata* and *Parametaria bella*. Figure 6 shows one of these trees, with the corresponding character state changes. The other three

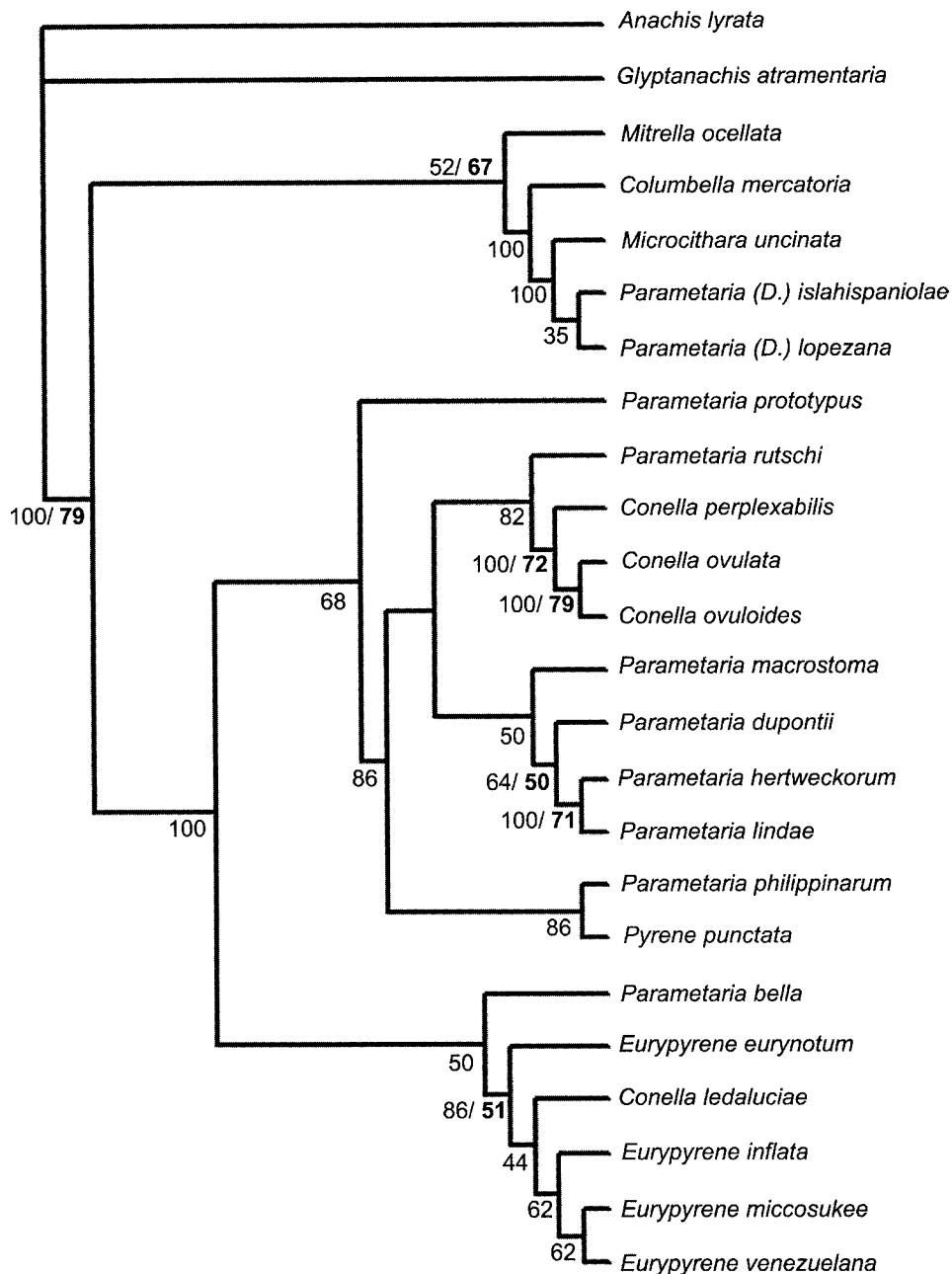


FIGURE 5—Fifty percent majority rule consensus of the 132 most parsimonious trees, with consensus indices. Bootstrap values of 50% or higher are given in bold after the consensus indices.

reconstructions in this group have *M. ocellata* basal to the entire ingroup, or *P. bella* is placed basal to the group of *Eurypyrene* species.

DISCUSSION

Phylogenetic relationships.—The primary objective of this study was to evaluate the monophyly and constituency of the three genera in question. In this study, a genus is considered to contain all species that are more closely related to the type species of that genus than to those of other genera and to be limited to a group defined by specific synapomorphies. The results of this study support the monophyly of *Conella* and the separation of

Microcithara uncinata and the two species in *Parametaria* subgenus *Dominitaria* from the rest of the ingroup. The constituencies of *Parametaria* and *Eurypyrene* are not strongly supported; tree support for these clades is poor and they have few or no unique diagnostic character states.

The results of this study are generally congruent with de-Maintenon (1999), a representative phylogeny for the Columbellidae. This is not surprising, although only about a quarter of the characters used in this analysis were carried over from the previous study. Both studies suggest moderate to strong support for two main columbellid clades roughly corresponding to the traditional subfamilies Columbellinae and Pyreninae. The ingroup

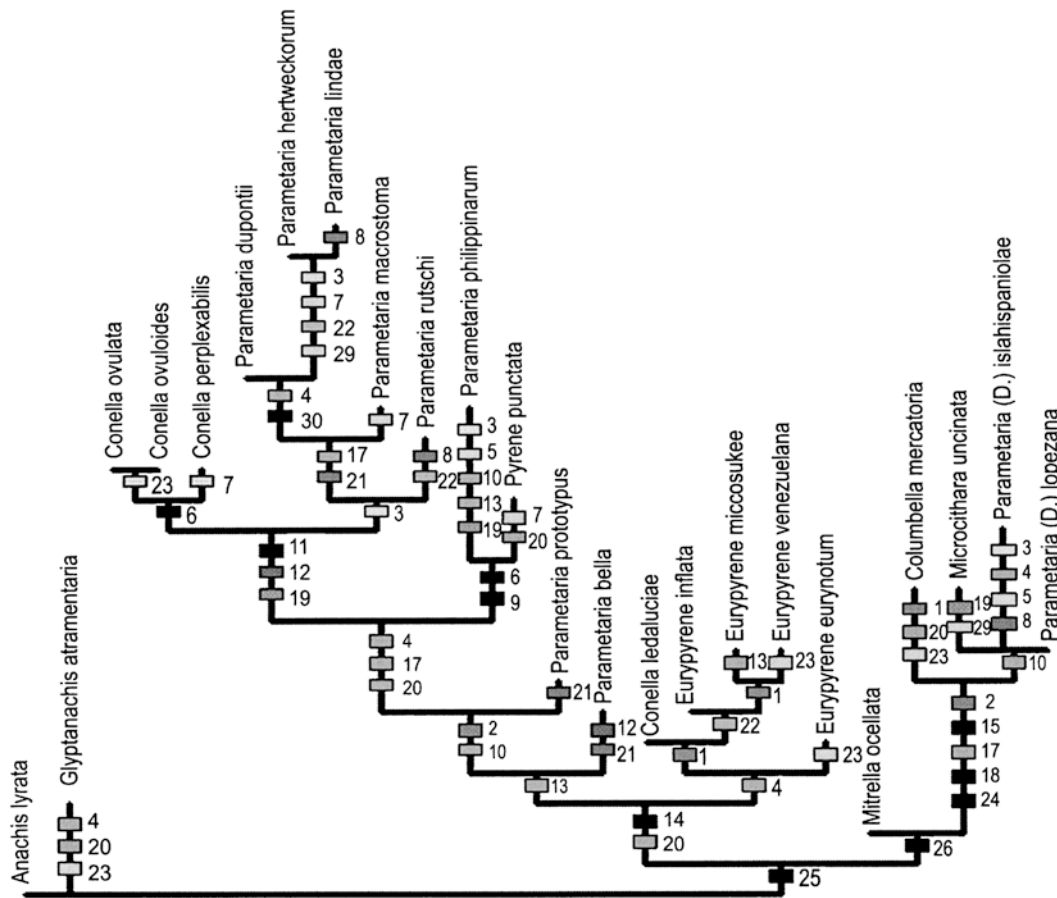


FIGURE 6—One of the four stratigraphically best trees, showing the character numbers that change on each branch. The shading of the boxes is determined by the rescaled consistency index; the darker the box, the higher the rescaled consistency index for that character.

clade comprised of *Parametaria (D.) islahispaniola* (Maury, 1917), *Microcithara uncinata*, and *Parametaria (D.) lopezana* (Jung, 1994) groups with columbelline species, such as *Columbella mercatoria* and *Mitrella ocellata*. The two extinct members of this basal group were assigned by Jung (1994) to *Parametaria*, new subgenus *Dominitaria* (based on the coniform shell), but differentiated from *Parametaria* sensu stricto by the “sculptured early teleoconch whorls and the higher spire” (Jung, 1994, p. 16). Based on the results of the analysis herein, these species are not closely related to *Parametaria*; the sculptured early teleoconch whorls occur frequently in *Columbella* Lamarck, 1799 and related taxa and spire height is variable throughout the columbellids. Their generic placement, however, is still uncertain, pending research to determine the monophyly and relationships of potentially closely related taxa such as *Microcithara*. *Microcithara uncinata* appears in the results of these analyses to be closely related to the two fossil species; however, the monophyly of *Microcithara*, which consists of three somewhat dissimilar extant species, has not been addressed and it seems premature to place these two species there.

The results suggest that *Conella* and *Parametaria* are more closely related to each other than either is to *Eurypyrene*, though support for this region of the tree is weak; these species are primarily characterized by their coniform or convex biconic shells, lacking the restricted funicle seen in most columbellids. The Indo-Pacific genus *Pyrene* and *Parametaria philippinarum* appear to be relatively basal offshoots of this clade. The external anatomy and shell morphology of the pyrenine columbellids tend

to be similar overall (similar radular morphology, conserved opercular form, few unique conchological characteristics), and relationships of the group are not strongly resolved, either in this analysis or in the previous analysis (deMaintenon, 1999).

A combination of bootstrap support for the overall tree and the topology of the shortest stratigraphically augmented trees do offer some taxonomic suggestions for the three genera in question. Based on these topologies, *Conella* is comprised of the three species *Conella ovulata* (the type species), *Conella ovuloides*, and *Conella perplexabilis*, as Jung (1994) suggested; the three species are collectively very similar, having a convex biconic shape and narrow aperture, and the grouping has moderately good bootstrap support, though the only unique character state they have (posterior labial denticles) they share with *Parametaria rutschi* (Jung, 1969). *P. rutschi* may be closely related to these, but the stratigraphically shortest tree places it with the *Parametaria* species. As noted by Jung (1994), *Conella ledaluciae* does not belong with this group, but appears to be more readily placed in *Eurypyrene*.

Eurypyrene is much more difficult to delimit; bootstrap support and the shortest stratigraphic tree suggest a grouping consisting of the type species, *Eurypyrene eurynotum*, plus four other species: *Conella ledaluciae*, *E. inflata*, *E. miccosukee*, and *E. venezuelana*. The characteristics of all these species are in agreement with Jung’s (1994) diagnosis, although he had not included *E. miccosukee*, only recently published, and *Conella ledaluciae*, which as *Eurypyrene ledaluciae* (Rios and Tostes, 1981) would be the only living species of the group. Radular morphology has not been reported for this species but may be informative. Both

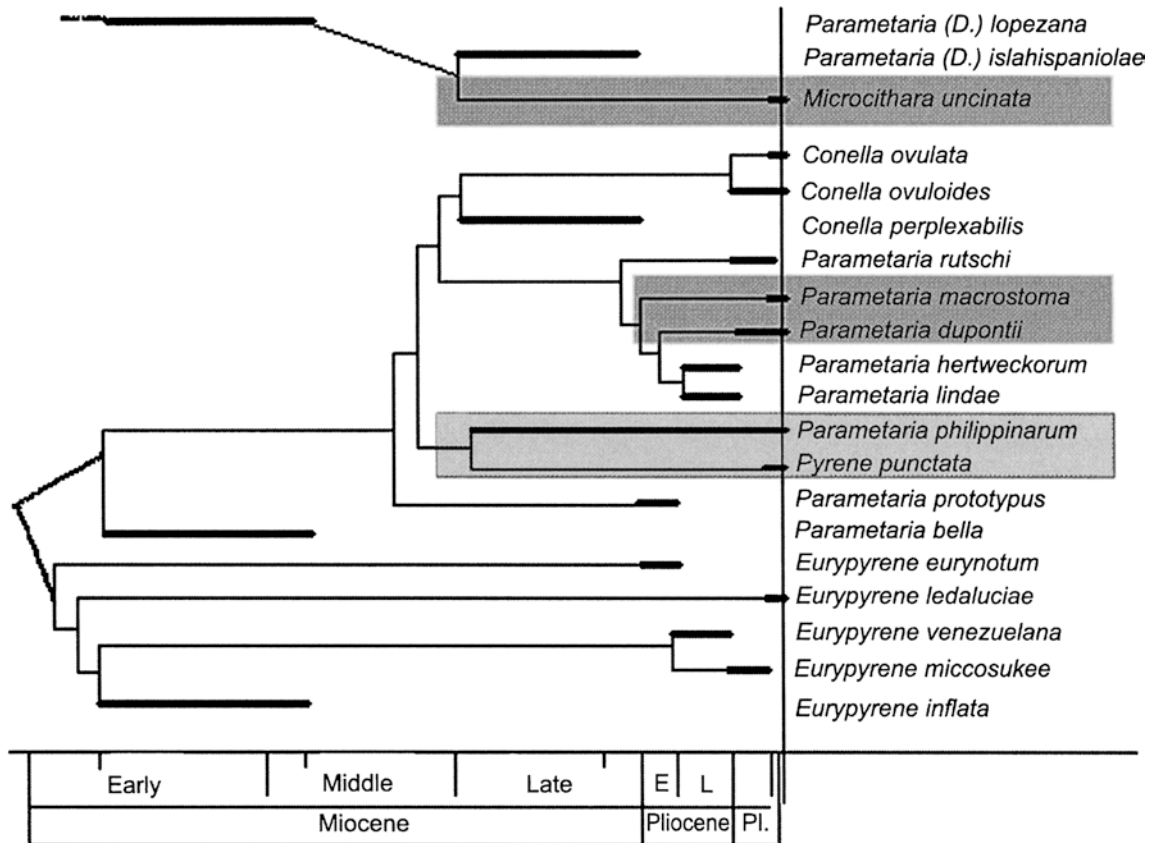


FIGURE 7—Stratigraphic reconstruction of the cladogram shown in Figure 6. The blocked areas represent regional groups, either Panamic (dark) or West Pacific (light), and dotted lines suggest deeper relationships.

of these species have the typical characteristics of the genus, including the large size, constricted funicle, bulbous protoconch, and denticulate posterior callus [also present in *Parametaria prototypus* (Guppy, 1867) and *P. bella*], however the calluses are weakly developed, especially in *E. ledaluciae*. One species included in Jung's (1994) analysis, *E. occidentalis* (Weisbord, 1962), is a large juvenile; as Jung (1994) suggested, it appears to be a specimen of *E. venezuelana*, and so it has been considered herein. *Parametaria bella* may also be a *Eurypyrene* from the results of this analysis; however, it is a small species with certain characteristics in common with *Parametaria* and *Conella* (i.e., the strongly ascending suture and regular axial ridges at the shoulder) and so its affinities are equivocal.

Parametaria is also difficult to delimit and the results of this study do not strongly recommend any particular solution. The coniform shape has apparently arisen in columbellids two or three times (depending on how *Parametaria philippinarum* is treated) and so is not a good indicator of relationships. Lacking this character, *Parametaria* in the traditional sense is quite heterogeneous. The terminal clade consisting of the three species *Parametaria dupontii* (the type species), *P. hertweckorum*, and *P. lindae* Petch, 1986 has low bootstrap support and one strong synapomorphy, the presence of variable spire height within species. Restricting membership of *Parametaria* to this group seems premature; most authors (i.e., Keen, 1971) consider at least *P. macrostoma* (Reeve, 1859) to be also a member of *Parametaria* and Jung (1994) also includes *P. rutschi* and *P. prototypus*; however, the present analysis does not support such an inclusive group. Each of these species has an intermediate combination of character states; *P. macrostoma*, for instance, has the typical characteristics

of a species of *Parametaria*, but it is much more similar to *Conella* in shape. *Parametaria* may simply be paraphyletic. Molecular or anatomical systematic analysis may be useful to provide better resolution to the living members of *Conella* and *Parametaria*, however, the relationships of the fossil species may never be well resolved.

The stratigraphically best trees out of the morphologically most parsimonious reconstructions have a few specific topological constraints that minimize ghost lineages. In the group containing *Microcithara uncinata* and both of the *Parametaria* subgenus *Dominitaria* species, the oldest species [(*Parametaria (D.) lopezana* from the early to middle Miocene Baitoa Formation] is moved to a more ancestral position and is also a metataxon; therefore that species is placed in an ancestral position in the stratigraphically adjusted phylogeny (Fig. 7). The stratigraphically shortest trees also place *Parametaria rutschi* with the *Parametaria* group rather than with *Conella*; *P. rutschi* is Pleistocene in age, whereas the oldest of the three *Conella* species, *C. perplexabilis*, is much older. Most of the *Parametaria* species are Pliocene to Recent. Long branches remain in the *Eurypyrene* group; however, these are primarily differentiated by shell size and shell sculptural characteristics. It is certainly possible that the older species in this group are ancestral, but this will require one or more additional morphological character state changes to take into account.

SYSTEMATIC SUMMARY

Jung (1994) provides an excellent diagnostic review of most of the species and all three genera investigated in this study, so the

following is intended to summarize the current status of the existing tropical American species in *Conella*, *Parametaria*, and *Eurypyrene*, as suggested through this research.

Genus CONELLA Swainson, 1840

Type species.—*Conella ovulata* (Lamarck, 1822).

Other species.—*Conella ovuloides* (C.B. Adams, 1850); *Conella perplexabilis* (Maury, 1917).

Genus EURYPYRENE Woodring, 1928

Type species.—*Eurypyrene eurynotum* Woodring, 1928.

Other species.—*Eurypyrene inflata* (Gabb, 1873); *Eurypyrene ledaluciae* (Rios and Tostes, 1981); *Eurypyrene miccosukee* Petuch, 1991; *Eurypyrene venezuelana* (Weisbord, 1962) = *Eurypyrene occidentalis* (Weisbord, 1962).

Genus PARAMETARIA Dall, 1916

Type species.—*Parametaria dupontii* (Kiener, 1850).

Other species.—*Parametaria hertweckorum* Petuch, 1991; *Parametaria lindae* Petuch, 1986.

GENERIC PLACEMENT UNCERTAIN

Parametaria bella Schmelz, 1995; *Parametaria macrostoma* (Reeve, 1859); *Parametaria philippinarum* (Reeve, 1859); *Parametaria prototypus* (Guppy, 1867); *Parametaria rutschi* Jung, 1969.

Biogeography and evolution of Eurypyrene, Conella, and Parametaria.—A stratigraphically corrected phylogeny for *Eurypyrene*, *Conella*, and *Parametaria* is shown in Figure 7. Some taxa require long temporal range extensions, but most species have autapomorphic characters supporting their monophyly.

The long range extensions and ghost taxa necessary to combine the stratigraphic record with the phylogeny require some comment. Ideally, the phylogeny and the stratigraphic record should match relatively well. When they do not, there may be several reasons for the discrepancy. Some columbellid taxa tend to be rare in the fossil record (and in many cases also in the Recent), and all of the species in this analysis have very restricted occurrences, typically only a single formation. Jung, in his monograph of the Neogene Dominican Republic columbellids (1994), included 13 species in his study, mostly from the genera examined here. Of these, eight were represented by five specimens or less and many were only found in a single stratigraphic section. Petuch (1986) named *Parametaria lindae* on the basis of only two specimens. Members of *Eurypyrene*, in particular, tend to be known from relatively few specimens, and the resulting phylogeny in this study suggests that a number of species probably existed in the Middle to Late Miocene that have not been found. It is certainly possible that some of the known species are ancestral and have undergone character state reversals in the course of their evolution, but there is no strong evidence for such state changes.

Corroborating the fossil record with an independent phylogeny provides a baseline for evaluating evolutionary patterns. Much of what we know about molluscan evolution in the American tropics is based on the *Strombina* Group, a diverse group of tropical American columbellids typically found in soft sediment habitats (Jackson et al., 1996). *Conella*, *Parametaria*, and *Eurypyrene* are less diverse columbellid groups that probably occurred associated with reefs or inshore reef rubble. Although their species diversities are very low, comparison of the patterns seen in these taxa may help us to understand the effect that habitat has on the history of diversification of tropical American molluscan taxa.

The diversification of the taxa in this analysis appears to divide into regional components to some degree. Most of the included species are Caribbean, including all of the *Eurypyrene* species, and the oldest members of the group. This is likely to be due in part to the poor quality of the Neogene east Pacific fossil record.

Microcithara uncinata and the two species placed in *Parametaria* (*Dominitaria*) Jung, 1994 show a split between the Caribbean fossil species and the extant Panamic species that may date back to before the late Miocene. The more Recent *Parametaria* species contain both Caribbean and Panamic members, with the only two living species being the Panamic *Parametaria* species. The most recent split in this line corresponding to the closure of the Panamanian Isthmus is between the two living Panamic *Parametaria* species and the two Pliocene fossil *Parametaria* species, both from south Florida. This is suggested to have occurred before the mid-Pliocene, but there is no evidence to suggest how long before that time this lineage might have split.

Another important event that has been traced in Neogene tropical American molluscan faunas is the Plio-Pleistocene pulse of origination and extinction that occurred in Caribbean and southeastern America (Allmon et al., 1993; Jackson et al., 1993, 1996; Budd et al., 1994, 1996; Budd, 2000). There is some evidence to suggest that enhanced originations occurred in the genera studied herein, in the divergence of the two Recent *Conella* species, the two Florida *Parametaria* species, and two of the *Eurypyrene* species. Extinctions occurred in the Pliocene and Pleistocene in several *Eurypyrene* species and four nominal Florida and Caribbean *Parametaria* species. The record for this group prior to the Pliocene is poor, however. It is worthwhile to note that none of the three genera went extinct.

In the eastern Pacific, in contrast, the columbellids of the *Strombina* Group show an increase in diversity from the Late Miocene through to the Recent (Jung, 1989; Jackson et al., 1993, 1996). This is undoubtedly due in part to the poorer quality of the eastern Pacific stratigraphic record (Coates et al., 1992; Coates and Obando, 1996). The species in *Conella*, *Eurypyrene*, and *Parametaria* have not undergone extensive radiations. *Parametaria* appears to be a paciphile genus; most of the fossil record is Caribbean, but the only surviving members are Panamic. *Eurypyrene* and *Conella* still survive solely in the Caribbean, however. *Eurypyrene ledaluciae*, the only survivor of the genus *Eurypyrene*, is restricted to deep water off Brazil, an area Vermeij (1978) suggested acts as a refugium for previously widespread Caribbean taxa.

Petuch (1982, 1988) has argued in favor of the differentiation of northern and southern Caribbean Neogene marine faunas, with the Caloosahatchian province in the north and the Gatunian province in the south. Some of the taxa in this study appear to show such a differentiation. Interestingly, none of the members of this group have been documented from the Gatun Formation. The group comprising the species of *Conella* is a southern clade, known primarily from the Caribbean. *Conella* is not found as a fossil in Florida, and the living species are rare there. *Microcithara uncinata* and its sister taxa also apparently represent a Gatunian/paciphile group, as no members of this group have been documented from Florida.

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