

EVOLUTION AND PHYLOGENETIC RELATIONSHIPS OF NEOGENE CORBULIDAE (BIVALVIA; MYOIDEA) OF TROPICAL AMERICA

LAURIE C. ANDERSON AND PETER D. ROOPNARINE

Department of Geology and Geophysics, Louisiana State University, Baton Rouge 70803, <laurie@geol.lsu.edu>
Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco 94118,
<roopnarine@calacademy.org>

ABSTRACT—We used 24 fossil and Recent species to construct character states of both composite and exemplar taxa for phylogenetic analyses of Neogene genera and subgenera of the Corbulidae from tropical America. All characters were conchologic and two matrices, which differed in the manner that commarginal-rib characters were coded, were analyzed using branch and bound searches and maximum parsimony. Character polarity was determined using *Corbula sensu strictu* as an outgroup. These analyses produced a limited number of robust and well-resolved cladograms that require only one ghost lineage. Such stable results indicate a high level of congruency among characters, and demonstrate that conchologic data sets can yield highly resolved cladograms.

Tropical American corbulids are not monophyletic, and include two major clades. Crown groups within these clades are endemic, and all genera endemic to tropical America first appear in the Miocene. In fact, generic diversity and body size peak in the upper Miocene of the Caribbean/western Atlantic. Range restrictions and extinctions of large-bodied genera from both corbulid clades contribute to a post-Miocene decline in body size in this region. The eastern Pacific does not experience a similar decline in diversity and body size. Diversity and morphologic trends in Caribbean corbulids coincide with regional environmental changes, in particular decreases in seasonality and productivity. Except for the extinction of *Bothrocorbula*, however, corbulid extinctions apparently predate faunal turnover reported for other molluscs.

Associated with these extinctions, we found evidence of geographic range restriction, but not range shifts, in corbulid genera, indicating that the geologic development of environmental refugia contributed more to survival than eurytopicity. Large-bodied genera of the southern Caribbean Gatunian Province (*Tenuicorbula*, *Panamicorbula*, and *Hexacorbula*) became restricted to the eastern Pacific. Range restriction to this high productivity refugium (i.e., paciphilic genera), rather than origination of new taxa, produced several corbulid genera now endemic to the region. Large-bodied genera from the Caloosahatchian Province of the southeastern U.S. (*Bothrocorbula* and *Bicorbula*), however, underwent global extinction. These subtropical and warm temperate taxa are presumably more eurytopic than their tropical counterparts, but do not exhibit range shifts in response to Neogene environmental change.

INTRODUCTION

CORBULID BIVALVES are some of the most abundant mollusks in Neogene sediments from marginal marine to neritic environments of tropical America (Jackson et al., 1999). These bivalves, therefore, were significant components of marine communities affected by Neogene environmental and climatic change in this region. Evolutionary responses of corbulids to these profound environmental changes have been documented (e.g., Anderson, 2001; Anderson and Roopnarine, 2003), but cladistic hypotheses have not been available to provide a phylogenetic context within which to examine this evolutionary change. Here we present cladistic analyses of tropical American corbulid genera and subgenera as well as additional selected taxa.

CORBULIDAE

The Corbulidae are small- to moderate-sized bivalves (most <3 cm in length) with a simple hinge often consisting of a cardinal tooth and socket-like resilifer in the right valve, and a cardinal socket and chondrophore in the left valve (Figs. 1–4). Corbulids range from subequal to greatly inequivalved with left and right valves differing in size, shape, and ornamentation (e.g., Figs. 1.1 and 1.4, 1.14 and 1.15, and 2.18 and 2.19).

Corbulids traditionally are placed within the Order Myoida (including the Hiatelloidea, Myoidea, and Pholadioidea) and Superfamily Myoidea. Molecular data indicate that this order is polyphyletic, although both morphologic and molecular (including

18S rDNA, 18S rRNA, 28S rRNA, and mitochondrial COI gene data) evidence support the Corbulidae and Myidae as sister taxa, and that this clade is either nested within or a sister group to part of the Veneroidea (Veneroidea, Mactroidea, Arcticoidea, and Corbiculoidea; Bernard, 1895, 1897; Purchon, 1990; Starobogatov, 1992; Adamkewicz et al., 1997; Waller, 1998; Campbell, 2000; Steiner and Hammer, 2000; Canapa et al., 2001; Giribet and Wheeler, 2002). Morton (1990), however, noted differences in shell structure and anatomical complexity between the Corbulidae and Myidae, called into question placement of the two families within the same superfamily, and proposed that for the Corbulidae alone, a close affinity with the Veneroidea was equally likely.

The earliest reported occurrences of corbulid bivalves are from the Jurassic of China (Yin and Fürsich, 1991), Kenya (Cox, 1965), India (Singh and Rai, 1980; Kanjilal, 1997; Fürsich et al., 2000), England (Duff, 1978; Harper et al., 2002), Portugal (Fürsich, 1981), Mexico (Alencaster de Cserna, 1963), and Canada (McLearn, 1924). Most of these occurrences, however, are equivocal because diagnostic features such as specimen hinges generally are not preserved and, thus, we have been unable to confirm reports of Jurassic corbulids from Africa and North America. At least part of the hinge or other indicatory features have been described and illustrated for *Jurassicornbula edwardi* (see Fürsich, 1981) from upper Jurassic sediments of the Lusitanian Basin in Portugal; for *Corbula* (*Corbula*) *haboensis* Kanjilal, 1997, *Corbulomima macneillii*, *C. mosae*, *Indocorbula lyrata*, and *I. basseae* (see Fürsich et al., 2000) from the Callovian of Kachchh,

FIGURE 1.—Numeric labels for arrows indicate illustrated character and character state respectively (see Appendix). 1–5, 7, *Corbula sulcata*, Recent, west Saharan Africa, SBMNH 345522, 1–3, 5, left valve, length 25 mm, $\times 2.1$, $\times 4.7$, $\times 3$, $\times 2.1$ respectively; 4, 7, right valve, length 26.3 mm, $\times 2$; 6, 8–10, 13, *C. gatunensis*, Miocene, Falcón, Venezuela, 6, left valve hinge, NMB 13666, length 17.1 mm, $\times 6.4$; 8–9, right valve, NMB 13665, length 24.4 mm, $\times 2.1$; 10, 13, left valve, NMB 13666, length 25.8 mm, $\times 2$; 11, 12, 14–18, *Varicorbula operculata*, Recent, Florida Atlantic Coast, TU R96, 11, 14, 17, 18, right valve, length 10.1 mm, $\times 5.2$, $\times 5$, $\times 31$, $\times 8$ respectively, 12, 15, 16, left valve, length 8.6 mm, $\times 5.9$, $\times 5.6$, $\times 7.8$ respectively.

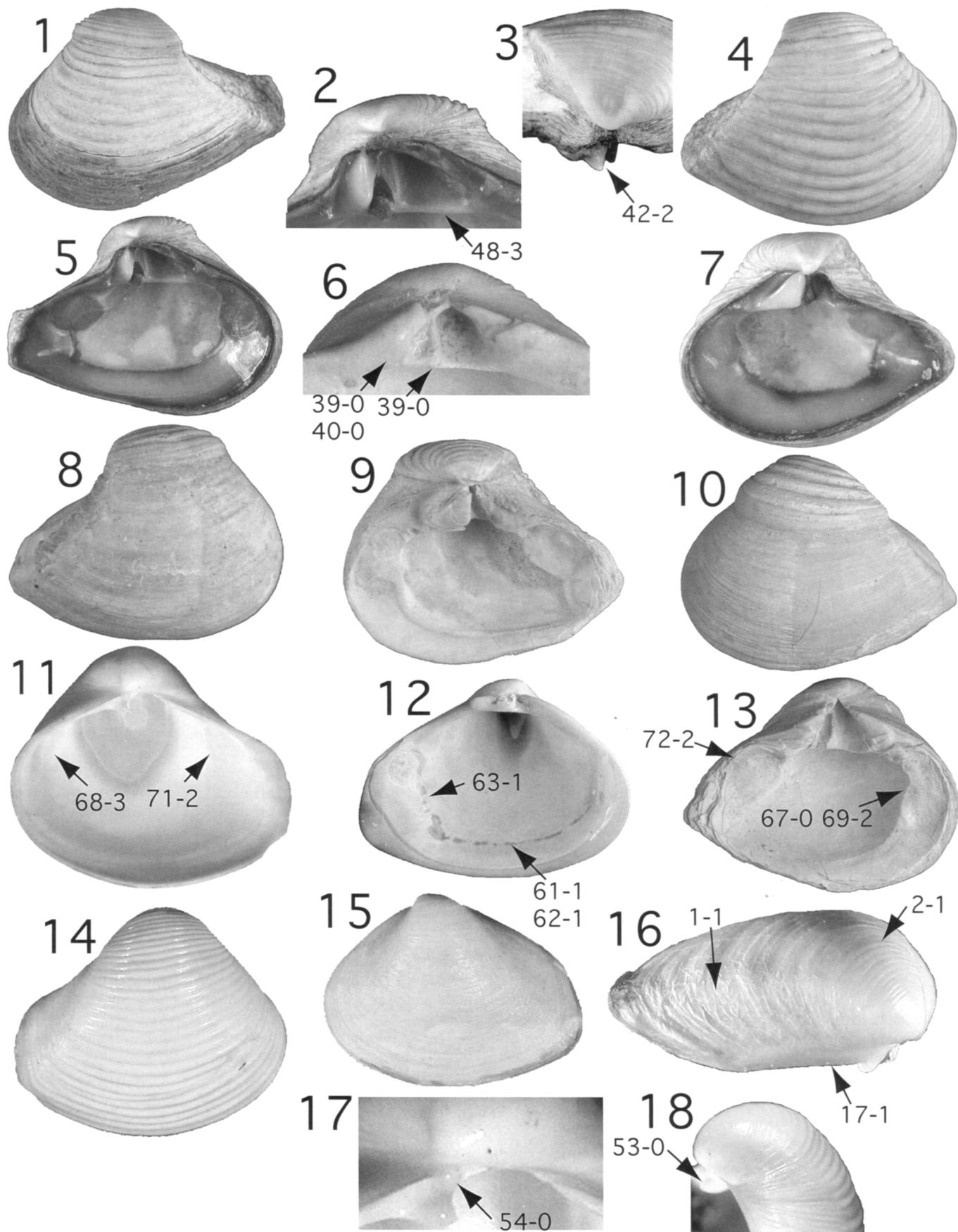


TABLE 1—Geographic and geologic ranges of corbulid genera compiled from primary literature.

	Panamic-Caribbean-W. Atlantic	E. Atlantic-Mediterranean	Indo-W. Pacific-Japan-Australia	Geologic range
<i>Serracorbula</i> ¹	X			Recent
<i>Guianadesma</i> ²	X			Neogene
<i>Pebasia</i> ²	X			Neogene
<i>Bothrocmbula</i>	X			Miocene-Pleistocene
<i>Hexacorbula</i>	X			Miocene-Recent
<i>Juliacorbula</i>	X			Miocene-Recent
<i>Tenuicorbula</i>	X			Miocene-Recent
<i>Panamicorbula</i>	X			Miocene-Recent
<i>Corbula s.s.</i>	X	X		Miocene-Recent
<i>Physoida</i>		X		Recent
<i>Semicorbula</i>		X		Miocene
<i>Anisocorbula</i>			X	Recent
<i>Notocorbula</i>			X	Recent
<i>Solidicorbula</i>			X	Recent
<i>Potamocorbula</i>			X	Recent
<i>Tiza</i>	X			Oligocene
<i>Vokesula</i>	X			Eocene-Oligocene
<i>Cuspicorbula</i>	X			Eocene
<i>Anapteris</i>	X			Eocene
<i>Pachydon</i> ²	X			Paleocene-Pliocene
<i>Bicorbula</i>	X	X		Eocene-Miocene
<i>Varicorbula</i>	X	X	X?	Eocene-Recent
<i>Cuneocorbula</i>	X	X		Eocene
<i>Lentidium</i>	X?	X	X?	Paleocene-Recent
<i>Janschinella</i>		X	X	Oligocene-Miocene
<i>Surobulia</i> ³	X			Cretaceous-lower Tertiary
<i>Ursirvus</i>	X			Cretaceous-Eocene
<i>Corbulamella</i>	X	X?		Cretaceous
<i>Caryocorbula</i>	X	X	X?	Cretaceous-Recent
<i>Caestocorbula</i>	X	X	X	Cretaceous-Eocene
<i>Parmicorbula</i>	X	X	X	Cretaceous-Eocene
<i>Eoursivivas</i>			X	Cretaceous
<i>Flexicorbula</i>			X	Cretaceous
<i>Nipponicorbula</i>			X	Cretaceous
<i>Pulsidis</i>			X	Cretaceous
<i>Jurassicorbula</i>		X		Jurassic
<i>Rostrocorbula</i>		X		Jurassic
<i>Corbulomima</i>		X	X	Jurassic-Cretaceous
<i>Hudsonella</i>			X	Jurassic
<i>Indocorbula</i>			X	Jurassic

¹ Coan (2002) considered the type species of *Serracorbula*, *S. tumaca*, a junior synonym of *Caryocorbula nasuta*.² Nonmarine.³ From Seymour Island, Antarctica.

India; for *Hudsonella sinensis* (see Yin and Fürsich, 1991) from the Bajocian of southern Qinghai Province, China; and for *Corbulomima macneillii* (see Duff, 1978) from the Jurassic Oxford Clay and *Rostrocorbula ibbetsoni* (see Harper et al., 2002) from the middle Jurassic Rutland Formation of England. These occurrences indicate that the Corbulidae were present at least along the Tethys margin by the middle Jurassic.

The distribution of living corbulid genera can be resolved into three broad biogeographic regions (Panamic-Caribbean-western Atlantic; eastern Atlantic-Mediterranean; and Indo West Pacific-Japan-Australia; Table 1). Tropical America is a distinct bioprovince throughout the Neogene, whereas genera present in the western Hemisphere that first appear in the Paleogene include several taxa whose ranges extend into western Europe (i.e., they are Tethyan). Genus-level biogeographic patterns prior to the Cenozoic

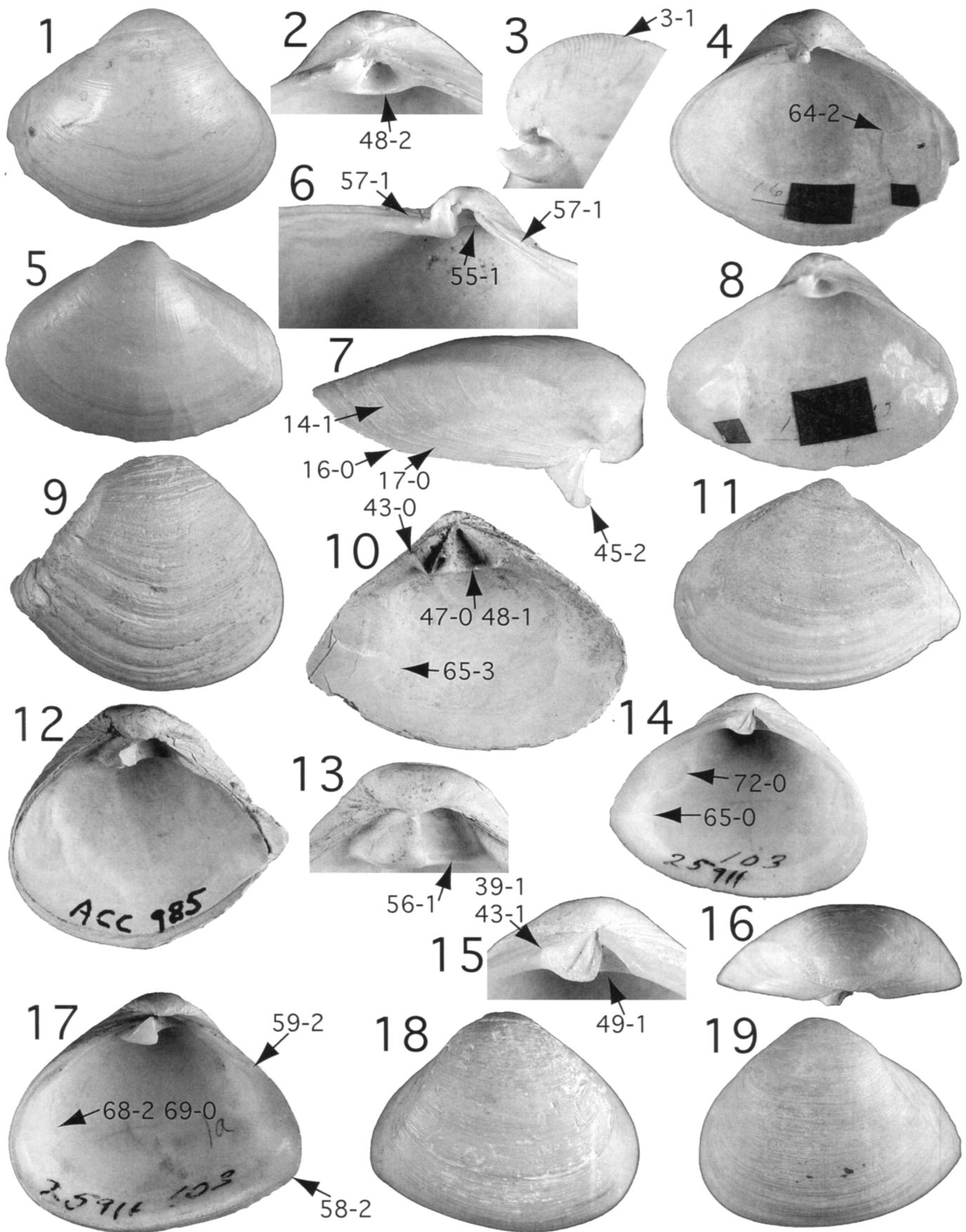
are unclear and, at present, primarily reflect taxonomic and monographic artifacts (e.g., the many genera described only from the Cretaceous of Japan).

Taxa analyzed.—Our analyses were conducted at the generic/subgeneric levels. Each taxon used is morphologically distinct, although the rank of these taxa is in flux. Some authors consider most or all to be separate genera, whereas others refer to them as subgenera, particularly of *Corbula*. For simplicity, we refer to all 12 taxa as genera. Based on our results (that tropical American corbulids are not monophyletic and only crown groups are endemic) a full taxonomic revision must await expanded phylogenetic analyses with broader taxon, geographic, and temporal coverage.

The 22 ingroup species used in our analyses represent approximately 15 percent of the total species diversity for the ingroup

FIGURE 2—Numeric labels for arrows indicate illustrated character and character state respectively (see Appendix). 1–8, *Bicorbula gallica*, Eocene Paris Basin, France, 1, 3, 4, 6, right valve, AMNH 16717, length 40.0 mm, $\times 1.3$, $\times 4$, $\times 1.4$, $\times 4$ respectively, 2, 5, 7, 8, left valve, AMNH 31976, length 32.4 mm, $\times 5.2$, $\times 1.6$, $\times 2.2$, $\times 1.7$ respectively; 9–13, *B. idonea*, middle Miocene Choptank Formation, Maryland, 9, 1/2, right valve, PRI 44840, length 30.7 mm, $\times 1.7$, 10–11, left valve, author's collection (Anderson), length 30.1 mm, $\times 2$, $\times 1.8$ respectively, 13, right valve hinge, author's collection (Anderson), length 30.4 mm, $\times 2.8$; 14–19, *Panamicorbula ventricosa* (= *P. inflata*), Recent, Ecuador, PRI 25911, 14–16, 19, left valve, length 28.0 mm, $\times 1.7$, $\times 4.9$, $\times 1.6$, $\times 1.8$ respectively, 17, 18, right valve, length 27.1 mm, $\times 2$, $\times 1.8$ respectively.





(Table 2). A large proportion of this diversity resides within *Caryocorbula* and to a lesser extent *Varicorbula*. If these genera are not monophyletic, their nodes likely will be the most unstable when new taxa are added to analyses, particularly at the species level. However, most interspecific differences among both *Caryocorbula* and *Varicorbula* species relate to subtle differences in continuous variables that describe valve outline shape and size. In contrast, most characters we used are conservative across a large number of Cenozoic species (at least of the Western Hemisphere) within these genera. We predict, therefore, that relationships among genera would be relatively robust as taxa are added in subsequent analyses at both the genus and species level.

In our analyses, we used both composite taxa (in which several species are used to construct generic-level character states) and exemplar species (in which one species defines the character states of a genus). We constructed composite taxa as much as possible (for eight genera) to produce a conservative data set of character states for genera. Up to four species define character states for each of these composite taxa (Table 3). Where possible, we used three species per genus including representatives of the type species as well as one species each from the lower and upper parts of a genus's stratigraphic range. Inclusion of more than two species for *Panamicorbula* and *Tenuicorbula* was impractical because of low species diversity and the rarity of individuals. In addition, we originally incorporated *Bothrocorbula synarmostes* into the analyses as a member of *Hexacorbula*, but reassigned it to *Bothrocorbula* once its character states were determined. As a result, *Hexacorbula* was represented by only two species and *Bothrocorbula* was represented by four.

Character states for four genera were defined using exemplar taxa. For *Varicorbula* and *Bicorbula*, tropical American species differed from the European type species (*V. gibba* and *B. gallica*) for character states typically diagnostic above the species level (i.e., hinge characters). Because of these combined geographic and morphologic discontinuities, the European type species were not combined with data on American species assigned to the same genera, and were included in the analyses as exemplar taxa of separate genera. As a result, *Bicorbula idonea* became an exemplar taxon because it is the only described Neogene tropical American species assigned to this genus. (American *Varicorbula* remained a composite taxon but one represented by two species.) The type species of *Cuneocorbula*, *C. biangulata* from the Eocene of the Paris Basin, was included originally as an outgroup taxon. Dall (1898) placed a number of western Atlantic fossil species in this genus, but Gardner (1926) subsequently erected the genus *Caryocorbula* for these American species. In initial analyses, *Cuneocorbula* fell within the ingroup (but not as a sister taxon to *Caryocorbula*) when specified as an outgroup taxon. We retained *Cuneocorbula* in subsequent analyses but did not specify it as an outgroup member.

We included *Corbula sulcata* (Fig. 1.1–1.5, 1.7) as an outgroup taxon both because the published temporal and geographic ranges of the genus (Recent, west Africa) were outside the study area, and because previous workers described the genus as lacking a chondrophore and placed it in a different subfamily than those found in tropical America (e.g., Vokes, 1945; Millard, 1997). In collecting data for this study, we discovered that *Corbula* s.s. has

TABLE 2—Estimated species diversity of ingroup taxa.

Genera	No. species in analysis	Est. species diversity (min)	Est. species diversity (max)
<i>Bicorbula</i>	2	8	15
<i>Bothrocorbula</i>	4	4	4
<i>Caryocorbula</i>	3	68	85
<i>Cuneocorbula</i>	1	3	4
<i>Hexacorbula</i>	2	7	8
<i>Juliacorbula</i>	3	7	8
<i>Panamicorbula</i>	2	3	3
<i>Tenuicorbula</i>	2	4	4
<i>Varicorbula</i>	3	27	39
Total	22	131	170

a fossil record in tropical America and is represented by *C. gatunensis* of the Panamanian and Venezuelan Miocene [placed in synonymy with *Hexacorbula hexacyma* by Woodring (1982) and originally chosen for our analyses for this reason; Fig. 1.6, 1.8–1.10, 1.13]. [In examinations of collections subsequent to our analyses, we found that Recent *C. dietziana* (western Atlantic) and *C. speciosa* (eastern Pacific) also were members of *Corbula* s.s.] All these species possess a distinct chondrophore (Fig. 1.2, 1.6). Early in ontogeny, the chondrophore in *Corbula* s.s. is very similar to the relatively flat and non-projecting chondrophore seen in genera such as *Caryocorbula* and *Bothrocorbula* (Fig. 4.11, 4.12). In later ontogeny, a resilifer-like pit develops on the anteroventral surface of the chondrophore and a posterior knob on the chondrophore's upper surface becomes greatly enlarged (Fig. 1.2, 1.6). This knob represents the left valve "tooth" in Lamarck's (1801) original description. *Corbula* was retained as an outgroup taxon and both *C. gatunensis* and *C. sulcata* were used to construct the character states for a composite *Corbula*.

Collections acronyms are as follows: AMNH—American Museum of Natural History, NMB—Naturhistorisches Museum, Basel, Switzerland, PRI—Paleontological Research Institution, SBMNH—Santa Barbara Museum of Natural History, TU—collections of Harold and Emily Vokes, UF—Florida Museum of Natural History, USNM—Smithsonian Institution, Natural History Museum.

CONCHOLOGIC CHARACTERS

All characters used in the analyses were conchologic and many were multistate (Appendix). Characters describe aspects of external ornament, valve shape, hinge, pallial line and sinus, and adductor muscle scars. Because corbulids are inequivaled, any trait that differed between valves in at least one genus was coded as two characters for left and right valves respectively. Polymorphic characters, those in which character states varied within a genus, were not included (e.g., the character "right valve commarginal rib shape" was not used because rib shape in the right valve varies among species within the genus *Corbula* s.s.; Fig. 1.4 vs. 1.8). Future species-level analyses will include broader taxon sampling and hence proper treatment of such polymorphic characters.

We ran analyses on two matrices: one of 73 and the other of 70 characters (Tables 4, 5). The two matrices differ only in that

FIGURE 3—Numeric labels for arrows indicate illustrated character and character state respectively (see Appendix). 1–7, *Tenuicorbula tenuis*, Recent, Colombia, PRI 25916a, 1, 3, 4, right valve, length 22.0 mm, $\times 2.5$, $\times 3.6$, $\times 2.6$ respectively, 2, 5–7, left valve, length 20.7 mm, $\times 13$, $\times 2.7$, $\times 2.6$, $\times 3.3$ respectively; 8–10, 12, *Juliacorbula scutata*, Pleistocene Bermont Formation, Florida, UF 83290, 8, 12, left valve, length 10.3 mm, $\times 5.6$, 9–10, right valve, length 10.1 mm, $\times 5.8$, $\times 5.6$ respectively; 11, 13, 15, 16, *Cuneocorbula biangulata*, Eocene Paris Basin, France, USNM 326895, 11, 15, left valve, length 6.9 mm, $\times 7.8$, 13, 16, right valve, length 9.4 mm, $\times 5.8$; 14, 17–20, *Varicorbula gibba*, Recent, Ireland, UF 17610, 14, 18, right valve, length 16.3 mm, $\times 3.1$, $\times 3$ respectively, 17, 19, 20, left valve, length 15.0 mm, $\times 3.1$, $\times 3.3$, $\times 9$ respectively.



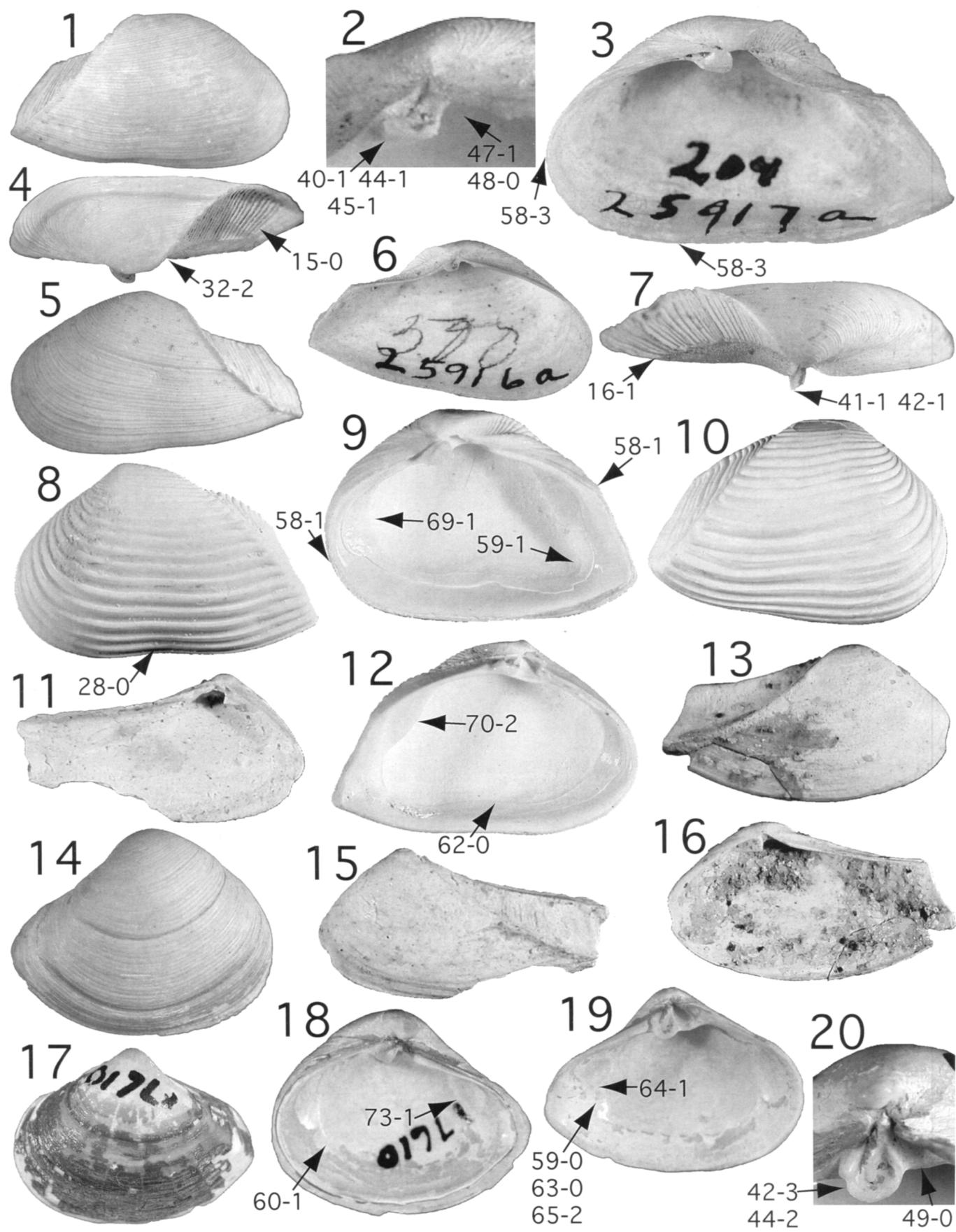


TABLE 3—Species used to construct generic-level character states.

Genera	Species used	Species distribution
<i>Bicorbula</i> European	<i>B. gallica</i> (Lamarck, 1801)	Eocene, France (type species)
<i>Bicorbula</i> American	<i>B. idonea</i> (Conrad, 1833)	Miocene, Maryland and Virginia
<i>Bothrocorbula</i>	<i>B. viminea</i> (Guppy, 1866)	Miocene-Pliocene, Greater Antilles (type species)
	<i>B. wilcoxii</i> (Dall, 1898)	Pliocene-Pleistocene, Florida
	<i>B. radiatula</i> (Dall, 1898)	Miocene, Florida
	<i>B. synarmostes</i> (Dall, 1898)	Miocene, Florida
<i>Caryocorbula</i>	<i>C. alabamensis</i> (Lea, 1833)	Eocene, Alabama (type species)
	<i>C. prenasuta</i> (Olsson, 1964)	Miocene, Panama
	<i>C. caribaea</i> (d'Orbigny, 1853?) ¹	Recent, western Atlantic
<i>Corbula</i>	<i>C. sulcata</i> Lamarck, 1801	Recent, Senegal (type species)
<i>Cuneocorbula</i>	<i>C. gatunensis</i> Toula, 1909	Miocene, Panama, Venezuela
<i>Hexacorbula</i>	<i>C. biangulata</i> (Deshayes, 1860)	Eocene, France (type species)
	<i>H. hexacyma</i> (Brown and Pilsbry, 1912)	Miocene, Panama (type species)
	<i>H. esmeralda</i> (Olsson, 1961)	Recent, eastern Pacific
<i>Juliacorbula</i>	<i>J. cubanaiana</i> (d'Orbigny, 1853?) ¹	Recent, western Atlantic (type species)
	<i>J. scutata</i> (Gardner, 1943)	Pleistocene, Florida
	<i>Juliacorbula</i> sp. a	Pliocene, Panama (Bocas del Toro)
<i>Panamicorbula</i>	<i>P. ventricosa</i> (A. Adams and Reeve, 1850)	Recent, eastern Pacific (type species <i>P. inflata</i> is junior synonym, see Coan, 2002)
<i>Tenuicorbula</i>	<i>P. canae</i> (Anderson, 1996)	Miocene, Dominican Republic
	<i>T. tenuis</i> (Sowerby, 1833)	Recent, eastern Pacific (type species)
	<i>T. melajoensis</i> (Jung, 1969)	Miocene, Trinidad
<i>Varicorbula</i> European	<i>V. gibba</i> (Olivier, 1792)	Miocene?-Recent, Europe (type species)
<i>Varicorbula</i> American	<i>V. operculata</i> (Philippi, 1848) ²	Recent, western Atlantic
	<i>V. chipolana</i> (Gardner, 1928)	Miocene, Florida

¹ The date of publication for d'Orbigny is the cause of much comment and speculation in the literature, with publication dates of 1842, 1845, 1846, and 1853 cited by various authors. Coan (2002) notes that text and plates of bivalves in both French and Spanish editions are now thought to have appeared in 1853.

² Mikkelsen and Bieler (2001) consider *V. operculata* to be a *nomen dubium* and use the synonym *V. disparilis* (d'Orbigny) instead, citing a publication date of 1842. As noted in footnote 1, however, the date of publication of this work is controversial. If, as Coan (2002) asserts, the publication date is 1853, another taxa *V. limatula* (Conrad, 1846), if synonymous (see Mikkelsen and Bieler, 2001), has priority.

five characters concerning commarginal rib distribution, thickness, shape, and expression in the 73-character data set are combined into two characters in the 70-character data set (Appendix). We constructed these two matrices because commarginal ribs are absent in both valves of *Cuneocorbula* (Fig. 3.13, 3.15) and *Panamicorbula* (Fig. 2.18, 2.19) and in left valves of *V. gibba* (Fig. 3.17) and *B. gallica* (Fig. 2.5). Therefore, characters describing aspects of ribs (characters 4–6 in the larger matrix) had to be coded as missing for these taxa, although the characters are “missing” because ribs are absent, rather than because they are not preserved. We did not add a “ribs absent” character state to characters 4–6 because doing so would have built redundancy into the matrix by coding the same character multiple times.

Most characters we used had discontinuous character states. For those describing the degree of expression of a trait, only characters with states that we could consistently distinguish because of morphologic gaps were retained. To identify stable codings, we edited characters and character states iteratively with Anderson producing initial descriptions and matrices, Roopnarine identifying character states difficult to reproduce consistently, and Anderson reevaluating these characters. Consequently, we reduced character states for six characters and omitted an additional eight characters to produce our 73-character matrix. Nevertheless, our phylogenetic results differ insignificantly from results presented using our initial matrices (Anderson and Roopnarine, 2001, 2002).

ANALYSES

Phylogenetic analyses were completed using PAUP* 4.0b10 (Swofford, 2002). In a first set of analyses for both matrices, characters were unordered and of equal weight. We also conducted a second set of analyses in which characters were reweighted according to the maximum value of their rescaled consistency indices (RC; using “reweight characters” option in PAUP*). Ten characters were autapomorphies, but were retained to qualify the distinctiveness of genera and because they may become informative in subsequent analyses incorporating additional taxa. Characters were polarized using *Corbula* s.s. as an outgroup. Analyses were conducted using branch and bound searches and maximum parsimony. Character state transformations were determined using accelerated transformation (ACCTRAN).

We used Bremer decay indices (Bremer, 1994) to compare the robustness of cladogram nodes. This decay index tracks the survival of nodes as the length of accepted cladograms increase incrementally. In other words, one computes a strict consensus tree incorporating the shortest tree(s) and those one step longer, and notes which nodes retain their resolution (by adjusting the trees retained to the shortest+1 using the Branch and Bound Analysis option in PAUP*). The process is repeated incrementally until all resolution is lost on the strict consensus tree.

FIGURE 4—Numeric labels for arrows indicate illustrated character and character state respectively (see Appendix). 1–6, *Caryocorbula prenasuta*, middle-upper Miocene Gatun Formation, Panama, NMB 18322, 1, 2, 4, left valve, length 11.9 mm, $\times 4.1$, $\times 5.2$, $\times 5.1$ respectively, 3, 5, 6, right valve, length 13.3 mm, $\times 3.6$, $\times 3.8$, $\times 4.5$ respectively; 7, 10–13, 15, *Bothrocorbula radiatula*, middle Miocene Oak Grove sand, Florida, TU 91, 7, 11, 12, left valve, length 11.7 mm, $\times 4.9$, $\times 4.7$, $\times 14.6$ respectively; 10, 13, 15, right valve, length 11.2 mm, $\times 4.9$, $\times 5.1$, $\times 12.6$ respectively; 8, 9, *Bothrocorbula viminea*, upper Miocene Cercado Formation, Dominican Republic, NMB 15906, 8, right valve, length 16.0 mm, $\times 3.8$, 9, right valve, length 16.3 mm, $\times 3.8$; 14, 16, 17–19, *Hexacorbula hexacyma*, middle-upper Miocene Gatun Formation, Panama, TU 1342, 14, 17, left valve, length 18.6 mm, $\times 3$, $\times 3.1$ respectively, 16, 18, 19, right valve, length 23.0 mm, $\times 2.4$, $\times 5.6$, $\times 2.5$ respectively.



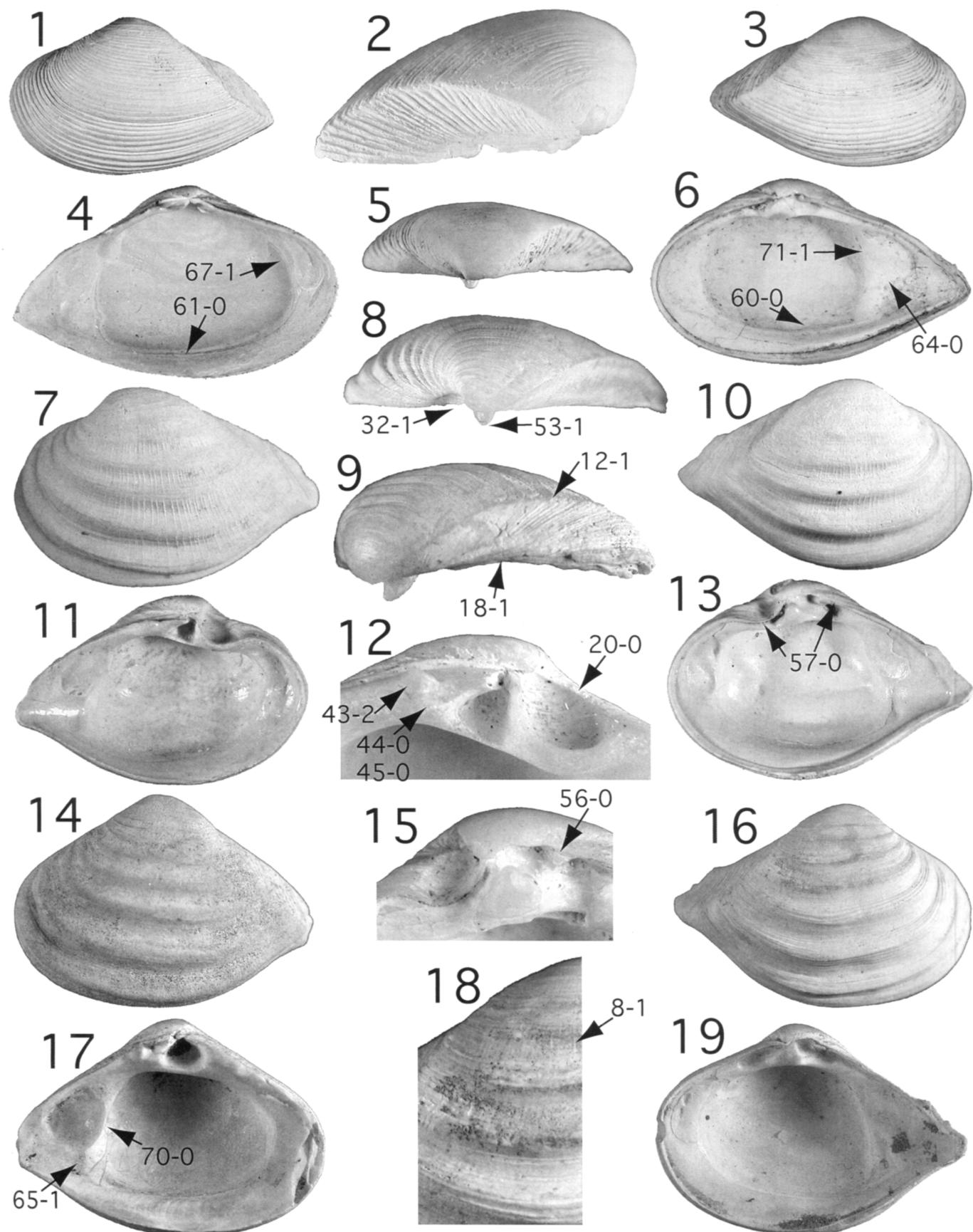


TABLE 4—73-character matrix.

<i>Bicorbula</i>	02200000000	0111100111	0011200101	0000021110	1101100111	2011010?00	1102321111	112
<i>B. gallica</i>	1011?22000	1111100111	00131011?1	0002003011	1101200211	0011110001	1102321211	112
<i>Bothrocorbula</i>	0221122210	0110000110	2100100101	1111111010	0020020200	1111000000	0100110020	022
<i>Caryocorbula</i>	0220011110	0000000111	2100100100	1000121110	0010010201	2011000000	0100221111	122
<i>Corbula</i>	0221411120	0111100021	0011200101	0002002000	1222010302	2011010001	0100110020	122
<i>Cuneocorbula</i>	000??0030	0111110111	32220001?0	12?2?0?0??	?????0?01	20111103??	?????11??	2??
<i>Hexacorbula</i>	0221121110	0110000111	2100100101	1000001010	0020000200	0111000000	0100110020	022
<i>Juliacorbula</i>	0220201130	0000010001	3222000000	1002102010	0020000211	0011110110	1000002212	212
<i>Panamicorbula</i>	000??0000	0111100011	0033211101	1002210010	0011010211	2011111200	1100002202	200
<i>Tenuicorbula</i>	0220300030	0000010001	3222000001	0202220011	1101111012	2011111310	1100002303	300
<i>Varicorbula</i>	1121012101	0101001111	1033101110	0002101010	1011020200	0000101001	1111221301	310
<i>V. gibba</i>	0021?12001	0101001111	1033100111	0002003010	1322110101	2011101001	1101221211	211

RESULTS

In the first set of analyses, in which characters were equally weighted, the 73-character matrix produced two most parsimonious trees [Fig. 5; tree length = 208, consistency index with autapomorphies excluded (CI) = 0.5758, and retention index (RI) = 0.5579]. In one tree (Fig. 5.1; subsequently referred to as Tree 1) American and European *Bicorbula* are sister taxa that occupy the most basal position in one of two ingroup clades. The other tree (Fig. 5.2) differs in that a clade incorporating both American and European *Varicorbula* is basal for this ingroup clade, and European and American *Bicorbula* branch off at the next two nodes. The 70-character matrix yields one most parsimonious tree with a topology identical to Tree 1 (Fig. 5.1; tree length = 203, CI = 0.5959, and RI = 0.5738). Similarly, when characters were weighted according to their RCs, both matrices produced a single most parsimonious tree with a topology identical to Tree 1 (Fig. 5.1; for the 73-character matrix, tree length = 78.79, CI = 0.7518, and RI = 0.7803; for the 70-character matrix, tree length = 78.92, CI = 0.7978, and RI = 0.8101).

Bremer decay indices.—Bremer decay indices indicate relatively robust cladogram nodes for both data sets (Fig. 6), with the number of trees increasing gradually as tree length is increased (Tables 6, 7). For both matrices, the most significant nodes are (*Juliacorbula* + *Tenuicorbula*) and (American + European *Varicorbula*). Support also is considerable for *Cuneocorbula* as the sister taxon of the (*Juliacorbula* + *Tenuicorbula*) clade, and *Panamicorbula* as sister to all three. The overall support also is strong for a clade comprising those taxa with *Bicorbula* and *Varicorbula*.

Both Bremer results and an examination of trees, one and two steps longer than the most parsimonious, indicate two areas of instability within the cladograms (Fig. 6). One area is the position of European and American *Bicorbula* relative to each other and to the *Varicorbula* clade. *Varicorbula* and *Bicorbula*, like *Corbula*, are more strongly inequivaled in shape and ornamentation than the other genera analyzed. Developing a stable hypothesis of relationships in this part of the cladogram may require the

addition of species from other inequivaled taxa, such as the Paleogene genus *Vokesula* and the western Pacific genus *Notocorbula*. Additional or alternative outgroups may also help resolve these relationships. As noted above, published information indicates that the geographic range of *Corbula* s.s. did not extend into tropical America. We now recognize, however, at least three Neogene tropical American species of *Corbula* s.s. Incorporating additional outgroups may clarify the status of *Corbula* s.s. relative to ingroup taxa as well as solidify relationships in the basal portions of the cladograms.

The other unstable area of the cladograms is the relationship among *Caryocorbula*, *Bothrocorbula*, and *Hexacorbula* (Fig. 6). These nodes are the only ones where Bremer values differ significantly between the two matrices. For the larger matrix, Bremer values are robust for the (*Hexacorbula* + *Bothrocorbula*) clade, but are relatively weak for *Caryocorbula* as sister to it. For the 70-character matrix, the node uniting the three taxa is relatively stable but the relationship among these taxa switches from (*Caryocorbula* + (*Bothrocorbula* + *Hexacorbula*)) in the most parsimonious tree to ((*Caryocorbula* + *Bothrocorbula*) + *Hexacorbula*) in a tree two steps longer than Tree 1.

Interestingly, the two matrices differ only in that five characters concerning commarginal rib distribution, thickness, shape, and expression in the 73-character data set are combined into two characters in the 70-character data set (see Appendix). For the larger matrix, character states in *Bothrocorbula* and *Hexacorbula* are identical for the five characters unique to that matrix, with three representing symplesiomorphies (characters 2–4) and two representing synapomorphies (characters 5 and 6). *Caryocorbula*, however, shares character states with *Bothrocorbula* and *Hexacorbula* for only two of these characters (2 and 3), both of which are symplesiomorphies. Of the remaining three characters, two are plesiomorphic (characters 5 and 6) and one is homoplasious (character 4; CI = 0.5) for *Caryocorbula*. Alternatively, the two characters unique to the smaller matrix have high CIs (CI = 1 and CI = 0.83 for character 2 and 3 respectively), although both

TABLE 5—70-character matrix.

<i>Bicorbula</i>	0230000011	1100111001	1200101000	0021110110	1100111201	1010?00110	2321111112
<i>B. gallica</i>	1012000111	1100111001	31011?1000	2003011110	1200211001	1110001110	2321211112
<i>Bothrocorbula</i>	0652210011	0000110210	0100101111	1111010002	0020200111	1000000010	0110020022
<i>Caryocorbula</i>	0341110000	0000111210	0100100100	0121110001	0010201201	1000000010	0221111122
<i>Corbula</i>	0721120011	11000211001	1200101000	2002000122	2010302201	1010001010	0110020122
<i>Cuneocorbula</i>	0000030011	1110111322	20001?012?	2?0?0?????	?0?0?01201	11103?????	?11?22??
<i>Hexacorbula</i>	0651110011	0000111210	0100101100	0001010002	0000200011	1000000010	0110020022
<i>Juliacorbula</i>	0431130000	0010001322	2000000100	2102010002	0000211001	1110110100	0002212212
<i>Panamicorbula</i>	0000000111	1100011003	3211101100	2210010001	1010211201	1111200110	0002202200
<i>Tenuicorbula</i>	0530030000	0010001322	20000001020	2220011110	1111012201	1111310110	0002303300
<i>Varicorbula</i>	1122101010	1001111103	3101111000	2101010101	1020200000	0101001111	1221301310
<i>V. gibba</i>	0022001010	1001111103	3100111000	2003010132	2110101201	1101001110	1221211211

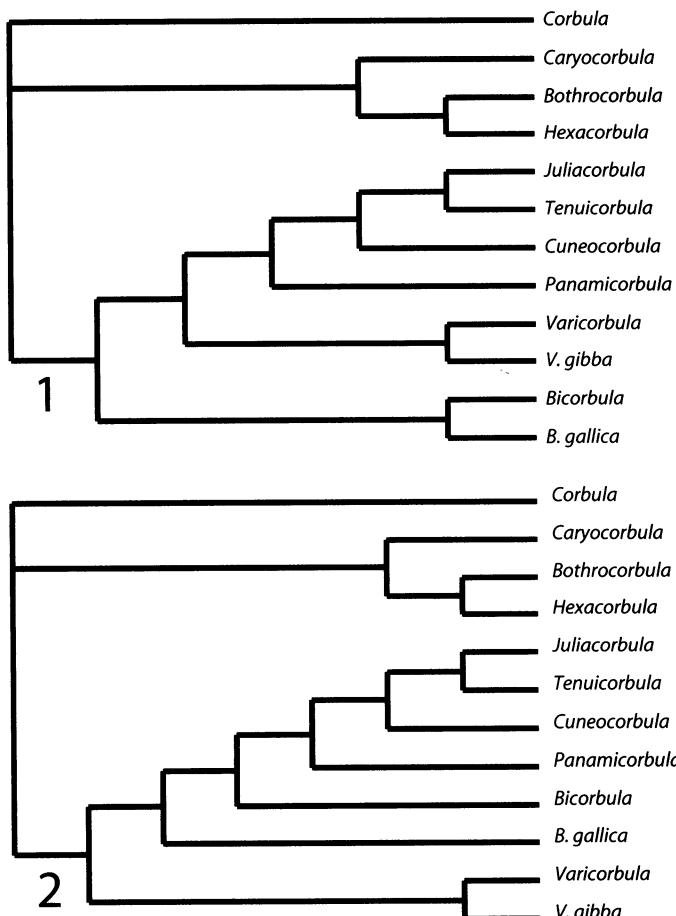


FIGURE 5—Two most parsimonious trees produced in analyses of 73-character matrix. See text for tree statistics. Analysis of 70-character matrix and of both matrices when characters are reweighted according to their RCs produces one most parsimonious tree with a topology identical to (1).

have a large number (up to eight) of character states. Therefore, these characters have little influence on the topology of cladograms produced from this matrix.

For *Bothrocorbula*, *Caryocorbula* and *Hexacorbula*, therefore, morphologic conservatism may make this clade less stable than other parts of the cladograms. Nonetheless, the configuration of the shortest trees is consistent with the fossil record (see next section).

Comparison to stratigraphic record.—Stratigraphic first appearances were tallied from the primary literature, and confirmed where possible from available collections. Except for *Bicorbula*, our results confirm published information on the first appearances of genera. The oldest species of both European and North American *Bicorbula* that we could confirm were from Eocene deposits. *Bicorbula* species reported from the Paleocene of North Dakota (*B. macriformis* and *B. subtrigonalis*) are, or are very closely allied with, *Pachydon* (a genus previously reported from Neogene freshwater deposits of western Amazonia; see Hartman and Anderson, 2002). Using published illustrations and descriptions, we could not confirm the identifications of other species referred to *Bicorbula* from Paleocene and Cretaceous deposits, or from post-Miocene deposits.

Both Tree 1 and the strict consensus tree for the larger matrix agree well with the fossil record and require only one ghost lineage (for *Panamicorbula*; Fig. 7). *Panamicorbula* is a rare genus

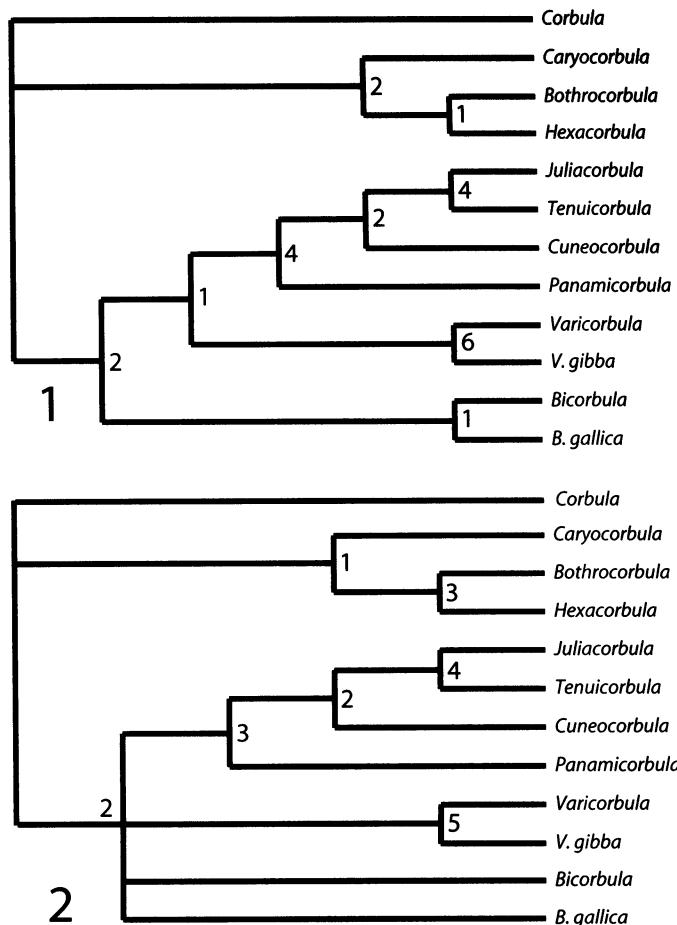


FIGURE 6—Bremer support indices labeled at each node for 1, one most parsimonious tree produced in analyses of 70-character matrix; 2, strict consensus tree produced in analyses of 73-character matrix.

reported from the Recent and Pleistocene of the tropical eastern Pacific (e.g., Seyfried et al., 1985; Coan, 2002) and upper Miocene of the Dominican Republic and Trinidad (Anderson, 1996). Therefore, it is not surprising that the stratigraphic position of this taxon may not be congruent with its phylogenetic position.

DISCUSSION

Our hypothesis of relationships among Neogene corbulid genera of tropical America is robust and well resolved, and is highly congruent with the fossil record. Tree topology is consistent between two data matrices and when characters are re-weighted. As outlined in the “Conchologic Characters” section, in spite of a revision in character state coding for six characters and deletion of eight other characters, our initial results (Anderson and Roopnarine, 2001, 2002) and those reported here are consistent. In

TABLE 6—Bremer Decay Index results for 73-character matrix.

Steps longer	Number nodes	Number new trees
0	7	2
1	7	3
2	6	3
3	4	5
4	2	16
5	1	31
6	0	50

TABLE 7—Bremer Decay Index results for 70-character matrix.

Steps longer	Number nodes	Number new trees
0	9	1
1	9	0
2	6	5
3	3	6
4	3	10
5	1	25
6	1	31
7	0	56

addition, Bremer decay indices illustrate that many nodes remain resolved in trees several steps longer than the shortest (Fig. 6), with the number of equally parsimonious trees increasing only gradually as tree length increases (Tables 6, 7).

Conchologic characters are often perceived as being less reliable than those based on soft-anatomy because of higher incidences of homoplasy (Harasewych, 1984; Wagner, 2001). Our results, however, as well as those of several others demonstrate that conchologic characters can yield highly resolved cladograms (Vermeij and Carlson, 2000; Roopnarine, 2001; Schneider and Carter, 2001; Wagner, 2001). In these studies, reliable characters range from potentially more consistent hinge-tooth morphologies (for bivalves) to possibly more homoplasious sculptural characters. At low taxonomic levels, however, many of these characters are synapomorphic and congruent in a number of distinct clades (Vermeij and Carlson, 2000; Miller, 1999; Roopnarine, 2001; this paper).

Biogeographic patterns.—Our results indicate that Neogene tropical American corbulids are not monophyletic, and can be divided into at least two major clades. In addition, tropical American corbulids are not strictly endemic, and both ingroup clades contain members whose geographic ranges extend beyond the region (Table 1). These cosmopolitan taxa are more basal members of their clades and first appear earlier in the geologic record (Fig. 7). Not surprisingly, biotic interchange, likely through the Tethyan Seaway, was more common before the Miocene. It is clear from our results, however, that American and European species in at least some of these genera, including *Varicorbula* and *Bicorbula*, may represent distinct clades. Additional work is needed to decipher patterns and timing of any divergence between European and American species in these genera.

The crown groups of both clades (*Bothrocorbula* + *Hexacorbula* and *Juliacorbula* + *Tenuicorbula*), however, are endemic to tropical America. These taxa, as well as the endemic genus *Panamicorbula*, first appear in the Miocene. Accepting these records without careful consideration may be problematic because only three corbulid species are described from the tropical American Oligocene (with an additional six described from the U.S. and Mexico Gulf Coast region), perhaps because Oligocene shallow-marine siliciclastic sediments with preserved aragonitic fossils are not widespread.

Nonetheless, corbulid generic diversity and body size are greater in the upper Miocene than in the remainder of the Neogene in the Caribbean/western Atlantic portion of tropical America (Anderson, 2001). Alternatively, in the eastern Pacific diversity and body size peak in the Holocene. The Miocene diversity and size peak in the Caribbean may be linked to elevated nutrient levels and primary productivity. Large corbulid species typically occur in deposits showing evidence of elevated nutrient availability (either from upwelling or runoff), and tend to be excluded from more oligotrophic deposits (Anderson, 2001). Nutrient and productivity levels were elevated in the Miocene of the Caribbean relative to today because of open circulation through the tropical

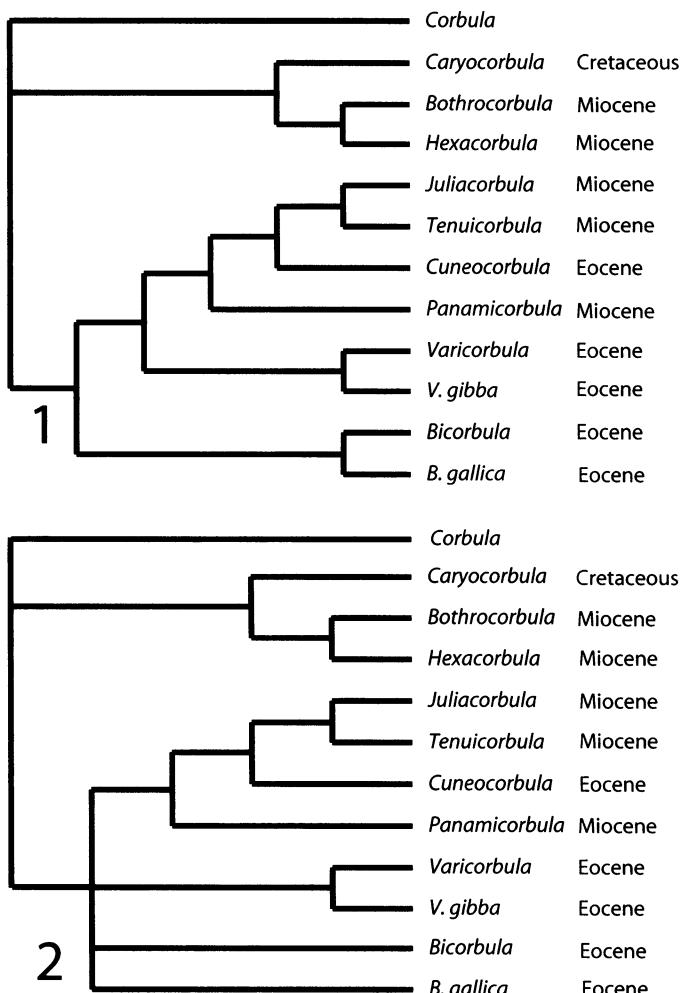


FIGURE 7—Stratigraphic first occurrences listed to the right of each ingroup genus name for 1, one most parsimonious tree produced in analyses of 70-character matrix; 2, strict consensus tree produced in analyses of 73-character matrix.

American Seaway (prior to 6 Ma; Collins, 1996; Collins et al., 1996a) and drainage of the Amazon-Orinoco fluvial system into the southern Caribbean (until ca. 8 Ma; Hooghiemstra and van der Hammen, 1998; Lundberg et al., 1998).

In the Caribbean/western Atlantic, corbulid body-size declined and generic-level extinction increased, with five of nine genera extirpated (*Hexacorbula*, *Panamicorbula*, and *Tenuicorbula* survive in the eastern Pacific) or extinct (*Bicorbula* and *Bothrocorbula*) in the Pliocene or Pleistocene. All five of these genera are large bodied whereas the four genera still present in the Caribbean/western Atlantic are exclusively small-bodied or include small-bodied species. In addition, both the extirpated and extinct groups include members from both clades we identified. Therefore, extinction from the Caribbean/western Atlantic portion of tropical America was not clade specific, but coincides with a trait distributed across clades, i.e., large body size. Even within *Caryocorbula*, a genus with a large size range, all large species in the Caribbean go extinct in the latest Miocene and do not reappear (through speciation, not as Lazarus taxa) until the latest Pliocene (Anderson and Roopnarine, 2003).

This extinction-driven decline in body size across corbulid genera clades is attributed to a decrease in nutrient availability and

primary productivity (Anderson, 2001). Changes in corbulid diversity and morphology coincide with evidence of latest Miocene–early Pliocene establishment of an essentially modern oceanic regime (8–6 Ma; Collins et al., 1996b) and increased carbonate deposition in the Caribbean Basin (starting 7.5 Ma; Collins et al., 1996a). Except for the post-Pliocene extinction of *Bothrocorbula*, however, extinctions in corbulids seem to predate late Pliocene species turnover and morphologic evolution in other molluscs that also are attributed to reduced nutrient levels (Vermeij, 1978; Petuch, 1982; Vermeij and Petuch, 1986; Allmon, 1992; Allmon et al., 1993, 1996; Collins et al., 1996a; Jackson et al., 1996; Roopnarine, 1996; Todd et al., 2002). Clearly, linking evolutionary patterns to causes in Neogene Caribbean molluscs is a more complex task than can be accomplished using large-scale compilations, especially those that do not encompass the Miocene. Close examination of ecologically diverse clades is needed to identify such cause(s) of morphologic evolution.

Corbulid genera undergo range restriction rather than range shifts during the course of Neogene environmental change in the Caribbean/western Atlantic. The three genera extirpated from the region after the Miocene (*Hexacorbula*, *Panamicorbula*, and *Tenuicorbula*) were part of the Neogene Gatunian Province that included both the Caribbean and tropical eastern Pacific. These genera survive today only in the tropical eastern Pacific, the largest extant remnant of the Gatunian Province. Unlike the Caribbean, nutrient availability and primary productivity increased in this region through the Neogene (Keigwin, 1982; Jones and Hasson, 1985; Teranes et al., 1996; Ibaraki, 1997). Species within *Caryocorbula* exhibit an analogous pattern. Body-size did not decline in the eastern Pacific after the Miocene and large-bodied *Caryocorbula* species still inhabit the area (Anderson, 2001).

Although the eastern Pacific served as a refugium for several genera, in contrast to other molluscan clades such as the strombinid gastropods (Jackson et al., 1996), a post-Miocene radiation of corbulid genera endemic to the eastern Pacific did not occur. The only described endemic genus is *Serracorbula*, whose type species, *Caryocorbula tumaca*, is considered a junior synonym of *C. nasuta* (see Coan, 2002). The pattern in corbulids is similar to that found in the venerid subfamily Chioninae, where in spite of an increase in species origination in the eastern Pacific, only one new and endemic genus (*Iliochione*) has evolved since the Pliocene (Roopnarine, 1996). Neither bivalve clade, therefore, produced significant evolutionary novelty in the post-Isthmian eastern Pacific, and modern endemic taxa primarily represent pacificophilic remnants that once had a broader geographic distribution.

Bothrocorbula and *Bicorbula*, both of which inhabited the Calloosahatchian Province of the southeastern U.S. (although *Bothrocorbula*'s range extended into the Gatunian Province), underwent global extinction after the Pleistocene and Miocene respectively. Because of their geographic distribution, these genera should at least have been more eurythermal, if not more eurytopic, than the tropical corbulid taxa that did not suffer global extinction. A tolerance to a more variable environment did not seem to confer a selective advantage to the more temperate genera. For *Bothrocorbula*, extinction coincides with the abrupt intensification of Northern Hemisphere Glaciation at the Pliocene–Pleistocene boundary (Cronin, 1991; Ishman, 1996; Prueher and Rea, 1998; Kleiven et al., 2002). In addition, neither *Bothrocorbula* or *Bicorbula* exhibit evidence of constricted or shifted geographic ranges over the Neogene in response to environmental change, which we do see in the three genera extirpated from the Caribbean portion of the Gatunian Province. Again, this pattern is similar to that of the Chioninae, where extinction of endemic tropical taxa pre-date a later pulse of extinction in the Calloosahatchian Province (Roopnarine, 1996). These contrasting patterns of range restriction between the Calloosahatchian and Gatunian genera indicate that the presence of refugia may be more critical to a taxon's

survival than eurytopicity, especially if that group is geographically restricted, as *Bothrocorbula* in particular was.

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APPENDIX

Description of characters and character states. Illustrations of character states in Figures 1–4 are noted after each description.

External ornament

1. Irregular fine anastomosing striae superimposed on surface of left and right valve	larger in left valve	1
absent	larger in right valve	2
present (Fig. 1.16, arrow 1–1)	20. Lunule	0
2. * Commarginal rib distribution on left valve	present (Fig. 4.12, arrow 20–0)	1
absent (Fig. 2.19)	absent	1
on early-formed portion of valve (Fig. 1.16, arrow 2–1)		2
across entire valve (Fig. 3.8)		3
3. * Commarginal rib distribution on right valve		0
absent (Fig. 2.18)	21. Left-valve shape	0
on early-formed portion of valve (Fig. 2.3, arrow 3–1)	subtriangular (Fig. 2.11)	0
across entire valve (Fig. 3.10)	ovate (Fig. 1.15)	1
4. * Commarginal rib width relative to interspaces	ovate triangular ("tear drop") (Fig. 4.1)	2
ribs < interspaces (Fig. 3.8)	rounded subtrapezoidal (Fig. 3.5)	3
ribs > interspaces (Fig. 1.14)		2
5. * Left-valve commarginal rib shape	22. Right-valve shape	0
Flatly rounded (Fig. 4.1)	subtriangular (see character 21)	0
Highly rounded (Fig. 4.7)	ovate triangular ("tear drop") (see character 21)	1
Wedge shaped (Fig. 3.8)	rounded subtrapezoidal (see character 21)	2
Ribbon like, flat (Fig. 3.5)		3
From rounded to low irregular with ontogeny (Fig. 1.1)	23. Left-valve posterior	0
6. * Commarginal ribs at keel	pointed (Fig. 4.7)	0
no change in expression (Fig. 3.8)	bluntly pointed (Fig. 1.10)	1
some flattening (Fig. 4.3)	bluntly truncated (Fig. 3.5)	2
die out before reaching keel (Fig. 4.14)	rounded (Fig. 1.15)	3
7. Left-valve radial ribs	24. Right-valve posterior	0
absent	pointed (see character 23)	0
fine (see character 8)	bluntly pointed (see character 23)	1
strong (Fig. 4.7)	bluntly truncated (see character 23)	2
8. Right-valve radial ribs	rounded (see character 23)	3
absent	25. Slope of dorsoposterior margin in left and right valves	0
fine (Fig. 4.18)	nearly parallel to anterior-posterior axis (Fig. 3.13)	0
strong (see character 7)	about 45 degrees to anterior-posterior axis (Fig. 2.5)	1
9. Keel expression	nearly perpendicular to anterior-posterior axis (Fig. 2.9)	2
indistinct (Fig. 2.18)	26. Left-valve inflation	0
low rounded (Fig. 1.14)	moderate (Fig. 4.7)	0
high rounded (Fig. 1.4)	high (Fig. 1.14)	1
high and sharp (Fig. 3.5)	27. Right-valve inflation	0
10. Left-valve keel	moderate (see character 26)	0
intersects ventral margin (Fig. 3.8)	high (see character 26)	1
dies out before reaching ventral margin (Fig. 1.15)	28. Midvalve depression	0
11. Right-valve keel	present (Fig. 3.8, arrow 28–0)	0
intersects ventral margin (see character 10)	absent	1
dies out before reaching ventral margin (see character 10)	29. Left and right valve size	0
12. Commarginal ornament on posterior slope of left valve continuous with	subequal (Fig. 4.1, 4.3)	0
ribs anterior of keel (Fig. 4.2)	inequivalved (Fig. 1.14, 1.15)	1
striae anterior of keel (Fig. 4.9, arrow 12–1)	30. Overall size (based on entire genus, not just species used for data on other character states),	0
13. Commarginal ribs on posterior slope of right valve continuous with	includes small species (<10 mm long)	0
ribs anterior of keel (see character 12)	includes only large species	1
striae anterior of keel (see character 12)		1
14. Sharpness of ornament on posterior slope of left valve	31. Hinge	0
sharp (see character 15)		0
low (Fig. 2.7, arrow 14–1)	31. Beak in right valve	0
15. Sharpness of ornament on posterior slope of right valve	extends past hinge area (Fig. 1.18)	0
sharp (Fig. 3.4, arrow 15–0)	does not extend past hinge area (Fig. 4.5)	1
low (see character 14)	32. Viewed dorsally, hinge plate in right valve	0
16. Escutcheon ridge expression of left and right valves	straight (Fig. 4.5)	0
rounded and indistinct (Fig. 2.7, arrow 16–0)	recessed at lunule (Fig. 4.8, arrow 32–1)	1
sharp and high (Fig. 3.7, arrow 16–1)	recessed at resilifer (Fig. 3.4, arrow 32–2)	2
17. Left-valve escutcheon floor	33. Sinuosity of left valve hinge plate	0
flat (Fig. 2.7, arrow 17–0)	not to slightly sinuous (Fig. 4.17)	0
upturned (Fig. 1.16, arrow 17–1)	strongly sinuous, recessed ventrally at lunule (Fig. 4.11)	1
18. Right-valve escutcheon floor	34. Sinuosity of right valve hinge plate	0
flat (see character 17)	slightly sinuous (see character 33)	0
depressed (Fig. 4.9, arrow 18–1)	strongly sinuous, recessed ventrally at lunule (see character 33)	1
19. Escutcheon symmetry	sinuous, recessed dorsally at resilifer (Fig. 2.17)	2
symmetrical in left and right valve	35. Hinge plate angle relative to anterior-posterior axis in left valve	0
	horizontal (Fig. 4.17)	0
	posterior up (Fig. 3.12)	1
	anterior up (Fig. 3.6)	2
	36. Hinge plate angle relative to anterior-posterior axis in right valve	0
	horizontal (see character 35)	0
	posterior up (see character 35)	1
	anterior up (see character 35)	2
	37. Hinge plate in left valve highest	0
	anterior of socket (Fig. 3.6)	0
	at chondrophore (Fig. 4.17)	1

posterior of chondrophore (Fig. 3.12)	2	present (Fig. 4.15, arrow 56–0)	0
either side of hinge (Fig. 2.8)	3	absent (Fig. 2.13, arrow 56–1)	1
38. Hinge plate in right valve highest at resilifer (Fig. 4.13)	0	57. Trough on right valve hinge plate for reception of left valve margin on front surface of hinge plate (Fig. 4.13, arrows 57–0)	0
anterior of tooth (Fig. 4.6)	1	on lower surface of hinge plate (Fig. 2.6, arrows 57–1)	1
39. Number of ridges on upper surface of chondrophore (left valve) two (Fig. 1.6, arrows 39–0)	0	58. Extent of trough in right valve margin for reception of left valve margin	
three (Fig. 2.15, arrow 39–1 points to posterior ridge)	1	around entire valve (Fig. 4.13)	0
40. Most prominent ridge on upper surface of chondrophore (left valve) posterior (Fig. 1.6, arrow 40–0)	0	present from ventral margin of anterior adductor muscle scar around hinge to ventral point of escutcheon (Fig. 3.9, between arrows 58–1)	
middle (Fig. 3.2, arrow 40–1)	1	present on all but posterior margin (Fig. 2.17, between arrows 58–2, 59–2)	2
41. Chondrophore projects (left valve) slightly past valve edge posterior of chondrophore, but is flush with valve edge anterior of socket (Fig. 2.16)	0	present on all but anteroventral margin (Fig. 3.3, between arrows 58–3)	3
beyond commissure (Fig. 3.7, arrow 41–1)	1		
42. Shape of chondrophore's outer edge viewed dorsally (left valve) straight (Fig. 2.16)	0		
v-shaped (Fig. 3.7, arrow 42–1)	1		
s-shaped (Fig. 1.3, arrow 42–2)	2		
rounded (Fig. 3.20, arrow 42–3)	3		
43. Knob on posterior ridge of chondrophore (left valve) absent (Fig. 2.10, arrow 43–0)	0		
present, small (Fig. 2.15, arrow 43–1)	1		
present, large (Fig. 4.12, arrow 43–2)	2		
44. Ridges and furrows on upper surface chondrophore (left valve) low relief (Fig. 4.12, arrow 44–0)	0		
moderate relief (Fig. 3.2, arrow 44–1)	1		
strong relief (Fig. 3.20, arrow 44–2)	2		
45. Proximal-distal shape and angle of chondrophore (left valve) downward angle and planar (Fig. 4.12, arrow 45–0)	0		
high downward angle proximally, upturned distally (scoop shaped) (Fig. 3.2, arrow 45–1)	1		
horizontal and planar with upturned end (Fig. 2.7, arrow 45–2)	2		
46. Cardinal socket angle relative to anterior-posterior axis (left valve) horizontal (Fig. 4.17)	0		
anterior up (Fig. 3.19)	1		
posterior up (Fig. 4.12)	2		
47. Hinge plate behind cardinal socket (left valve) present (Fig. 2.10, arrow 47–0)	0		
absent (Fig. 3.2, arrow 47–1)	1		
48. Lateral walls of cardinal socket (left valve) do not wrap around socket opening (Fig. 3.2, arrow 48–0)	0		
wrap slightly around both anterior and posterior sides (Fig. 2.10, arrow 48–1)	1		
wrap strongly around both anterior and posterior sides (Fig. 2.2, arrow 48–2)	2		
wrap around anterior side only (Fig. 1.2, arrow 48–3)	3		
49. Rim on hinge plate at ventral margin of cardinal socket (left valve) present (Fig. 3.20, arrow 49–0)	0		
absent (Fig. 2.15, arrow 49–1)	1		
50. Cardinal tooth and beak (right valve) far apart (Fig. 4.13)	0		
closely spaced but tooth below beak (Fig. 4.6)	1		
overlap, distal tip of tooth above beak (Fig. 3.3)	2		
51. Cardinal tooth angle relative to anterior-posterior axis (right valve) horizontal (Fig. 4.19)	0		
posterior up (Fig. 4.13)	1		
anterior up (Fig. 3.18)	2		
52. Cardinal tooth position relative to beak (right valve) directly below beak (Fig. 1.9)	0		
below and posterior of beak (Fig. 4.15)	1		
53. Cardinal tooth projects (right valve) does not project beyond beak (Fig. 1.18, arrow 53–0)	0		
projects beyond beak (Fig. 4.8, arrow 53–1)	1		
54. Tooth-like knob, formed at dorsoanterior point of external valve below beak, above tooth (right valve)			
present (Fig. 1.17, arrow 54–0)	0		
absent	1		
55. Resilifer pit (right valve) on front surface of hinge plate (Fig. 4.13, 4.15)	0		
under beak, on lower surface of hinge plate (Fig. 2.6, arrow 55–1)	1		
56. Secondary vertical wall subdividing resilifer pit (right valve)			

Pallial line and sinus

59. Thickness of pallial sinus scar thick (Fig. 3.19, arrow 59–0)	0
thin (Fig. 3.9, arrow 59–1)	1
60. Distance of pallial line to ventral margin of right valve close to valve margin (Fig. 4.6, arrow 60–0)	0
far from valve margin (Fig. 3.18, arrow 60–1)	1
61. Angle of pallial line in left and right valves relative to anterior-posterior axis oblique (higher anterior, lower posterior) (Fig. 4.4, arrow 61–0)	0
parallel (Fig. 1.12, arrow 61–1)	1
62. Pallial line in left and right valves sinuous (Fig. 3.12, arrow 62–0)	0
straight (Fig. 1.12, arrow 62–1)	1
63. Orientation of pallial sinus in left and right valves perpendicular to anterior-posterior axis (Fig. 3.19, arrow 63–0)	0
oblique to anterior-posterior axis (Fig. 1.12, arrow 63–1)	1
64. Pallial sinus intersects posterior adductor muscle scar in left and right valves at midscar (Fig. 4.6, arrow 64–0)	0
at anteroventral point of scar (Fig. 3.19, arrow 64–1)	1
along lower anterior edge of scar (Fig. 2.4, arrow 64–2)	2
65. Expression of pallial sinus in left valve no invagination (Fig. 2.14, arrow 65–0)	0
does not extend to anterior edge of posterior adductor muscle scar (Fig. 4.17, arrow 65–1)	1
extends to anterior edge of posterior adductor muscle scar (Fig. 3.19, arrow 65–2)	2
extends beyond anterior edge of posterior adductor muscle scar (Fig. 2.10, arrow 65–3)	3
66. Expression of pallial sinus in right valve no invagination (see character 65)	0
does not extend to anterior edge of posterior adductor muscle scar (see character 65)	1
extends to anterior edge of posterior adductor muscle scar (see character 65)	2

Adductors

67. Orientation of anterior adductor muscle scar relative to commissure in left valve low oblique angle (Fig. 1.13, arrow 67–0)	0
moderate angle (Fig. 4.4, arrow 67–1)	1
high oblique angle (see character 68)	2
68. Orientation of anterior adductor muscle scar angle relative to commissure in right valve low oblique angle (see character 67)	0
moderate angle (see character 67)	1
high oblique angle (Fig. 2.17, arrow 68–2)	2
nearly perpendicular (Fig. 1.11, arrow 68–3)	3
69. Anterior adductor muscle scar of left and right valves not embedded in valve wall (Fig. 2.17, arrow 69–0)	0
slightly embedded in valve wall (Fig. 3.9, arrow 69–1)	1
deeply embedded in valve wall (Fig. 1.13, arrow 69–2)	2
70. Orientation of posterior adductor muscle scar relative to commissure in left valve low oblique angle (Fig. 4.17, arrow 70–0)	0
moderate angle (see character 71)	1

high angle (Fig. 3.12, arrow 70–2)	2	than interspaces, and which show no change in expression at keel (Fig. 2.11)	2
nearly perpendicular (see character 71)	3	across entire valve surface with flatly rounded ribs that are thinner than interspaces, and which flatten at keel (Fig. 4.1)	3
71. Orientation of posterior adductor muscle scar relative to commissure in right valve		across entire valve surface with wedge shaped ribs that are thinner than interspaces, and which show no change in expression at keel (Fig. 3.8)	4
low oblique angle (see character 70)	0	across entire valve surface with flat topped, ribbon-like ribs that are thinner than interspaces, and which show no change in expression at keel (Fig. 3.5)	5
moderate angle (Fig. 4.6, arrow 71–1)	1	across entire valve surface with highly rounded ribs that are thicker than interspaces, and which die out at keel (Fig. 4.7)	6
high oblique angle (see character 70)	2	across entire valve surface, ribs rounded in early ontogeny, later be- coming low and irregular, ribs thicker than interspaces and flatten at keel (Fig. 1.1)	7
nearly perpendicular (Fig. 1.11, arrow 71–2)	3		
72. Posterior adductor muscle scar of left valve		3. Commarginal rib distribution on right valve	
not embedded in valve wall (Fig. 2.14, arrow 72–0)	0	absent (Fig. 2.18)	0
slightly embedded in valve wall (see character 73)	1	on early-formed portion of valve (Fig. 2.3, arrow 3–1)	1
deeply embedded in valve wall (Fig. 1.13, arrow 72–2)	2	across entire valve surface with ribs that are thicker than interspaces, and which flatten at keel (Fig. 1.14)	2
73. Posterior adductor muscle scar of right valve		across entire valve surface with ribs that are thinner than interspaces, and which show no change in expression at keel (Fig. 3.1)	3
not embedded in valve wall (see character 72)	0	across entire valve surface with ribs that are thinner than interspaces, and which flatten at keel (Fig. 4.3)	4
slightly embedded in valve wall (3.18, arrow 73–1)	1	across entire valve surface with ribs that are thicker than interspaces, and which die out at keel (Fig. 4.16)	5
deeply embedded in valve wall (see character 72)	2		

*These characters are combined into the following two characters to form a 70-character matrix. Commarginal ribs are absent in both left and right valves in *Cuneocorbula* and *Panamicorbula* and in the left valves of *V. gibba* and *B. gallica*. Therefore, characters 4–6 had to be coded as missing data although they are not present rather than not observed.

2. Commarginal rib distribution on left valve

absent (Fig. 2.19)	0
on early-formed portion of valve (Fig. 1.16, arrow 2–1)	1
across entire valve surface with flatly rounded ribs that are thinner	