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Close evolutionary affinities between freshwater corbulid bivalves from the Neogene of western Amazonia and Paleogene of the northern Great Plains, USA

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Abstract

Freshwater corbulid bivalves found in Miocene deposits of western Amazonia have been considered products of an endemic radiation of a marine clade within the large lacustrine system occupying the region at that time. Our reexamination of Paleocene freshwater corbulids of the Tongue River Formation of western North Dakota and eastern Montana, however, extends the stratigraphic and geographic range of three Amazonian taxa—*Pachydon, Ostomya,* and *Anticorbula*—to the Paleocene of the northern Great Plains of the United States. Both Paleocene and Miocene freshwater corbulid taxa occur in large freshwater systems with an intermittent marine connection. To test the phylogenetic relationships of one particularly widespread Paleocene species (*Pachydon mactriformis*), we conducted cladistic analyses using maximum parsimony and heuristic searches of matrices of conchologic characters. Seven species of *Pachydon* and *Pebasia dispar* from the western Amazonian Neogene, *Pachydon mactriformis* from the Paleocene of North Dakota, representative species of eight neotropical marine corbulid genera, and three additional corbulid taxa were included. *Corbula* was the outgroup. All analyses produced similar regions of stability within trees. One such area is a *Pachydon* crown group that includes *P. mactriformis*, indicating that Paleocene and Miocene *Pachydon* are not convergent. Our results also indicate that *Pachydon* does not represent a separate basal radiation within the family. However, we have not resolved a robust sister clade relationship for the *Pachydon* crown group. Two Amazonian Neogene taxa do not fall within the *Pachydon* crown group, and their phylogenetic position is not resolved. At this time, we do not have sufficient evidence to refine the definitions of *Pachydon* and Pachydontinae as monophyletic clades. Although we have evidence that three genera of corbulid bivalves (*Pachydon, Ostomya,* and *Anticorbula*) in the Pebas Formation are not endemic and have long geologic histories, a species-level radiation occurs within the Amazonian Miocene, especially within *Pachydon*. In this radiation, morphologic and ecologic divergence is dramatic, and one species, *P. obliquus*, successfully invaded and dominated extreme, dysoxic habitats.

Keywords: Bivalvia; Corbulidae; Freshwater; Neogene; *Pachydon*; Paleogene; Pebas Formation; Tongue River Formation; Western Amazonia; Williston Basin

1. Introduction

Corbulid bivalves of the Neogene Pebas Formation of northern Peru and correlative units in adjacent areas of Brazil, Colombia, and Ecuador are considered products of an endemic radiation of a marine clade in a large freshwater system, often referred to as Lake Pebas (Wesselingh et al., 2002). The molluscan fauna of this unit has high endemicity (several assemblages well over 90% endemic species) and flocklike species groups with extreme morphological variation, particularly in the cochliopine gastropods and corbulid bivalves (Wesselingh et al., 2002). For freshwater corbulid bivalves, most of six genera and 19 species that occur in the Pebas Formation are extinct, and none to date is well documented outside of northern South America (Wesselingh et al., 2002). Nonetheless, soon after Gabb (1869) first described the Pebas fauna, Meek (1876) noted similar corbulid species in freshwater deposits from the Late Cretaceous and Paleocene of the Williston Basin of the northern Great Plains of the USA (now western North Dakota and easternmost Montana). Later systematic treatments by Stanton (1920) and Cvancara (1966), however, placed these species respectively in *Corbula s.s.*

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Bruguière, 1797, and *Bicorbula* Fischer, 1887, both of which are marine taxa. These reassignments generally reflected the prevailing thought that the taxa were indicative of a marine influence in otherwise freshwater deposits.

Reexamination of Paleocene corbulids of the Tongue River Formation of western North Dakota and easternmost Montana indicates that the relationship between these taxa and Neogene freshwater corbulids of South America must be reconsidered (Hartman and Anderson, 2002; Anderson and Hartman, 2003). In this article, we compare the depositional settings and corbulid faunas, including initial phylogenetic results, of the Paleocene Tongue River and Miocene Pebas formations. Our results indicate that corbulid species of the Pebas Formation appeared as part of an endemic radiation but that three genera have a much earlier evolutionary origin and broader geographic range.

1.1. Pachydon *and other Miocene freshwater corbulid genera of western Amazonia*

Corbulids generally are characterized by relatively small (most <3 cm in length) and inequivalved shells that often have a subtrigonal shape (e.g. Fig. 1). The left valve typically is smaller, and differences in valve size, shape, and ornamentation range from subequal to highly inequivalved, including concavo-convex shells (Fig. 2, images 1, 2, 4, 5). Corbulids also have relatively simple hinges. A cardinal tooth in the right valve is located to the anterior of a socketlike resilifer (Fig. 1, image 5). The left valve has an anterior cardinal socket and posterior chondrophore (Fig. 1, image 2).

The morphology of the freshwater genus *Pachydon* Gabb, 1869, conforms to this basic corbulid body plan (Fig. 3). Diagnostic features of the genus include a prosogyrous umbo and beak that is strongly expressed in the type species *P. obliquus* Gabb, 1869 (Fig. 3, images 1, 2, 4, 5, 8). A strong cardinal tooth that is bluntly rectangular, a strong keel (especially in the left valve), and valve surfaces lacking sculpture except for fine concentric striae also are typical features of *Pachydon*. In addition, *Pachydon* species commonly possess a deeply impressed, rugose anterior adductor muscle scar and nonplanar commissure.

Other previously described freshwater genera of corbulids from the Pebas Formation include the extant *Anticorbula* Dall, 1898 (also commonly referred to by its junior synonym *Guianadesma* Morrison, 1943) and two extinct taxa, *Pebasia* Nuttall, 1990, and *Ostomya* Conrad, 1874. Extant *Anticorbula*

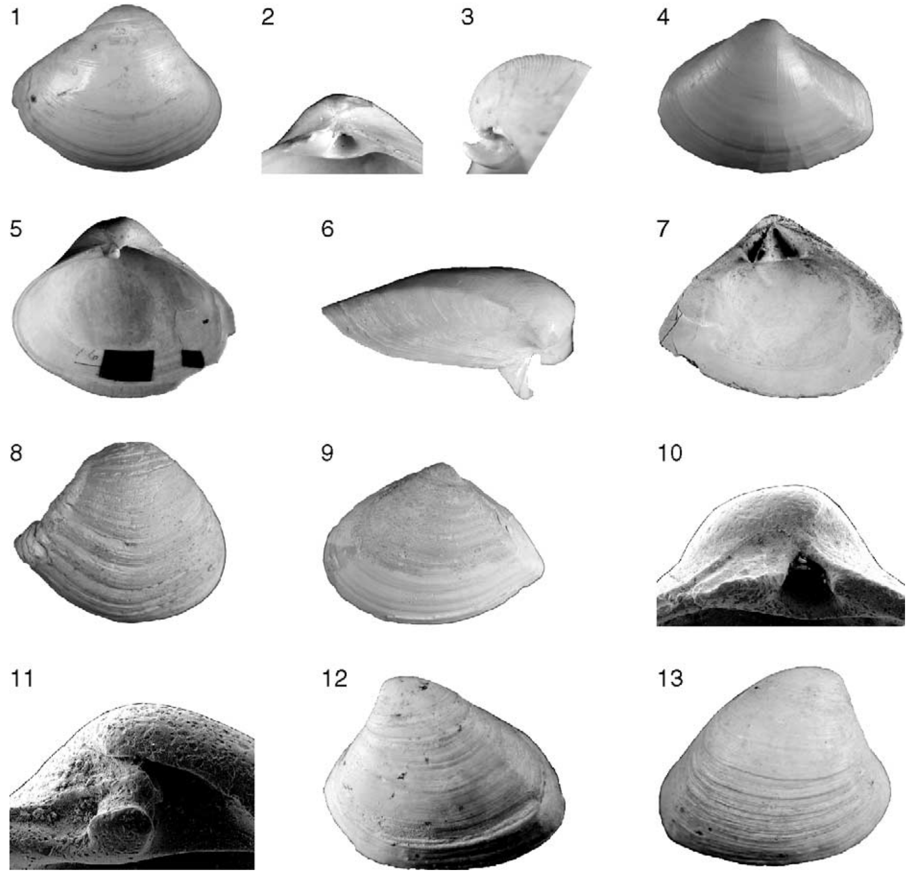

Fig. 1. (Images 1-6) *Bicorbula gallica*, Eocene, Paris Basin, France, (1, 3, 5) right valve, American Museum of Natural History (AMNH) 16717, length 40 mm, X1.3, X5, X1.1, respectively, (2, 4, 6) left valve, AMNH 31976, length 32.4 mm, X4.1, X1.6, X1.4, respectively. (Images 7–9) *B. idonea*, middle Miocene Choptank Formation, Maryland, (7, 9) left valve, author's collection (Anderson), length 30.1 mm, X1.6, X1.5, respectively, (8) right valve, Paleontological Research Institution (PRI), Ithaca, NY, PRI 44840, length 30.7 mm, X1.3. (Images 10–13) *Pachydon mactriformis*, Paleocene Tongue River Formation, North Dakota, (10) left valve hinge, University of Minnesota Paleontology Collection (UMPC) 12413b, X10, (11) right valve hinge, UMPC 12409, X17, (12) left valve, Hartman S2095 (Locality L0039), length 15.7 mm, X3.1, (13) right valve, Hartman S2096 (Locality L0039), length 19.0, X2.4.

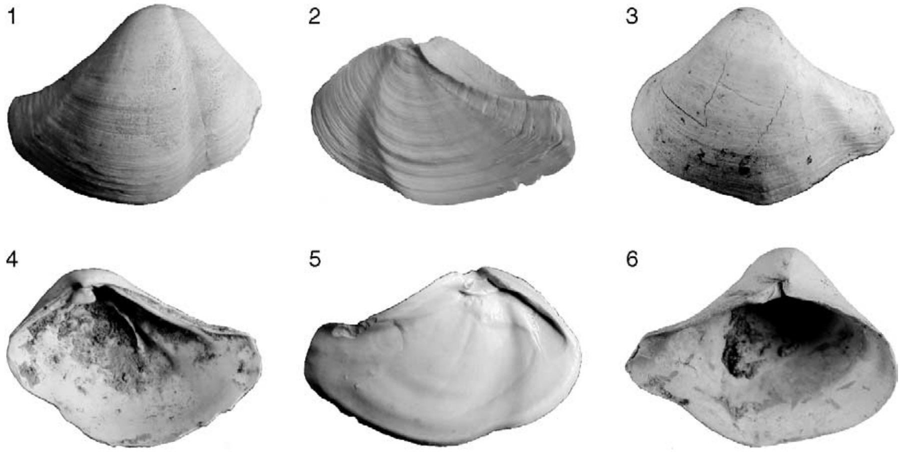

Fig. 2. (Images 1, 2, 4, 5) *Pebasia dispar*, Miocene Pebas Formation, Peru, (1, 4) right valve, author's collection (Anderson), length 13.1 mm, X3.8, (2, 5) left valve, author's collection (Anderson), length 14.1 mm, X3.5, X3.8, respectively. (Images 3, 6) *Pachydon erectus*, left valve, Miocene Pebas Formation, Peru, author's collection (Anderson), length 20.6 mm, X2.6.

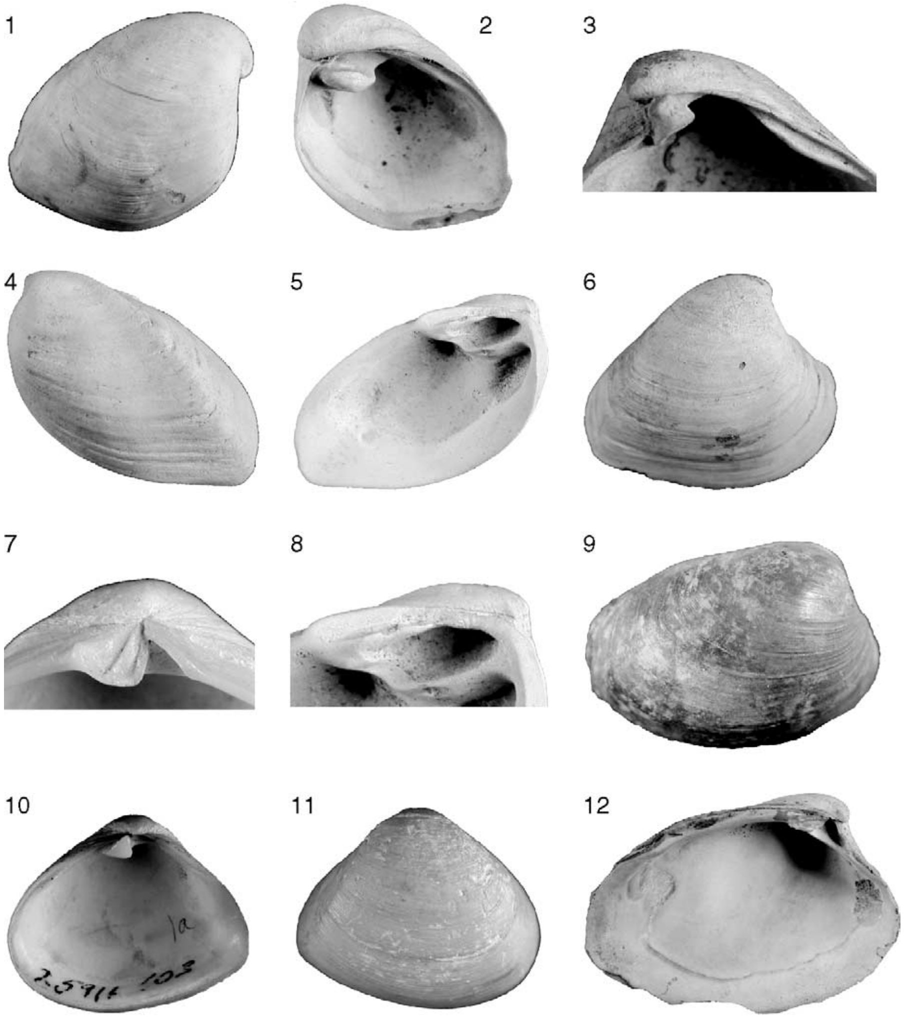

Fig. 3. (Images 1, 2, 4, 5, 8) *Pachydon obliquus*, Miocene Pebas Formation, Peru, (1, 2) right valve, author's collection (Anderson), length 11.5 mm, X3.8, X3.3, respectively, (4, 5, 8) left valve, author's collection (Anderson), length 13.0 mm, X3.5, X3.5, X6, respectively. (Images 3, 6) *Pachydon cuneatus* right valve, Miocene Pebas Formation, author's collection (Anderson), length 16.4 mm, X5.2, X 2.7, respectively. (Images 7, 10, 11) *Panamicorbula ventricosa* (=*P. inflata*), Recent, Ecuador, PRI 25911, (7) left valve, length 28.0 mm, X5.9, (10, 11) right valve, length 27.1 mm, X1.6. (Images 9, 12) *Pachydon tenuis*, Miocene Pebas Formation, Peru, (9) right valve, author's collection (Anderson), length 26.5 mm, X2, (12) left valve, author's collection (Anderson), length 25.7 mm, X 2.2.

live in uppermost estuarine to fluvial environments of the Guyanas, as well as in floodplain environments of the Brazilian and possibly Peruvian Amazon (Morrison, 1943; Leistikow and Janssen, 1997; Simone, 1999). Unlike most other corbulids, which are infaunal, *Anticorbula* lives byssally attached to hard substrates, often nestling (Nuttall, 1990; Leistikow and Janssen, 1997; Simone, 1999). This habit is reflected in its shell, which resembles that of nestling myoid bivalves with irregular kidney-shaped valves, indistinct umbos, and nonplanar commissures (Fig. 4, images 13–15, 17, 18). In addition to the Pebas Formation, fossil *Anticorbula* occur in the early Miocene Chaguaramas and Pliocene La Piedras formations of Venezuela (described as *Ostomya mencheri* by Palmer 1945, see also Nuttall 1990) and the Oligo-Miocene Colorado Formation of Colombia (described as *O. colombiana* by Pilsbry and Olsson 1935, see Nuttall 1990). We extend the geologic range of this genus to the Paleocene.

Anticorbula has been placed in both the Lyonsiidae (Morrison, 1943; Simone, 1999) and the Corbulidae (Nuttall, 1990; Leistikow and Janssen, 1997). On the basis of hinge characters, we consider *Anticorbula* a corbulid. In *Anticorbula*, a resilifer pit is located under the umbo in the right valve and on

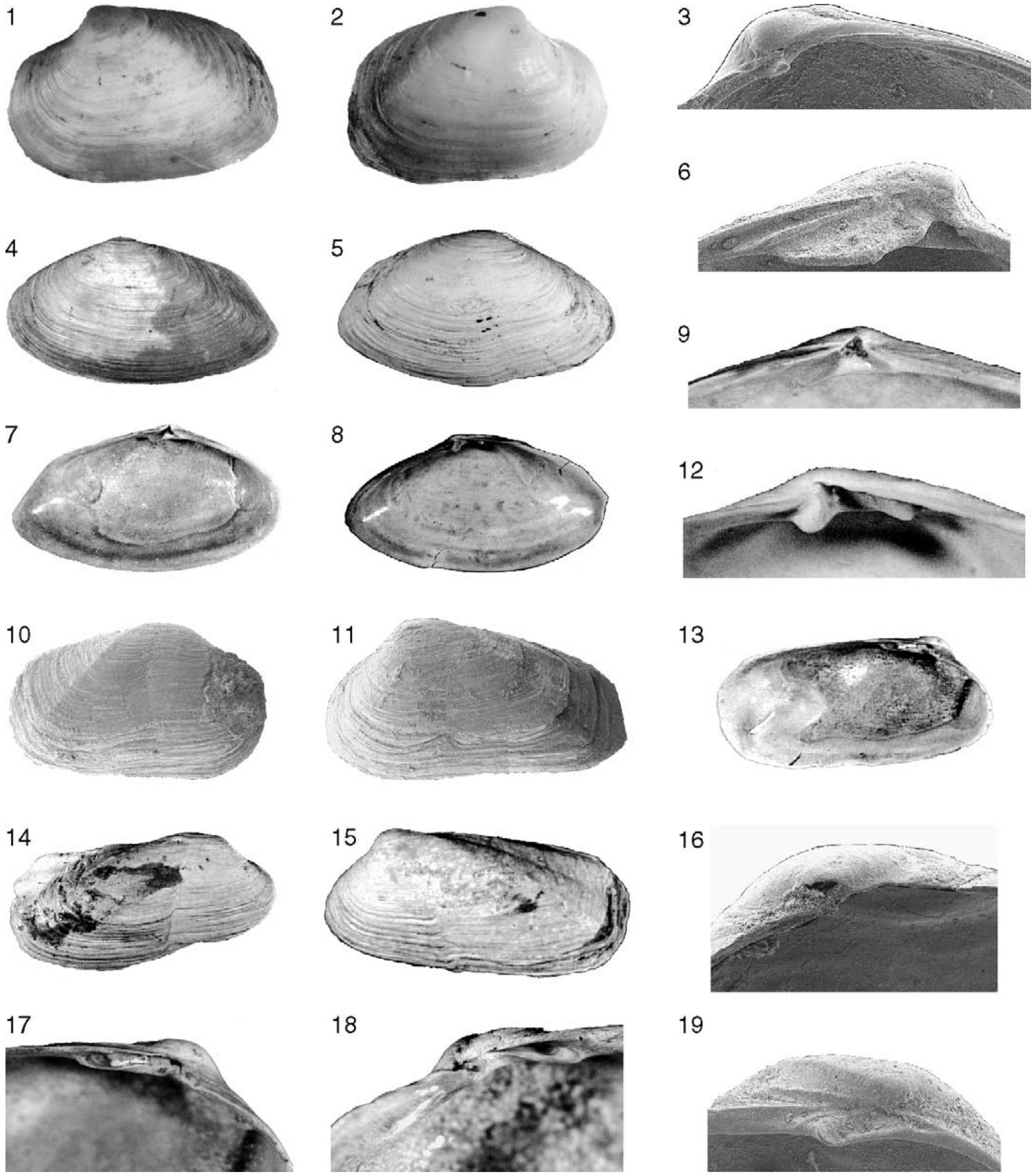

Fig. 4. (Images 1–3, 6) *Ostomya* sp., middle? Paleocene Tongue River Formation, Montana, (1) left valve, Hartman S2108 (Locality L0049), length 10.1 mm, X5, (2) right valve, Hartman S2107 (Locality L0049), length 10.4 mm, X4.7, (3) right valve, Hartman S2289, X37, (6) left valve, Hartman S2291, X32. (Images 4, 5, 7–9, 12) *Ostomya papyria*, Miocene Pebas Formation, Peru, (4, 7, 9) left valve, Rijks Museum voor Geologie en Mineralogie (RGM) 456187 (sample F707), length 9.1 mm, X5.7, X5.7, X19, respectively, (5, 8, 12) right valve, RGM 456190 (sample F70), length 9.1 mm, X5.6, X5.6, X25, respectively. (Images 10, 11, 16, 19) *Anticorbula* sp., middle? Paleocene Tongue River Formation, Montana, (10) right valve, Hartman S2287 (Locality L0049), length 8.9 mm, X5.5, (11) left valve, Hartman S2283 (Locality L0049), length 7 mm, X7.8, (16) right valve hinge, Hartman S2281 (Locality L0049), X20, (19) left valve hinge, Hartman S2286 (Locality L0049), X15.6. (Images 13–15, 17, 18) *Anticorbula* sp., Miocene Pebas Formation, Peru, (13, 15, 17) left valve, RGM 456185 (sample F707), length 6.4 mm, X8.3, X9.2, X20, respectively, (14, 18) right valve RGM 456184 (sample F707), length 9 mm, X5.5, X17, respectively.

an obliquely projecting, reduced chondrophore in the left valve (Fig. 4, images 13, 16–19; cf. *Bicorbula gallica* (Lamarck, 1801), Fig. 1, images 1–6). In addition, remnants of the hinge plate and possibly of cardinal dentition are present. Such features also are present in *A. mencheri* from the Pliocene Las Piedras Formation of Venezuela. In contrast, members of the Lyonsiidae lack a hinge plate and have resilifers in both valves. These resilifers are oriented perpendicular to the commissure and located underneath and posterior to the umbos. This orientation is functionally possible because members of this family possess a lithodesma (calcareous plate attached to and reinforcing the ventral side of the ligament but not attached to the hinge of either valve). Whereas Simone (1999) infers that a mantle extension he observed filling a hollow region in the ligament of *A. fluviatilis* (H. Adams, 1860) could be a vestigial lithodesma, we argue that the orientation of ligament attachments and evidence of a reduced hinge plate and dentition indicate that *Anticorbula* is a corbulid bivalve.

Pebasia is an extinct genus reported only from the Pebas Formation. The genus is highly distinctive, with a concavo-convex shell, nonplanar commissure, and hinge that corresponds well with the basic corbulid plan, although modified to accommodate the unusual shell shape (Fig. 2, images 1, 2, 4, 5). A pleurothetic (resting on one valve) life position with possible strong byssal attachment is suggested for this genus (Savazzi and Yao, 1992).

Ostomya also is extinct, with previous valid reports only from the Pebas Formation (Nuttall 1990 reassigned other taxa previously placed in *Ostomya* to *Guianadesma*, a junior synonym of *Anticorbula*), although we extend its range to the Paleocene of North America. The genus is nearly equivalved, with ovate valves that have a small umbo (Fig. 4, images 1–9, 12). In the left valve, the cardinal socket is very small, and the chondrophore is prominent, trough-shaped, and directed posteroventrally at about a 45° angle to the hinge line. This genus is considered by some authors to be a member of the Lyonsiidae (e.g. Vokes, 1945), but hinge features, including a hinge plate, a cardinal tooth and resilifer pit in the right valve, and a cardinal socket and chondrophore in the left valve, support the assignment of *Ostomya* to the Corbulidae (Fig. 4, images 3, 6–9, 12; see also Nuttall, 1990).

1.2. Paleocene freshwater Corbulidae of North America

Meek (1876) placed three species of corbulids from the Late Cretaceous and 'Eocene' (now Paleocene) of western North Dakota and eastern Montana in *Pachydon* (*Pachyodon* of Meek), designating it a subgenus of *Corbula*. These species were collected from dominantly fluvial and paludal environments (Hartman, 1976; Chevren and Jacob, 1985; Rogers, 1998) of the Campanian Judith River Formation and the Paleocene Fort Union Group. Subsequent authors (Stanton, 1920; Cvancara, 1966) reported two of these species—'*Corbula*' *subtrigonalis* Meek and Hayden, 1856, and '*C.*' *mactriformis* Meek and Hayden, 1856—from the Cannonball Formation, a unit within the Fort Union Group that represents marine incursions into the Williston Basin. In addition, Cvanacara (1966) reassigned these species to *Bicorbula*, a genus of marine bivalves, whose type species *B. gallica* is from Eocene strata of the Paris Basin.

Ongoing stratigraphic work (Hartman and Kihm, 1992, 1995; Lund et al., 2002) indicates that at least one of these species, '*C.*' *mactriformis* (Fig. 1, images 10–13), has a wide distribution in Paleocene nonmarine sediments of western

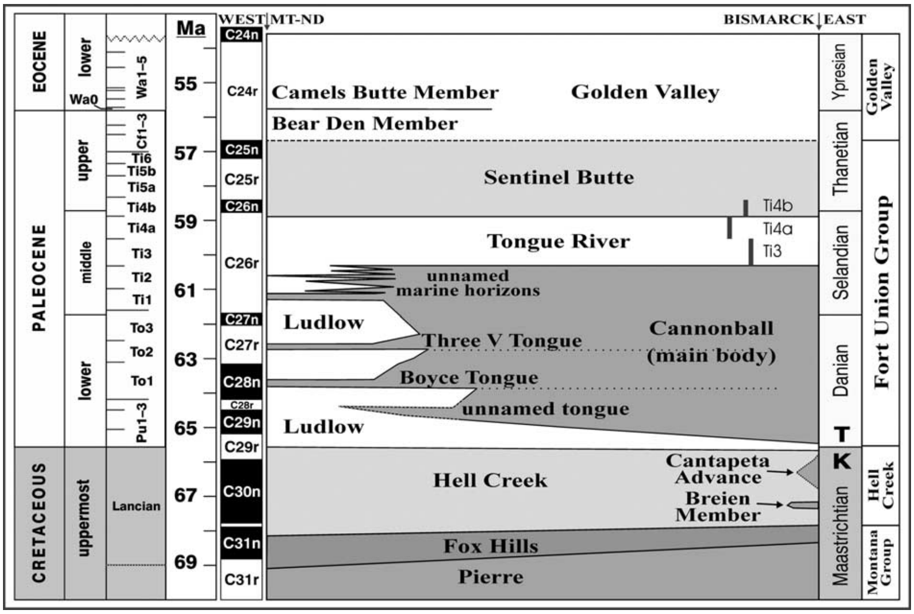

Fig. 5. Uppermost Cretaceous and Paleocene chronostratigraphy of fossil-bearing strata in the eastern Williston Basin of western North Dakota, USA. Illustrated, from the left, are system, series, North American Land Mammal "Age" (NALMA), geochronometric age (in millions of years), magnetic polarity, chronostratigraphic correlation of strata across western North Dakota, global stages, and formation names (revised framework from Hartman et al., 2005; see also Lund et al., 2002; see Vuke et al., 2003, for chronostratigraphic framework of same interval in Montana).

North Dakota and southeastern Saskatchewan. It occurs from the upper part of the Ludlow Formation (~62 Ma, Torrejonian (To) North American Land Mammal Age (NALMA); Fig. 5) to the lower part of the Sentinel Butte Formation (Ravenscrag Formation of Canada) (~58 Ma, Tiffanian-4 [Ti4] NALMA) but is most common in the Tongue River Formation (~61–59 Ma, Ti2–Ti4 NALMA biochron). In these units, '*C.*' *mactriformis* typically is found as part of unabashedly freshwater molluscan assemblages (we discuss this further in Section 2). As currently defined, specimens reported from the Cannonball previously assigned to '*C.*' *mactriformis* may not be conspecific with individuals from freshwater facies (see Taylor, 1975).

Type material of '*C.*' *mactriformis* and further collections from the Tongue River Formation (Hartman, unpublished data) are within the range of morphologies observed in *Pachydon* and do not closely resemble *B. gallica*, the type species of *Bicorbula,* or *B. idonea* (Conrad, 1833), a Miocene species of the Atlantic Coastal Plain (Fig. 1). All these genera have subdued or absent concentric sculpture, whereas valves of '*C.*' *mactriformis*, like *Pachydon*, are prosogyrous, giving them a triangular-chordate shape (Fig. 1, images 10, 13, cf. especially *P. cuneatus* Conrad, 1871, Fig. 3, images 3, 6). In addition, the hinge of '*C.*' *mactriformis* is highly reminiscent of *Pachydon*, including a lateral toothlike groove posterior to the right valve hinge and a massive, bluntly rectangular cardinal tooth (Fig. 1, image 11). These similarities confirm a close phylogenetic relationship with Amazonian Neogene *Pachydon*, and therefore, we refer '*C.*' *mactriformis* to *Pachydon*. Additional undescribed taxa with strong affinities to *Ostomya* and *Anticorbula* also have been collected from Tongue River Formation localities (Fig. 4).

2. Geological and environmental context of the corbulids studied

The Pebas Formation is a poorly defined unit several hundreds to a thousand meters thick that covers over 1 million km^2 in Colombian, Peruvian, Ecuadorian, and Brazilian Amazonia. The unit was deposited in the East Andean foreland basin and adjacent pericratonic basins of the South American Craton. Most of the Pebas Formation is of late early–early late Miocene age (Hoorn, 1993, 1994).

The Pebas Formation is typified by 3–7 m thick, predominantly coarsening-upward parasequences, often capped by lignites. Fine-grained, brilliant blue-green smectitic clays and fine, immature, feldspar-rich sands characterize the formation. Channel lithosomes occur with common inclined heterolithic stratification (Räsänen et al., 1998). Fossils are common, especially within the basal clays and above the lignites of parasequences. Relationships with underlying and overlying geological units are poorly defined (Hoorn, 1993; Wesselingh et al., 2002).

Nuttall (1990) reconstructed the depositional setting of the Pebas Formation as a series of shallow lakes, streams, and swamps of varying salinities on the basis of the molluscan fauna. Hoorn (1993) and Hoorn et al. (1995), using palynologic and sedimentologic data, concluded that the Pebas Formation was deposited in a fluviolacustrine environment with marine influence. On the basis of ichnofossils and tidal deposits, Gingras et al. (2002) inferred a marginal marine environment. Vonhof et al. (1998, 2003) and Wesselingh et al. (2002) both concluded, on the basis of Sr-isotope and molluscan data, respectively, that the Pebas Formation represented a large, long-lived, complex lacustrine system that was episodically influenced by marine incursions, although salinities probably never exceeded 5‰.

In the North American western interior, Paleocene deposits represent an alluvial system that intertongued with marine deposits during the Laramide orogeny. Intercalated terrestrial and marine to brackish-water deposits are documented throughout the early stages of the orogeny by persistent shoreline fluctuations for nearly 7 my, from the Maastrichtian to the Selandian (Diemer et al., 1996; Hartman et al., 1999; Wroblewski and Steel, 1999; Tibert et al., 2001; Lund et al., 2002; Belt et al., 2002, 2004a,b, 2005). Sea-level fluctuations are recorded as far west as eastern Montana and throughout all but the youngest intervals of the Tongue River Formation (Hartman, 1993a; Hartman et al., 1998, 1999; Tibert et al., 2001; Hartman and Anderson, 2002; Belt et al., 2004b, 2005). Depositional continuity between brackish and freshwater facies is evident in the lower part of the Tongue River Formation in western North Dakota (Diemer et al., 1996; Tibert et al., 2001; Belt et al., 2004b). Furthermore, the Cannonball Sea deepened throughout the Paleocene (Hartman et al., 1999, in prep.), which indicates open circulation with an oceanic source and faunal exchange across the Dakota Isthmus of Erickson (1999). Final regression of the Cannonball Sea commenced in the Selandian (Ti2 NALMA), according to microfossil, mammalian, and molluscan data (Hartman et al., 1999), and moved completely out of the study area within the Ti3 NALMA biochron (Hartman et al., 1999; Kihm and Hartman, 2004).

Nevertheless, corbuld-bearing beds in the Tongue River Formation are generally associated with freshwater molluscan assemblages. In 39 of 44 localities where *P. mactriformis* is reported, the species is associated with single species of freshwater gastropods, such as *Lioplacodes nebrascensis producta* (White, 1883; Pleuroceridae), *Campeloma nebrascense* (Meek and Hayden, 1860; Viviperidae), and New Genus A *limneaformis* (Meek and Hayden, 1856), as well as with fragmentary material of freshwater mussels (Unionidae). *Pachydon mactriformis* also occurs in monospecific assemblages at five localities. Tibert et al. (2001) described the ostracode fauna (including *Bisulcocypridae*, *Candona*, and *Darwinula*) from one such locality (Golden Valley County, in the Ti2 NALMA biochron; Hunter, 1999; Belt et al., 2004b) as indicative of fresh water. *Ostomya* and *Anticorbula* are found at a single locality in eastern Montana and are associated with a diverse assemblage of freshwater snails, Sphaeriidae specimens, and a few fragmentary remains of freshwater mussels (Unionidae).

Although corbulids occur in freshwater deposits of the Tongue River Formation, some occurrences apparently coincide with either a sea-level highstand or significant progradation. For example, four monotypic localities of *P. mactriformis* are located relatively far to the east (Grant and Burleigh counties in central North Dakota, near Estevan in Saskatchewan) and high in the section (Ti3 and Ti4), suggesting a temporal and geographic propinquity to final regression of the Cannonball Sea. In addition, the presently known stratigraphic horizon of *Ostomya* and *Anticorbula* (laterally correlative to the upper part of the Ludlow Formation in North Dakota; Torrejonian pre-Ti3 NALMA biochron; Hartman, 1993b) coincides with an earlier sea-level highstand and transgression of the Cannonball Sea.

3. Phylogenetic analyses: Taxa analyzed

Seven species of Amazonian Neogene *Pachydon*, *Pebasia dispar* (Conrad, 1874), and the Paleocene *Pachydon mactriformis* were incorporated into phylogenetic analyses (Table 1). Representative species of eight genera reported in Neogene marine deposits of the western Atlantic, Caribbean, and eastern Pacific also were included. These species are the type species for their respective genera, with two additions. One addition is *Bicorbula idonea* (Fig. 1, images 7–9), a species from the Neogene of the western Atlantic that is sufficiently distinct from the type species of *Bicorbula*, *B. gallica* (Fig. 1, images 1–6), to warrant separate inclusion. Similarly, *Varicorbula disparilis* (d'Orbigny, 1853?) is added as a representative of western Atlantic species assigned to *Varicorbula* Grant and Gale, 1931, because these species differ from the European type species *V. gibba* (Olivi, 1792) for character states typically diagnostic beyond the species level. The type species of *Cuneocorbula* Cossmann, 1886, *C. biangulata* (Deshayes, 1860) from the Eocene of the Paris Basin, was included because in previous analyses of marine corbulid taxa (Anderson and Roopnarine, 2003), this genus fell within the ingroup.

Four species of the genus *Corbula* were used as outgroup taxa. *Corbula* was selected as an outgroup because previous workers have 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). However, *Corbula* possesses a chondrophore, although it is distinctive from other corbulid taxa (Anderson and Roopnarine, 2003). We used four species of *Corbula* as outgroup taxa because they show highly variable sculptural features.

4. Phylogenetic analyses: Conchologic characters

All characters used in the analyses were conchologic and describe aspects of external ornament, valve shape, hinge, pallial line and sinus, and adductor muscle scars (Appendix A). Because corbulids are inequivalved, any trait that differed between valves in at least one genus was coded as separate characters for the left and right valves.

Table 1
Species used in phylogenetic analyses

Genera	Species used	Species distribution
Bicorbula European	*B. gallica* (Lamarck, 1801*)*	Eocene, France (type species)
Bicorbula American	*B. idonea* (Conrad, 1833)	Miocene, Maryland and Virginia
Bothrocorbula	*B. viminea* (Guppy, 1866)	Miocene–Pliocene, Greater Antilles (type species)
Caryocorbula	*C. alabamiensis* (Lea, 1833)	Eocene, Alabama (type species)
Corbula	*C. sulcata* Lamarck, 1801	Recent, Senegal (type species)
	C. gatunensis Toula, 1909	Miocene, Panama and Venezuela
	C. dietziana C.B. Adams, 1852	Recent, western Atlantic
	C. speciosa G.B. Sowerby I, 1833	Recent, eastern Pacific
Cuneocorbula	*C. biangulata* (Deshayes, 1860)	Eocene, France (type species)
Hexacorbula	*H. hexacyma* (Brown and Pilsbry, 1912)	Miocene, Panama (type species)
Juliacorbula	*J. cubanaiana* (d' Orbigny, 1853?)[a]	Recent, western Atlantic (type species)
Panamicorbula	*P. ventricosa* (A. Adams and Reeve, 1850)	Recent, eastern Pacific (type species *P. inflata* is junior synonym; see Coan, 2002)
Tenuicorbula	*T. tenuis* (G.B. Sowerby I, 1833)	Recent, eastern Pacific (type species)
Varicorbula European	*V. gibba* (Olivi, 1792)	Miocene?-Recent, Europe (type species)
Varicorbula American	*V. operculata* (Philippi, 1848)[b]	Recent, western Atlantic
Pachydon	*P. mactriformis* (Meek and Hayden, 1856)	Paleocene, North Dakota
	P. obliquus Gabb, 1869	Miocene, western Amazonia (type species)
	P. trigonalis Nuttall, 1990	Miocene, western Amazonia
	P. tenuis Gabb, 1869	Miocene, western Amazonia
	P. sp. cf. *tenuis* Gabb, 1869	Miocene, western Amazonia
	P. carinatus Conrad, 1871	Miocene, western Amazonia
	P. erectus Conrad, 1871	Miocene, western Amazonia
	P. cuneatus Conrad, 1871	Miocene, western Amazonia
	Pebasia dispar (Conrad, 1874)	Miocene, western Amazonia

[a] 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.

[b] Mikkelsen and Bieler (2001) consider *V. operculata* (Philippi, 1848) to be a *nomen dubium* and use the synonym *V. disparilis* (d'Orbigny) instead, citing a publication date of 1842. As noted in the previous note 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 (Mikkelsen and Bieler, 2001), has priority.

Table 2
Seventy-three character matrix

	10	20	30	40	50	60	70
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890 123
Bicorbula idonea	2200000000	0001111001	0011001100	0000021110	1101100101	20111010?0	1102320010 012
Bicorbula gallica	011?2?2200	0011111001	2011001301	0002003011	1101200201	0011111001	1102320110 012
Bothrocorbula viminea	2211122221	1001100001	1122210000	1111111010	0020020200	1111100000	0100110020 022
Caryocorbula alabamiensis	2200011111	1000000001	0022210000	1000121110	0010010201	2011100000	0100220010 022
Corbula sulcata	2215511112	2001111002	0012001101	0002002000	1222010312	2011101001	0100110020 022
Corbula gatunensis	2214411112	2001111002	0012001100	0002002000	1222010302	2011101001	0100110020 022
Corbula dietziana	2216503112	2000111002	0022001101	0002101000	0222000301	0011110001	0100110020 022
Corbula speciosa	2216503112	2000101002	0022001101	0002001000	0222000302	0011111001	0101110020 122
Cuneocorbula biangulata	00?????003	3001111111	001132220?	12?2?0?0??	??????0?21	201111103?	?????00?1 1??
Hexcorbula hexachyma	2211122111	1001100001	0022210000	1000001010	0020000200	0111100000	0100110020 022
Juliacorbula cubaniana	2202200113	3000000110	0022322200	1002102010	0020000201	0011011010	1000001111 112
Panamicorbula ventricosa	00?????000	0001111001	0011003310	1002210010	0011010201	2011111120	1100001101 100
Tenuicorbula tenuis	2203300003	3000000110	0011322201	0202220011	1101111002	2011111130	1100001101 100
Varicorbula operculata	1217011210	0101010001	0022103300	0002101010	1011020200	0000010101	1111220100 110
Varicorbula gibba	021?0?1200	0101010001	0011103301	0002003010	1322110111	2011010101	1101220110 111
Pachydon mactriformis	00?????000	0111111001	0000433300	1000111211	1300020223	1121201001	1112330010 011
Pachydon obliquus	00?????002	1001111012	0000533300	0000114110	0001020220	1111201001	1101030141 101
Pachydon tenuis	00?????000	0001111001	3200543301	1002114010	000102022?	1??1?010??	0101000131 110
Pachydon cf. *tenuis*	00?????000	0111111002	3200543301	1011114010	0001020222	11113110?1	1101000140 001
Pachydon cuneatus	00??????00	000111100?	2000433300	1002111010	??01020222	1111301011	110100?13? 111
Pachydon carinatus	00?????003	1001111101	0000543301	1022114010	0001020221	1111311001	0000110040 111
Pachydon erectus	00?????201	0011111101	2020001310	1002200010	0011010301	00112010?1	0100111131 022
Pachydon trigonalis	00?????110	0111111001	0022003300	0000114010	0001020203	1111401021	1111221121 111
Pebasia dispar	00?????100	001111111?	3013602021	0002001010	2000000303	00014110??	11001?0110 111

We ran analyses on two matrices: one of 73 and the other of 68 characters (Tables 2 and 3). Two characters were autapomorphies but are retained to qualify the distinctiveness of the taxa. The two matrices differ only in that seven characters pertaining to commarginal rib distribution, thickness, shape, and expression in the 73-character data set are combined into two characters in the 68-character data set (Appendix A). We constructed these two matrices because commarginal ribs are absent in either the left or both valves of several taxa. Therefore, characters that describe aspects of ribs

Table 3
Sixty-eight character matrix

	10	20	30	40	50	60	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345678
Bicorbula idonea	2200000011	1100100110	0110000000	2111011011	0010120111	010?011023	20010012
Bicorbula gallica	0120000111	1100120110	0130100020	0301111012	0020100111	1100111023	20110012
Bothrocorbula viminea	6722110011	0000111222	1000011111	1101000200	2020011111	0000001001	10020022
Caryocorbula alabamiensis	3311110000	0000100222	1000010001	2111000100	1020120111	0000001002	20010022
Corbula sulcata	8911220011	1100200120	0110100020	0200012220	1031220111	0100101001	10020022
Corbula gatunensis	7811220011	1100200120	0110000020	0200012220	1030220111	0100101001	10020022
Corbula dietziana	9Q11220001	1100200220	0110100021	0100002220	0030100111	1000101001	10020022
Corbula speciosa	9Q11220001	0100200220	0110100020	0100002220	0030200111	1100101011	10020122
Cuneocorbula biangulata	0000330011	1111100113	2220?12?2?	0?0???????	?0?2120111	1103??????	?00?11??
Hexacorbula hexachyma	6711110011	0000100222	1000010000	0101000200	0020001111	0000001001	10020022
Juliacorbula cubaniana	4411330000	0011000223	2220010021	0201000200	0020100110	1101010000	01111112
Panamicorbula ventricosa	0000000011	1100100110	0331010022	1001000110	1020120111	1112011000	01101100
Tenuicorbula tenuis	5500330000	0011000113	2220102022	2001111011	1100220111	1113011000	01101100
Varicorbula operculata	1621001010	1000100221	0330000021	0101010110	2020000000	1010111112	20100110
Varicorbula gibba	0620001010	1000100111	0330100020	0301013221	1011120110	1010111012	20110111
Pachydon mactriformis	0000001111	1100100004	3330010001	1121113000	2022311212	0100111123	30010011
Pachydon obliquus	0000210011	1101200005	3330000001	1411000010	2022011112	0100111010	30141101
Pachydon tenuis	0000000011	1100132005	4330110021	1401000010	2022?1??1?	010??01010	00131110
Pachydon cf. *tenuis*	0000001111	1100232005	4330110111	1401000010	2022211113	110?111010	00140001
Pachydon cuneatus	00?0000011	1100?20004	3330010021	11010??010	2022211113	0101111010	0?13?111
Pachydon carinatus	0000310011	1110100005	4330110221	1401000010	2022111113	1100100001	10040111
Pachydon erectus	0020100111	1110120200	0131010022	0001000110	1030100112	010?101001	11131022
Pachydon trigonalis	0011001111	1100100220	0330000001	1401000010	2020311114	0102111112	21121111
Pebasia dispar	0010000111	1111?30136	0202100020	0101020000	0030300014	110??11001	?0110111

for these taxa (characters 3–7 in the larger matrix) had to be coded as missing, although these characters are ‘missing’ only because ribs are absent, not because they are not preserved. We did not add a ‘ribs absent’ character state to characters 3–7 because doing so would have built redundancy into the matrix by coding the same character multiple times (see also Mikkelsen, 1998; Strong and Lipscomb, 1999).

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, as outlined by Anderson and Roopnarine (2003).

5. Phylogenetic analyses

Phylogenetic analyses were completed using PAUP* 4.0b10 (Swofford, 2002). Characters were polarized using four species of *Corbula s.s.* as outgroup taxa. Analyses were conducted using maximum parsimony and heuristic searches (see Table 4). For these searches, we used tree bisection-reconnection as the branch-swapping algorithm and both simple stepwise addition (*Bicorbula idonea* as the reference taxon) and random addition (10,000 replicates) to add taxa to develop the trees. In the first set of analyses, 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 (RCI, using the ‘reweight characters’ option in PAUP*). Character state transformations were determined using accelerated transformation.

We used both Bremer decay indices (Bremer, 1988, 1994) and bootstrapping to compare the robustness of the cladogram nodes. The Bremer decay index tracks the survival of nodes as the length of the accepted cladograms increases incrementally. In other words, we compute a strict consensus tree that incorporates the shortest tree(s) and those one step longer and then note which nodes retain their resolution (e.g. by adjusting the trees retained to the shortest +1 in the heuristic analysis option in PAUP*). The process is repeated incrementally until all resolution is lost in the strict consensus tree. We used heuristic analyses with simple addition to compute the Bremer indices.

In bootstrapping (Felsenstein, 1985), characters from the original matrix are randomly (and independently) resampled to create new matrices to construct cladograms. Summary cladograms for replicate bootstraps show the frequency with which each node is recovered from the replicate analyses. We ran bootstraps of heuristic searches using both simple addition (10,000 bootstrap replicates) and random addition (1000 bootstrap replicates with 100 random addition replicates per bootstrap).

6. Phylogenetic results

Analyses of the 73-character matrix, using either simple or random addition, produced a single, most parsimonious tree (Fig. 6a; Table 5; tree length = 347, consistency index with autapomorphies excluded [CI] = 0.438; retention index [RI] = 0.595). In this tree, *Pachydon mactriformis* falls within a crown group clade that includes most Miocene *Pachydon* species. This crown group is nested within the more diverse of two clades of marine Corbulidae. Two Amazonian Neogene species, *Pebasia dispar* and *Pachydon erectus* Conrad, 1871, do not fall within the *Pachydon* crown group but occupy more basal positions in the larger of the two ingroup clades.

Reweighting characters according to their RCI has a minimal effect. Heuristic analyses using both random and simple additions produce a single, most parsimonious tree (Fig. 6b; Table 5; tree length = 89.22, CI = 0.591, RI = 0.716). The only difference between the equal weight and RCI trees is the branching order of *P. obliquus* and *P. cuneatus* in the *Pachydon* crown group.

Bremer decay indices indicate relatively robust cladogram nodes for the simple addition, equal weight tree (Fig. 6a), although the number of trees increases rapidly at tree lengths greater than two steps longer than the most parsimonious (Table 6). The most robust nodes (Bremer value = 6) support crown groups among marine taxa, in particular for (*Juliacorbula* + *Tenuicorbula*), *Cuneocorbula* as the sister taxon of (*Juliacorbula* + *Tenuicorbula*), and (*Caryocorbula* + (*Bothrocorbula* + *Hexacorbula*). Support also is considerable (Bremer value = 4–5) for (American + European *Varicorbula*), (*Bothrocorbula* + *Hexacorbula*), the defined ingroup as a whole, and the crown group clade including all freshwater corbulids except *Pebasia dispar* and *Pachydon erectus*.

Bootstrap results are comparable to the Bremer indices. There are slight differences between the bootstraps analyses using simple addition (Fig. 6c, 10,000 replicates) and random addition (Fig. 6d, 1000 bootstrap replicates with 100 random

Table 4
Analyses conducted for each data matrix

Analysis	Addition sequence	Character weight
Heuristic	Simple (*Bicorbula idonea* reference taxon)	Equal
Heuristic	Random (10,000 replicates)	Equal
Heuristic	Simple (*Bicorbula idonea* reference taxon)	RCI
Heuristic	Random (10,000 replicates)	RCI
Bremer (heuristic)	Simple (*Bicorbula idonea* reference taxon)	Equal
Bootstrap (heuristic; 10,000 replicates)	Simple (*Bicorbula idonea* reference taxon)	Equal
Bootstrap (heuristic; 1000 replicates)	Random (100 replicates)	Equal

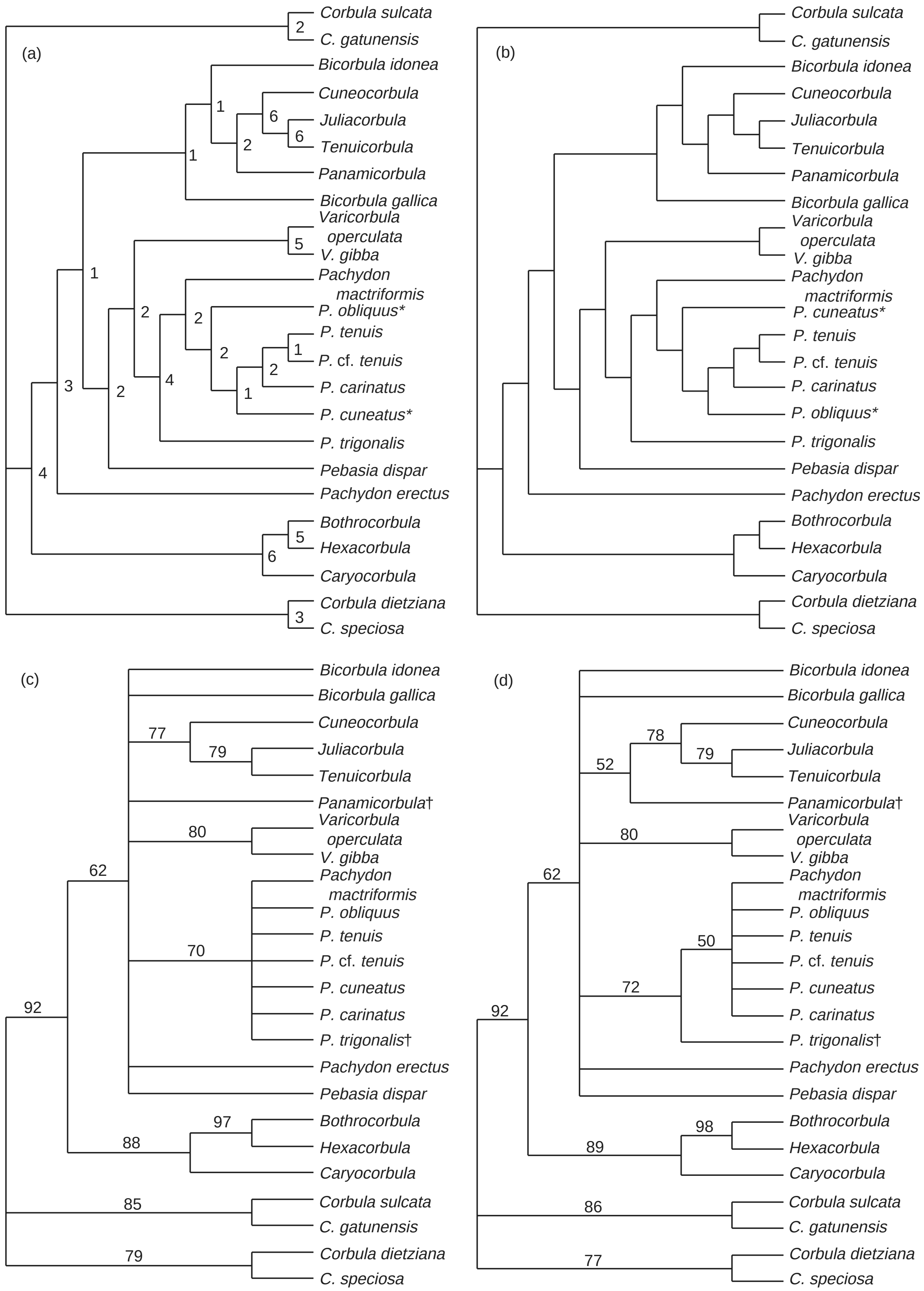

Fig. 6. Phylogenetic results for the 73-character matrix. (a) The single most parsimonious tree resulting from heuristic analyses in which characters are equally weighted and either simple or random (10,000 replicates) stepwise addition is used. Bremer decay indices are indicated by the numbers at each node. (b) The single most parsimonious tree resulting from heuristic analyses (simple and random addition), in which characters are weighted according to their RCI values. Taxa whose

Table 5
Tree statistics for 73-character matrix

Weight	Stepwise addition	Number of trees	Length	CI	RI	Topology
Equal	Simple or random	1	347	0.438	0.595	Fig. 6a
RCI	Simple or random	1	89.22	0.591	0.716	Fig. 6b

Table 6
Bremer decay index results for 73-character matrix

Steps longer	Number of nodes	Number of new trees
0	21	1
1	16	6
2	9	61
3	7	375
4	5	1638
5	3	6444
6	0	22151

replicates per bootstrap); the latter recovers greater than 50% support for *Panamicorbula* as a sister to [*Cuneocorbula*+(*Juliacorbula*+*Tenuicorbula*)] and *Pachydon trigonalis* Nuttall, 1990, as basal to the rest of the *Pachydon* crown group.

Results based on the 68-character matrix are broadly similar to those from the 73-character matrix. When characters are equally weighted, simple addition produces 33 most parsimonious trees, and random addition recovers 35. The topology of strict consensus trees from these two analyses and tree statistics are identical (Fig. 7a; Table 7; for both trees, length = 335; CI = 0.445; RI = 0.586), and the consensus tree closely resembles the majority consensus trees for the bootstrap analyses of the 73-character matrix (Fig. 6c,d). When characters are weighted according to their RCIs, both simple and random addition produce the same single most parsimonious tree and very similar tree statistics (Fig. 7b; Table 7). The resulting tree differs from other analyses in that *Pachydon erectus* is basal to the entire ingroup, and the two *Bicorbula* species are sister taxa.

Bremer decay indices and bootstrap results indicate less robust cladogram nodes than for the 73-character matrix, although the relative support for most nodes remains the same (Fig. 7a,c,d; Table 8). One exception is the much lower support for (*Bothrocorbula*+*Hexacorbula*) (Fig. 7a,c,d versus Fig. 6a,c,d). The overall topology of the bootstrap consensus trees, however, matches that of the bootstrap using simple addition for the 73-character matrix (Fig. 6c).

All our analyses thus point to similar regions of stability and instability within trees. Of interest here is that a *Pachydon* crown group that includes *P. mactriformis*, the Paleocene species from North Dakota, is robust. Synapomorphic characters for this clade include a right-valve hinge plate that is not sinuous and is angled, with the posterior higher than the anterior (characters 34 and 36). (Note that all characters are referred to using their number in the larger matrix.) In addition, the cardinal tooth is similarly oriented and located below and posterior to the beak (characters 51 and 52), and the left valve hinge plate is narrowest at the cardinal socket (character 37). The particular character states cited in the 'Introduction' section as diagnostic for *Pachydon* are synapomorphic at a higher, less robust node, which excludes *P. trigonalis*. These characters include the prosogyrate, right-angle chordate valves (characters 23–26), a well-developed lateral toothlike groove posterior to the right valve hinge (character 49), and a robust rectangular cardinal tooth (character 55), as well as a right valve pallial sinus that extends anterior to the posterior adductor muscle scar (character 66). Of these traits, only those character states describing chordate valve outlines for valve shape (states 4 and 5 for character 25; 3 and 4 for character 26) and prosogyrous beaks and umbos for both valves (state 0 for characters 23 and 24) correspond closely and thus may not be independent. These traits were retained in our analyses because prosogyry and valve outline shape do not appear to be redundant in several species not yet incorporated in our analyses (e.g. *Tiza alta* (Conrad, 1848), *Corbula (Caryocorbula) betsyae* Marincovich, 1993 and *C. tahitensis* Lamarck, 1818).

The node for the entire ingroup also is robust, which indicates that freshwater corbulids do not represent a separate basal radiation within the family. The ingroup is supported by several synapomorphies (reversals occur for several of these character states in some derived clades), including a larger left valve escutcheon (character 20), a low rounded left valve keel (character 10), and a chondrophore with three ridges on the dorsal surface and straight outer margin (characters 39 and 42).

Our analyses do not resolve a robust sister clade relationship for the *Pachydon* crown group. Given similar habitat requirements and Neogene geographic distribution patterns, we might infer a close relationship between *Pachydon* and *Panamicorbula* (Pilsbry, 1932). *Panamicorbula* (Fig. 3, images 7, 10, 11) is reported from marine incursion levels of the Pebas Formation, and its fossil and modern occurrences are in fine-grained, brackish-water sediments (Vermeij and Wesselingh, 2002; Wesselingh et al., 2002). Our phylogenetic results, however, place *Pachydon* within the same major clade as *Panamicorbula*, but the relationships among groups in that clade are not well resolved. For both matrices, when this node does resolve, we have recovered a sister group relationship with *Varicorbula*. Synapomorphies supporting this node include a rounded posterior margin (characters 27 and 28) and lateral walls of the cardinal socket that wrap strongly around both sides of the socket opening (character 48).

◀ positions differ between sections a and b are indicated by an asterisk (*). (c) Consensus tree with support indicated for each node for bootstrap analysis (10,000 replicates) using a heuristic search with equally weighted characters and simple stepwise addition. (d) Consensus tree with support indicated for each node for bootstrap analysis (1000 replicates) using a heuristic search with equally weighted characters and random stepwise addition (100 replicates per bootstrap). Taxa whose positions differ between sections c and d are indicated by a dagger (†).

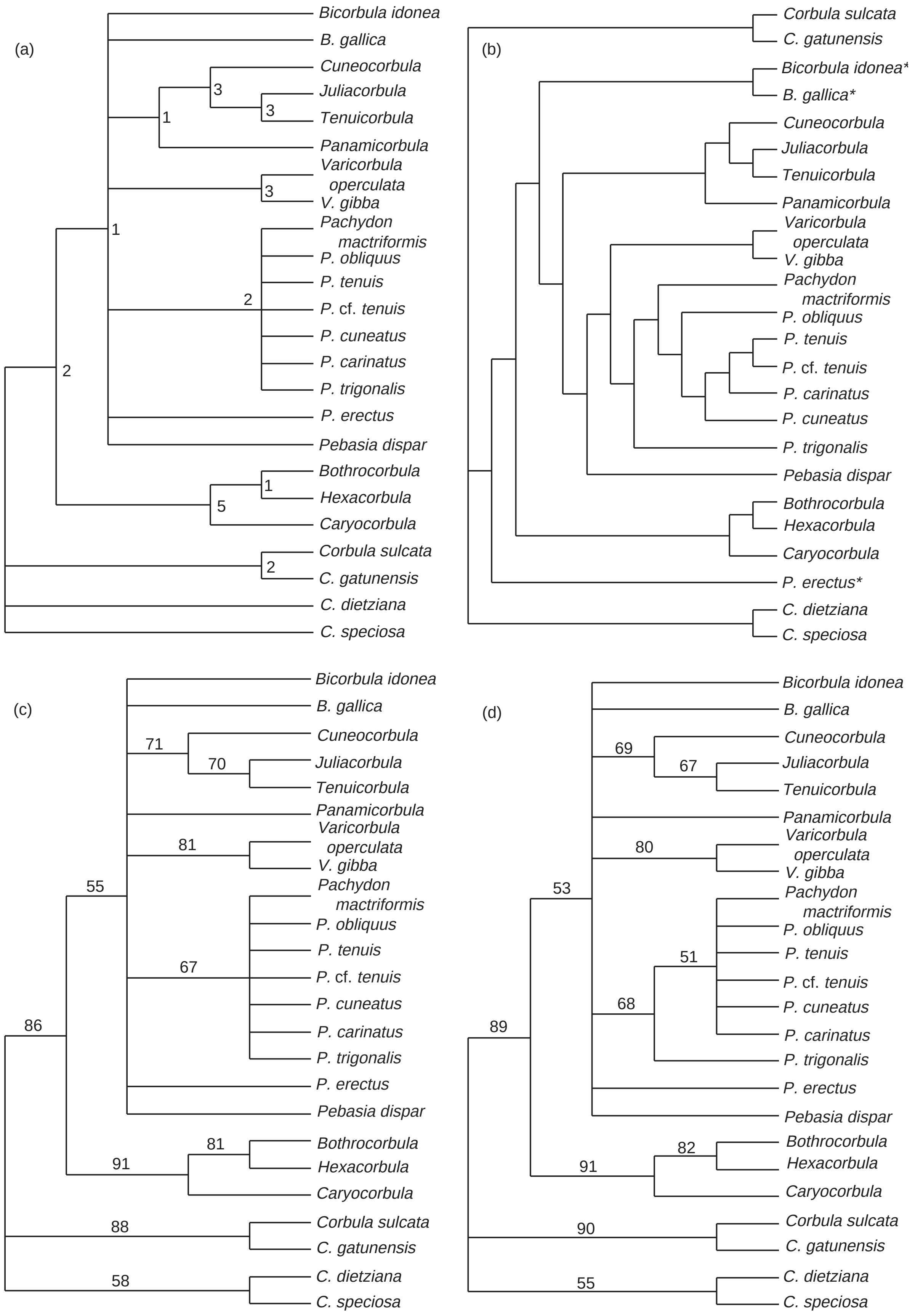

Fig. 7. Phylogenetic results for the 68-character matrix. (a) Strict consensus tree resulting from heuristic analyses, in which characters are equally weighted and either simple or random (10,000 replicates) stepwise addition is used. Bremer decay indices are indicated by the numbers at each node. Taxa whose positions differ from

Table 7
Tree statistics for 68-character matrix

Weight	Stepwise addition	Number of trees	Length	CI	RI	Topology
Equal	Simple	33	335	0.445	0.586	Fig. 7a
	Random	35	335	0.445	0.586	
RCI	Simple	1	98.88	0.613	0.702	Fig. 7b
	Random	1	99.34	0.612	0.702	

Table 8
Bremer decay index results for 68-character matrix

Steps longer	Number of nodes	Number of new trees
0	10	33
1	7	336
2	4	1899
3	1	8210
4	1	30769
5	0	102403

Finally, two Amazonian Neogene taxa (*Pebasia dispar* and *Pachydon erectus*) do not fall within the *Pachydon* crown group, although we are cautious about accepting the polyphyletic nature of *Pachydon* at this time. Although these species never fall within the crown group, their phylogenetic positions are neither stable nor well resolved from one analysis to the next. *Pebasia dispar* (Fig. 2, images 1, 2, 4, 5) consistently falls in the larger ingroup clade, but its relationship with other clade members is not stable. When it does resolve, it appears basal to (*Varicorbula* + crown *Pachydon*). The position of *Pachydon erectus* (Fig. 2, images 3, 6) is particularly unstable. In most analyses, it was part of the larger ingroup clade and, when resolved, is the basal taxon in this clade. In one analysis, however, the species is shown as basal to the entire ingroup. Our results thus may call into question the existing definitions of *Pachydon* and its subfamily Pachydontinae, but we do not have sufficient evidence to redefine these taxa as monophyletic groups. Further analyses incorporating additional species with morphologic affinities to *Pebasia dispar* and *Pachydon erectus* (Fig. 2), such as *P. ledaeformis* (Dall, 1872) and *P. elongates* (Boettger, 1878), may help resolve some of these relationships.

In summary, our phylogenetic analyses produced relatively robust and comparable results across data sets, search parameters, and measures of cladogram node robustness. In all analyses, *Pachydon mactriformis* falls within a crown group clade that includes most Miocene *Pachydon* species. Synapomorphic characters supporting this clade are not closely associated with the possession of a prosogyrous beak and umbo, a trait typically used to define the genus. We could not resolve a robust sister clade relationship for the *Pachydon* crown group. Nonetheless, this crown group is nested within a clade of marine Corbulidae, and the ingroup node is robust across analyses, indicating that freshwater corbulids do not represent a separate basal clade within the family. Two Amazonian Neogene species, *Pebasia dispar* and *Pachydon erectus*, do not fall within the *Pachydon* crown group, and their phylogenetic placement is not, at present, well resolved.

7. Additional faunal similarities: *Ostomya* and *Anticorbula*

At present, our phylogenetic analyses only incorporate two of six genera and seven of nineteen species of freshwater corbulids from the Pebas Formation, as well as one Paleocene species from the Tongue River Formation. However, additional similarities exist between the corbulid faunas of these units. In particular, we recognize previously undocumented occurrences of the corbulid genera *Ostomya* and *Anticorbula* in the lower part of the Tongue River Formation in easternmost Montana (Hartman, 1993b; Vuke et al., 2003, as the Tongue River Member following Montana Bureau of Mines and Geology usage).

Ostomya was first described by Conrad (1874) and has not been reported previously outside the Amazonian Neogene. The type species of this genus, *O. papyria* Conrad, 1874, has nearly equivalved, ovate shells with small umbos (Fig. 4, images 4, 5, 7–9, 12). The left valve has a very small cardinal socket and prominent, trough-shaped chondrophore that is directed posteroventrally. An undescribed species of corbulid closely resembling *O. papyria* occurs at one locality in the Tongue River Formation (Hartman, 1993b). It is more quadrate than *O. papyria*, with a broader umbo and more subdued keel (Fig. 4, images 1–3, 6), and more strongly prosogyrous. However, the hinges of these two species are highly congruent (hinge characters are typically diagnostic at the genus level).

An undescribed species of *Anticorbula* occurs at the same locality as *Ostomya*. This genus is not previously reported outside of northern South America or prior to the Miocene. The ornament, valve shape, and hinge of the Tongue River specimens (Fig. 4, images 10, 11, 16, 19) closely match those of Neogene *Anticorbula* (Fig. 4, images 13-15, 17, 18).

8. Discussion

Our results indicate that three genera of freshwater corbulid bivalves (*Pachydon, Ostomya,* and *Anticorbula)* present in the Miocene Pebas Formation of western Amazonia are long-lived genera that occupied freshwater environments in the Americas since at least the Paleocene. For *Pachydon,* phylogenetic results strongly support the placement of the

◀ those resolved in consensus trees for bootstrap analyses of the 73-character matrix (Fig. 6c,d) are indicated by an asterisk (*). (b) The single most parsimonious tree resulting from heuristic analyses (simple and random addition) in which characters are weighted according to their RCI values. Taxa whose positions differ from that resolved in the 73-character matrix when characters are weighted with their RCIs (Fig. 6b) are indicated by an asterisk (*). (c) Consensus tree with support indicated for each node for bootstrap analysis (10,000 replicates) using a heuristic search with equally weighted characters and simple stepwise addition. (d) Consensus tree with support indicated for each node for bootstrap analysis (1000 replicates) using a heuristic search with equally weighted characters and random stepwise addition (100 replicates per bootstrap).

Paleocene species *P. mactriformis* within a *Pachydon* crown group. Therefore, the Paleocene and most Miocene representatives of *Pachydon* are not convergent but form a monophyletic clade.

Corbulids are not reported (nor have we observed them) from other Paleogene freshwater deposits of the Americas. As a result, *Pachydon*, *Ostomya*, and *Anticorbula* each have long, and to date unrecorded, geologic histories (about 50 Ma) and disjunct geographic distributions. Inferring monophyly for these genera requires substantial phylogenetic support, especially given that many freshwater molluscan groups are polyphyletic. At least for *Pachydon*, for which we have established phylogenetic hypotheses, we have this support. Our overall tree topologies are consistent with those for tropical American marine corbulids when freshwater taxa are excluded (Anderson and Roopnarine, 2003). In addition, a variety of characters that are not redundant with the prosogyrous valves typical of *Pachydon* support the robust node uniting the crown group. Finally, several of these features are traits that are evolutionarily conservative in bivalves (e.g. hinge features).

In part, these geographic and temporal gaps relate to the ephemeral nature of the large freshwater systems in which these corbulids thrive, as well as to the low preservation potential of both freshwater facies and molluscan remains within these facies. For example, in the northern Great Plains, Eocene–Miocene deposits occur as isolated remnants, mostly on the tops of buttes. Within these Cenozoic deposits, paleoenvironments are primarily terrestrial, and fluvial-deltaic deposits similar to that preserved in the Tongue River Formation are absent.

Given this geologically discontinuous record and the extremely low present-day diversity of freshwater corbulids (i.e. one species of *Anticorbula*), it is difficult to infer with great confidence the geographic history of these bivalves. The known geographic distributions of these genera suggest one of three possible paleobiogeographic scenarios. In the first scenario, genera originate and disperse across both continents prior to Middle Jurassic rifting of the Americas. This rifting commenced at about the same time that corbulids first appear in the fossil record (for a review, see Anderson and Roopnarine, 2003). These early records of corbulids occur in marine to brackish-water deposits. *Pachydon*, however, does not represent a separate basal radiation within Corbulidae but is a derived clade, so its origin probably postdates the Middle Jurassic.

In a second biogeographic scenario, genera originate and disperse across both continents in the late Cretaceous when extensive island arc formation may have provided a nearly continuous terrestrial corridor through the Caribbean (Iturralde-Vinent and MacPhee, 1999). A continuous land connection may not have been required for dispersal and exchange of freshwater corbulids between the Americas. Modern freshwater *Anticorbula* tolerate low-salinity brackish waters (Leistikow and Janssen, 1997), and according to Sr-isotope data, some Miocene *Pachydon* species lived in salinities that may have reached 5‰ (Vonhof et al., 1998, 2003). In addition, occurrences of *P. mactriformis* in the Tongue River Formation coincide with maximum transgression of the Cannonball Seaway, indicating that this species may have tolerated brackish-water salinities.

In the third biogeographic scenario, genera originate in North America by the Paleocene and disperse to South America by the Miocene, probably via some vector such as migratory water fowl. This scenario requires the fewest ad hoc assumptions about the missing geologic record but also is nearly impossible to test.

Additional work incorporating Mesozoic and Paleogene genera may help resolve the basal relationships within clades, narrow temporal gaps, and biogeographic ambiguities. We are not aware of any taxa with strong morphologic affinities to *Pachydon*, although two genera, *Tiza* de Gregorio, 1890, and *Hudsonella* Yin and Fürsich, 1991, have been allied with Pachydontinae. Vokes (1945) erected the subfamily Pachydontinae and included both *Pachydon* and *Tiza*, a genus described from the marine Oligocene Mint Springs Formation of Mississippi. As in *Pachydon*, *Tiza* has very subdued sculpture and a lateral toothlike groove on a long posterior slope in the right valve. However, *Tiza* also has a very different shell shape (nearly comma shaped, with a strongly concave dorsoposterior slope), lacks prosogyrous valves, and has both a triangular, hooked-shaped cardinal tooth and a relatively flat chondrophore with subdued dorsal ridges typical of other corbulid genera (see also Nuttall, 1990).

Yin and Fürsich (1991) considered the hinge of *Hudsonella*, which they described from a brackish-water faunule from the Middle Jurassic of Qinghai Province, China, to closely resemble those of *Pachydon* and *Tiza*. Although we have not examined their material, their illustrations show that the type species, *H. sinensis* (Chen, 1976), is distinct in that it has an inflated shell with a triangular shape and prominent rostrum and a triangular, hooked cardinal tooth. The chondrophore of *Hudsonella*, however, has a similar shape and orientation to that of *Pachydon*.

Although *Pachydon, Ostomya*, and *Anticorbula* all have long geologic histories, an apparent radiation at the species level, especially within *Pachydon*, nevertheless occurs in the Amazonian Miocene. The delay between clade origination and species radiation may seem at odds with some well-known taxa, such as east African cichlids, that formed species flocks through explosive speciation rates that coincide with geologically recent lake basin flooding (e.g. Meyer et al., 1990; Rossiter and Kawanabe, 2000). However, long evolutionary histories have been inferred for various endemic lacustrine clades, particularly in gastropods. For example, in Tankganyikan gastropods, four major lineages predate lake formation by as much as 40 my, according to mitochondrial DNA divergence estimates (Wilson et al., 2004). In addition, Hausdorf et al. (2003), using similar evidence, concluded that the stem group for one major Lake Baikal gastropod lineage (Baicaliidae; Rissooidea) predates the origin of the Baikal rift, whereas another lineage (Benedictiinae;

Rissooidea) probably arose autochthonously within the basin but in rift lakes predating Lake Baikal.

The radiation of Amazonian Neogene *Pachydon* may have originated with a single species, *P. hettneri* (Anderson, 1928) during the early Miocene (Wesselingh and Macsotay, 2006). This species occurs in assemblages that also contain undisputed fluvial taxa (Pilsbry and Olsson, 1935), a habitat similar to that of modern *Anticorbula*. The radiation of *Pachydon* resulted in high morphologic divergence, ranging from the strongly prosogyrous and obliquely deformed shells of *P. obliquus* (Fig. 3, images 1, 2, 4, 5, 8) to the elongated valves of *P. tenuis* Gabb, 1869 (Fig. 3, images 9, 12). In addition, the apparently endemic *Pebasia dispar* (Fig. 2, images 1, 2, 4, 5), with its concavo-convex shell, is an extreme example of inequivalvity in corbulids. Furthermore, it appears that at least one *Pachydon* species, *P. obliquus*, was especially successful in invading dysoxic environments. This species is the most common *Pachydon* in the Pebas Formation and occurs in a variety of facies, including organic- and clay-rich intervals in which articulated specimens that are in situ or show signs of minimal transport dominate the assemblages (Wesselingh et al., 2002). *Pachydon* may have been preadapted for an invasion of such freshwater dysoxic habitats because several marine corbulid species have documented tolerances of low-oxygen conditions, fine sediments (they are efficient at producing pseudofeces), and turbid waters (Pearson, 1972; Lande, 1975; Lewy and Samtleben, 1979; HRS-Brenko, 1981; Kiørboe and Møhlenberg, 1981; Weigelt and Rumohr, 1986; Jensen, 1990; Lamprell et al., 1998; Wesselingh et al., 2002).

Extinction of Amazonian corbulids, with the exception of *Anticorbula*, probably is associated with the tectonic reorganization of northwestern South America during the early Late Miocene. During this time, the western margin of the South American Craton was exhumed, which obliterated Lake Pebas and led to the establishment of the modern Amazon River system (Wesselingh et al., 2002, references therein). Unfortunately, well-dated fossiliferous deposits that might be used to test this inference are lacking in the region.

9. Conclusions

The stratigraphic and geographic range of *Pachydon, Ostomya,* and *Anticorbula*, all previously thought to be endemic to the Neogene of northern South America, are extended to the Paleocene of the northern Great Plains of the United States. Both Paleocene and Miocene freshwater corbulid taxa occur in large, freshwater systems with an intermittent marine connection. Phylogenetic analyses indicate that *P. mactriformis* is part of a crown group containing most Miocene *Pachydon* species, and thus, Paleocene and Miocene species are not convergent. This robust crown group rests within a marine clade, although sister group relations to the *Pachydon* clade are not resolved. The records of *Pachydon, Ostomya,* and *Anticorbula* include large temporal gaps and disjunctive biogeographic distributions. Biogeographic dispersal probably postdates the Middle Jurassic origin of the family, based on the relatively derived position of *Pachydon*, and we infer that dispersal occurred no earlier than the Late Cretaceous via either direct dispersion of species or a dispersal vector such as migratory waterfowl. Despite the long stratigraphic ranges of some freshwater Corbulidae, these bivalves undergo an endemic radiation within the Miocene Lake Pebas that is accompanied by high morphologic divergence and invasion and faunal dominance of dysoxic habitats. Major extinction of freshwater corbulids probably is associated with the tectonic reorganization of northwestern South America that started in the late Miocene and eventually destroyed the Lake Pebas lacustrine system as the modern-day Amazon River system developed.

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Appendix A

A.1. Description of characters and character states

External ornament

1.*	Commarginal rib distribution on left valve	
	absent	0
	on early-formed portion of valve	1

	across entire valve	2
2.*	Commarginal rib distribution on right valve	
	absent	0
	on early-formed portion of valve	1
	across entire valve	2
3.*	Commarginal rib width relative to interspaces (left and right valves)	
	ribs < interspaces	0
	ribs > interspaces	1
4.*	Left valve commarginal rib shape	
	flatly rounded	0
	highly rounded	1
	wedge shaped	2
	ribbonlike, flat	3
	from highly rounded to low irregular with ontogeny	4
	from wedge-shaped to low irregular with ontogeny	5
	from wedge-shaped to flat ribbon with ontogeny	6
	regular to irregular flatly rounded with ontogeny	7
5.*	Right valve commarginal rib shape	
	flatly rounded	0
	highly rounded	1
	wedge-shaped	2
	ribbonlike, flat	3
	from rounded to low irregular with ontogeny	4
	from wedge-shaped to rounded with ontogeny	5
6.*	Commarginal ribs at keel (left valve)	
	no change in expression	0
	some flattening	1
	die out before reaching keel	2
7*.	Commarginal ribs at keel (right valve)	
	no change in expression	0
	some flattening	1
	die out before reaching keel	2
	no change in expression to some flattening with ontogeny	3
8.	Left valve radial ribs	
	absent	0
	fine	1
	strong	2
9.	Right valve radial ribs	
	absent	0
	fine	1
	strong	2
10.	Keel expression (left valve)	
	indistinct	0
	low rounded	1
	high rounded	2
	high and sharp	3
11.	Keel expression (right valve)	
	indistinct	0
	low rounded	1
	high rounded	2
	high and sharp	3
12.	Left valve keel	
	intersects ventral margin	0
	dies out before reaching ventral margin	1
13.	Right valve keel	
	intersects ventral margin	0
	dies out before reaching ventral margin	1
14.	Commarginal ornament on posterior slope of left valve continuous with	
	ribs anterior of keel	0
	striae anterior of keel	1
15.	Commarginal ribs on posterior slope of right valve continuous with	
	ribs anterior of keel	0
	striae anterior of keel	1
16.	Sharpness of ornament on posterior slope of left valve	
	sharp and regular	0
	low and irregular	1
17.	Sharpness of ornament on posterior slope of right valve	
	sharp and regular	0
	low and irregular	1
18.	Escutcheon ridge expression of left valve	
19.	rounded and indistinct	0
	sharp and high	1
20.	Escutcheon ridge expression of right valve	
	rounded and indistinct	0
	sharp and high	1
21.	Escutcheon symmetry	
	symmetrical in left and right valve	0
	larger in left valve	1
	larger in right valve	2
22.	Lunular area right valve	
	absent	0
	present, forms pit	1
	flat with indistinct margin	2
	flat with distinct margin	3
23.	Lunular area left valve	
	absent	0
	present, forms pit	1
	flat with distinct margin	2
Valve Shape		
23.	Orientation of beak and umbo (right valve)	
	both prosogyrate	0
	both orthogyrate	1
	beak prosogyrate, umbo orthogyrate	2
24.	Orientation of beak and umbo (left valve)	
	both prosogyrate	0
	both orthogyrate	1
	beak prosogyrate, umbo orthogyrate	2
	opisthogyrate	3
25.	Left valve shape	
	equi-subtriangular	0
	ovate	1
	ovate triangular (“tear drop”)	2
	rounded subtrapezoidal	3
	right triangle cordate	4
	elongate right angle cordate	5
	kidney-shaped	6
26.	Right valve shape	
	equi-subtriangular	0
	ovate triangular (“tear drop”)	1
	rounded subtrapezoidal	2
	right triangle cordate	3
	elongate right angle cordate	4
27.	Left valve posterior	
	pointed	0
	bluntly pointed	1
	bluntly truncated	2
	rounded	3
28.	Right valve posterior	
	pointed	0
	bluntly pointed	1
	bluntly truncated	2
	ounded	3
29.	Left valve inflation	
	low	0
	moderate-high	1
	concave	2
30.	Commissure	
	planar	0
	nonplanar	1
	strongly sinuous	2

(*continued on next page*)

Hinge

31.	Beak in right valve	
	extends past hinge area	0
	does not extend past hinge area	1
32.	Viewed dorsally, hinge plate in right valve	
	straight	0
	recessed at lunule	1
	recessed at resilifer	2
33.	Sinuosity of left valve hinge plate	
	straight to slightly sinuous	0
	strongly sinuous, recessed ventrally at lunule	1
	sinuous, recessed dorsally at resilifer	2
34.	Sinuosity of right valve hinge plate	
	straight to slightly sinuous	0
	strongly sinuous, recessed ventrally at lunule	1
	sinuous, recessed dorsally at resilifer	2
35.	Hinge plate angle relative to anterior–posterior axis in left valve	
	horizontal	0
	posterior up	1
	anterior up	2
36.	Hinge plate angle relative to anterior–posterior axis in right valve	
	horizontal	0
	posterior up	1
	anterior up	2
37.	Hinge plate in left valve highest (narrowest)	
	anterior of socket	0
	at chondrophore	1
	posterior of chondrophore	2
	either side of hinge	3
	at socket	4
38.	Hinge plate in right valve highest	
	at resilifer	0
	anterior of tooth	1
	at posterior end of hinge plate	2
39.	Number of ridges on upper surface of chondrophore (left valve)	
	two	0
	three	1
40.	Most prominent ridge on upper surface of chondrophore (left valve)	
	posterior	0
	middle	1
41.	Chondrophore projects (left valve)	
	slightly past valve edge posterior of chondrophore, but is flush with valve edge anterior of socket	0
	beyond commissure	1
	does not project	2
42.	Shape of chondrophore's outer edge viewed dorsally (left valve)	
	straight	0
	v-shape	1
	s-shaped	2
	rounded	3
43.	Knob on posterior ridge of chondrophore (left valve)	
	absent	0
	present, small	1
	present, large	2
44.	Ridges and furrows on upper surface chondrophore (left valve)	
	low relief	0
	moderate relief	1
	strong relief	2
45.	Proximal-distal shape and angle of chondrophore (left valve)	
	downward angle and planar	0
	high downward angle proximally, upturned distally (scoop-shaped)	1
	horizontal and planar with upturned end	2
	horizontal, trough-shaped, closely spaced ridges and furrow parallel to valve margin	3
46.	Cardinal socket angle relative to anterior-posterior axis (left valve)	
	horizontal	0
	anterior up	1
	posterior up	2
	nearly perpendicular	3
47.	Hinge plate behind cardinal socket (left valve)	
	present	0
	absent	1
48.	Lateral walls of cardinal socket (left valve)	
	do not wrap around socket opening	0
	wrap slightly around both anterior and posterior sides	1
	wrap strongly around both anterior and posterior sides	2
	wrap around anterior side only	3
49.	Lateral toothlike groove in left valve posterior of chondrophore	
	absent	0
	forms a triangular depression just behind chondrophore	1
	well developed	2
50.	Cardinal tooth and beak (right valve)	
	tip of tooth and beak far apart	0
	tip and beak closely spaced but tooth below beak	1
	tip and beak overlap, distal tip of tooth above beak	2
	tooth emerges from space directly below beak (no space, no overlap)	3
51.	Cardinal tooth angle relative to anterior-posterior axis (right valve)	
	horizontal	0
	posterior up	1
	anterior up	2
52.	Cardinal tooth position relative to beak (right valve)	
	directly below beak	0
	below and posterior of beak	1
53.	Cardinal tooth projects (right valve)	
	tip does not project beyond beak	0
	tip projects beyond beak	1
	base only projects beyond beak	2
54.	Toothlike knob, formed at dorsoanterior point of external valve below beak, above tooth (right valve)	
	present	0
	absent	1
55.	Tooth shape	
	triangular, shallow hook shape	0
	triangular, deep hook shape	1
	rectangular, not hooked	2
	massive square, deep hook shape	3
	triangular, not hooked	4
56.	Resilifer pit (right valve)	
	on front surface of hinge plate	0
	under beak, on lower surface of hinge plate	1
57.	Secondary vertical wall subdividing resilifer pit (right valve)	
	present	0
	absent	1
58.	Trough on right valve hinge plate for reception of left valve margin	
	on front surface of hinge plate	0
	on lower surface of hinge plate	1
59	Extent of trough in right valve margin for reception of left valve margin	
	around entire valve	0
	present from ventral margin of anterior adductor muscle scar around hinge to ventral point of escutcheon	1
	present on all but posterior margin	2
	present on all but anteroventral margin	3

Pallial Line and Sinus

60.	Distance of pallial line to ventral margin of right valve	
	close to valve margin	0
	far from valve margin	1
61.	Angle of pallial line in left and right valves relative to anterior-posterior axis	
	oblique (higher anterior, lower posterior)	0
	parallel	1

62. Pallial line in left and right valves	
sinuous	0
straight	1
63. Orientation of pallial sinus in left and right valves	
perpendicular to anterior-posterior axis	0
oblique to anterior–posterior axis	1
64. Pallial sinus intersects posterior adductor muscle scar in left and right valves	
at midscar	0
at anteroventral point of scar	1
along lower anterior edge of scar	2
65. Expression of pallial sinus in left valve	
no invagination	0
does not extend to anterior edge of posterior adductor muscle scar	1
extends to anterior edge of posterior adductor muscle scar	2
extends beyond anterior edge of posterior adductor muscle scar	3
66. Expression of pallial sinus in right valve	
no invagination	0
does not extend to anterior edge of posterior adductor muscle scar	1
extends to anterior edge of posterior adductor muscle scar	2
extends beyond anterior edge of posterior adductor muscle scar	3

Adductors

67. Orientation of anterior adductor muscle scar relative to commissure in left valve	
low oblique to moderate angle	0
high oblique angle	1
68. Orientation of anterior adductor muscle scar angle relative to commissure in right valve	
low oblique to moderate angle	0
high oblique angle to nearly perpendicular	1
69. Anterior adductor muscle scar of left and right valves	
smooth or ridged, not embedded in valve wall	0
smooth or ridged, slightly embedded in valve wall	1
smooth or ridged, deeply embedded in valve wall	2
pitted, deeply embedded in valve wall	3
pitted, recessed within pit	4
70. Orientation of posterior adductor muscle scar relative to commissure in left valve	
low oblique to moderate angle	0
high oblique angle to nearly perpendicular	1
71. Orientation of posterior adductor muscle scar relative to commissure in right valve	
low oblique to moderate angle	0
high oblique angle to nearly perpendicular	1
72. Posterior adductor muscle scar of left valve	
Not embedded in valve wall	0
slightly embedded in valve wall	1
deeply embedded in valve wall	2
73. Posterior adductor muscle scar of right valve	
not embedded in valve wall	0
slightly embedded in valve wall	1
deeply embedded in valve wall	2

*These characters are combined into the following two characters to form a 68-character matrix.

2. Commarginal rib distribution on left valve	
absent	0
on early formed portion of valve	1
across entire valve surface with flatly rounded ribs that are thinner than interspaces, and that show no change in expression at keel	2
across entire valve surface with flatly rounded ribs that are thinner than interspaces, and that flatten at keel	3
across entire valve surface with wedge shaped ribs that are thinner than interspaces, and that show no change in expression at keel	4
across entire valve surface with flat topped, ribbonlike ribs that are thinner than interspaces, and that show no change in expression at keel	5
across entire valve surface with highly rounded ribs that are thicker than interspaces, and that die out at keel	6
across entire valve surface, ribs highly rounded in early ontogeny, later becoming low and irregular, ribs thicker than interspaces and flatten at keel	7
across entire valve surface, ribs wedge shaped in early ontogeny, later becoming low and irregular, ribs thicker than interspaces and flatten at keel	8
across entire valve surface, ribs wedge shaped in early ontogeny, later becoming ribbonlike, ribs thicker than interspaces with no change at keel	9
3. Commarginal rib distribution on right valve	
absent	0
on early-formed portion of valve	1
across entire valve surface, ribs flatly rounded, thinner than interspaces, with no change in expression at keel	2
across entire valve surface, ribs flatly rounded, thinner than interspaces, with flattening at keel	3
across entire valve surface, wedge-shaped ribs, thinner than interspaces, with no change in expression at keel	4
across entire valve surface, flat topped, ribbonlike ribs, thinner than interspaces, with no change in expression at keel	5
across entire valve surface, flatly rounded ribs, thicker than interspaces with some flattening at keel	6
across entire valve surface, highly rounded ribs, thicker than interspaces, that die out at keel	7
across entire valve surface, ribs highly rounded in early ontogeny, later becoming low and irregular, ribs thicker than interspaces and flatten at keel	8
across entire valve surface, ribs wedge shaped in early ontogeny, later becoming rounded, ribs thicker than interspaces and flatten at keel	9
across entire valve surface, ribs thicker than interspaces, ribs wedge shaped with no change in expression in early ontogeny, later becoming rounded, with flattening at keel	Q

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