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ROLE OF CONSTRAINT AND SELECTION IN THE MORPHOLOGIC EVOLUTION OF *CARYOCORBULA* (MOLLUSCA: CORBULIDAE) FROM THE CARIBBEAN NEOGENE

Laurie C. Anderson and Peter D. Roopnarine

ABSTRACT

We examined patterns of morphologic evolution in *Caryocorbula,* a common bivalve genus of the Caribbean Neogene, to evaluate the roles that constraint and selection play in its apparent morphologic conservatism. With multivariate analyses using landmark-based geometric morphometrics, we examined the relationship of valve size and outline shape within the *Caryocorbula* + (*Bothrocorbula* + *Hexacorbula*) clade, and within 21 morphospecies of *Caryocorbula*, all from Neogene deposits of the Caribbean region. We found that each genus is morphologically distinct both in shape and size, and that *Caryocorbula* shows strong interspecific allometry that persists despite species turnover and the vagaries of geographic and temporal sample coverage.

Persistence of this allometric trend indicates that constraints shape *Caryocorbula* morphology. Constraint mechanisms may relate to 1) space limitations in the inequivalved shells that characterize Corbulidae, and/or 2) the need for functional articulation of unequal valves through a complex shell accretion history. Alternatively, environmental conditions, particularly nutrient availability, may control the spatial and temporal distribution of large *Caryocorbula*, but constraint via pleiotropy could restrict the shape of these bivalves. Finally, although constraints appear to play an important role in the morphologic evolution of Neogene *Caryocorbula*, an adaptive relationship of size and shape to environment is not precluded, as illustrated for *Caryocorbula* species from the late Miocene-early Pliocene of the northern Dominican Republic. The morphology of these species falls along the interspecific allometric curve, but each is also characteristic of a particular paleoenvironmental setting, with valve size and shape tracking with inferred depth and physical energy gradients.

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INTRODUCTION

Species of *Caryocorbula*, one of the most abundant genera of molluscs in the Neogene of the Caribbean (Jackson et al. 1999), typically have been identified using qualitative descriptions of valve outline shape and valve size. This genus, however, is relatively conservative in its morphology, making qualitative methods for alpha-level taxonomy difficult. Using multivariate analyses of landmark data, we examined the relationship of size and shape within the clade *Caryocorbula* + (*Hexacorbula* + *Bothrocorbula*) (Figure 1, Figure 2) and within *Caryocorbula* to document patterns of morphologic evolution in these taxa, focusing on the Caribbean Neogene. We found that *Caryocorbula* exhibits a strong interspecific allometric trend through the Neogene in this region; a trend that persists through speciation and extinction events, and across environmental gradients. We see roles for both constraint and selection in shaping these morphologic patterns.

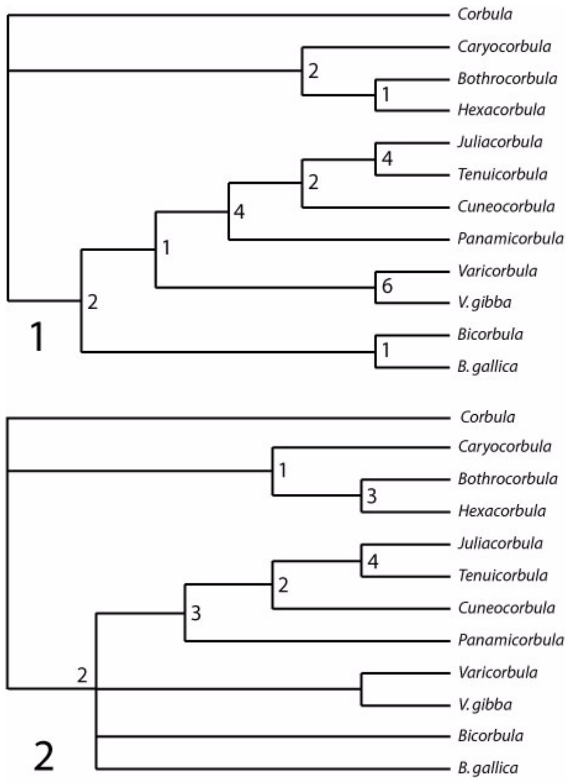

Figure 1. Trees resulting from cladistic analyses using maximum parsimony of conchologic characters for tropical America Neogene corbulid genera. Characters polarized using *Corbula* as an outgroup. Each node is labeled with its Bremer decay index. **1.1** One most parsimonious tree derived from analysis of a 70-character matrix (tree length = 203; consistency index (CI) = 0.5959; and retention index (RI) = 0.5738). **1.2** Strict consensus of two most parsimonious trees derived from analysis of a 73-character matrix (tree length = 208; CI = 0.5758; and RI = 0.5579). After Anderson and Roopnarine (2003).

Allometry and Constraint

Allometry can be defined as differential growth of body parts as the size of an organism increases. Klingenberg (1998) noted that allometric studies could be divided into two schools with different emphases. Studies in what he terms the Huxley-Jolicouer School are concerned with patterns of size covariation among several morphologic traits, in particular size covariation that fits the equation of simple allometry ($y=bx^a$ where a is a constant that does not equal one (1) if the two traits are measured on the same scale). In such studies, shape is of peripheral importance. Allometric studies in the Gould-Mosimann School focus on the relationship of shape and size, and give simple allometry no special status (i.e., allometry represents any type of non-isometric growth), except to note that it often fits empirical data well (e.g., Gould 1966, 1975, 1977; Jungers et al. 1995).

Allometry is often categorized by the types of data collected for study (see Cock 1966; Gould 1966). With static or intraspecific allometry, the covariation of traits among individuals within a particular ontogenetic stage of a single species is recorded. Ontogenetic allometry involves the determination of covariation among traits across ontogenetic stages of given species (but not necessarily within one individual, which is termed longitudinal allometry). The allometry tracked in this study is interspecific allometry, defined as allometry among species of different sizes within a single clade at the same growth stage (i.e., adult).

Broadly defined, constraints are mechanisms that limit or channel adaptive response in adult body plans, and allometry and morphologic constraints have been linked by a number of authors. For instance, Maynard Smith et al. (1985) note that allometric relations among adults of different species (interspecific allometry) that resemble growth stages of a single species (ontogenetic allometry) are strongly suggestive evidence of constraint. Further, Gould (1966) notes that interspecific allometry (as we document here for *Caryocorbula*) is the most likely type of allometry to illustrate change that must occur as size increases (i.e., shape that is functionally constrained by size).

Although discussed widely, constraint terminology has defied attempts at standardization, with categories and definitions of constraints varying among authors. For instance, phyletic constraints have been defined in related but non-interchangeable ways as adaptations retained in new ecologic settings (i.e., phyletic inertia; Gould and Lewontin

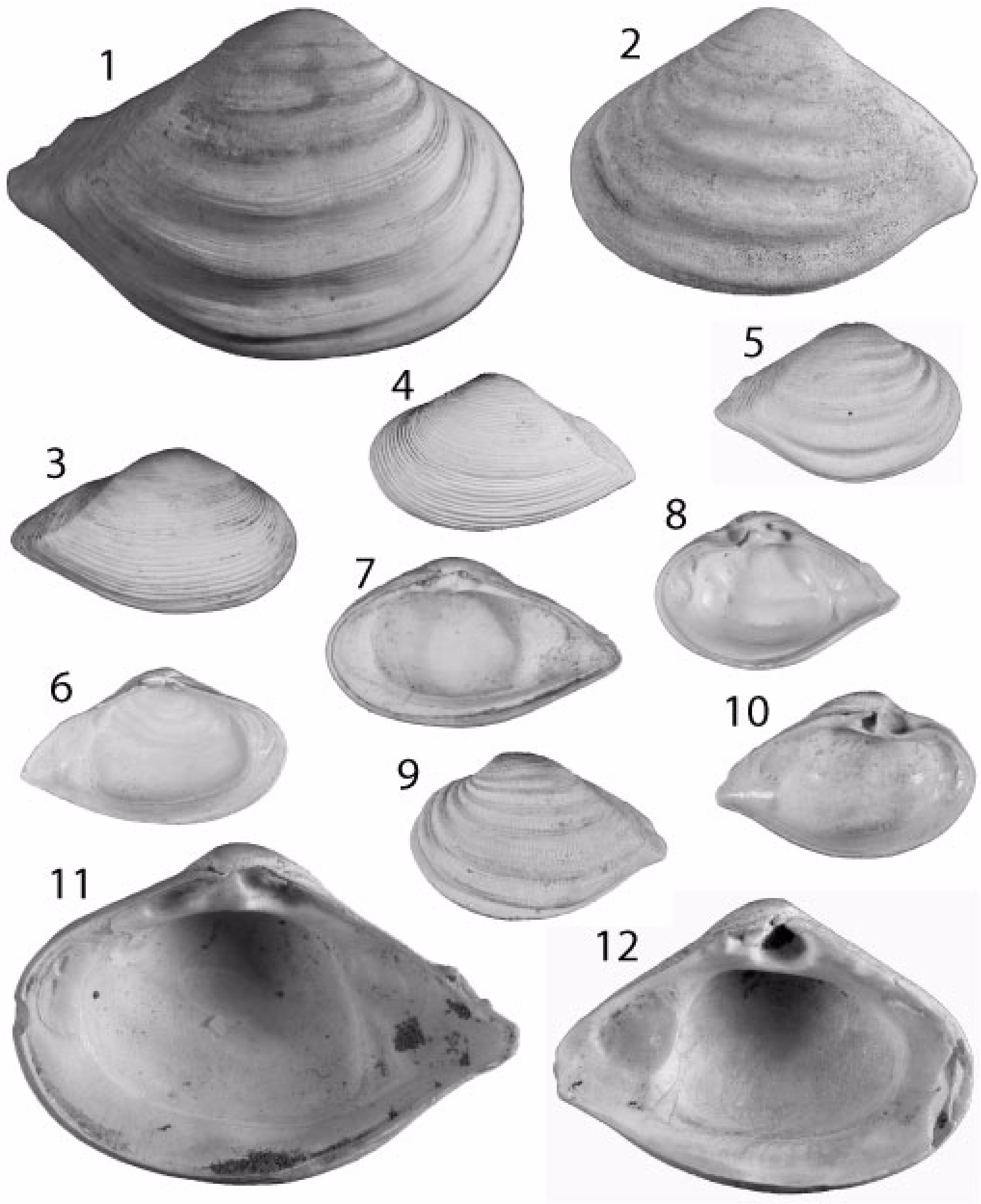

Figure 2. Illustrations of *Caryocorbula, Bothrocorbula,* and *Hexacorbula* valves, all X4. **2.1, 2.2, 2.11, 2.12,** *Hexacorbula hexacyma*, middle-upper Miocene Gatun Formation, Panama, TU 1342, **2.1, 2.11,** length 23.0 mm, **2.2, 2.12,** length 18.6 mm; **2.3, 2.4, 2.6, 2.7** *Caryocorbula prenasuta*, middle-upper Miocene Gatun Formation, Panama, NMB 18322, **2.3, 2.7,** length 13.3 mm, **2.4, 2.6,** length 11.9 mm; **2.5, 2.8 - 2.10,** *Bothrocorbula radiatula*, middle Miocene Oak Grove sand, Florida, TU 91, **2.5, 2.8,** length 11.2 mm; **2.9, 2.10,** length 11.7 mm.

1979) and as "establishment of a particular ontogeny to the exclusion of other options" (Raff 1996). Further, a similar concept of historical constraint has been defined as inherited allometries channeling evolutionary change (Gould 2002), as the form of ancestral species setting the course of evolutionary change (Thomas and Rief 1993), and as the evolutionary history of an organism limiting the developmental pathways that can evolve (Richardson and Chipman 2003).

As is apparent from these definitions, constraint terminology also includes a mix of pattern definition and process inference, and is often vague about causal mechanisms, primarily because these mechanisms are difficult to determine, even within living species. In addition, processes underlying specific constraints may be recategorized from one author to the next, so that pleiotropy, for example, has been listed as a mechanism of developmental constraint (Cheverud

Table 1. Constraint classification of Richardson and Chipman (2003).

Constraint Category	Type of Constraint	Definition
Generative (limited production of variant phenotypes during ontogeny)	Historical	Evolutionary history of organism limits developmental pathways because of current form or patterning mechanism available
	Developmental buffering	Genetic changes occur without phenotypic effect because of feedback loops and buffering in developmental pathways
	Genetic	Bias in appearance of certain genotypes due to nature of genetic system, probability of mutation, or recombination
	Physical	Physical properties of egg or embryo, extra-embryonic membranes and environment, limit or bias evolutionary change during development
Selective (limited survival of variant phenotypes during ontogeny or phylogeny)	Horizontal	Some developmental pathways influence many different developmental processes; changes in pathways likely deleterious because of pleiotropy
	Vertical	Changes in early developmental stages may have multiple effects on later stages, and are thus constrained
	Structural	Organisms limited in form because exceeding certain physical boundaries is selected against (i.e., limitations caused by physical laws)
	Functional	Functional integration of different systems limit morphologic variability

1984), genetic constraint (Gould and Lewontin 1979, Atchley and Hall 1991, Schwenk 1995, Schlichting and Pigliucci 1998), and horizontal constraint (Richardson and Chipman 2003).

The types of mechanisms considered to be constraints are the topic of considerable discussion. For example, the most widely quoted constraint definition is that of Maynard Smith et al. (1985) who defined developmental constraints as "biases in production of variant phenotypes, or limitations on phenotypic variability caused by the structure, character, composition or dynamics of the developmental system." A number of authors have attempted to narrow this definition, including Fusco (2001) who, using the term reproductive constraint, defined constraint as a "bias on the production of new ontogenetic trajectories caused by current mechanism of transmission of hereditary factors and laws of epigenetic interaction." In this definition, only phenomena that bias the organization of new ontogenetic trajectories are included, with phenomena that are properly natural selection acting during development excluded (see also Schlichting and Pigliucci 1998). Alternatively, Richardson and Chipman (2003) draw a distinction between what they call generative and selective constraints but consider both as types of constraint (Table 1). In this classification, generative constraints limit production of certain phenotypes during ontogeny and result in non-random production or nonproduction of variants. Selective constraints arise by natural selection acting during embryonic development, and remain approximately constant through a broad range of environments.

Clearly, the classification of constraint's causal mechanisms remains in flux. We do not attempt here to make further contributions to this situation. Instead, in the discussion below we will examine the possible role of constraint, and causal mechanisms of constraint, in the morphologic evolution of *Caryocorbula* using the broadly inclusive but clearly defined classification developed by Richardson and Chipman (2003).

MATERIALS AND METHODS

Phylogenetic Analyses

Phylogenetic analyses, which are described in detail in Anderson and Roopnarine (2003), are only briefly outlined here. 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 used in the analyses were conchologic, and character polarity was determined using *Corbula* as an outgroup. We ran analyses on two matrices: one of 73 and the other of 70 characters, which differed in the manner that commarginal-rib characters were coded. Phylogenetic analyses using branch and bound searches and maximum parsimony were completed in PAUP* 4.0b10 (Swofford 2002).

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 increases 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. The process is repeated incrementally until all resolution is lost on the strict consensus tree.

Morphometric Analyses

We used landmark-based geometric morphometrics to quantify size and shape variation (Bookstein 1991). Geometric morphometrics are used increasingly for morphometric studies because the methods allow 1) complete separation of size and shape into distinct variables, 2) segregation of shape into uniform and non-uniform components (see below), and 3) powerful means to visualize morphologic differences using thin plate spline (tps) techniques. Further, the shape variables derived from geometric morphometric analyses can be incorporated into commonly used multivariate analyses including analysis of covariance (ANCOVA; Rosas and Bastir 2002), multivariate regression (Zelditch and Fink 1995; Penin and Berge 2001; Rosenberg 2002), principal components analysis (Zelditch et al. 2003), and canonical variates analysis (multivariate version of discriminate analysis; this study). In fact, a number of authors have used geometric morphometrics in allometric studies both within species (Zelditch et al. 1993; Zelditch and Fink 1995; Rosas and Bastir 2002) and among species (Fink and Zelditch 1995; Penin and Berge 2001; Rosenberg 2002; Zelditch et al. 2003).

In geometric morphometrics, ordinary Cartesian coordinates of geometrically homologous points (i.e., landmarks) are used to define the distributions of specimens in Kendall shape space around a Procrustean distance-minimized common reference form (Rohlf 1996). Specimen deviation from this consensus form is then calculated as the location of the specimen on a series of principal warp vectors (= partial warp scores). The principal warps are the principal axes of a normal Euclidean space tangential to the curved Kendall shape space, and are termed the non-uniform component of shape description because they summarize localized shape variation at variable geometric scales. The projection of the shape space distributions (i.e., partial warp scores) into Euclidean space is a mathematical convenience that permits their use in normal univariate and multivariate analyses. An additional component of shape description is the uniform or affine transformations of global stretching/compressing and shearing. Together, the uniform and non-uniform shape components provide a complete description of specimen shape.

In geometric morphometric studies, centroid size, the square root of the sum of squared distance of a series of measured landmarks to their common centroid, is often used as an estimate of overall size. Centroid size is a desirable measure of geometric scale because it is the only scaling variable that is uncorrelated with shape measures in the absence of allometry (Bookstein 1991). It, therefore, presents a clean and interpretable separation between organismal shape and size.

As part of this study, we defined 21 morphospecies of *Caryocorbula* represented by 1,145 specimens and used these species, along with 4 species of *Bothrocorbula* and *Hexacorbula* represented by 134 specimens, in a series of geometric morphometric analyses. Samples used were from Neogene deposits of Venezuela, Panama, Costa Rica, Dominican Republic, and Jamaica, as well as samples of Holocene corbulids collected in the Caribbean and Gulf of Mexico (Table 2, Table 3, Appendix). Collections acronyms are as follows: NMB--Naturhistorisches Museum, Basel, Switzerland, and TU—collections of Harold and Emily Vokes (now housed at the Paleontological Research Institution, Ithaca, New York and the Florida Museum of Natural History, Gainesville, Florida).

Because corbulids are inequivalved, we used only right valves in analyses, but captured landmarks of both internal and external views of specimens (Figure 3). Traditional species-level diagnostic characters within these genera are valve outline shape and valve size. Expression of ribs, and the lunular pit in *Bothrocorbula*, are used to a lesser extent for species discrimination. External landmarks generally track valve outline shape directly. The internal landmarks used are only indirectly related to traditional species-level features, although the relative placement of internal features is influenced by valve shape. Most internal landmarks, however, can be registered with greater precision, because more represent either the intersection of features, or maxima of curvature on very tight curves (Figure 3).

Centroid size was computed for both internal and external views using *Shape* (Cavalcanti 1996). However, only centroid size based on internal landmarks are used to illustrate allometry because the measure is based on more precisely placed landmarks (and an additional landmark) than external centroid size. Both uniform and non-uniform (partial warp) scores were computed using the program *tpsRelw* (Rohlf 2002) with scores for internal and external landmarks calculated separately. We computed scores for all three genera and for *Caryocorbula* only. For each data set, we examined the homogeneity/heterogeneity of uniform and non-uniform scores using relative warp analysis, a

Table 2. Stratigraphic and geographic locations of *Caryocorbula* samples. If a unit spans an epoch boundary, it is listed in both. A "?" indicates provisional placement in an epoch. Unnamed units are identified by their geographic location.

EPOCH (Age)	Florida	Greater Antilles	Venezuela	Costa Rica	Panama
Holocene	Florida	Dominican Republic Jamaica Cuba	Venezuela Grenada		
Upper Pleistocene					
Middle Pleistocene					
Lower Pleistocene (Calabraian)			Mare Cumaná	Moin	
Upper Pliocene (Gelasian)			Mare Cumaná?	Moin	Escudo de Veraguas unnamed unit (Isla Colon) unnamed unit (Valiente Peninsula)
Upper Pliocene (Piacenzian)		Bowden		Quebrada Chocolate Rio Banano	Escudo de Veraguas Cayo Agua Shark Hole Point (Bruno Bluff Member) unnamed unit (Isla Colon) unnamed unit (Valiente Peninsula) unnamed unit (Isla Solarte)
Lower Pliocene (Zanchlean)		Mao Gurabo unnamed unit (Rio Yaque del Norte, Dominican Republic)	Punta Gavilán		
Upper Miocene (Messinian)		Gurabo Cercado unnamed unit (Rio Mao, Dominican Republic)	Caujarao		
Upper Miocene (Tortonian)		Cercado unnamed unit (Rio Mao, Dominican Republic)	Caujarao Buenevara Adentro		Upper Gatun Middle Gatun Lower Gatun
Middle Miocene (Serravalian)			Buenevara Adentro		Lower Gatun
Middle Miocene (Langhian)			Cantaure		
Lower Miocene (Burdigalian)			Cantaure La Candelaria beds		
Lower Miocene (Aquitanian)					

modified principal components analysis. For *Caryocorbula*, we used these results as a first step in defining morphospecies. Group identifications (among genera and among *Caryocorbula* species) were tested further with canonical variates analysis (CVA) of the same scores. In preliminary analyses, CVAs in which scores of internal and external landmarks were combined produced better discrimination among identified groups than did CVAs where internal and external landmarks were analyzed separately. Therefore, with one exception, these combined results were used to visualize morphologic variability in our datasets. For *Caryocorbula*, initial CVA results were used to test and refine orig-

Table 3. Stratigraphic and geographic locations of *Bothrocorbula* and *Hexacorbula* samples. If a unit spans an epoch boundary, it is listed in both. A "?" indicates provisional placement in an epoch.

EPOCH (Age)	Greater Antilles	Venezuela	Costa Rica	Panama, Colombia
Holocene				
Upper Pleistocene				
Middle Pleistocene				
Lower Pleistocene (Calabraian)				
Upper Pliocene (Gelasian)				
Upper Pliocene (Piacenzian)	Bowden		Rio Banano	
Lower Pliocene (Zanchlean)	Gurabo			Tubara?
Upper Miocene (Messinian)	Gurabo Cercado			Tubara?
Upper Miocene (Tortonian)	Cercado	Buenevara Adentro		Gatun
Middle Miocene (Serravalian)		Buenevara Adentro		Gatun
Middle Miocene (Langhian)	Baitoa	Lagunillas? Cantaure		
Lower Miocene (Burdigalian)	Baitoa	Cantaure		
Lower Miocene (Aquitanian)				

inal morphospecies interpretations, which were then used in the CVAs reported here.

RESULTS

Size and Shape among *Caryocorbula*, *Bothrocorbula,* and *Hexacorbula*

A CVA of uniform and non-uniform shape components reveals that each genus of the *Caryocorbula* + (*Bothrocorbula* + *Hexacorbula*) clade is morphologically distinct both in shape (Wilks' lambda = 0.002, p<0.0001; 98.9% of specimens correctly assigned to genus; Figure 4) and size (Figure 5). Qualitatively, these genera are most readily distinguished by sculptural differences and by the presence of a lunule in *Bothrocorbula* (Figure 2.8, Figure 2.10). CVA results highlight more subtle but consistent differences related to the shape of valve outlines among genera (see also Figure 2). At one extreme on CVA Axis 1, *Bothrocorbula* has a slightly narrowed keel and a very broadly rounded anterior margin. In addition, the dorsal ends of the adductor muscle scars, especially the anterior, are positioned more toward the center of the valve. *Bothrocorbula* and *Hexacorbula* separate primarily on the second CVA axis. *Hexacorbula* has a narrower and more dorsally positioned rostral area accompanied by posterior expansion of the shell behind the umbo. *Caryocorbula* separates from the other genera primarily on CVA Axis 1 and differs most notably in having a much broader rostral area.

Relative warp analysis of the three genera highlights interspecific allometry in *Caryocorbula* that is not observed in either *Bothrocorbula* or *Hexacorbula* (illustrated in Figure 6 using internal landmarks; Note: because we used landmark techniques, the relationship of size and shape is not due to the use of shape variables containing size information, a pervasive problem for distance metrics). The CVA axes do not record this allometry because non-allometric features related to the dorso-ventral breadth of the rostral area (broad in *Caryocorbula*, narrower in *Hexacorbula* and *Bothrocorbula*) separate the genera in the analysis. In contrast, the first Relative Warp axis describes shape deformation related to valve elongation and rostrum position. Valves with high positive scores on Relative Warp Axis 1 are, relative to the standard reference form, compressed anteroposteriorly, have adductor muscle scars and ventral point of the pallial sinus (Landmark D on Figure 3) that are directed inward and upward, and have a ventrally displaced rostrum (Figure 6). Valves with high negative values on Relative Warp Axis 1 are dorsoventrally compressed with a strongly upturned rostrum, have posterior adductor muscle scars that are displaced inward and downward, and the ventral point of the pallial sinus positioned upward and inward.

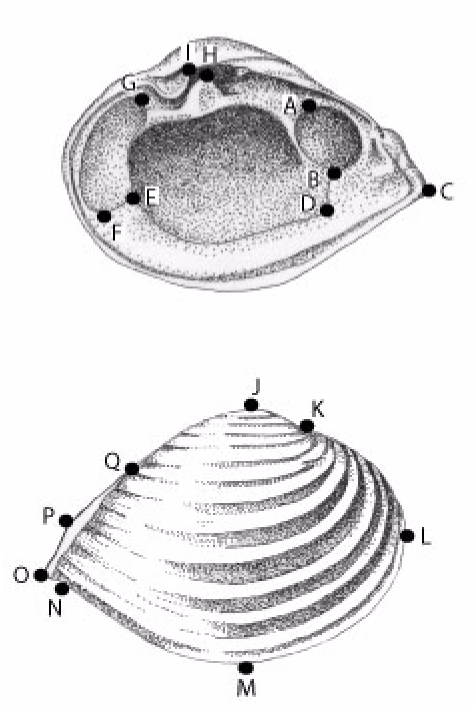

Figure 3. Landmarks used for *Caryocorbula*, *Hexacorbula,* and *Bothrocorbula*. Landmarks are defined as follows: (A) maximum curvature along dorsal margin of posterior adductor muscle scar; (B) intersection of pallial line with posterior adductor muscle scar; (C) posterior-most point on ventral side of rostrum; (D) posterior-most point of pallial line; (E) intersection of pallial line with anterior adductor muscle scar; (F) maximum curvature along ventral margin of anterior adductor muscle scar; (G) maximum curvature along dorsal margin of anterior adductor muscle scar; (H) dorsal-most point of cardinal tooth; (I) beak position; (J) maximum curvature of umbo; (K) maximum curvature along dorsoanterior slope; (L) maximum curvature along anterior margin; (M) maximum curvature along ventral margin; (N) maximum curvature anterior of keel along ventral margin; (O) intersection of keel with ventral margin; (P) posterior-most point on dorsal side of rostrum; (Q) intersection of keel with dorsoposterior margin.

Juvenile corbulids tend to be extremely thin valved until they approach adult size (Goodwin et al. 2003). As a result, preservation of juveniles should be extremely rare, and the specimens used for all genera in these analyses probably represent valves of adults. Therefore, the absence of observed allometry in *Bothrocorbula* and *Hexacorbula* may reflect the absence of small species in these genera (i.e., allometry not obvious over relatively narrow size ranges; see Figure 5). The lack of small species, however, indicates that size is an important morphologic feature in *Bothrocorbula* and *Hexacorbula* in spite of the absence of observed interspecific allometry in their valves.

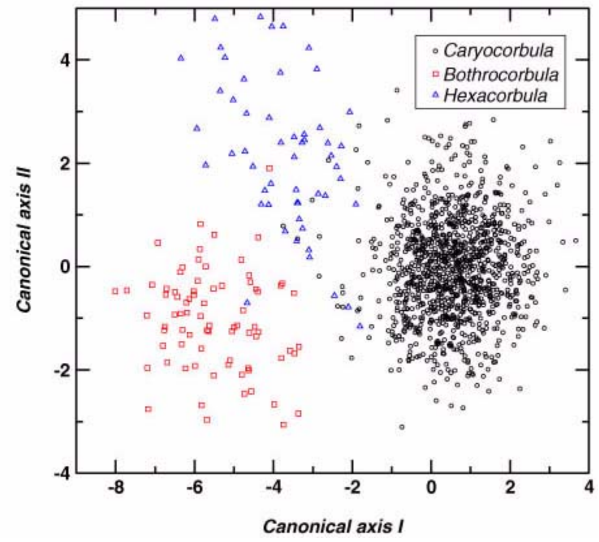

Figure 4. Separation of *Caryocorbula, Bothrocorbula,* and *Hexacorbula* on the first two canonical variates analysis (CVA) axes using uniform and non-uniform shape components derived from both internal and external landmarks. Genera are morphologically distinct (Wilks' lambda = 0.002, $p<0.0001$; 98.9% of specimens correctly assigned to their genus).

Interspecific Allometry in *Caryocorbula*

Neogene *Caryocorbula* from the Caribbean expresses a strong interspecific pattern of allometry (Figure 6, Figure 7). The CVA Axis 1 illustrated in Figure 7, like the Relative Warp Axis in Figure 6, describes valve elongation and rostral position, although the axes are reversed. Therefore, small species have relatively low CVA Axis 1 scores and tend to be shortened anteroposteriorly with a ventrally positioned rostrum. Larger specimens are progressively more elongate through dorsoventral shortening and have a more dorsally positioned to upturned rostrum (Figure 7).

This allometric trend persists throughout the Neogene, as illustrated when specimens from six broad time slices are plotted separately or when allometric curves for time slices are compared (Figure 8, Figure 9; Note: time intervals in these figures were not analyzed separately but are displayed separately to highlight temporal patterns). In Figure 8, allometric trajectories (fit with logarithmic equations) for each time slice generally follow the overall allometric trend (black line on Figure 8), although the overall trend can be offset (i.e., y-intercepts differ) from one time interval to another. A notable exception is the "middle" Pliocene interval (purple line on Figure 8) where size is somewhat truncated, and where *Caryocorbula* sp. C, which has a morphology that does not fall along the general allometric trend, is found (orange dia-

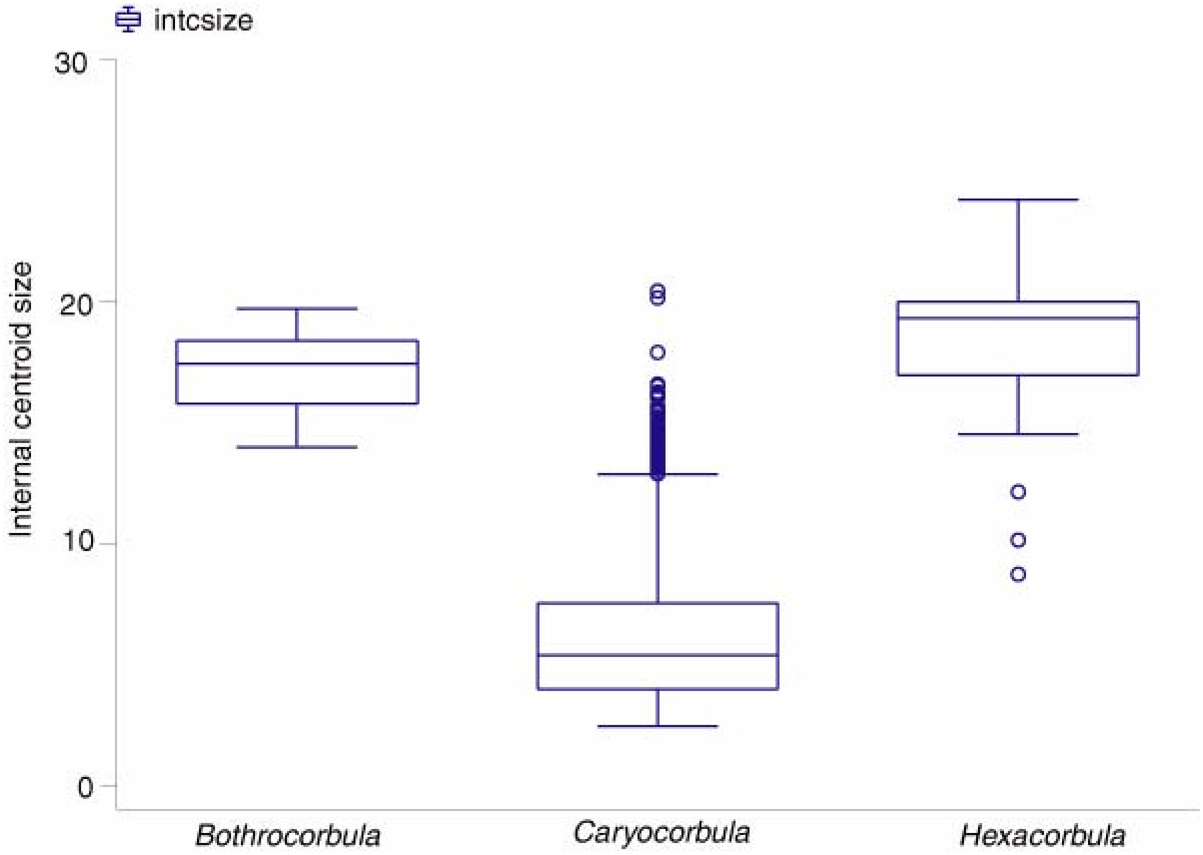

Figure 5. Spindle diagrams illustrating centroid size derived from internal landmarks for *Bothrocorbula*, *Caryocorbula*, and *Hexacorbula*. For each genus, the line within the box is median size, the box represents the 25% and 75% boundaries, brackets mark the 5% and 95% boundaries, and circles represent outliers.

mond in Figure 7 and Figure 9; further discussed below and in the Discussion section).

The constancy of this allometric trend is not dependent on a few abundant long-lived species (Figure 9). Instead, different species of a given size from different localities or times tend to have very similar shapes. For instance, *C. sericea* (from the upper Pliocene Bowden, Moin, and Escudo de Veraguas formations of Jamaica, Costa Rica, and Panama, respectively) and *C. lavalleana* (from the lower Pliocene Gurabo and Mao formations of the Dominican Republic and Holocene collections from Cuba and Venezuela) anchor the bottom of the curve from the Mio-Pliocene to Holocene, but reoccupy morphospace vacated by another species, *Caryocorbula* sp. A, from the upper lower to lower middle Miocene Cantaure Formation of Venezuela (Figure 9). In addition to species turnover, the allometric pattern in *Caryocorbula* persists in spite of uneven geographic and environmental sampling over time (see Table 2; Appendix).

Three time intervals show some variance from the overall allometric pattern. First, the middle-upper Miocene interval is missing small caryocorbulids with high negative values on CVA Axis 1 but includes the largest *Caryocorbula* from the Caribbean Neogene. (This is also the interval in which corbulid generic diversity peaks in the Caribbean [Anderson 2001; Anderson and Roopnarine 2003].) Second, in the Mio-Pliocene, the allometric curve is truncated dramatically, without an apparent change in curve shape (Figure 8, Figure 9). This extinction of large-bodied *Caryocorbula* species is part of an extinction of large species of all corbulid genera present in the Caribbean. These extinctions have been attributed to a decrease in nutrient availability and primary productivity in the Caribbean that commenced at this time (Anderson 2001). Third, the “middle” Pliocene, as well as the middle to upper Miocene, each contain a handful of individuals from species (*Caryocorbula* sp. B and *Caryocorbula* sp. C) that are offset from the overall allometric trend (Figure 7, Figure 9).

There are few similar studies to which we can compare our results, making it difficult to infer how common or rare such interspecific allometric trends are. Although studies of allometry and scaling are common, most studies track allometry within spe-

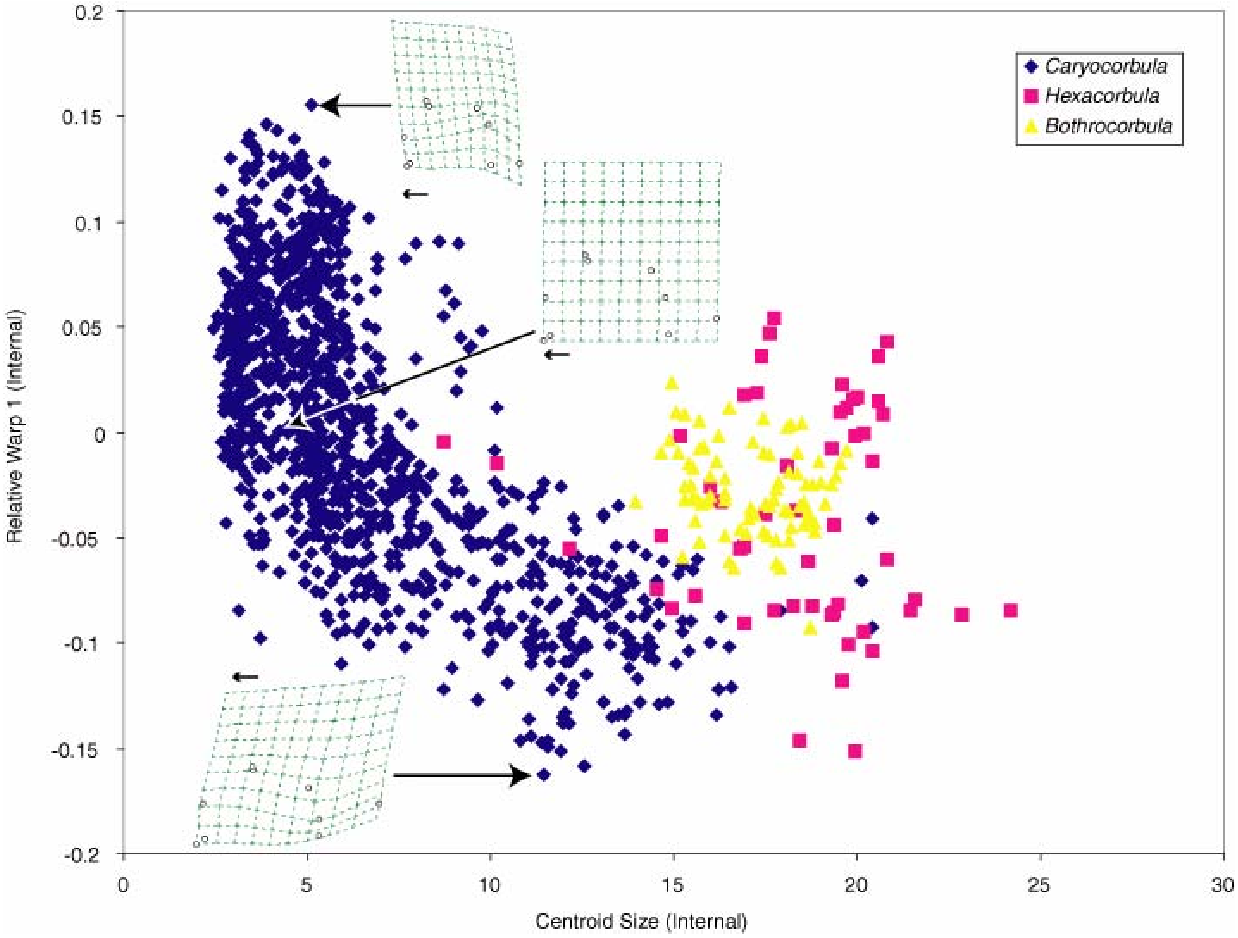

Figure 6. Centroid size based on interior landmarks vs. Relative Warp Axis 1 for an analysis of internal landmarks of *Bothrocorbula*, *Caryocorbula*, and *Hexacorbula*. Thin plate splines of internal landmarks are illustrated for three specimens to show variation in shape deformation along the first relative warp axis (small arrows point toward valve anterior).

cies, and of those that track allometry among species most studies focus on covariation in the size (i.e., length, mass, volume) of two traits (i.e., those of the Huxley-Jolicouer School). Very few studies have documented the relationship of size and shape among species (i.e., the Gould-Mosimann School). For the "Huxleyan" data sets, interspecific allometry is relatively common, and observed in vertebrates in general (Jerison 1973) and in terrestrial mammals (Christiansen 2002), primates (Majoral et al. 1997), deer (Gould 1974), and horses (Radinsky 1984). For the few "Gouldian" data sets (including two studies using the geometric morphometric techniques we employ; Penin and Berge 2001, Rosenberg 2002), a range of allometric trends among species are documented including differing allometric slopes for species (e.g., Rosenberg 2002), similar trends that offset along the size axis (similar to the pattern we see for species pooled by time interval, Figure 8; e.g., Emlen 1996), or a combination of differing trends and trend offsets (e.g., Kawano 2000).

DISCUSSION

Determining the cause of interspecific allometry in *Caryocorbula* requires a series of inferences (Figure 10). The consistent correlation of size and shape in *Caryocorbula* that is not seen in its sister clade (*Bothrocorbula* + *Hexacorbula*), implies that this relationship is genetically based and is an emergent property of *Caryocorbula* as a whole. Further, because a clear and persistent allometric pattern is present in a data set where paleoenvironmental conditions were neither constant nor sampled consistently over geologic time, neither ecophenotypic plasticity nor natural selection can be the cause of *Caryocorbula* allometry. Finally, a role for constraints in this interspecific allometry is indicated because this trend persists through multi-

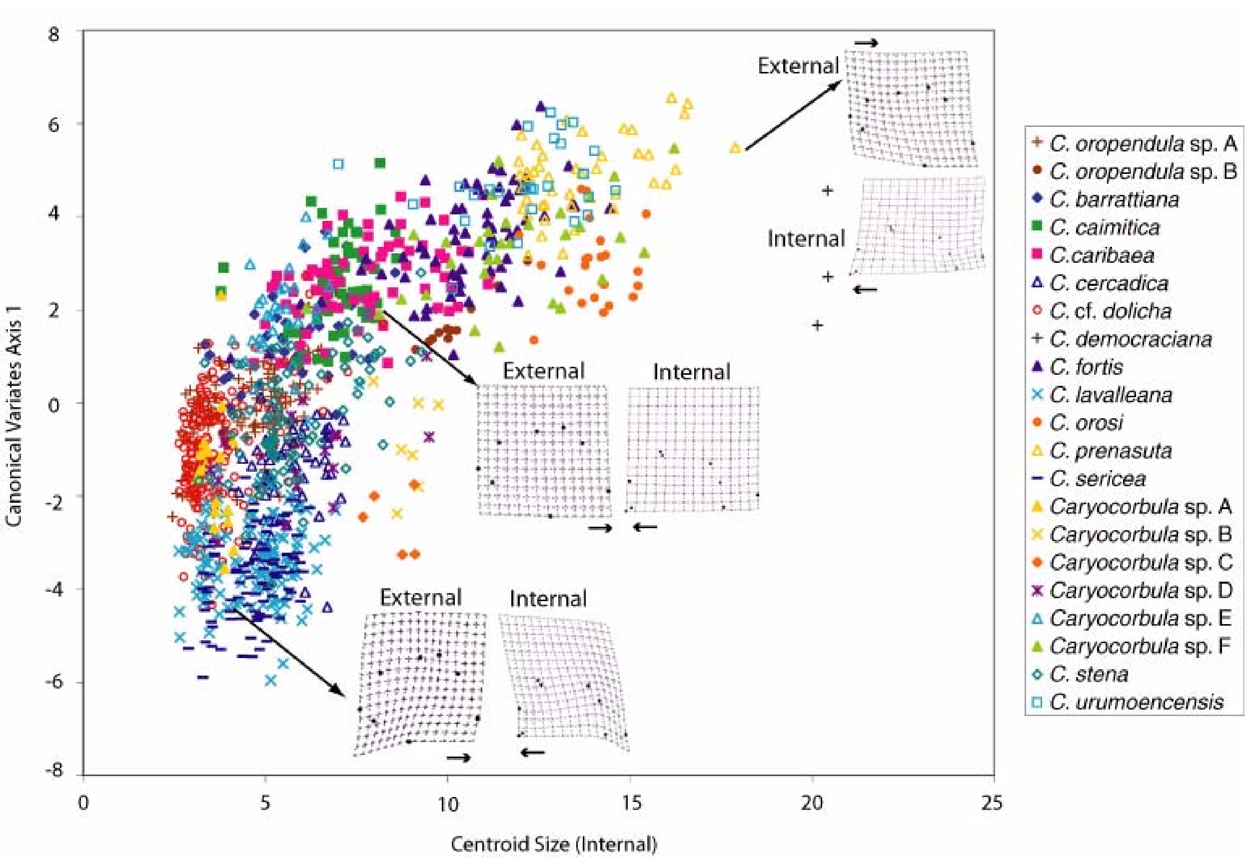

Figure 7. Centroid size based on interior landmarks vs. CV Axis 1 for *Caryocorbula* (based on uniform and non-uniform shape components derived from both internal and external landmarks for a dataset including only *Caryocorbula*). Thin plate splines of internal and external landmarks are illustrated for three specimens to show variation in shape deformation along the first relative warp axis (small arrows point toward valve anterior).

ple speciation and extinction events (see Gould 1966; Maynard Smith et al. 1985).

As outlined in the introduction, constraint studies lack a common terminology. We have chosen to use the recent classification of Richardson and Chipman (2003) as a basis for discussion of constraint in *Caryocorbula*. Within this classification (Table 1), the most likely mechanisms to explain the interspecific allometry in *Caryocorbula* are either historical (a type of generative constraint) or horizontal (a selective constraint) constraints.

Richardson and Chipman (2003) define historical constraints as generative constraints in which the evolutionary history of an organism limits the developmental pathways that it can evolve, either because of current form (e.g., Resnik 1995; but see Schwenk 1995) or because of the patterning mechanisms available to it (e.g., Gould 1989). *Caryocorbula*, and perhaps other corbulids, may be subject to historical constraint through their characteristically inequivalved condition. In corbulids, the smaller left valve fits partially to completely into the right valve. One way that the inequivalved condition may constrain morphology is by limiting internal space. In fact, we see a pattern consistent with this limitation in our data. Most *Caryocorbula* species (and most corbulid species for that matter) have relatively inflated valves. In our dataset, only two *Caryocorbula* species have uninflated valves (*Caryocorbula* sp. B and *Caryocorbula* sp. C). Perhaps not coincidentally, these two species are also the ones that do not fit into the overall allometric trend (Figure 7).

In addition to limits on internal space, historical constraints acting through the ontogeny of valve accretion in corbulids may play a significant role in determining valve shape. Many corbulids experience an initial period of valve-edge accretion producing a very thin shell (Goodwin et al. 2003). In this initial phase, left and right valves can be nearly equivalved, even in highly inequivalved genera such as *Varicorbula* (Anderson 1996). This valve-edge accretion phase is followed by a phase where accretion occurs predominantly onto valve inner surfaces, making the growth trajectory highly oblique to perpendicular to the commissure plane (Wrigley 1946; Goodwin et al. 2003). This change in growth direction may accompany the develop-

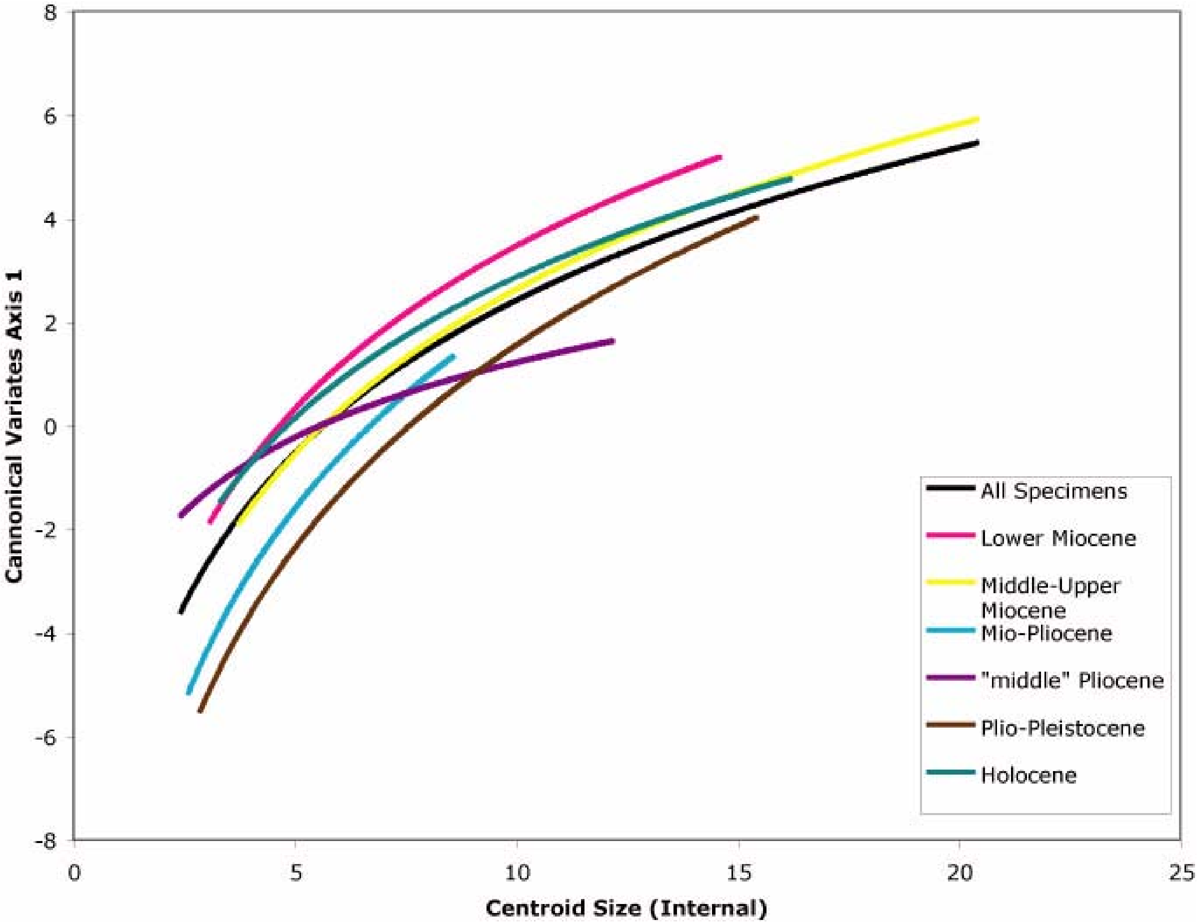

Figure 8. Allometric curves (fit with a logarithmic function) for all *Caryocorbula* (black line) and for the same data subdivided by time interval. Time intervals correspond to the following Ages in Table 2: Lower Miocene = Burdigalian + Langhian; Middle-Upper Miocene = Serravalian + Tortonian; Mio-Pliocene = Messinian + Zanchlean; “middle” Pliocene = Piacenzian; Plio-Pleistocene = Gelasian + Calabraian; Holocene = Holocene.

ment or accentuation of the inequivalved condition. Adult valve shape may be constrained, therefore, by the need for functional valve articulation between valves that differ in size and shape in the latter phase of this complex accretionary history.

It is also possible that horizontal constraints (Richardson and Chipman 2003), in which some developmental pathways influence many different processes in development so that changes in any pathway are likely to have a negative selective value because of pleiotropic effects (see also Raff 1996). For instance, selection may be acting on *Caryocorbula* size, but if shape is linked to size by pleiotropy, an interspecific allometric trend such as we document would result (see Gould 1977; Gould and Lewontin 1979; Cheverud 1984; Norris 1991). In previous work, we have called on regional changes in nutrient availability as a cause of dramatic size trends in corbulid and chionine bivalves of the Caribbean Neogene (e.g., Roopnarine 1996; Anderson 2001). More specifically, we have inferred that speciation and extinction of large-bodied members of these clades are controlled by changes in nutrient availability and primary productivity. Therefore, for *Caryocorbula*, environmental conditions (i.e., increased nutrient availability) could allow the evolution of large-bodied species, but constraints could restrict the species that arise to a narrow range of shapes.

Although interspecific allometry in *Caryocorbula* may be a byproduct of constraint, this allometric trend, nonetheless, can have adaptive significance (Gould and Lewontin 1979; Maynard Smith et al. 1985; Norris 1991; Amundson 1994; Levinton 2001). In other words, constraint may channel morphologic variability but natural selection nevertheless acts as the underlying force for change (Bell 1987; Gould 1989; Landman 1989; Geary et al. 2002). In fact, evidence that the correlation of size and shape are adaptive in *Caryocorbula* can be inferred through examination of areas where precise paleoenvironmental data are available, such as Neogene deposits of the Dominican Republic (Figure 11).

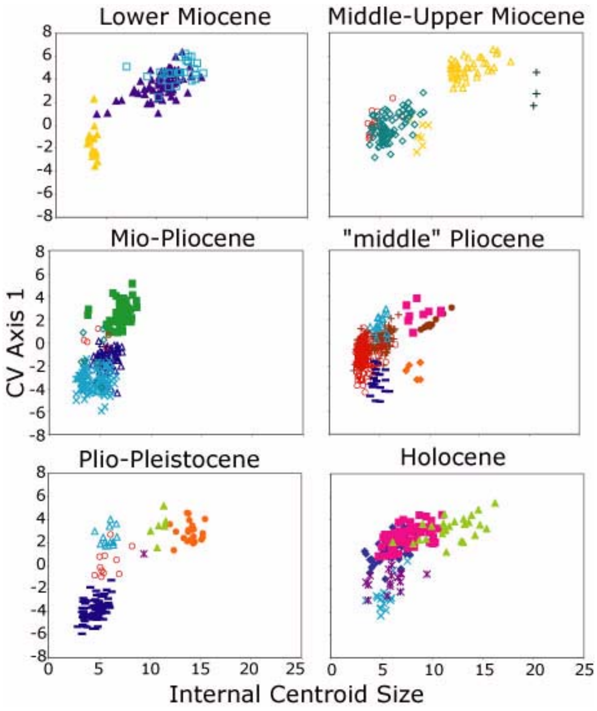

Figure 9. Centroid size based on interior landmarks vs. CV Axis 1 for *Caryocorbula.* Data are identical to Figure 7 and Figure 8 but scores are separated onto plots representing same time intervals as in Figure 8. Symbols as in Figure 7.

In these late Miocene and early Pliocene sediments, valve morphology, sediment type, and inferred water depths are closely related, and this relationship cannot be explained by taphonomic processes such as transport and size sorting (Anderson 1994, 1996). Valves of the relatively large *C. caimitica* occur in marginal- to shallow-marine sands and silts with evidence of sediment movement and where bioclasts are concentrated into lenses, burrows, or lenticular beds. Such strata with concentrated bioclasts were probably deposited in higher energy conditions in which *C. caimitica* would be less susceptible to disinterment because of its larger size, and would be capable of more efficient and deeper burial because of its elongate shape and more prominent rostrum (Stanley 1970). The morphologically intermediate *C. cercadica* also is found in shallow-marine deposits, but those formed in a lower energy setting, as indicated by the species' occurrence in lenticular beds rich in bioclasts with a silty matrix. Finally, valves of the small species *C. lavalleana* typically occur in deeper-water deposits of finer-grained sediment where bioclasts are dispersed through the matrix, indicating low energy conditions. The triangular shape of *C. lavalleana* would increase its buoyancy within these softer sediments.

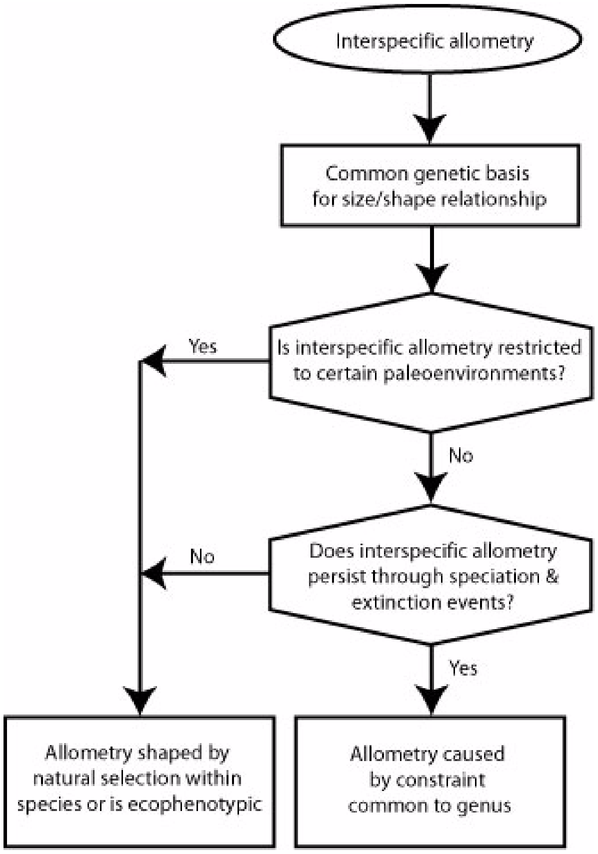

Figure 10. Flowchart illustrating evidence used to infer a major role for constraint in interspecific allometry in *Caryocorbula*.

Further evidence to support an adaptive explanation for valve shape may be gleaned from *Caryocorbula* sp. B and *Caryocorbula* sp. C, which do not fall within the allometric trend (Figure 7). These species have valve outline shapes typical of species with smaller body sizes. These un-elongated moderate-sized species may have compensated for a lack of anterior-posterior streamlining with a thinner profile provided by their relatively uninflated valves.

CONCLUSIONS

Difficulties in qualitatively identifying Neogene morphospecies of Caribbean *Caryocorbula* are caused by an interspecific allometric trend that very likely has a genetic basis. In addition, the persistence of this trend through speciation and extinction events, its presence across paleoenvironments, and its resiliency despite sampling effects indicates that the allometry arises from some mechanism of constraint. Based on the strong correlation of *Caryocorbula* morphology to paleoenvironment, however, selection must still

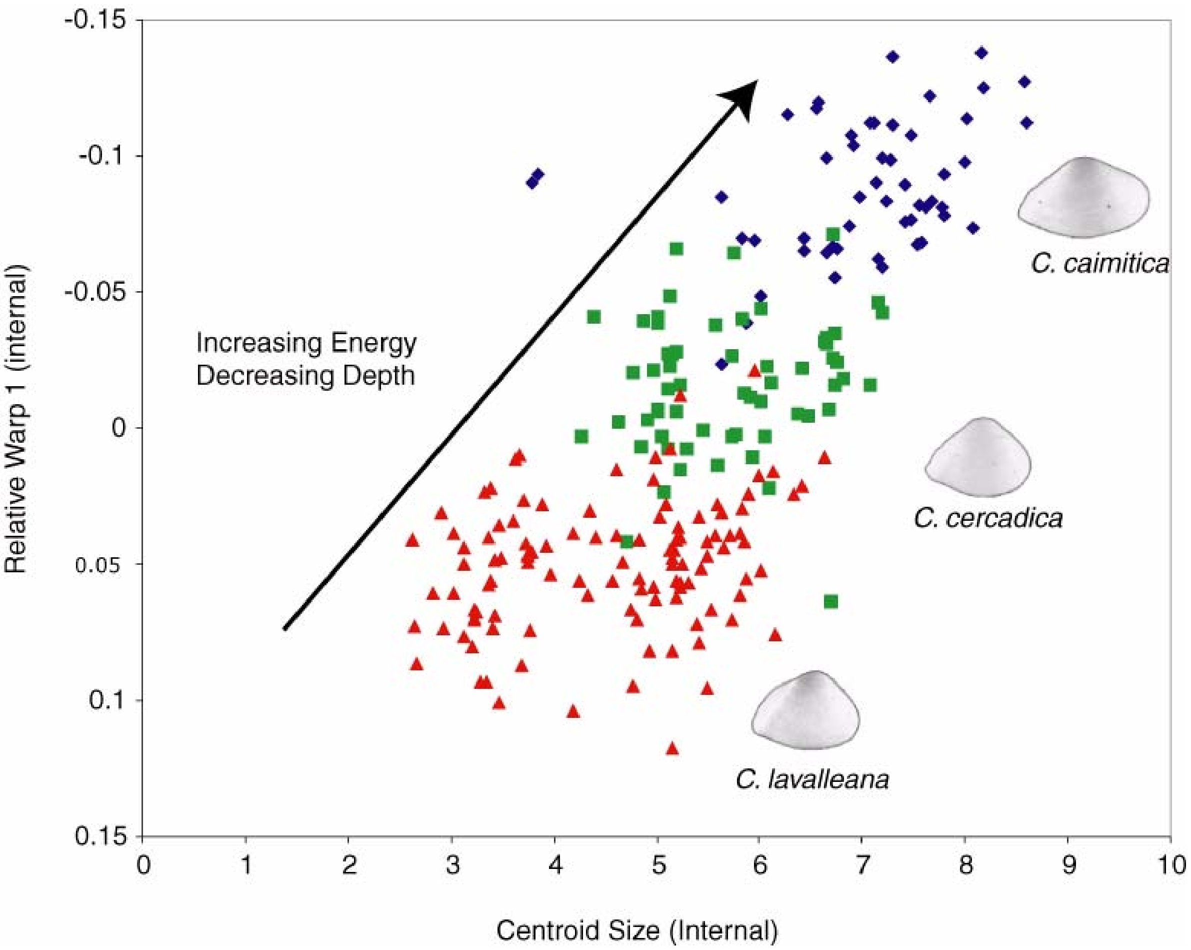

Figure 11. Centroid size based on interior landmarks vs. Relative Warp Axis 1 for uniform and non-uniform shape components based on internal landmarks of *Caryocorbula* from the Dominican Republic Mio-Pliocene. These results represent a separate analysis from that illustrated in Figure 7 and Figure 9. External views of representatives of each of the three species analyzed also are illustrated.

play an important role in the morphologic evolution of this genus.

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APPENDIX

Samples used in analyses. Unnamed units are identified by their geographic location.

Species	Horizon	Formation (for fossil) Locality (for Holocene)	# Valves
Caryocorbula			
C. oropendula sp. A	Upper Pliocene (Piacenzian)	Quebrada Chocolate	101
		Rio Banano	23
C. oropendula sp. B	Upper Pliocene (Piacenzian)	Rio Banano	11
C. barrattiana	Holocene	Jamaica	16
		Grenada	6
		Venezuela	17
C. caimitica	Upper Miocene (Tortonian - Messinian)	Cercado	52
C. caribaea	Holocene	Dominican Republic	11
		Grenada	10
		Cuba	2
		Jamaica	24
		Florida	12
		Venezuela	2
	Upper Pliocene (Piacenzian-Gelasian)	unnamed unit (Isla Colon)	5
	Upper Pliocene (Piacenzian)	Cayo Agua	4
C. cercadica	Upper Miocene (Tortonian-Messinian)	unnamed (Rio Mao)	61
C. cf. *dolicha*	Upper Pliocene - Lower Pleistocene (Gelasian – Calabraian)	Moin	11
	Upper Pliocene (Piacenzian-Gelasian)	unnamed unit (Valiente Peninsula)	16
		unnamed unit (Islan Colon)	2
	Upper Pliocene (Piacenzian)	Cayo Agua	93
		unnamed unit (Isla Solarte)	17
		Shark Hole Point (Bruno Bluff Mem.)	35
	Lower Pliocene (Zanchlean)	Punta Gavilán	8
	Upper Miocene (Tortonian - Messinian)	Caujarao	15
C. democraciana	Upper Miocene (Tortonian-Messinian)	Caujarao	3
C. fortis	Lower-Middle Miocene (Burdigalian-Langhian)	Cantaure	56
	Lower Miocene (Burdigalian)	La Candelaria beds	12
C. lavalleana	Holocene	Cuba	9
		Venezuela	8
	Lower Pliocene (Zanchlean)	unnamed unit (Rio Yaque del Norte)	33
		Mao	17
	Upper Miocene-Lower Pliocene (Messinian - Zanchlean)	Gurabo	53
	Upper Miocene (Tortonian-Messinian)	unnamed unit (Rio Mao)	8
C. orosi	Upper Pliocene-Lower Pleistocene (Gelasian-Calabraian)	Moin	22

APPENDIX (continued).

Species	Horizon	Formation (for fossil) Locality (for Holocene)	# Valves
C. prenasuta	Upper Miocene (Tortonian-Messinian)	Caujarao	7
	Upper Miocene (Tortonian)	middle-upper Gatun	9
	Middle-Upper Miocene (Serravalian-Tortonian)	lower Gatun	27
C. sericea	Upper Pliocene-Lower Pleistocene (Gelasian-Calabraian)	Moin	42
	Upper Pliocene (Piacenzian-Gelasian)	Escudo de Veraguas	41
	Upper Pliocene (Piacenzian)	Bowden	19
Caryocorbula sp. A	Lower-Middle Miocene (Burdigalian-Langhian)	Cantaure	18
Caryocorbula sp. B	Middle - Upper Miocene (Serravalian - Tortonian)	Buenevara Adentro	7
Caryocorbula sp. C	Upper Pliocene (Piacenzian)	Shark Hole Point (Bruno Bluff Mem.)	5
Caryocorbula sp. D	Holocene	Venezuela	16
	?Upper Pliocene - Lower Pleistocene (?Gelasian - Calabraian)	Cumaná	1
Caryocorbula sp. E	?Upper Pliocene - Lower Pleistocene (?Gelasian - Calabraian)	Cumaná	3
	Upper Pliocene - Lower Pleistocene (Gelasian - Calabraian)	Mare	10
	Upper Pliocene (Piacenzian-Gelasian)	Escudo de Veraguas	18
Caryocorbula sp. F	Holocene	Venezuela	25
	?Upper Pliocene - Lower Pleistocene (?Gelasian - Calabraian)	Cumaná	5
	Upper Pliocene - Lower Pleistocene (Gelasian - Calabraian)	Mare	1
C. stena	Lower Pliocene (Zanchlean)	Punta Gavilán	7
	Upper Miocene (Tortonian)	middle-upper Gatun	50
	Middle-Upper Miocene (Serravalian-Tortonian)	lower Gatun	32
C. urumoencensis	Lower-Middle Miocene (Burdigalian-Langhian)	Cantaure	27
Bothrocorbula	Upper Pliocene (Piacenzian)	Rio Banano	1
		Bowden	2
	Upper Miocene-Lower Pliocene (Messinian-Zanchlean)	Gurabo	11
	Upper Miocene (Tortonian-Messinian)	Cercado	44
		unnamed unit (Rio Mao)	17
	Lower – Middle Miocene (Burdigalian-Langhian)	Baitoa	5
Hexacorbula	?Upper Miocene -?Lower Pliocene (?Messinian - ?Zanchlean)	Tubara	1
	Middle-Upper Miocene (Serravalian-Tortonian)	Buenevara	18
		Gatun	29
	Lower-Middle Miocene (Burdigalian-Langhian)	Cantaure	5