

Relationships among *Venericardia* (Bivalvia: Carditidae) on the U.S. Coastal Plain during the Paleogene

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Rapidly changing Venerid (Bivalvia: Cardinaria) in the U.S. Coastal Plain

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Abstract.—Despite the abundance and diversity of *Venerid* bivalves on the U.S. Coastal Plain during the

The genus is now extinct and its closest living relatives are believed to belong to *C. ...* Conrad 1867 (Heaslip, 1968).

The objective of this study is to reconstruct the evolutionary relationships among selected U. S. Coastal Plain venericard species. The resulting phylogeny will allow the identification of major clades and the exploration of the validity of historical and current venericard classification. Specifically, it will be determined whether external ornamentation types (alticostate and planicostate) and originally proposed subtaxa (*C. ...*, *G. ...*, *...*, and *...*) represent monophyletic groups within *...*.

Materials

...—Eighteen ingroup species of venericards (Table 1) were selected for examination, representing approximately 30% of venericard species on the U.S. Coastal Plain during the Paleogene. The ingroup consisted of representatives from four major originally proposed subtaxa: *C. ...*, *G. ...*, *...*, and *...* (Table 1). Two to 11 species were selected from each original subtaxon, including the type species (if found on the U.S. Coastal Plain) and additional abundant or well-preserved species. The selected species included representatives from across the Paleogene, with the greatest number occurring during the Eocene due to the clade's high Eocene diversity (Table 1).

Two species closely related to venericards were included as outgroups to polarize characters:

aspects of shell shape, size, external ornament, hinge teeth, adductor muscle scars, and pallial line. Characters were primarily based on qualitative observations of venericard specimens and were differentiated into states that were identifiable by eye, but not easily measured. Quantitative characters based on continuous measurements (characters 1, 12–16) were

ornamentation was excluded from analysis, the planicostates formed a monophyletic group in the majority of most parsimonious trees. Eight of the more derived planicostate species (*V. planicosta*, *V. m. m. m.*, *V. m. m. m.*, *V. m. m. m.*, *V. m. m. m.*, *V. m. m. m.*, *V. m. m. m.*, and *V. m. m. m.*) were monophyletic in every most parsimonious tree (supported by character 8), whereas the more basal planicostate species (*V. m. m. m.*, *V. m. m. m.*, and *V. m. m. m.*) fell outside this clade in 30% of most parsimonious trees. The persistence of the planicostate clade when the external ornamentation characters were given less weight indicates that planicostate venericards are united by similarities beyond their smooth-ribbed ornamentation (e.g., primarily shell shape [2] and size [1]).

Although the monophyletic status of

Chlamydomonas species than other allicostate species. However, a member of *Chlamydomonas*, .

Within the alticostates, the proposed *Colletes* species (*C. hirsuta*, *C. vernalis*, and *C. albicollis*) and *Colletes* species (*C. albicollis* and *C. hirsuta*) all

use and loan of museum specimens. We also thank W. Allmon, D. Dockery, E. Fenlon, L. Ivany, E. Robinson, J. Sessa, and L. Ward for numerous useful discussions and field support. G. Hunt provided insightful comments that improved the manuscript. K. Ohman assisted with photography and compiled stratigraphic and geographic ranges. E. Fenlon contributed to field collection, specimen identification, and the development of characters. Suggestions from two anonymous reviewers were greatly appreciated. Research was supported by the National Science Foundation (EAR-0718745) and the National Center for Ecological Analysis and Synthesis.

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among the species’ geographic ranges are generally associated with changes in sea level. All species from the Paleocene and Eocene occurred in Alabama, and frequently occurred in additional nearby states, such as Arkansas, Georgia, Louisiana, Mississippi, and Texas. Species with more recent stratigraphic ranges have slightly different geographic ranges. For example, *Carditella* occurred during the late Oligocene in Florida and North Carolina and *Carditella* occurred during the early Miocene in Florida. Although *Carditella* and *Carditella* group together in the phylogeny, their similar geographic ranges are most likely a function of outcrop availability (Miller et al., 2005).

Our phylogeny reconstructed the evolutionary relationships among Paleogene venericard species on the U.S. Coastal Plain and indicates that smooth-ribbed planicostate venericards evolved once from alticostate venericards. The phylogeny also suggests that the alticostates are paraphyletic to the planicostates and that venericard taxonomy should be revised to reflect monophyletic groups within the alticostates. Future work should focus on resolving the evolutionary relationships among alticostate venericards by including additional species from each proposed subtaxa and Paleocene species in phylogenetic analyses.

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A . . . D c - 1 - - - c a aq a c a aq
 1 a - - - - 1 - c a a - -

1. Size: 0 = tiny (width <1 cm); 1 = small (width 1-3 cm);

45. Intercostal shape across middle of largest specimen: 0 = “U”-shape; 1 = “V”-shape; 2 = flat.
46. Intercostal shape on umbone: 0 = “U”-shape; 1 = “V”-shape; 2 = flat.
47. Adductor muscle scar depth: 0 = shallow; 1 = deep.
48. Pallial line intersection with anterior adductor muscle scar: 0 = intersection at middle of muscle scar; 1 = intersection at posterior edge of muscle scar.
49. Pallial line shape: 0 = smooth, uniform curve; 1 = bends in corner.
50. Hinge size: 0 = narrow; 1 = wide.
51. Two morphs with differing inflation: 0 = observed; 1 = not observed.

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