Modes of Larval Development and Rates of Speciation in Early Tertiary Neogastropods

Abstract. *Although most warm-water molluscs have planktotrophic larval stages, some living families of tropical neogastropods are dominated by nonplanktotrophic development. Fossil protoconchs of early Tertiary neogastropods indicate that some families became progressively dominated by nonplanktotrophic development through time. This trend may be the result of higher speciation rates for nonplanktotrophs and a unidirectional trend in developmental change.*

Paleobiologists have been interested in the larval development of fossil gastropods because of its influence on biogeographic distribution and evolutionary rates. Fossil species that had planktotrophic larval stages have been shown to have had broader geographic distributions and greater evolutionary longevities than species that had nonplanktotrophic larval stages (*1–4*). Most, if not all, neogastropod families had species with planktotrophic development in the early Tertiary.

In view of this fact and the general predominance of the planktotrophic mode of development in modern warm-water marine faunas (*5*), it is surprising that all living species of the warm-water neogastropod families Volutidae and possibly Fasciolariidae have nonplanktotrophic dispersal (*6, 7*). I suggest that differential rates of speciation and an irreversible trend in developmental change may have influenced larval developmental patterns in these families through the Tertiary.

A survey of the larval developmental types of the neogastropod families Volutidae, Fasciolariidae, Nassariidae, Mitridae, Buccinidae, and Olividae through the Paleocene-Eocene interval was undertaken. All are carnivores except for nassariids which are nonselective deposit feeders and scavengers (*8*).

The results of this analysis, as expressed in Fig. 1, indicate that nonplanktotrophic development was a relative rarity among the six families during the Paleocene and part of the early Eocene (*9*). The relative proportions of nonplanktotrophics among families increased late in the early Eocene and early in the middle Eocene and again in the late middle Eocene. The late Eocene was characterized by continued high proportions of nonplanktotrophs.

At present only two principal geographic trends in larval development types are known in living marine invertebrates. Although the literature on developmental types in deep water marine environments is sparse, there seems to be a trend of increasing number of nonplanktotrophic species with increasing water depth (*5*). In addition, there is a trend of increasing numbers of planktotrophics with decreasing latitude. These environmentally related gradients do not explain the change in developmental types seen in early Tertiary neogastropods. Early Tertiary deposits show no trends toward deeper water environments, and therefore progressively deeper water faunas are not being collected through time. In addition, modern volutids show no preference for deep water. Of 17 species of west Atlantic volutids documented [all of those described by Weaver and duPont (*10*) that are represented by enough specimens to reliably establish ranges], ten live in water depths of about 20 m or less and four extend into the littoral zone.

Continental plate positions established by paleomagnetic data (*11*) show little change in the paleolatitude of the Gulf Coast region through the early Tertiary; therefore a change in latitude cannot be invoked to explain changes in developmental types in the early Tertiary.

There is a cooling trend in the middle to late Eocene that is the beginning of a general climatic deterioration following a long interval of relatively mild world climates (*12*). If the present-day correlation of larval development and latitude is linked to temperature, a cooling episode might be expected to produce larger numbers of nonplanktotrophs. The increase in proportions of nonplanktotrophs in the early Eocene predates the middle to late Eocene cooling interval, but more detailed work on paleotemperatures and their chronology needs to be carried out before any firm statements can be made on this correlation.

It has been suggested that a species that is restricted to a certain habitat or food resource may find it advantageous to have a low-dispersal mode of reproduction so that its particular requirement is fully exploited (*6*). In this case, volutids and fasciolariids should exhibit the most specialized habitat requirements among the neogastropods. Yet in studies of areas where several neogastropod families coexist, volutid and fasciolariids usually exhibit as broad or broader prey preferences than do the Muricidae and Conidae (both families have large numbers of planktotrophs) (*8, 13–15*), and they do not seem to exhibit unusual substrate restrictions.

I suggest that the shift to nonplanktotrophy does not rely on an adaptive advantage to nonplanktotrophic development (*16*). The fossil record indicates that species with nonplanktotrophic development speciate more readily than do

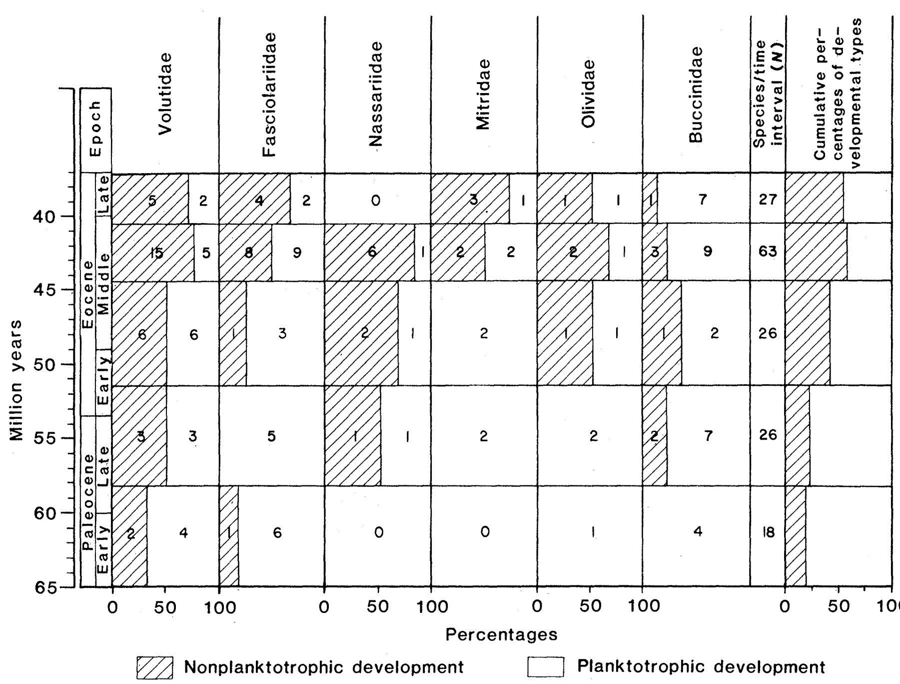

Fig. 1. Relative percentages of developmental types for six neogastropod families in the early Tertiary.

planktotrophic forms, probably because populations of nonplanktotrophic species face a higher probability of geographic isolation (*1, 3*). Any geographic setting that promotes the isolation of populations of nonplanktotrophic species but not high dispersal forms, should result in the diversification of nonplanktotrophs at a rate greater than that for high dispersal forms.

The Gulf of Mexico coastal plain was subjected to a number of major shoreline transgressions and regressions during the early Tertiary, possibly as a result of global sea-level changes. Regressive intervals were accompanied by the building of large deltas in southern and eastern Texas and the Louisiana-Mississippi area (*3*). Successive paleogeographic reconstructions (*3*) suggest a pattern whereby nonplanktotrophs and planktotrophs achieved gulf-wide ranges during transgressive intervals when deltas were reduced. The ranges of many of the nonplanktotrophs may have been attenuated by deltas during regressive periods while most of the planktotrophic forms were able to disperse around these barriers.

This process of range-partitioning and speciation can lead to higher numbers of nonplanktotrophs relative to planktotrophs, but it does not explain how a group of species may remain dominated by nonplanktotrophs after the range-dividing mechanism ceased to act. A trend has been noted in the marine invertebrates whereby planktotrophic species give rise to nonplanktotrophs but that the reverse is rarely true (*17–19*). Evidence from the Eocene seems to support a unidirectional trend in developmental change (*16*). Several early Tertiary genera that were exclusively planktotrophic gave rise to nonplanktotrophic species. However, no genus that contained all nonplanktotrophic species gave rise to a planktotrophic form.

Given these two trends—a high rate of diversification for nonplanktotrophs and a unidirectional trend in developmental change—if a situation ever arose where a group became completely nonplanktotrophic, it would remain so, even after pressures prompting rapid nonplanktotrophic speciation were removed. Only allochthonous species of the same taxon, migrating from an area where planktotrophic development had not been lost, would be likely to introduce new planktotrophs (*20*). Differential speciation rates and the relative irreversibility of developmental change are probably not the only processes in action promoting increasing proportions of nonplanktotrophs among neogastropods, but these processes must be taken into account when considering changes in developmental types through time.

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9. Development type was determined from the morphology of the protoconch by the criteria explained in (*3*). Hansen (*3*), also comments on taxonomy and geologic ranges. Out of 188 species that met the criteria (*3*), 128 had specimens that retained a protoconch preserved well enough so that a larval determination could be made. Although recovery percentages vary among families, there is no reason to suspect a difference in recovery rate between the two developmental types. The species analyzed should represent an unbiased sampling of the developmental types of the six families. A stratigraphic chart was divided into five time intervals corresponding to transgressive-regressive cycles for the Gulf Coast. Any species that has some part of its range within a particular interval is counted within that interval. Many species are therefore counted more than once in the tabulation in Fig. 1. No species of Nassariidae and Mitridae were recorded for the early Paleocene and none of Nassariidae in the late Eocene. This reflects on absence of preserved protoconchs and not of the species. There is a conspicuous increase in numbers of species late in the middle Eocene that may be partly due to unusually numerous exposures of the Upper Lisbon and Cook Mountain formations. It is possible that the higher number of exposures has allowed more nonplanktotrophs (with narrower ranges) to be sampled during this interval. It is difficult to assess this factor at present, but even if late middle Eocene data are excluded, the overall trend, as depicted in the cumulative percentages, persists.
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20. This hypothesis does not require all neogastropods to show a uniform trend in developmental change through the Cenozoic. Nonplanktotrophs will increase most dramatically when geographic range-dividing mechanisms are at work. If isolating processes are curtailed, this trend could stop or even reverse itself unless the group has already become totally nonplanktotrophic. The lack of a trend in the Buccinidae suggests that these processes were not pervasive.
21. I thank P. Chambers, N. Gilinsky, J. Lang, R. Linsley, and G. Vermeij for discussion and criticism. Supported by the Geology Foundation of the University of Texas at Austin.

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Liposomal Blockade of the Reticuloendothelial System: Improved Tumor Imaging with Small Unilamellar Vesicles

Abstract. *The reticuloendothelial system of mice bearing EMT6 tumors was effectively blocked by intravenous injections of small unilamellar vesicles that incorporated a 6-aminomannose derivative of cholesterol in the lipid bilayer. Neutral liposomes loaded with indium-111–nitrilotriacetic acid were then injected. Fifty percent more radioactivity was deposited in tumors of the animals with blocked reticuloendothelial systems than in controls. Twenty-four hours after the injection of radioactive vesicles, well-defined tumor images were observed in whole-body gamma camera scintigraphs. Biodistribution studies showed that tumors from animals with blocked reticuloendothelial systems had more than twice the radioactivity per gram than any other tissue analyzed.*

Phospholipid vesicles, or liposomes, have potential applications in the delivery of biologically active molecules to specific targets in vivo (*1–3*). A variety of substances has been successfully incorporated into liposomes and administered under experimental conditions (*4, 5*). Nevertheless, liposomes have not found widespread use in diagnosis or therapy because they are rapidly cleared from the circulation by the reticuloendothelial system (RES) and concentrated in the liver and spleen (*6*). New *et al.* (*7*) and Alving *et al.* (*8*) applied this phenomenon to treat leishmaniasis in animals. Liposome-entrapped antileishmanial drugs were injected under the assumption that they would concentrate in reticuloendothelial cells, where the parasite proliferates. The encapsulated drugs were approximately 700 times more effective than an equal dose of unencapsulated drugs. Such a method, however, would not allow targeting of liposomes to nonhepatic tissues or malignancies.

Attempts have been made to alter liposome biodistribution by blocking the RES with such substances as carbon, methyl palmitate, latex beads, and dextran sulfate as well as with unlabeled liposomes (*9–13*). The blocking agents were administered before or with labeled