an 8 to 10 percent velocity decrease. If dilatancy precedes the quake, then a theoretical treatment (*14*) based on parallel, vapor-filled cracks oriented vertically for a normal-faulting mechanism yields only a 5 percent velocity decrease for the Tonga rays which arrive at WHA at 25° off the vertical. However, inasmuch as both the depth of the anomalous zone and the degree of crack orientation are conjectural, the reported time delay is not unreasonable.

If cracks are present and are indeed vertically parallel, a horizontal seismic wave traveling to WHA would experience a maximum velocity decrease of about 17 percent (*14*). Local Hawaiian earthquakes could serve as sources for such horizontal paths, but increased relative residual scatter is anticipated since waves incident to WHA and the reference station will not, for this case, share a common ray path over the major part of the path length.

The very localized (less than 20 km) horizontal extent of the anomalous zone is much smaller than estimates for thrust earthquakes reported in the literature (*15*); indeed, it encompasses only a small fraction of the aftershock zone. Perhaps this is characteristic of normal and strike-slip faulting and is responsible for the negative reports of velocity changes preceding earthquakes with nonthrust mechanisms. Such a small anomalous region for a large earthquake could be explained in terms of a very restricted zone of intense stress buildup (*16*) where the break initiated, whereas the rest of the much larger rupture surface remained at a lower stress state throughout the observed precursory period. Then, as for the case reported here, only the rare occurrence of a large shallow earthquake beneath an existing, long-term seismic array will make possible the identification of a travel time delay small in both magnitude and horizontal dimension.

ARCH C. JOHNSTON
Cooperative Institute for Research
in Environmental Sciences,
University of Colorado/National
Oceanic and Atmospheric
Administration, Boulder 80309

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Larval Dispersal and Species Longevity in Lower Tertiary Gastropods

Abstract. *Species longevity in Lower Tertiary volutids (Gastropoda) is primarily controlled by a combination of developmental type and environmental tolerance. Larval dispersal may be an important factor in molluskan evolutionary rates.*

Ecologic factors affecting evolutionary rates in invertebrates have been the subject of a great deal of discussion (*1*). Various rate controls have been proposed, including feeding type (*2*), environmental tolerance (*1, 3, 4*), and population size (*5*). We discuss here how evolutionary rates may be influenced by larval dispersal, in particular for Lower Tertiary Volutidae (Gastropoda).

Larval dispersal has a significant effect on the geographic distribution of mollusks (*6, 7*). Living species with long-lived planktonic larvae may regularly cross the Atlantic Ocean while those with short or no planktonic stages are unable to cross any oceanic basins. Even local geographic irregularities such as brackish water coves and inlets may be a barrier to dispersal (*8*). The pronounced effect of larval type on species biogeography has generated studies relating the dispersal of fossil invertebrates to modes of speciation (*9*) and evolutionary rates (*4, 7, 10*).

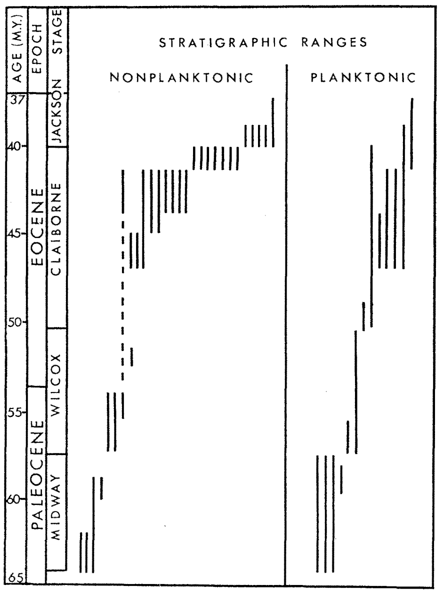

Fig. 1. Geologic ranges of species with nonplanktonic or planktonic larval stages.

The Paleocene-Eocene outcrops of the North American Gulf Coast provide a suitable framework for testing the effect of dispersal on species longevity. The stratigraphy has been extensively studied and molluskan fossils are generally well preserved.

In order to minimize the effect of factors other than dispersal (factors such as feeding type or morphologic complexity), a single family of gastropods, the Volutidae, was chosen for detailed analysis. Modern volutids are ecologically and morphologically a relatively homogeneous group (all burrowing carnivores-scavengers), and fossil species have an adequate proportion of both planktonics and nonplanktonics (living species have only nonplanktonic development).

Larval development for each species was determined by the criteria of Shuto (*9, 11*), and of the 42 taxa in the study

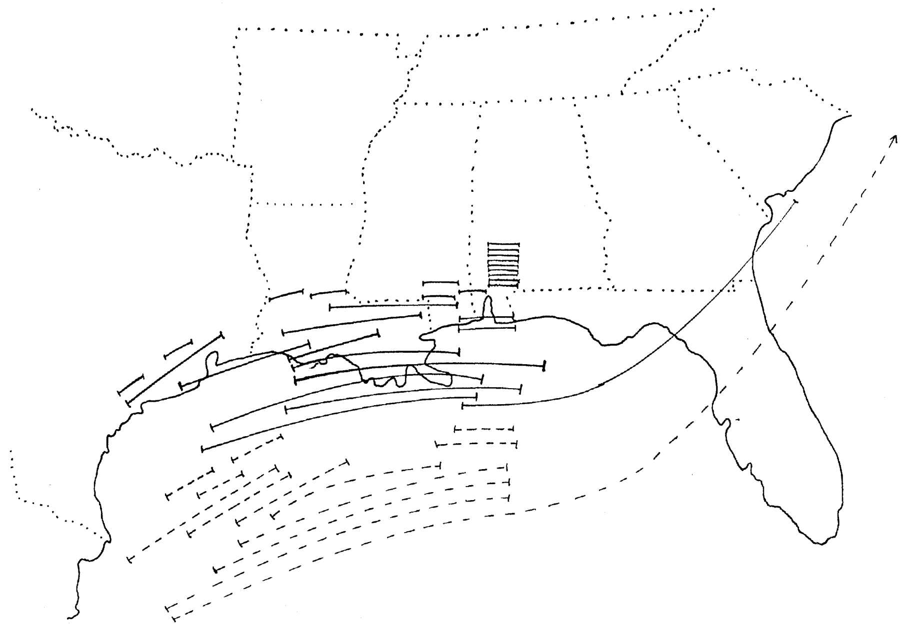

Fig. 2. Geographic distributions of all species, using maximum range in one interval for each. Solid line, nonplanktonics; dashed line, planktonics.

area (*12*), 29 were found to have nonplanktonic larvae, and 13 to have planktonic larvae. The stratigraphic range for each species was quantified by summing the durations of the geologic formations in which each was present (*13*, *14*). In order to measure geographic ranges, a Paleocene-Eocene outcrop distribution map of the Gulf Coast was divided into geographic units approximately 75 km wide (± 5 km, in order to keep major collecting areas within one unit). Each species was mapped as continuously present between its two most distant localities within time-equivalent formations. This range was quantified by counting the intervening geographic units.

Under the above criteria, planktonics were found to have a mean species duration of 4.4 million years, compared to 2.2 million years for nonplanktonics. Geographic distribution for a species covered an average of 7.8 units for planktonics and 3.5 units for nonplanktonics. Values for longevity and distribution for planktonics are significantly higher as determined by the Mann-Whitney U test (two-tailed test for large samples, $z < .01$ and .05 respectively; see Fig. 1). Paleogeographic maps compiled for maximum marine transgressions and regressions show recurrent delta formation during regressive periods in southeast Texas and the Mississippi River Valley (*15*). During periods of regression, nonplanktonics tended to have their ranges restricted by these deltaic areas, while planktonics were generally able to disperse around them. In periods of delta submergence, both developmental types tended to be widespread, although nonplanktonics retained a higher proportion of restricted ranges. When all ranges are combined (Fig. 2), it can be seen that nonplanktonics have a restricted species distribution well within the limits of their overall range, while planktonics tend to have restricted distributions toward the edges of their normal range. This seems to corroborate Shuto's (*9*) observation that planktonic forms speciate near the edges of their distribution while nonplanktonics speciate within their total range.

The broad distributions of nonplanktonics during periods of submergence and the restricted ranges of some planktonics indicate differences in environmental tolerance among the volutids. Tolerance to environmental variations (eurytopy) has been suggested as having an effect on species longevity and distributions (*3*, *4*). Species that are highly tolerant of changes in environment (eurytopic) are able to cross barriers because of their adaptability to extreme conditions. Such eurytopic forms tend to have wide ranges and can cope with environmental disturbances, which result in greater species longevity. If some of the volutids are more eurytopic than others, then the simple model of larval duration, biogeographic spread, and evolutionary rate is complicated by at least one other ecologic variable (eurytopy) that may affect species longevities.

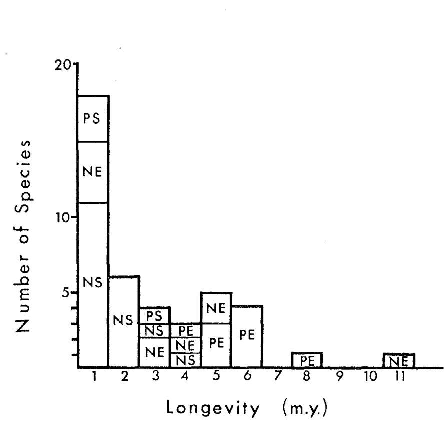

Fig. 3. Developmental type and environmental tolerance of each species with longevity. *N*, nonplanktonic; *P*, planktonic; *S*, stenotopic; *E*, eurytopic; *m.y.*, million years.

To include this variable, environmental tolerance was estimated from relative abundance data that I collected, and from geographic distribution within a single 1- to 2-million-year time interval. The interval of maximum geographic distribution for each species was used as a measure of its tolerance. A species present in several different sedimentary regimes, or distributed over more than four geographic units in a single time horizon, was labeled eurytopic. A species present, at its maximum interval of distribution, in only one sedimentary type or in four geographic units or less was called stenotopic. A graph of larval type and environmental tolerance on longevity (Fig. 3) reveals that nearly all long-lived species are both planktonic and eurytopic (*16*). The majority of the short-lived forms are both nonplanktonic and stenotopic. Intermediate species are mainly nonplanktonic-eurytopic or planktonic-stenotopic. This arrangement corresponds to a model wherein environmental tolerance and dispersal combine to produce very long, very short, or intermediate species durations. In other words, two forces are at work: high dispersal and eurytopy both tend to extend species longevities, and low dispersal and stenotopy tend to curb them. When planktonic larvae and eurytopy occur together, species durations are greater than that expected from the independent influence of each factor. Similarly, when the two restraining forces, stenotopy and nonplanktonic larvae, are in operation together, species exhibit high turnover. Other combinations result in intermediate species durations.

If planktonic-eurytopic species of volutids are long-lived, why are there no planktonic volutids today? Figure 1 shows that while at the beginning of the Paleocene planktonics and nonplanktonics are about equally represented, the nonplanktonics steadily increase in number with time, particularly during rapid sea-level fluctuations in the Upper Middle Eocene. Environmental changes of this sort may favor species groups that can respond faster evolutionarily. It is possible that the planktonics were outcompeted by the nonplanktonics.

Evidence presented here supports the hypothesis that larval ecology has an effect on evolutionary rates. Along continental shelves, nonplanktonic, low dispersal species are easily isolated by local barriers during periods of regression. The subsequent increase in rates of extinction and speciation decreases average species longevity. Planktonic, high-dispersal species are less frequently isolated and tend towards long species duration. In any group of organisms, however, evolutionary rates will be influenced by a number of factors. Within the ecologically and morphologically uniform group of Lower Tertiary volutids, species longevities are primarily controlled by a combination of two factors, dispersal and environmental tolerance. Whether these factors control mollusks in general or even other families of gastropods is yet unknown, because many other ecologic controls must be taken into account.

THOR A. HANSEN
Department of Geology and Geophysics,
Yale University, New Haven,
Connecticut 06520

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11. Shuto's (*9*) criteria are size of embryonic whorl and shape and ornamentation of protoconch whorls. Primarily, a small and pointed apex indicates a planktonic larval stage while a large and blunt apex is characteristic of nonplanktonic forms.
12. The volutid nomenclature of Palmer and Brann (*14*) was adopted. Only species that passed the following criteria were used: (i) a part of their range must include Alabama, Mississippi, Louisiana, or Texas, (ii) only fully named species were used (for example, not *Athleta* sp.), (iii) species based on a single unique specimen or species poorly described and in which the sole type has been lost were disqualified, and (iv) all subspecies were included under the specific name.
13. Published reports on nannofossils and planktonic foraminifera allow correlation of Gulf Coast Paleocene-Eocene stratigraphy with the new Paleocene time scale of J. Hardenbol and W. A. Berggren (*Bull. Am. Assoc. Pet. Geol.*, in press). For a similar scale, see W. A. Berggren, *Lethaia* **5**, 195 (1972).
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16. The single long-lived nonplanktonic-eurytopic species is a problematical form present in one formation in the Upper Paleocene and one formation in the Upper Middle Eocene. Whether it is truly a single species is questionable, but it passed all the criteria of (*12*) and so is included.
17. I thank R. Dodge, E. Kauffman, D. Rhoads, N. Sohl, V. Tunnicliffe, and K. Waage for comments and criticism. Thanks go to J. B. C. Jackson and R. Scheltema for discussion.

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Aeolanthus biformifolius De Wild.: A Hyperaccumulator of Copper from Zaïre

Abstract. Aeolanthus biformifolius *(Labiatae) from Shaba Province, Zaïre, has been shown to be a hyperaccumulator of copper. The copper content of the total plant during the rest period after the rainy season was 1.3 percent (dry weight basis) and is easily the highest copper concentration ever found in living material. This species should be classified as a "copper flower" because of its exclusive occurrence over mineralized ground.*

Numerous studies have been concerned with the vegetation associated with copper mineralization in south-central Africa, namely, Shaba Province, Zaïre (*1, 2*), and the "Copper Belt" in Zambia (*3, 4*) and Rhodesia (*5–7*). Several plants have been described as "copper flowers" and are of considerable interest for mineral exploration. Typical copper flowers include *Becium homblei* (De Wild.) Duvign. et Plancke in Zambia and Rhodesia (*3, 6, 7*), *Haumaniastrum katangense* in the vicinity of Lubumbashi, and *H. robertii* around Kolwezi in Shaba Province, Zaïre (*2*). More recently, the copper and cobalt contents of African

Table 1. Copper concentrations (in micrograms per gram, dry weight) in *Aeolanthus biformifolius* compared with values for other accumulator species in south-central Africa.

Species	Location	Organ	Mean copper concentration	Reference
Aeolanthus biformifolius	Shaba (Étoile)	Basal leaves (1/7/77)	2,600	*
A. biformifolius	Shaba (Étoile)	Basal leaves (2/2/77)	2,150	*
A. biformifolius	Shaba (Étoile)	Flower stems (1/7/77)	3,500	*
A. biformifolius	Shaba (Étoile)	Flower stems (2/2/77)	2,150	*
A. biformifolius	Shaba (Étoile)	Corms (1/7/77)	2,600	*
A. biformifolius	Shaba (Étoile)	Corms (2/2/77)	11,800	*
A. biformifolius	Shaba (Étoile)	Corms (3/24/77)	13,700	*
A. biformifolius	Shaba (Étoile)	Whole plant (2/2/77)	10,000	*
A. biformifolius	Shaba (Étoile)	Whole plant (3/24/77)	13,700	*
Ascolepis metallorum	Shaba (Dikuluwe)	Leaves	1,200	(*2*)
Becium aureoviride	Shaba (Niamumenda)	Leaves	210	(*2*)
B. homblei	Zambia	Leaves	324	(*3*)
Crotalaria cornetii	Shaba	Leaves	12	(*9*)
C. peschiana	Shaba	Leaves	268	(*9*)
C. prolongata	Zambia	Leaves	15	(*9*)
Eragrostis boehmii	Shaba (Tilwizembe)	Leaves	78	(*2*)
Fimbristylis exilis	Rhodesia (Copper King)	Leaves	420	(*7*)
Haumaniastrum homblei	Shaba	Leaves	74	(*8*)
H. katangense	Shaba	Leaves	75	(*8*)
H. robertii	Shaba	Leaves	662	(*8*)
H. robertii	Shaba (Mupine)	Leaves	1,960	(*2*)
Indigofera dyeri	Rhodesia (Copper King)	Leaves	890	(*8*)
Pandiaka metallorum	Shaba (Dikuluwe)	Leaves	740	(*2*)
Triumfetta dikuluwensis	Shaba (Dikuluwe)	Leaves	123	(*2*)

*This study.