ABSTRACT—A global taphonomic and biometric study of five lineages of the radiolarian genus Phacopinus during the last 6 million years shows: (1) phylogenetic change was gradual but occurred as variable rates (r) a trend toward decreasing size in all lineages but with common reversals of trend; (2) the two speciation events that occurred during the interval were both gradual (r = 50,000 yrs); (3) of the two extinction events one was gradual, the other abrupt; (4) the extinctions eliminated the larger species and within species phylogenetic trends result in the elimination of larger morphotypes. (5) Hybridization between lineages is common, particularly in regions of strong speciation.

Our data suggest that for many microfossil taxa, the systematic species concepts may not be valid, nor is the peripheral isolate "allopatric" mode of speciation. Hierarchical models of speciation, structure, and geographic speculation thereby appear to be fruitful concepts for future research.

INTRODUCTION

Deep-sea microfossil records provide an unusual opportunity to study and compare patterns of geographic change within lineages. We have studied geographic and temporal patterns of morphologic evolution in the genus Phacopinus, a common and diverse member of the Naeglia radiolarian assemblage. The study integrates traditional taxonomic analysis and biometric data from globally distributed samples taken throughout the Vidal-Pinedo section (Plate 1).

Five major species level lineages are recognized (Table 2). P. phacopodis (Boeckel) is a polyphyletic group in which we recognize at least three morphologically distinctive subseries. P. panspermia Sigalov, while not examined in this study, is morphologically very similar to P. trilimbus and may constitute a fourth subspecies. P. phacopidus (Boeckel) is also polyphyletic, with two recognizable species—P. p. panspermia and P. p. phacopidus. The extinct lineages P. major Kastl and P. princina (Kastl) are more narrowly monotypic, while P. lawesii (Coghill) represents a large group whose internal phylogenetic relationships are not yet clearly discerned.

Each Phacopinus lineage has a distinctive geographic distribution over the past 5 million years (Figure 1). P. phacopidus and P. p. phacopidus are common in both tropical and subtropical waters. The other taxa are less widely distributed. P. phacopidus was entirely restricted to tropical environments. P. sowerbyi is and has been common only in the subtropical regions.

Table 1: Cores Examined

<table>
<thead>
<tr>
<th>Core</th>
<th>Lat.</th>
<th>Long.</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEUF 158</td>
<td>71°</td>
<td>86°</td>
</tr>
<tr>
<td>DEUF 378</td>
<td>71°</td>
<td>86°</td>
</tr>
<tr>
<td>DEUF 348</td>
<td>61°</td>
<td>12°</td>
</tr>
<tr>
<td>DEUF 58</td>
<td>60°</td>
<td>16°</td>
</tr>
<tr>
<td>DEUF 22</td>
<td>3°</td>
<td>7°</td>
</tr>
</tbody>
</table>


TAPHONOMY

Examination of numerous samples (only a subset of which are shown in Figure 1) reveals a complex taphonomic pattern of evolution in Phacopinus (Figure 1). Seven million years ago, three species of Phacopinus existed—one each in low, middle, and high latitudes. Each species is distinctly different from the others over most of its geographic range, but in regions of intense speciation intermediate forms between the species are occasionally seen. With the passage of 1 million years, the morphologies and abundances of these lineages change.
Figure 1. Relative abundance of species in biometrically analyzed populations of *Pterocanium*. Sample sizes shown in boldface.
### Table 2: Morphosystematic Analysis of *P. r. mediterraneus*

<table>
<thead>
<tr>
<th>Character</th>
<th>Male numbers of continuous variable character states (character intermediate)</th>
<th>Type of morphological intermediate</th>
<th>Number of provinces in each morphological intermediate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trich</td>
<td>Valid</td>
<td>Invalid</td>
<td>Total</td>
</tr>
<tr>
<td>Sclerite</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

#### Figure 7: Diagram of lineage relationships in *P. r. mediterraneus*. Lighter shaded areas are regions of morphologic intermediation.

P. audax, P. trifidis, and intermediate forms all occur in subtropical sediments. *Chrysaola* in the morphology of *P. r. mediterraneus* are seen which pre-figure later evolutionary trends. By 4.5 Ma (Mio- cene), P. audax and P. trifidis have entered their range into subtropical waters. Typical P. mediterraneus forms are common, but so are forms intermediate between P. australis and P. mediterraneus. P. auricula is already widespread in the equatorial Indian Ocean, together with intermediates between P. auricula and P. mediterraneus. A few early forms of P. auricula are also seen, mostly in the equatorial Pacific. Thus, in the 4.5 million years between 6 Ma and 4.5 Ma, P. auricula has evolved, although the presence of intermediate forms suggests that this event is not yet complete. At 3 Ma, individual lineages are well defined, and intermediates are rare. P. auricula is a common member of the assemblage in equatorial zones, and P. auricula has spread into the equatorial and subtropical Pacific. In the latest part of the Pliocene and in the early Pleistocene, P. auricula and P. auricula become extinct. Within the P. auricula lineage, a shift from distinct P. auricula morphology to P. auricula morphotype is evident. **SUMMARY**

It is not yet possible to quantify the majority of the diagnostic characters given in Table 2. Thus, biometric data only partially document the morphologic intermediation.
Figure 3: Gradual phyletic trends in mean thorax width of Pterocanium lineages. Narrow lines represent standard deviation of samples, heavy lines 95% confidence intervals of means. For sample locations and sizes see Figure 1.

Logical patterns seen through the microscope. The measurements made however do indicate both the gradual rate of morphologic change and its particular nature. In P. pristimum (Figure 3) an initial increase in thoracic width in the early Pleistocene is followed by a reversal in trend and a phylogenic size decrease throughout the late Pleistocene, eventually terminating in the abrupt extinction of the lineage at the base of the Pliocene. Phylogenic size decrease is also seen in the mean thoracic width of P. audax, and in the mean thoracic width of P. trilobatum populations from the equatorial Pacific (Figure 3).

Variation in individual characters is very high for all radiolarian taxa examined, as is covariation. Size variation between individuals within a population is similar in one case to variation between taxa as well. This is shown in Figure 4, where nearly symmetric axes of thoracic size variation in populations of P. pristimum and P. trilobatum are colinear with the axis of between taxa differentiation. This uniformity of pattern however does not hold for comparisons of other taxa, for example P. trilobatum to P. pristimum (Figure 4).

Apparent hybridization between the P. pristimum and P. trilobatum lineages in the Pliocene follow-
ing differentiation in the Pliocene is indicated in Figure 6. Initially distinct, these taxa became progressively harder to distinguish as inter-
mediates became more common. Convergence is seen not only in size, but in many other diagnostic characters as well. Despite this phenomenon, re-
cent populations of these lineages still display two distinct modes.

**DISCUSSION**

Certain generalizations about planktonic foraminif-
ner protist evolution may be drawn from our study of
*Peneroplis*. The tempo of evolution is very gradual, both during geologic change and during speciation. The phylogenetic pattern observed is at least some-
times reminiscent of Eldredge and Gould’s (1972) hypo-
thesis that most evolution is gradual — i.e., that
it is produced primarily by Neotenic speculation of
small peripheral isolates, followed by knobs — does not seem to hold for these planktonic, deep-
sea organisms. Possible reasons for this may be
found in the distinctive biological characteristics
of this group of protists.

Many workers have previously noted that in deep-
sea holoplankton, a fluke environment with continu-
ous mixing regimes in large populations, spread over
large areas, not small (a few species Alkathuria)
scattered isolates which are stable over hundreds of
years. These relatively large populations are

![Figure 4: Scatterplot showing variation in thorax measurements for composite populations of *Peneroplis* species.](image)

The pattern of convergence in size is evident, with the most recent populations showing the most divergence. This indicates that the evolutionary history of these species is complex, involving both gradual and rapid changes.

Isolation may be difficult to achieve for reasons of population structure as well. Complex geographic variation is quite marked in protistan holoplankton (cf. the Foraminifera, for example, see Kenner, 1976). This, together with observations of common hybridization and rapid evolution (particularly in Radiolaria, e.g., Grütz, 1976; this study) implies that most planktonic marine microfossil groups possess a typically protist population structure of synapomorphies, or perhaps a plant-like one of synagones (Grütz, 1975). The evolution of reproductive isolating mechanisms in (relatively) simple protists may therefore be more difficult than in more complex marine organisms.

Eldredge and Goin (1980) have argued that within-species trends may not be related to higher-
level, mesoscale lineage patterns. Gradual, within-species phenotypic size decreases in common to spot *Peneroplis* lineages studied. This is similar to a larger-scale trend towards smaller forms in *Peneroplis*, created by the extinction of relatively large *P. advena* and *P. pristinus*, and the origin of relatively small *P. praetextum*. Although "ancient" and "modern" evolutionary trends are similar in our data, some characters...
In conclusion, both empirical observations of micro-fossil variation and theoretical considerations suggest that evolution in marine protistan holothurians generally does not proceed by the rapid development of discrete species in small, isolated environments. Alloplecy is an important mechanism of evolution in the deep-sea, but the relative rarity of alloplecy events, and the huge size of the population involved, distinguish it from the model used by Eldredge and Gould. Para-patric and clonal models of evolution by contrast are largely independent of absolute population size, nor do they require complete geographic isolation to operate (Edelson, 1970). These models of speciation may often be more appropriate than alloplecy when studying protistan evolution in the planktonic marine realm.

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