

## EVOLUTION OF THE RADIOLARIAN SPECIES-COMPLEX *PTEROCANIUM*: A PRELIMINARY SURVEY

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**ABSTRACT**—A global taxonomic and biometric study of the radiolarian genus *Pterocanium* defines 5 major lineages over the last 6 million years: *Pterocanium charybdeum*, *P. praetextum*, *P. korotnevi*, *P. prismatium*, and *P. audax*. *P. charybdeum* is divided into 4 subspecies: *P. charybdeum charybdeum* (n. comb.), *P. charybdeum trilobum* (n. comb.), *P. charybdeum grandiporus* (n. comb.), and *P. charybdeum allium* (n. subsp.).

Sympatric or parapatric speciation of *P. prismatium* and *P. praetextum* from ancestral *P. charybdeum* was observed over a one-half million year interval in the latest Miocene and early Pliocene. Measurements of thoracic dimensions and qualitative observations suggest substantial, gradual phyletic evolution in the 5 lineages studied. Morphological intermediates between formerly distinct lineages were observed and suggest the possibility of hybridization and reticulate evolution in *Pterocanium*.

### INTRODUCTION

THE LAST few years have seen a resurgence of interest in using fossil data to construct and test evolutionary hypotheses. Deep-sea micropaleontologic data is of particular importance to this work, as nowhere else in the fossil record can be found such a combination of stratigraphic continuity, geographic control, and large sample sizes (Prothero and Lazarus, 1980; Lipps, 1981).

To use these unique records, we must understand certain factors. Geographic variation, for example, can make individual fossil sequences difficult to interpret (Gould and Eldredge, 1977; Bookstein et al., 1978). Taxonomic assumptions, stratigraphic resolution, measurement techniques, and sampling artifacts can also affect our ability to use microfossil sequences to study evolutionary pattern. To assess the importance of these factors in evolutionary micropaleontology, we have carried out an exploratory study of the late Neogene evolution of the radiolarian genus *Pterocanium* (Ehrenberg, 1847). Great emphasis was laid on detailed systematic analysis of this taxon, and on securing a glob-

ally comprehensive set of stratigraphically continuous sequences suitable for our analysis. These data provide an unusually complete picture of evolutionary change in this group over the last 6 million years.

### GEOGRAPHIC AND STRATIGRAPHIC CONTROL

We selected for an initial taxonomic survey several composite sedimentary sequences that represent most of the world's radiolarian biogeographic regions (Goll, 1976). These cores are shown in Figure 1. With the exception of the lower latitude Atlantic basin, all major oceanographic regions are represented in our core set. Ages of sediments in these cores were determined by correlation of these biostratigraphic and magnetostratigraphic datum levels to the standardized time scales provided by LaBreque et al. (1977), Mankinen and Dalrymple (1979), Theyer and Hammond (1974), Theyer et al. (1978), Hays and Opdyke (1967), and Hays (1970). More detailed analysis was done on a subset of these cores.

For each of 4 regional stratigraphic sequences used in the detailed phase of this project, several levels, spaced about 1.5 million years apart, were sampled for initial analysis. These levels were located at magnetic reversal datum levels and form globally

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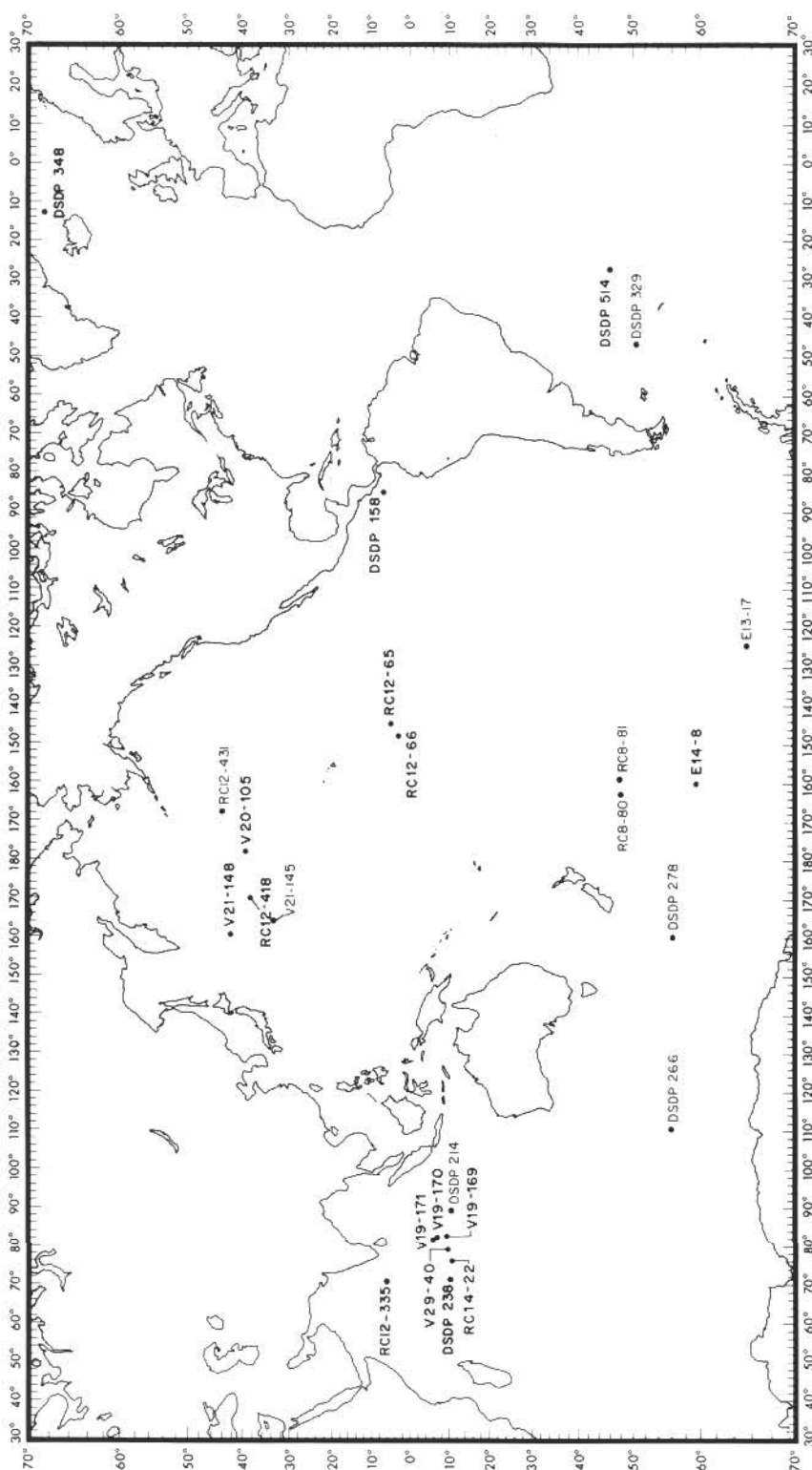


FIGURE 1.—Locations of all deep-sea sediment cores used in this study. The stratigraphies of cores selected for detailed analysis are discussed in the text. For those cores not mentioned elsewhere, see: DSDP 266, Hayes, Frakes et al. (1975); DSDP 278, Kennett, Houtz, et al. (1975); DSDP 329, Barker, Dalziel, et al. (1977); DSDP 348, Talwani, Udintsev, et al. (1976); DSDP 514, Ludwig, Krashennnikov, et al. (1980). Stratigraphy of RC8-81 based on senior author's unpublished data.

synchronous time 'slices' approximately 100,000 years thick. These time slices allowed us to examine patterns of geographic variation independent of patterns of temporal change. For those cores lacking paleomagnetic information, we sampled at the level which graphic correlation analysis (Shaw, 1964) of biostratigraphic datum levels determined to be equivalent to the magnetic reversal of interest. The levels chosen were mid magnetochron 6 (6.1 Ma), 'c' event of the Gilbert (4.4 Ma), the base of the Gauss (3.4 Ma), the base of the Olduvai event of the Matuyama (1.9 Ma), and core top (0.0 Ma) (Ma= mega-annum, or 1 m.y.b.p.). More detailed stratigraphic coverage was added later by taking additional interspaced samples as needed. Comments on each of the sites follows.

**Equatorial Indian Ocean.**—Six piston cores were used to study *Pterocanium* evolution in the equatorial Indian Ocean. Opdyke and Glass (1969) studied the paleomagnetic stratigraphy and biostratigraphy of cores V19-169, V19-170, and V19-171, while Burckle and Opdyke (1977) have reported on the paleomagnetic and biostratigraphic data for cores RC14-22 and V29-40. This information has been combined with additional radiolarian stratigraphic data from these five cores and the radiolarian stratigraphy to paleomagnetic stratigraphy correlation charts of Theyer and Hammond (1974) and Theyer et al. (1978) to create a correlated set of cores covering the entire Pleistocene and Pliocene (Figure 2). This composite sequence provides a nearly continuous record of this portion of *Pterocanium*'s evolutionary history in the equatorial Indian Ocean. Preservation of *Pterocanium* specimens was generally good, although breakage sometimes made biometric analysis difficult. Late Miocene coverage of the equatorial Indian Ocean was provided by piston core RC12-335 and Deep Sea Drilling Project drill cores 214 and 238 (Figure 3). The lowermost 50 cm of RC12-335 contains abundant, well preserved radiolarians. The occurrence of the radiolarian stratigraphic indicator species *Stichocorys delmontensis*, *Didymocyrtis antepenultima*, *Spongaster berminghamsi*, and *Acrobotrys tritubus*, together with the absence of *Trisolenia omnitubus* and *Diartus hughesi*, indicate an age for this sediment of  $\sim 6.8 \pm 0.2$  Ma. Bio-

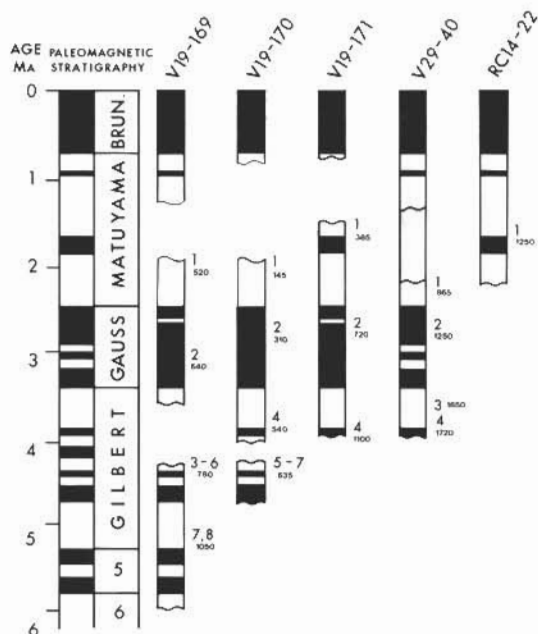


FIGURE 2—Composite piston core set from the equatorial Indian Ocean. Bold numbers refer to the following radiolarian datum levels: 1, top *Pterocanium prismatium*; 2, top *Stichocorys peregrina*; 3, top *Spongaster pentas*; 4, top *Didymocyrtis* (formerly *Ommatartus*) *penultima*; 5, bottom *Spongaster tetras*; 6, top *Spongaster berminghamsi*; 7, top *Trisolenia* (formerly *Solenosphaera*) *omnitubus*; 8, top *Acrobotrys tritubus*. Smaller numbers associated with each datum level are depth to datum in core in centimeters.

Hiatuses within cores (shown in figure by gaps) cause clustering and non alignment of datum levels. Exception is shaded interval of core V29-40, where loss of a sediment section subsequent to coring has occurred and is responsible for apparent displacement of datum level. The magnetic polarity interpretation presented here for V29-40 is based on the raw data given by Burckle and Opdyke (1977) and not their black and white polarity interpretation, which was erroneously drafted (Opdyke, personal commun.).

stratigraphic data for DSDP sites 214 and 238 was taken from the relevant initial report volumes (Von der Borch et al., 1974; Fisher et al., 1974). Radiolarian preservation in these drill cores was on average only fair, although no substantial loss in *Pterocanium* diversity is thought to have taken place.

**Tropical Pacific.**—The biostratigraphy (Saito et al., 1975) and magnetostratigraphy

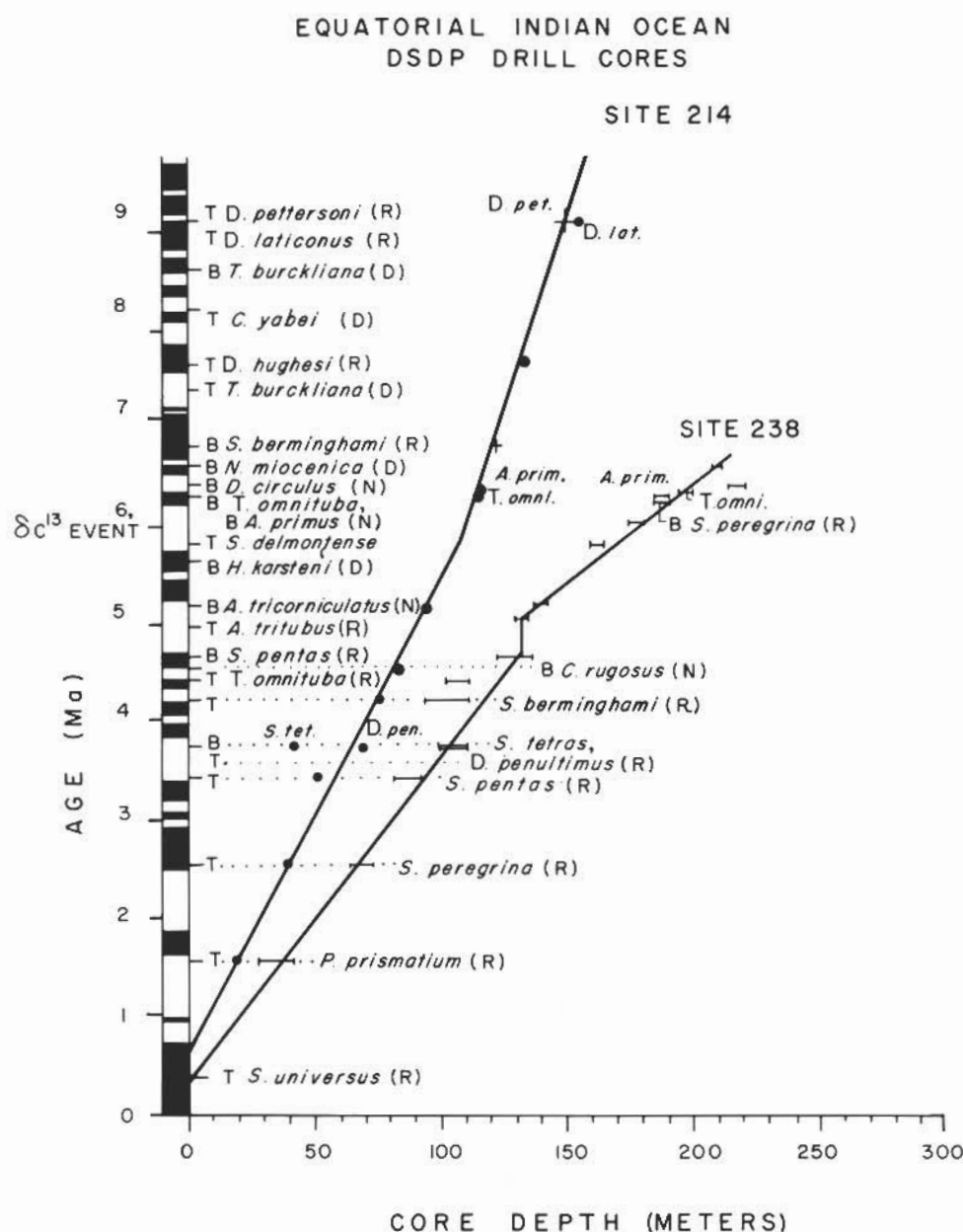


FIGURE 3—Biostratigraphic correlation of equatorial Indian Ocean drill sites to inferred paleomagnetic reversal time scale, using site report data and calibrations discussed in the text, and the late Miocene carbon isotope shift of Vincent et al. (1980). T, top, B, bottom, D, diatom, R, radiolarian, N, nannofossil. Bars for site 238 reflect sampling uncertainty in placement of datum levels; in site 214 this uncertainty is so small that datum levels can be plotted simply as dots.

(Foster and Opdyke, 1970) of piston cores RC12-65 and RC12-66 is well documented (Figure 4). Preservation of *Pterocanium* was generally good throughout these cores, with

breakage of specimens only occasionally becoming significant. We have also examined low latitude Pacific DSDP Site 158 (Figure 5), which has a near constant sedimentation

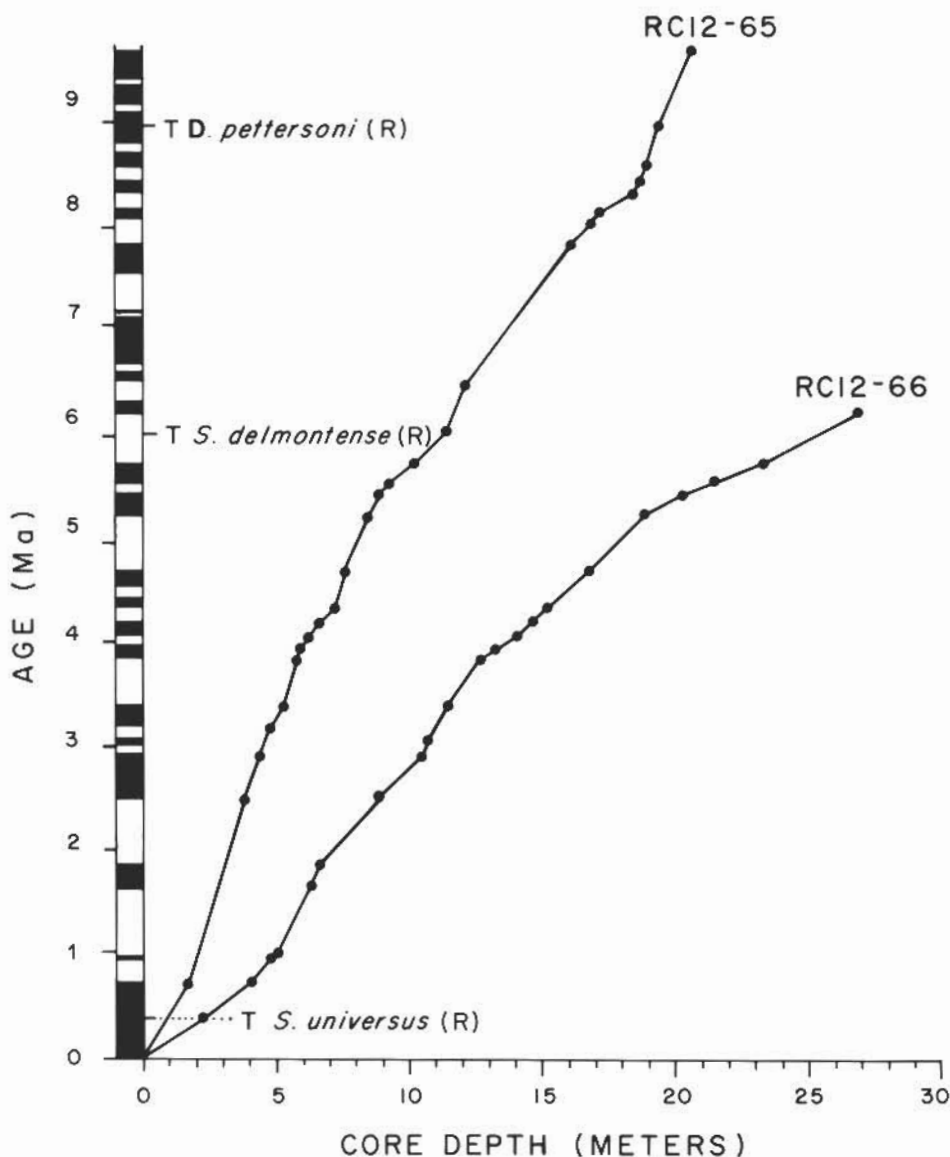


FIGURE 4—Age-depth relationships for equatorial Pacific Ocean piston cores. Unless noted, datum levels are paleomagnetic reversal boundaries. Sources of calibration discussed in text.

rate of more than 4 cm/1000 years (Bukry, 1973; Dinkelman, 1973; Burckle and Opdyke, 1977; Keigwin, 1979; Theyer and Hammond, 1974; Theyer et al., 1978) and provides a record from approximately 3 Ma to about 7 Ma. Preservation of *Pterocanium* was very good in this material, although abundances were sometimes low.

*North Pacific.*—We selected 5 piston cores from the North Pacific for detailed analysis:

V21-145, V21-148, RC12-418, RC12-431, and V20-105. These cores contain a radiolarian fauna representative of the northern margin of the North Pacific subtropical gyre and the North Pacific subpolar gyre. They have a combined stratigraphic range from the Upper Miocene to the Recent, with a gap in the latest Miocene and basal Pliocene. All these cores have undergone detailed biostratigraphic and magnetostratigraphic anal-

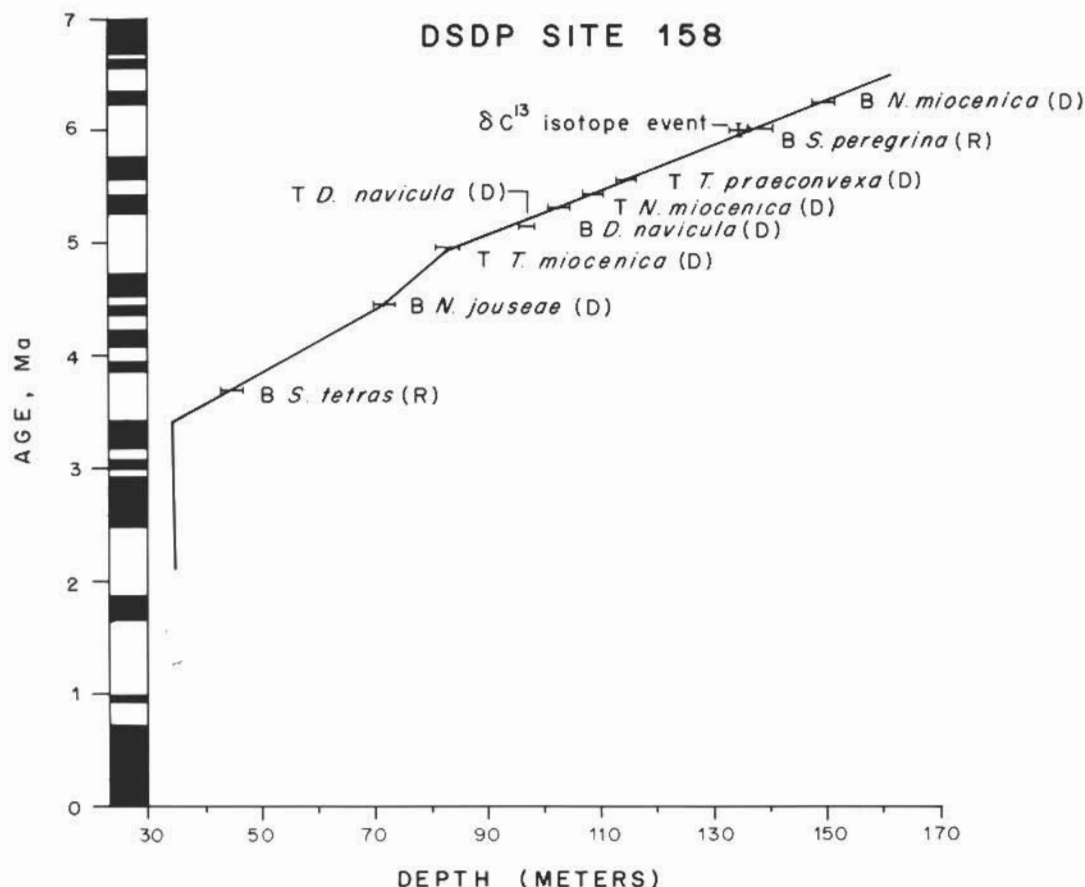


FIGURE 5—Correlation of DSDP drill site 158 to inferred paleomagnetic reversal time scale. Sources of calibration in text.

ysis (Figure 6). Preservation of *Pterocanium* in this suite of cores was generally good, in part due to the resistance to dissolution typical of high latitude forms.

**Antarctic.**—Previous workers on Antarctic stratigraphy have noted the presence of *Pterocanium* in the Pliocene and early Pleistocene of the Southern Ocean (Hays and Opdyke, 1967; Keany, 1979). We selected piston cores E14-8, E13-17, RC8-80 and RC8-81 in the South Pacific to investigate the Antarctic history of these taxa (Figure 7). Core E14-8 contains well preserved specimens of *Pterocanium*. Core E13-17 is barren of microfossils through much of the Pliocene, but contains well preserved radiolarians in the Pleistocene and in the latest Miocene (magnetochron 5). Subantarctic cores RC8-80 and RC8-81 contain well preserved radiolarians in the latest

Miocene and early Pliocene. Stratigraphies for younger portions of these cores have not been satisfactorily determined. Because continuous late Miocene sections are not available from the Southern Ocean, we did not examine in detail the earlier Southern Ocean history of *Pterocanium*.

#### METHODS

**Sample preparation.**—Randomly settled slides (Moore, 1973) were prepared from the acid cleaned >63 micrometer size fraction, and scanned for *Pterocanium* specimens.

**Systematic methodology.**—Our approach to phylogeny reconstruction was essentially stratophenetic (Gingerich, 1979). Closely spaced morphologically transitional sequences clearly indicated immediate ances-

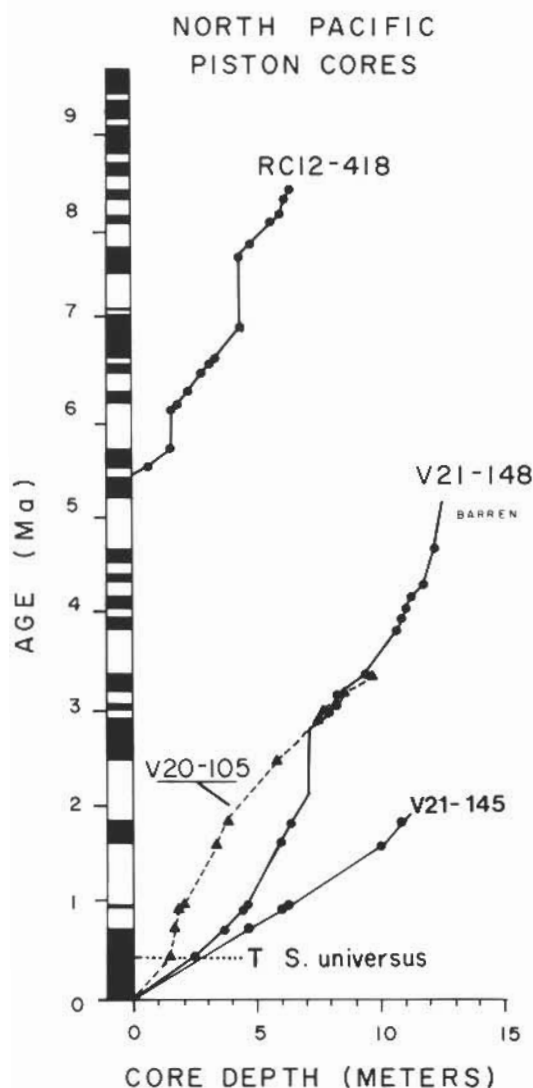


FIGURE 6—Age-depth relationships for North Pacific piston cores. Unless noted, datum levels are paleomagnetic reversal boundaries. Sources of calibration from Opdyke and Foster (1970), Hays (1970), Haq et al. (1980), and Burckle and Opdyke (personal commun.).

try, eliminating the need for more complex morphological systematic analysis. This approach is justified when the fossil record is reasonably complete (Prothero and Lazarus, 1980; Lazarus and Prothero, 1984).

**Morphologic analysis.**—Rates of morphologic change are ideally studied using biometric techniques rather than more subjective assessments of morphologic state.

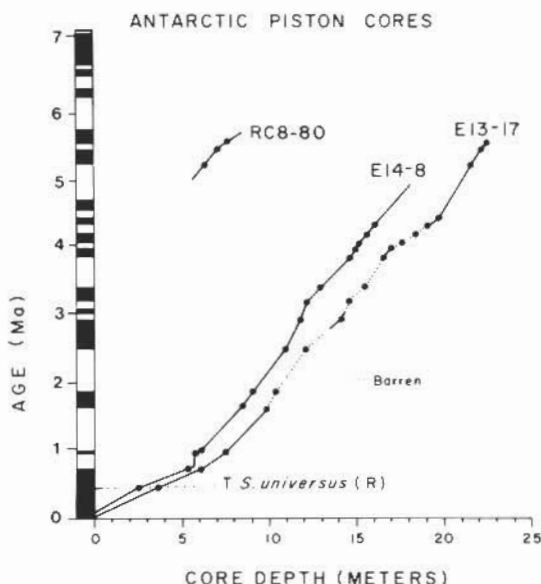


FIGURE 7—Age-depth relationships for Antarctic piston cores. Unless noted, datum levels are paleomagnetic reversal boundaries. Sources of calibration: Hays and Opdyke (1967), McCollum (1975), Burckle and Opdyke (1977), and Keany (1979).

However, at present our ability to quantify radiolarian morphology is very limited. Thus the nature of data in this analysis, with certain exceptions, is that of the 'character state' approach of classical taxonomy. In a few instances biometric data proved useful. Measurements were made using two types of measuring tools. Eyepiece micrometers on Wild M20 research microscopes (40× objectives and 10× oculars), and with a resolution of  $\pm 3$  micrometers, were used for the majority of the measurements. A microcomputer digitizer system with a resolution of  $\sim \pm 0.7$  micrometers was used for a few of the most recently acquired measurements.

We measured four characters of the *Pterocanium* skeleton (Figure 8). Pore and bar measurements proved to be most useful in general characterizations of taxa. Thorax width and length was more clearly resolved by eyepiece micrometer methods, and these data provide simple measures of overall size and shape.

#### TAXONOMY

In order to define the higher level systematic hypothesis that delimits the range of ra-



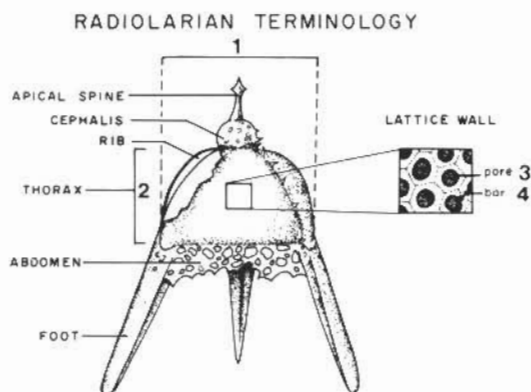


FIGURE 8—Diagrammatic representation of a *Pterocanium* specimen showing terminology and location of biometric measurements. 1, Width of base of thorax, 2, length of thorax, 3, mean pore diameter, 4, mean bar width. Pore and bar values from central/lower portion of thorax wall, as shown.

diolarian lineages under investigation it was necessary to revise the genus *Pterocanium*. Although this revision is incomplete, it is adequate for the purposes of this project.

The large majority of generic descriptions that concerned us originated with the works of Ehrenberg (1847) and Haeckel (1881), which were subsumed and elaborated on by Haeckel (1887). These authors did not have available to them sufficient material of any one species to properly evaluate the significance of the characters they were using in their taxonomic work. As a result, many generic level distinctions have since been shown to be based on characters that vary in local populations within a single species. Additionally these earlier workers defined most taxa on the basis of single characters—a practice which generally results in highly unstable classifications.

In our conception, the general morphologic type that embraces the lineages in question is a nassellarian with a small spherical cephalis and thorax possessing three thoracic ribs, which are prolonged into three-bladed basal feet. These feet are simply terminated. The thorax, which may bear an irregular abdomen, is also distinctly terminated, but is not closed. Forms assigned to this "pterocaniid" skeletal type have been divided by Haeckel (1887) into some half dozen genera: *Lychn-*

*ocanium*, *Theopodium*, *Pleuropodium*, *Lychnodictyum*, *Dictyophimus*, *Pterocorys*, *Podocyrtis*, and *Pterocanium*. The artificial nature of most of these taxa can be seen immediately when compared, using more recent data on character variation.

*Lychnodictyum*, for example, is distinguished from *Pterocanium* largely by the presence in the latter of an abdomen (Haeckel, 1887, p. 1329). In the context of pterocaniids this never amounts to much more than a delicate "veil." We have observed populations of *P. trilobum* that may have well developed veils or may have no discernible development of this character. In most populations some specimens possess at least rudiments of a veil, while others do not. The veil, in particular, may also be affected in some instances by the degree of preservation, for it is unusually delicate and therefore easily dissolved.

The distinction between *Lychnodictyum* and *Lychnocanium* is similarly invalid. The presence or absence of lattice-work in the bases of the feet is the primary criterion used to distinguish these two genera. But within the range of intergradational morphotypes that we assign to the single species *P. charybdeum*, we see a complete gradation between forms with well developed lattice-work and forms with nearly solid foot bases.

Other problems arise because of inconsistencies in original works as to the meaning of a particular generic distinction. On the basis of the plates and discussion, it is not clear whether *Dictyopodium* fits the definition of "pterocaniid" given above. Haeckel distinguished this genus both on the presence of lattice-work in the feet and on whether the feet originate at the base of the thorax or within it. As to the former, Haeckel seems to mean not the lattice-work seen only in the proximal portion of the foot (as in his definition of *Pterocanium*), but instead a more distal fenestration. We consider these two characters to be unrelated. The origination point of the feet is also difficult to use. Haeckel himself changed his assignment of the forms pictured in his Plate 73; the lettering on the plate refers specimens 1–6 to *Dictyopodium*, while captions on the facing page (prepared at a later date; Haeckel, 1887, p. iv) assigned the same specimens to *Pterocanium*.

A final problem results from the fact that



# RELATIVE ABUNDANCE OF *PTEROCANIUM* SPECIES IN LATE NEOGENE OCEANS

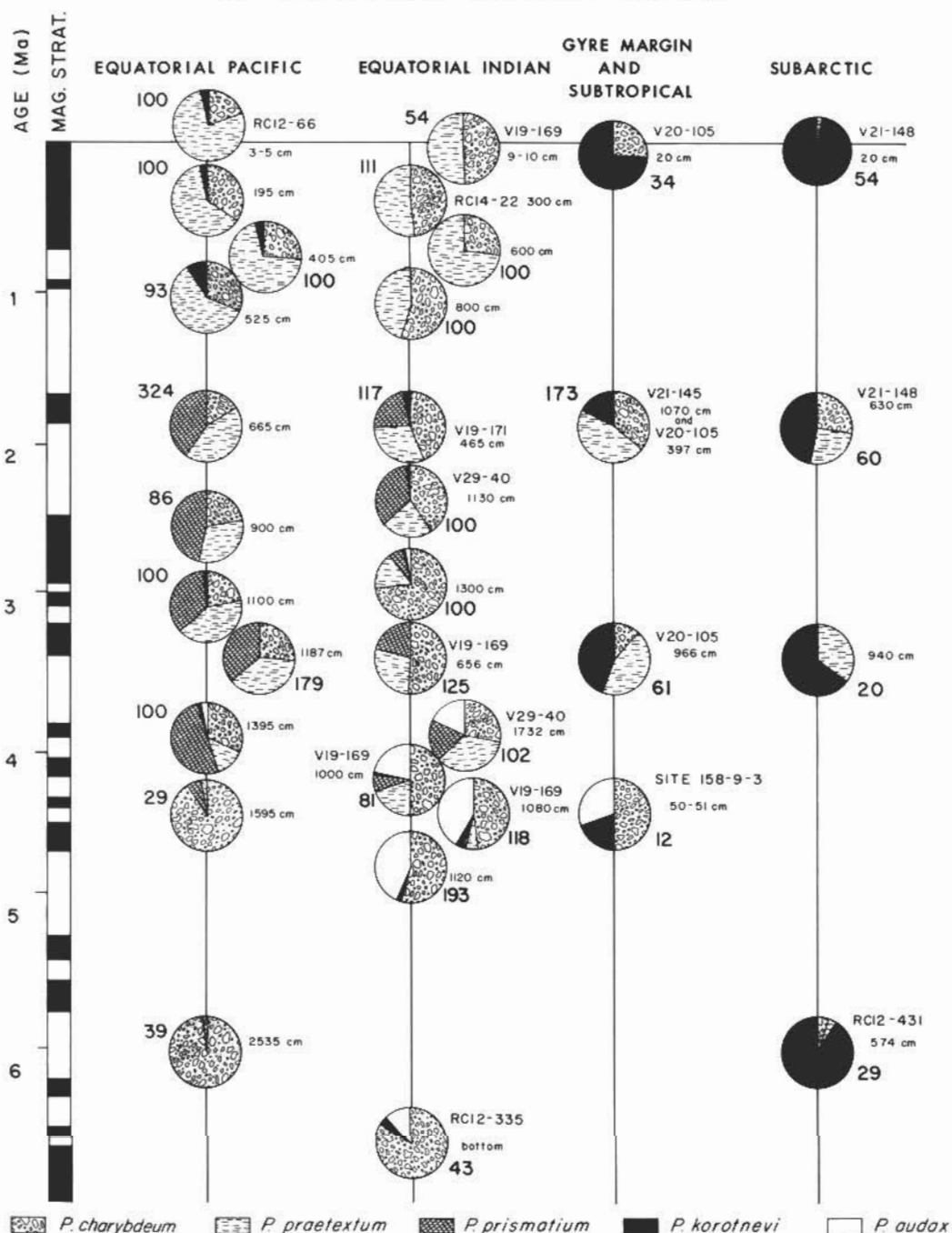


FIGURE 9—Chart showing relative abundance of *Pterocanium* species in late Miocene to Recent sediments from globally distributed sections. Center of each graph placed at estimated age as inferred from stratigraphic analysis. Sample sizes used to estimate relative abundances shown by bold numbers next to each graph. Populations of intermediate specimens have arbitrarily been divided evenly between end members. Many intermediate levels have been examined but not tabulated.

many characters, which in modern classifications are thought to represent family level distinctions, were not considered in Haeckel's work. For example, the structure of the cephalis was considered by Riedel (1967) to be of great importance in distinguishing the families Theoperidae and Pterocorythidae. *Pterocorys aquila* Haeckel (1887) is, on the basis of his Plate 71, fig. 5, clearly assignable to the Theoperidae, and probably to *Pterocanium*, in our revised definition. Yet *Pterocorys campanula*—Plate 7, fig. 3—equally clearly belongs in the Pterocorythidae, based on the figured structure of the cephalis. This point has also been made by Nigrini (1970).

Given the problems alluded to above, it may eventually become necessary to synonymize the majority of the pterocaniid generic taxa listed in Haeckel, or at least revise generic definitions. Formal revision must however wait until more information is obtained on pterocaniid stratigraphy and systematic characters. Until such information is available we formally restrict ourselves to revising just *Pterocanium*.

*Subgeneric taxa in Pterocanium.*—Taxonomic assignment within *Pterocanium* was based on morphologic, stratigraphic, and biogeographic criteria. Morphologic clusters presenting discrete groupings over most of their observed stratigraphic ranges and which also show both geographic and stratigraphic continuity were considered distinct species. Morphologic intergradation was seen between species (as defined above) at certain stratigraphic levels in some regions, and these intermediate forms were noted separately. Subspecies were erected for morphotypes that contain stratigraphic, geographic, or phylogenetic information, but never attained the discreteness needed to be recognized as a species. Hence they are, at most, reference points in a morphologic continuum.

Whether our taxonomic species represent actual biological species cannot be determined at present. Further work, both biometric and on living material, will be needed to clarify additional taxonomic detail.

The result of this phase of our project was the identification of 5 fairly distinct lineages and several subspecific level taxa. These taxa, however, do not represent the total diversity present in our study interval. Much work still needs to be done, in particular on the system-

atics of some of the more common higher latitude forms, but, because of the additional time required, these forms could not be included in this study. The taxa included in our analysis are: *Pterocanium charybdeum* (with 4 subspecies), *P. praetextum* (with 2 subspecies), *P. korotnevi*, *P. audax*, and *P. prismatium*. The description and evolution of each of these taxa is given below, while the character state information used in our analysis is summarized in Table 1.

We wish to emphasize, once more, that variability is so common to taxonomic characters in these radiolarians that no single character can be considered as conclusively diagnostic. Accurate classification is generally possible only when several characters are used in the evaluation. Nor can all individuals be unambiguously assigned to one of the taxa formally recognized, even if all the characters listed are used in classification. Morphologic variation in Radiolaria is very complex. Particularly at subspecific levels, it is difficult to adequately encompass this variation in Linnaean typologic constructs.

*Deposit of type materials.*—All designated type specimens are on deposit at the U.S. National Museum, Washington, D.C.

#### SYSTEMATIC PALEONTOLOGY

##### Genus PTEROCANIUM (Ehrenberg, 1847)

*Pterocanium* EHRENBURG, 1847, p. 54.

*Type species.*—*Podocyrthis charybdea* MÜLLER, 1855, p. 492.

*Diagnosis.*—Nassellarians with spherical cephalis and more or less pyramidal thorax, possessing 3 typically 3-bladed feet extending from base of thorax and continuing to apex of thorax as thoracic ribs. Base of thorax terminated by distinct peristome. Abdomen, when present, thin and irregularly terminated. Proximal portion of feet often porous. Feet terminate distally in simple point. Pores of thorax increase in size from apex to base, bars are typically rectangular in cross section, often forming raised frames around pores. Apical horn of cephalis invariably present, cylindrical, and may develop small distal thorns. A secondary cephalic spine may also be present. Spherical or subspherical imperforate cephalis is relatively small, heavy walled, and covered with widely scattered

TABLE 1—Characters useful in distinguishing taxa within *Pterocanium*. All are continuous variates rather than binary characters. One end-member state designated as 0, the other extreme by 2, and intermediate conditions by 1. Taxa scores represent average condition, but considerable variation is to be expected, and mosaic individuals are common, particularly within species.

| No. | Name                      | Polarity of end member states                                   | <i>P. charybdeum</i> |         |        | <i>P. praetextum</i> |       |         | <i>P. korot.</i> | <i>P. pris.</i> | <i>P. audax</i> |
|-----|---------------------------|---|----------------------|---------|--------|----------------------|-------|---------|------------------|-----------------|-----------------|
|     |                           |   | chary.               | trilob. | allium | grandi.              | prae. | eucolp. |                  |                 |                 |
| 1   | Apical spine length       | long (0) to short (2)   | 1                    | 0       | 1      | 0                    | 1     | 1       | 2                | 1               | 0               |
| 2   | Apical spine thorns       | prominent (0) to absent (2)                                     | 2                    | 1       | 2      | 2                    | 2     | 2       | 2                | 2               | 0               |
| 3   | Cephalis                  | sphere (0) to hemisphere (2)                                    | 0                    | 1       | 0      | 1                    | 0     | 0       | 1                | 0               | 2               |
| 4   | Thorax size               | large (0) to small (2)  | 0                    | 0       | 1      | 0                    | 2     | 2       | 1                | 0               | 0               |
| 5   | Thorax wall shape         | flat (0) to inflated (2)  | 0                    | 1       | 1      | 1                    | 2     | 1       | 1                | 0               | 1               |
| 6   | Thorax rib shape          | straight (1), sharply bent (2), simply curved (3), recurved (4) | 1                    | 4       | 1      | 4                    | 1     | 1       | 3                | 2               | 4               |
| 7   | Thorax pore size          | large (0) to small (2)  | 2                    | 0       | 1      | 0                    | 2     | 2       | 1                | 0               | 0               |
| 8   | Th. pore shape & distrib. | regular (0) to irregular (2)                                    | 1                    | 0       | 2      | 0                    | 1     | 1       | 0                | 1               | 0               |
| 9   | Thorax bar width          | narrow (0) to wide (2)  | 0                    | 2       | 0      | 1                    | 0     | 0       | 2                | 1               | 2               |
| 10  | Thorax bar thickness      | smooth (0) to framed (2)  | 0                    | 1       | 1      | 1                    | 1     | 1       | 2                | 0               | 2               |
| 11  | Accessory body spines     | prominent (0) to absent (2)                                     | 1                    | 1       | 0      | 1                    | 0     | 1       | 2                | 0               | 2               |
| 12  | Foot length               | long (0) to short (2)   | 1                    | 1       | 2      | 0                    | 0     | 1       | 0                | 1               | 1               |
| 13  | Foot thickness            | thin (0) to thick (2)   | 0                    | 1       | 0      | 1                    | 0     | 0       | 2                | 1               | 2               |
| 14  | Foot shape                | straight (0) to curved (2)                                      | 1                    | 2       | 1      | 1                    | 0     | 1       | 1                | 0               | 0               |
| 15  | Foot attachment           | parallel (0) to angled (2)                                      | 2                    | 2       | 1      | 1                    | 0     | 0       | 1                | 0               | 2               |
| 16  | Foot base                 | porous (0) to hyaline (2)                                       | 0                    | 1       | 1      | 1                    | 0     | 0       | 1                | 2               | 1               |
| 17  | Abdominal veil            | prominent (0) to absent (2)                                     | 1                    | 1       | 1      | 0                    | 0     | 0       | 2                | 1               | 2               |

pores, partially or more commonly nearly entirely filled with deposits of silica. Distinguished from *Lithomelissa* and related forms by distinct peristome, small spherical generally imperforate cephalis, and prominent feet.

*Comments.*—The type species for this genus was given by Foreman and Riedel (1972) as "*Lithocampe aculeata*" Ehrenberg, 1844. By the rules of nomenclature a type species must be a validly described species, with description, type specimens, etc. Ehrenberg's "species," however, was not figured, has no known type material, and was described only in the vaguest manner. Redescription of Ehrenberg's material would eliminate this problem, but no locality information was given by him that would permit creating a valid definition for his proposed species. Thus "*Lithocampe aculeata*" is not a valid species name, and cannot serve as the type for a valid genus. The genus must be based on the first validly defined species. We follow the earlier determination of Petrushevskaya (1971) who considered the type species to be *P. prosperinae*, which we feel is a junior synonym of *P. charybdeum*. *P. charybdeum* is, to our knowledge, the oldest validly described species which has been associated by the author with the generic name *Pterocanium*.

Species such as *Dictyophimus infabricatus* Nigrini, 1968 are not included in this revision, despite certain similarities in overall form. Only those taxa specifically listed are newly included in the formal definition of *Pterocanium*. Taxa previously assigned to *Pterocanium* by other authors and not directly mentioned here are retained in the genus, pending further work.

Repeated evolution of identical characters seems to be very common in Radiolaria, thus none of the characters given can individually be considered diagnostic. Generic assignment must be based, instead, on as many of the criteria given as is feasible. Further, it must be understood that this definition of *Pterocanium* is based on analysis of late Miocene to Recent material only. The taxonomic status of Paleogene forms with similar character suites is uncertain.

#### PTEROCANIUM CHARYBDEUM (Müller), 1855

*Podocyrthis charybdea* MÜLLER, 1855, p. 492.

*Pterocanium prosperinae* EHRENBURG, 1858, p. 34–35.

*Pterocanium prosperinae* BENSON, 1966 (in part), p. 405–408, Pl. 27, fig. 4 (only).

*Pterocanium charybdeum* (Müller), MÜLLER, 1858, p. 43–45, Pl. 6, figs. 7–10; PETRUSHEVSKAYA, 1971, p. 228–229, fig. 113, I, II, (?)IV, (?)V, but not III.

*Dictyopodium trilobum* HAECKEL, 1860, p. 839; HAECKEL, 1862, p. 340, Pl. 8, figs. 6–10.

*Pterocanium trilobum* (Haeckel), HAECKEL, 1887, p. 1333; POPOFSKY, 1913, p. 390–392; HAYS, 1965, p. 177–178, Pl. 3, fig. 10; NIGRINI, 1967, p. 71–72, Pl. 7, figs. 3a, b; PETRUSHEVSKAYA, 1971, p. 229–230, fig. 112, IV–VI; RENZ, 1973, p. 187, Pl. 5, fig. 17.

*Pterocanium gravidum* HAECKEL, 1887, p. 1329, Pl. 73, fig. 3.

*Pterocanium grandiporus* NIGRINI, 1968, p. 57, Pl. 1, fig. 7.

*Diagnosis.*—Cephalis of moderate size, spherical or subspherical, and weakly to fairly heavily silicified. Apical spine moderate to long. Thorax large, variable in shape but generally pyramidal to conical. Thoracic pores moderate to large, subcircular to polygonal, bars moderate to thin. Feet flared, curved to greater or lesser extent, and porous at base. Development of abdomen variable, but usually only present on occasional specimens.

*Distribution.*—Tropical and subtropical waters of all the oceans from at least the late Miocene to the Recent.

*Comments.*—*P. charybdeum* is a highly variable species, within which early workers recognized several species-level taxa. We have not been able to detect any truly discrete morphologic clusters within *P. charybdeum*, and for this reason we have broadened the definition of the species to include these earlier taxa. Subspecies are used where possible to denote patterns of covariation of characters within *P. charybdeum*. Illustrations and descriptions of Müller (1855, 1858), Ehrenberg (1858), Haeckel (1860, 1862, 1887), and Popofsky (1913) are too general to serve as a reliable guide at the subspecific level, and thus some early descriptions can be assigned only to the species, but not to a particular subspecies. We have tried, where possible, to follow Nigrini (1967, 1968) and Petrushevskaya (1971) in interpreting this earlier nomenclature.

Four subspecies of *P. charybdeum* are recognized in this study. *P. charybdeum*'s distribution has previously been described from surface sediments by Nigrini (1967, 1968, 1970). This pattern was also seen in our

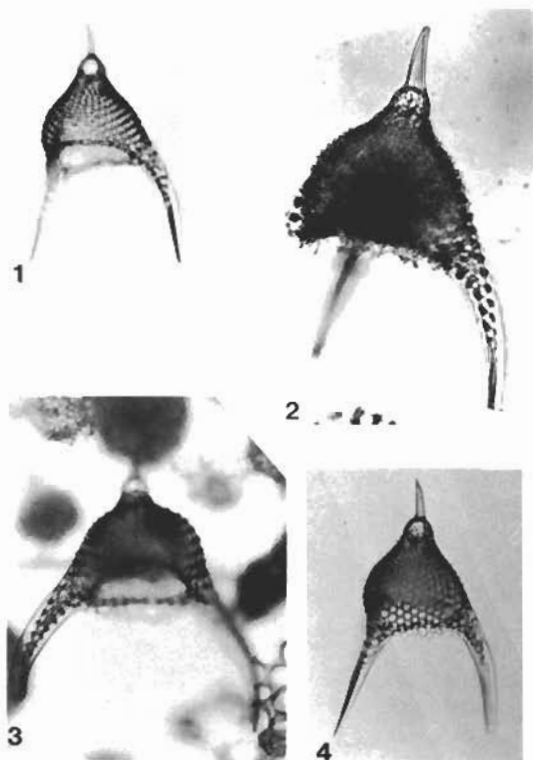


FIGURE 10—*Pterocanium charybdeum trilobum*. 1, specimen from eastern equatorial Pacific (158-9-2, 50-51 cm; T39.2; thoracic width 105 micrometers). In this and subsequent photographs, values in parentheses refer respectively to sample; England Finder coordinates; and maximum width of the thorax for the figured specimen. 2, individual showing heavy thorax, curved feet and "necked" cephalic suture. Early Pliocene of Indian Ocean (V19-169, 1,080 cm; W25; thoracic width 120 micrometers). 3, another example (same slide) with heavy curved feet (thoracic width 95 micrometers). 4, same specimen as in A, focused to show structure of cephalis. Note faint rugosity near tip of apical horn.

downcore studies (Figure 9). Nigrini, however, did not recognize any subspecies. One of our subspecies—*P. c. grandiporus*—was previously given specific rank by Nigrini (1968).

*PTEROCANIUM CHARYBDEUM TRILOBUM*  
Haeckel, n. comb.  
Figures 10.1–10.4

*Pterocanium trilobum* (Haeckel), HAYS, 1965, p. 177–178, Pl. 3, fig. 10; NIGRINI (in part), 1967, p. 71–72, Pl. 7, fig. 3a (only);

(?)PETRUSHEVSKAYA, 1971, p. 229–230, fig. 112, IV–VI; KLING (in part), 1973, p. 638, Pl. 4, figs. 6–8 (only).

*Pterocanium prosperinae* BENSON (in part), 1966, p. 405–408, Pl. 27, Fig. 4 (only).

*Pterocanium charybdeum* (Müller), PETRUSHEVSKAYA (in part), 1971, p. 228–229, fig. 113, I (only).

**Diagnosis.**—Cephalis weakly silicified. The internal septal ring at the collar stricture is weakly developed or absent, and the base of the cephalis is thus relatively unconstricted or "open." Apical horn large. Thorax flared, recurved, cylindrical; apex in some specimens drawn out into neck which merges smoothly into exterior of cephalis. Thorax nearly the same size as in *P. charybdeum charybdeum*. Lattice wall of thorax coarser than in *P. c. charybdeum*, pores larger, circular, bars thick, surface relatively rough. Feet in most specimens more widely flared at juncture with thorax than in *P. c. charybdeum* and more convex. Feet are also more robust and less porous than in *P. c. charybdeum*. Abdominal veil usually absent.

**Distribution.**—*P. c. trilobum* is the most widely distributed taxon in our samples. It has been a common member of the tropical and subtropical assemblages at least since the late Miocene. It is significantly more abundant and more heavily silicified in the Indian Ocean than in samples from the Pacific basin. Pleistocene specimens from the North Pacific also, in some cases, may be assigned to *P. c. trilobum*, although it is often difficult to distinguish in this North Pacific material between *P. c. trilobum* and *P. c. grandiporus*. A few individuals assignable to *P. c. trilobum* were also found in latest Pliocene and early Pleistocene sediments in the Antarctic, as first noted by Hays (1965). Heavy silicification in this Antarctic population produces a superficial resemblance to *P. korotnevi*, but the thorax size, shape, and foot structure are still far more similar to *P. c. trilobum*.

**Comments.**—*P. c. trilobum* seems to have been the ancestor of the late Miocene subspecies *P. c. allium*. *P. c. trilobum* shares several characteristics with *P. audax*, including a relatively heavy, coarse thorax and a weak collar stricture. Foot structure is also similar, as both taxa have relatively thick, slightly porous or non-porous foot bases. Only the straight foot shape and distal apical horn thorns of *P. audax* clearly and consistently



separate the two taxa in most samples. In late Miocene and early Pliocene samples from the equatorial Indian Ocean and the Equatorial Pacific even these distinctions are occasionally violated, and individuals with completely transitional morphologies can be seen. Because transitional specimens between these two taxa are not found in samples from other regions and other time intervals, their presence was not felt to be a sufficient reason to synonymize *P. c. trilobum* with *P. audax*. The occurrence of these morphological intermediates does imply a close relationship between the two taxa. It also supports the synonymy of *Pterocanium* with *Lychnodictyum*, the Haeckelian genus to which *P. audax* was originally assigned by Riedel (1953).

**PTEROCANIUM CHARYBDEUM CHARYBDEUM**

Müller, n. comb.

Figures 11.1–11.4, 13.3

(?)*Dictyopodium trilobum* HAECKEL, 1862, p. 340, Pl. 8, figs. 6–10.

(?)*Dictyopodium challenger* HAECKEL, 1878, p. 47, fig. 35.

(?)*Lychnodictyum challenger* (Haeckel), HAECKEL, 1887, p. 1231.

*Pterocanium trilobum* (Haeckel), (?)HAECKEL, 1887, p. 1333; NIGRINI (in part), 1967, p. 71–72, Pl. 7, fig. 3b (only).

**Diagnosis.**—Heavily silicified cephalis is strongly constricted internally by well developed septal ring at collar stricture; (i.e., not “open” at base), bears relatively small apical horn. Thorax moderately large, uninflated to slightly inflated flared tetrahedron. Feet moderately robust, project from basal vertices of thorax, are collinear with thoracic edges, and have only a slight convex curvature. Lattice wall of thorax thin, bars wider than thick, pores often polygonal. Thoracic lattice continues into base of feet. Abdominal veil weakly developed.

**Distribution.**—This subspecies represents the other common form of *P. charybdeum*, and, like *P. c. trilobum*, is found in tropical and subtropical regions from the late Miocene to the Recent. *P. c. charybdeum* is more abundant than *P. c. trilobum* in most Pacific samples, and this geographic difference prompts us to formally describe this morphology.

**Comments.**—*P. c. charybdeum* is very similar to members of the *P. praetextum* lin-

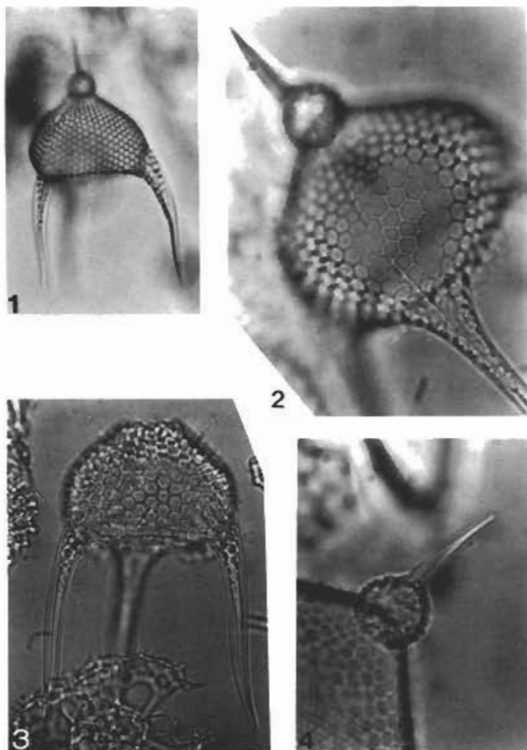


FIGURE 11-1-4, *Pterocanium charybdeum charybdeum*. 1, overview showing general dimensions (thoracic width 95 micrometers). 2, individual from the equatorial Pacific, focused to show polygonal pore structure and prominent thorax rib continuing into foot (RC12-66, 0–2 cm; Z48.1; thoracic width 105 micrometers). 3, a morphologically intermediate individual with long, nearly parallel *P. praetextum*-like feet (RC12-66, 665 cm; W34.1; thoracic width 110 micrometers). 4, same as 2, focus on cephalis. Note well developed demarcation between cephalis and thorax.

eage, a similarity we believe may have been the result of an intertwined evolutionary history. Relative to *P. praetextum*, *P. c. charybdeum* is larger, has more widely angled feet, a more tetrahedral thorax, and less development of an abdominal veil. These differences may be used to separate “typical” *P. c. charybdeum* from *P. praetextum* except during the early Pliocene and the late Pleistocene. At these times many individuals, although classified as *P. c. charybdeum*, are noticeably intermediate in size, thoracic shape, pore dimensions, and foot development. In the early Pliocene, these intermediate types

are, in fact, a major element of the *Pterocanium* assemblage, along with abundant *P. c. trilobum*, and *P. c. allium*. As this time interval coincides with the earliest known specimens of *P. praetextum*, these intergradational forms are thought to be related to the origin of the *P. praetextum* lineage. The late Pleistocene intermediates are less readily explained, but may possibly represent hybridization between *P. praetextum* and *P. charybdeum*.

**PTEROCANIUM CHARYBDEUM ALLIUM n. subsp.**  
 Figures 12.1–12.6

**Diagnosis.**—Cephalis moderately silicified, but usually “closed” at base (c.f. diagnosis of *P. c. charybdeum*). Apical horn small. Thorax flared inflated cylinder, but not noticeably recurved. Sometimes weak flattening towards tetrahedral shape. Thorax slightly smaller than in *P. c. trilobum*, lattice wall thin, pores small, polygonal, bars rectangular, wider than thick. Feet only weakly flared, thin, short, and weakly pored at base. Abdominal veil sometimes present.

**Etymology.**—Specific name refers to resemblance of inflated thorax of this species to a bulb of garlic (Latin “allium”).

**Distribution.**—*P. c. allium* is common in tropical and subtropical sediments in the late Miocene, and is more or less restricted to this stratigraphic interval. Earlier Miocene, Pliocene, and Pleistocene populations of *P. charybdeum* are usually assignable to one of the other recognized subspecific taxa.

**Comments.**—The importance of *P. c. trilobum*, aside from its potential use as a stratigraphic form, lies in the ancestral nature of its morphology. It is in many respects intermediate between *P. charybdeum*, *P. praetextum*, and *P. prismatium*. As noted earlier, *P. c. allium* was derived from earlier populations of *P. c. trilobum* by reduction in foot and apical horn length and by an increase in the degree of silicification of the base of the cephalis. Further differentiation resulted in the demise of *P. c. allium* and the evolution of *P. c. charybdeum*, *P. praetextum*, and *P. prismatium*.

**PTEROCANIUM CHARYBDEUM (Müller)**  
**GRANDIPORUS** Nigrini, n. comb.  
 Figures 13.1, 13.2

*Pterocanium grandiporus* NIGRINI, 1968, p. 57, Pl. 1, fig. 7.

**Diagnosis.**—Lightly silicified cephalis is open at base, and possesses long thin apical spine. Thorax moderate to large, formed of two conic sections joined together by a more nearly horizontal section, resulting in a distinctively stepped profile to the thoracic outline. Thoracic pores somewhat irregular but generally subcircular and surrounded by weak polygonal frames. Pores fairly large, bars of moderate thickness. Feet long, thin, moderately flared and slightly convex, only weakly pored at base. Abdominal veil sometimes present. Veil has relatively large irregular pores and a ragged termination.

**Distribution.**—Restricted to the subtropical and eastern equatorial provinces of the Pacific.

**Comments.**—Nigrini (1968) defined *P. c. grandiporus* as a separate species, based primarily on the size of the thoracic pores, and secondarily on the relatively long feet and apical spine. In our material we have found that all these characteristics—particularly pore size—are largely gradational with *P. c. trilobum* (Fig. 14). For this reason we do not feel that *P. c. grandiporus* should be given separate specific rank, although it is a sufficiently distinctive morphotype—with a characteristic biogeographic distribution—to justify its retention as a formal taxon.

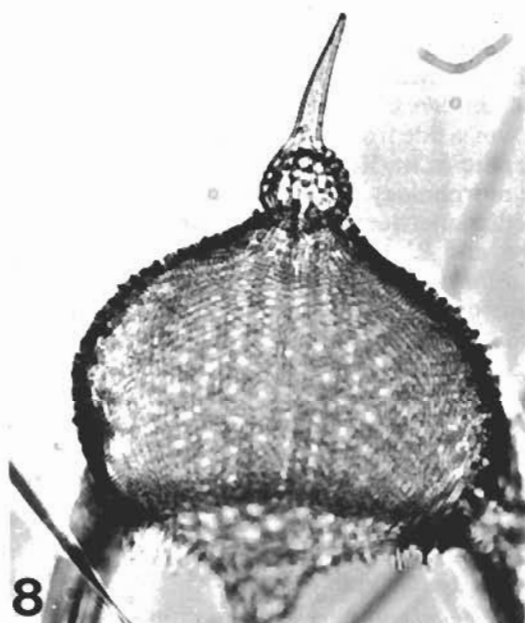
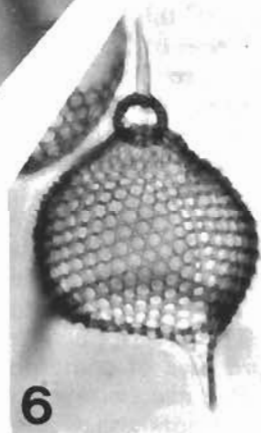
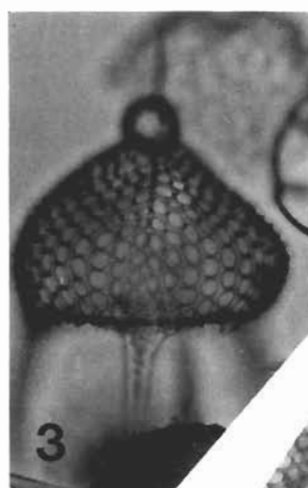
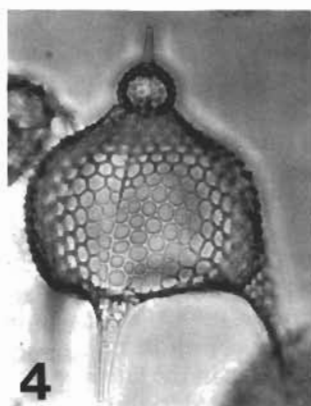
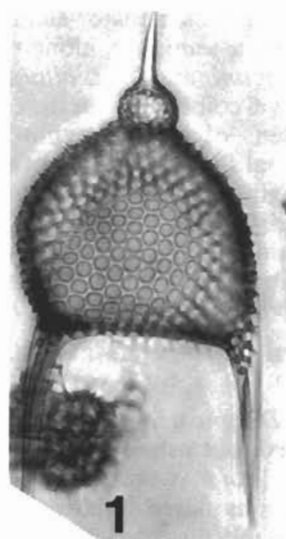
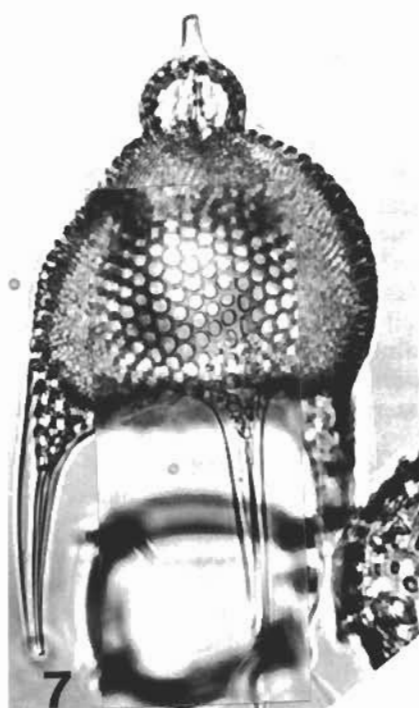
**PTEROCANIUM PRAETEXTUM**  
 (Ehrenberg), 1872

*Lychnocanium praetextum* EHRENBURG, 1872a, p. 316; 1872b, p. 297, Pl. 10, fig. 2.

There are two forms of *P. praetextum* according to Nigrini (1967), a low latitude and a high latitude form. Our results are in agreement with this interpretation. The relative abundances of the species as a whole are given in Figure 9.

**Comments.**—Nigrini (1967, 1970) and Johnson and Nigrini (1980, 1982) have presented distribution maps for this species that indicate biogeographic ranges of the two subspecies are largely non-overlapping. In this work we prefer to describe the range of *P. p. praetextum* as residing entirely within the range of the more cosmopolitan *P. p. eucolpum*. This description is more in accord with the presence of common (though subordinate) *P. p. eucolpum* in most equatorial samples of Radiolaria where *P. p. praetextum* dominates.





## PTEROCANIUM PRAETEXTUM (Ehrenberg)

EUCOLPUM Haeckel, Nigrini, 1967

Figures 15.1–15.4

*Pterocanium praetextum* (Ehrenberg) *eucolpum* Haeckel, NIGRINI, 1967, p. 70, Pl. 7, fig. 2.*Pterocanium eucolpum* HAECKEL, 1887, p. 1332, Pl. 73, fig. 4.*Pterocanium bicornae* HAECKEL, 1887, p. 1332, Pl. 73, fig. 5.(?) *Pterocanium tricolpum* HAECKEL, 1887, p. 1331–1332, Pl. 73, fig. 1; POPOFSKY, 1913, p. 392.*Pterocanium* sp. PETRUSHEVSKAYA, 1971, fig. 112, VII.*Pterocanium praetextum* (Ehrenberg), RENZ (in part), 1973, p. 186–187, Pl. 5, fig. 16a (only).

**Diagnosis.**—Cephalis is heavily silicified “closed” sphere (basal pores small), and is only slightly smaller than cephalis of *P. charybdeum*. Apical horn usually small. Thorax irregular hemisphere, much smaller than thorax of *P. charybdeum*. Thorax lattice wall thin, pores small, polygonal, bars thin. Feet are long, nearly straight or slightly convex, and usually subparallel. Feet are usually connected by thin abdominal veil of very finely pored lattice work.

**Distribution.**—*P. p. eucolpum* is widely distributed in temperate through tropical waters of the world ocean. This pattern has been typical throughout *P. p. eucolpum*’s stratigraphic range, from its origin near the Miocene–Pliocene boundary to the present day.

**Comments.**—*P. p. eucolpum* is the phylogenetically older of the two subspecies of *P.*

*praetextum*, and morphologically more similar to its ancestor(s)—*P. charybdeum* and/or *P. korotnevi*. Transitional series are noted in the discussions of those two lineages. *Pterocanium bicornae*, as figured by Haeckel (1887, Pl. 73), apparently differs from his *P. eucolpum* (on the same plate) only in the presence of a second apical horn. We do not feel that this difference in a single character is of any taxonomic significance, given the variability of individual characters in *Pterocanium*. We have, therefore, synonymized the two species. However, other pterocaniids with two apical horns (such as “*Pterocanium* sp.,” Nigrini and Moore, 1979) may still belong to different species, and are excluded from our synonymy.

## PTEROCANIUM PRAETEXTUM (Ehrenberg)

PRAETEXTUM Nigrini, 1967

Figures 16.1–16.4

*Pterocanium praetextum* (Ehrenberg) *praetextum* NIGRINI, 1967, p. 68, Pl. 7, fig. 1.(?) *Pterocanium monopylum* POPOFSKY, 1913, p. 388.*Pterocanium prosperinae* BENSON (in part), 1966, p. 405–408, Pl. 27, fig. 3 (only).*Pterocanium praetextum* (Ehrenberg), BENSON, 1966, p. 408–410, Pl. 27, fig. 6; Pl. 28, fig. 1; PETRUSHEVSKAYA, 1971, p. 230, fig. 114, I, II, III; RENZ (in part), 1973, p. 186–187, Pl. 5, fig. 16b (only).(?) *Pterocanium charybdeum* (Müller), PETRUSHEVSKAYA (in part), 1971, p. 228–229, fig. 113, III (only).

For additional synonymy see Nigrini, 1967.

FIGURE 12—1–6, *Pterocanium charybdeum allium*, n. subsp. 1, holotype displaying characteristic almost parallel thin feet; nearly nonporous foot-bases; circular, regular pores; and secondary spines on thorax. Inflated thorax and necking of thorax at cephalic suture are not very well developed on this specimen (RC12-66, 1875 cm; F49; thoracic width 130 micrometers). This photograph and 2, 4, 5, and 6 were created by multiple exposures of the same specimen at different focal planes. 2–6, paratypes showing variation in *P. c. allium*. All but 3 are from same slide as holotype. 2, individual with short, thin parallel feet; inflated, “necked” thorax; and secondary spines on cephalis (D23; thoracic width 110 micrometers). 3, specimen from the late Miocene of the Indian Ocean displaying thoracic outline characteristic of *P. c. allium* (locality and magnification unrecorded). 4, individual with prominent “neck” to apex of thorax (Z33.4; thoracic width 125 micrometers). 5, specimen with unusually long feet (C15.3; thoracic width 125 micrometers). 6, example of thorax inflation (Y51.4; thoracic width 125 micrometers). 7, *Pterocanium* of uncertain species from early Pliocene with inflated thorax (but no “necking” of apex) and thin, parallel feet. Lack of necking and small size of thorax are reminiscent of *P. praetextum eucolpum* (RC12-66, 1,305 cm; F20; thoracic width 105 micrometers). Montage of photographs from different focal planes. 8, *Pterocanium charybdeum* uncertain subspecies. Individual has *P. c. allium*-like thorax and cephalis, but feet (not shown) are strongly curved and more typical of *P. c. trilobum* (RC12-66, 2,535 cm; D33/4; thoracic width 135 micrometers).

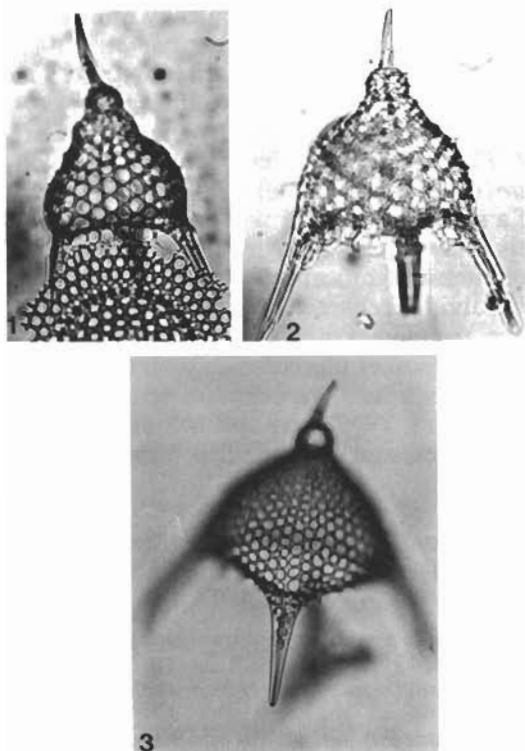


FIGURE 13—1, *Pterocanium charybdeum grandiporus*, focused to show large pores, stepped profile of thorax (RIS-32 PS, top; G20; thoracic width 110 micrometers). 2, *P. c. grandiporus* showing indistinct cephalic suture and flared feet (RIS-32 PS, top; J22; thoracic width 115 micrometers). 3, *P. c. charybdeum* showing pyramidal thorax and thin flared feet (thoracic width 100 micrometers).

**Diagnosis.**—Similar in most characteristics to *P. p. eucolpum* above, *P. p. praetextum* differs from *P. p. eucolpum* chiefly in the shape of the thorax, which in *P. p. praetextum* has a pentagonal outline. This effect is created by subconical inflated sections of the thorax wall which lie between the three thoracic ribs, which, consequently, are sunken into the thorax. The feet of *P. p. praetextum* tend to be straighter and more parallel than in *P. p. eucolpum*, and the abdominal veil is often better developed. In both subspecies of *P. p. praetextum*, but particularly in *P. p. praetextum*, small needle-like spines are seen projecting from the surface of the thorax.

**Distribution.**—*P. p. praetextum* is ex-

tremely common in modern equatorial assemblages of Radiolaria, where it is by far the most common form of *Pterocanium*. This dominance developed gradually over the last five million years, and until one million years ago *P. p. eucolpum* was the most common form of *Pterocanium* in tropical sediment samples. *P. p. praetextum* is not found outside of the equatorial province, and may bear a clinal relationship to the phylogenetically older *P. p. eucolpum*, which dominates in subtropical waters.

#### PTEROCANIUM PRISMATIUM Riedel, 1953

Figures 17.1–17.4

*Pterocanium prismatium* RIEDEL, 1957, p. 87–88, Pl. 3, figs. 4, 5.

**Diagnosis.**—Cephalis thick-walled, complete sphere, apical horn small. Thorax very large, consisting of an upper short tetrahedron that joins the cephalis to a more distal triangular prism section. Lattice walls are thin, pores moderately large, somewhat irregular, circular to polygonal and are often distinctly elongated longitudinally. Bars are of moderate thickness, and generally lack prominent frames. Short flat triangular spines are often found projecting from the upper thorax, particularly along thoracic ribs. Feet are moderately robust and of medium length, extend in parallel from base of thoracic prism. Base of feet are weakly porous. Abdominal veil occasionally present, generally poorly developed.

**Distribution.**—*Pterocanium prismatium* first evolved in the early Pliocene and became extinct in the latest Pliocene. During its entire history it was restricted to equatorial waters (Figure 9). It was more common during most of this time in the Pacific than in the Indian Ocean, where its stratigraphic distribution is rather spotty.

**Comments.**—Of all the lineages of *Pterocanium* in our study, *P. prismatium* is the only one whose evolutionary history has been previously investigated (Kellogg and Hays, 1975). This species is also a well known stratigraphic indicator of the Pliocene–Pleistocene boundary. Hays (1971) has investigated in detail the relationship between the extinction of this lineage and the Olduvai magnetic event.

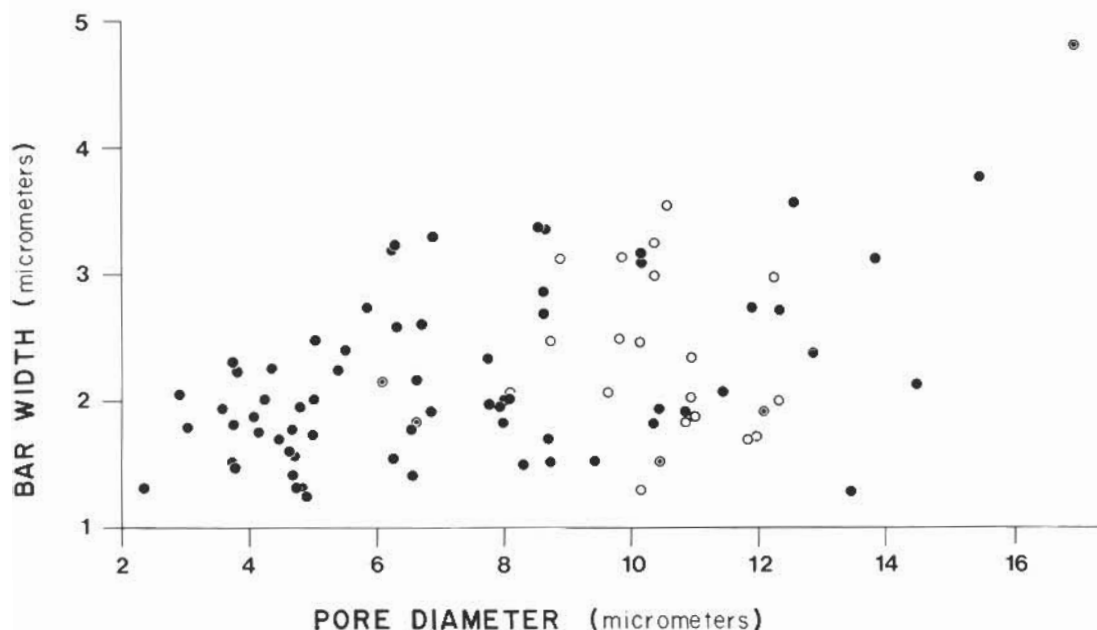


FIGURE 14—Comparison of thorax lattice wall pore and bar dimensions in *P. c. grandiporus* to those of other *P. charybdeum*. Different geographic areas and stratigraphic levels are included to represent the range of pore and bar dimensions in *P. charybdeum*: RIS-32 and RIS-34 (eastern equatorial Pacific, Recent); DSDP 238, core 11, section 4 (equatorial Indian, Pliocene); and DSDP 238, core 18, sections 2 and 4 (latest Miocene). *P. c. grandiporus* data from RIS samples only. Each dot represents one specimen. Measurements were made with an electronic digitizer and are accurate to approx.  $\pm 0.7$  micrometers. Circles, *P. c. grandiporus*; solid dots, other *P. charybdeum*; bull's-eyes, intermediate forms.

**PTEROCANIUM KOROTNEVI (Dogiel), 1952**  
Figures 18.1–18.5

*Pterocorys korotnevi* Dogiel, DOGIEL and RESHETNYAK, 1952, p. 17, fig. 11.

(?)*Lychnocanium sigmopodium* HAECKEL, 1887, p. 1228, Pl. 61, fig. 15.

*Pterocanium prosperinae* BENSON (in part), 1966, p. 405–408, Pl. 27, fig. 5 (only).

*Pterocanium korotnevi* (Dogiel), NIGRINI, 1970, Pl. 3, figs. 10, 11; KLING, 1973, p. 638, Pl. 4, figs. 1–4; Pl. 10, figs. 6–9.

*Lychnocanium korotnevi* (Dogiel), PETRUSHEVSKAYA, 1971, fig. 111, I.

*Lychnocanium* sp. cf. *L. sigmopodium* Haeckel, RENZ, 1973, p. 185–186, Pl. 5, fig. 14.

*Lychnocanoma* sp. cf. *L. grande* Campbell and Clark, 1944, KLING, 1973, Pl. 4, figs. 9, 10; REYNOLDS, 1980, p. 766, Pl. 1, figs. 21, 22.

*Pterocanium trilobum* (Haeckel), KLING (in part), 1973, p. 638, Pl. 4, fig. 5 (only).

*Lychnocanoma* sp. SAKAI, 1980, p. 711, Pl. 9, figs. 1a, b.

**Diagnosis.**—Cephalis hemispherical, somewhat irregular, and relatively large. Api-

cal spine small. Thorax small, hemispherical, very thick walled. Pores small, circular, surrounded by raised frames, bars correspondingly thick. Feet moderately long and very robust, flared, straight or slightly concave, essentially unpored even at base. No veil.

**Distribution.**—*P. korotnevi* has, at one time or another, existed in most of the polar waters of the world. At present it is restricted to the North Pacific, but in the Miocene it may also have been common in the Antarctic.

**Comments.**—Forms transitional in morphology between *P. korotnevi* and *P. p. eucolum* are very common in the early Pliocene in cores located in transitional North Pacific–Subtropical locations. On morphologic grounds either *P. korotnevi* or *P. charybdeum* could be ancestral to *P. p. eucolum*—or both could be.

The detailed history of this taxon has not yet been worked out, for it is not only taxonomically complex, its restriction to high lat-

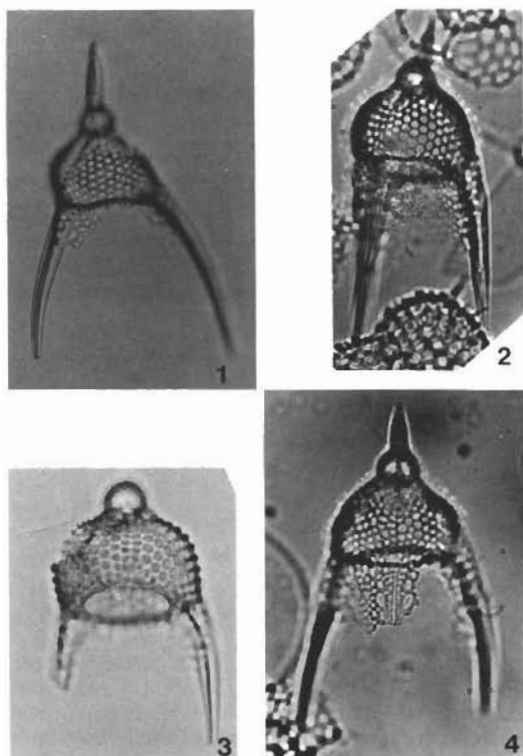


FIGURE 15—*Pterocanium praetextum eucolpum*. 1, individual with flared legs and irregular thorax outline (thoracic width 70 micrometers). 2, 3, specimens showing subparallel legs, rounded outline to thorax 2, RC12-66, 205 cm; L17.3; thoracic width 70 micrometers. 3, thoracic width 60 micrometers. 4, specimen intermediate between 1 and 2+3 (RC12-66, 85–87 cm;  $\times 14$ ; thoracic width 80 micrometers).

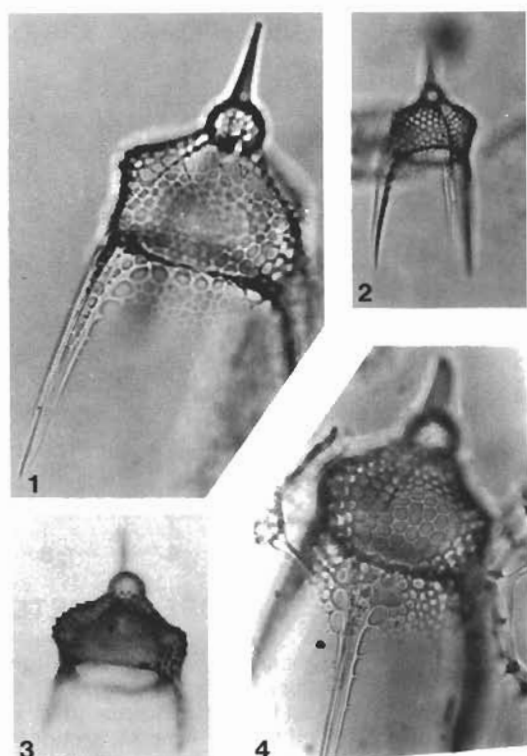


FIGURE 16—*Pterocanium praetextum praetextum*. 1, focus showing spherical cephalis (thoracic width 60 micrometers). 2, individual with nearly complete, subparallel feet (thoracic width 60 micrometers). 3, specimen showing inflated lobes of thorax and intervening sunken rib areas (thoracic width 60 micrometers). 4, equatorial Pacific individual (RC12-66, 0–2 cm; Z37/8; thoracic width 75 micrometers), focus on pore structures.

itude sediments makes it much more difficult to determine its stratigraphic distribution. With the development of reliable high latitude zonations for the pre-Pliocene, it will be possible to trace this group's evolutionary history in more detail.

In recent sediments a more or less complete gradation exists between forms with small thoraxes, traditionally assigned to *P. korotnevi*, and more robust forms which previously were assigned to *Lychnocanoma* sp. or *Lychnocanoma* sp. cf. *L. grande*. According to Kling (1973), Reynolds (1980), and Sakai (1980), these robust forms are restricted to the Pleistocene. Several taxa similar to *Lychnocanum grande* in morphology exist in Pliocene and earlier sediments from the

North Pacific, including the type material of *L. grande* from the California Miocene. Some of these forms are stratigraphically useful. Although these earlier forms may also be conspecific with *P. korotnevi*, no further formal revision is attempted until a complete re-examination of the earlier material is possible.

#### PTEROCANIUM AUDAX (Riedel) n. comb.

Figures 19.1–19.4, 20.1, 20.2

*Lychnodictyum audax* RIEDEL, 1953, p. 810–811, Pl. 85, fig. 9; SANFILIPPO and RIEDEL, 1974, p. 1022–1023, Pl. 2, fig. 8; SAKAI, 1980, p. 711, Pl. 8, figs. 1a, b.

**Diagnosis.**—Cephalis hemispherical, thin walled. Apical horn (Figure 20) very long and



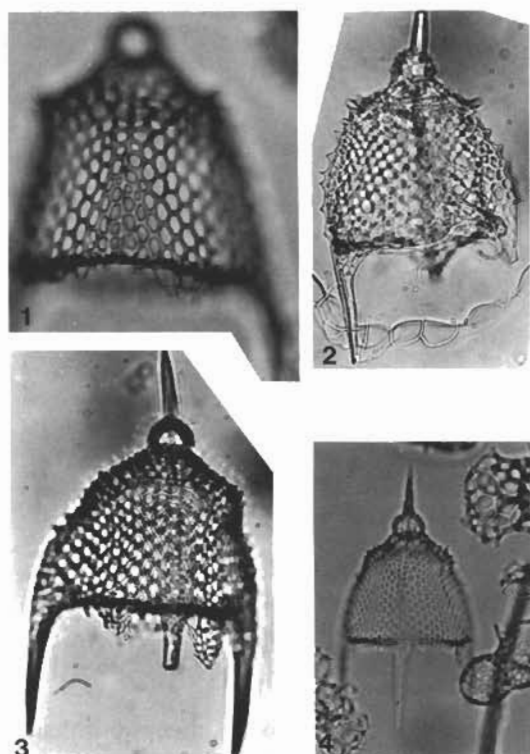


FIGURE 17—*Pterocanium prismatium*. 1, specimen showing how pores in thorax align along thorax rib (thoracic width 95 micrometers). 2, individual with prominent cusped secondary spines along thorax rib (RC12-66, 665 cm; YX46; thoracic width 125 micrometers). 3, specimen (RC12-66, 1,300 cm; P31; thoracic width 165 micrometers) with well developed subparallel feet. Note thin bars framing pores visible in plane of focus. 4, specimen displaying prismatic to concave nature of thorax walls (thoracic width 90 micrometers).

very thick, bears cluster of thorns near tip. Thorax very large, in the form of an elongate slightly recurved cone that merges smoothly with the base of the cephalis. Thoracic ribs marked only by alignment of pores to either side of a poreless band on surface of thorax—there is usually no external ridge or depression. Pores large, irregularly circular, bars often very thick, usually cylindrical and smooth, but may occasionally be faceted by development of funnels on exterior of pores. Feet are thick, moderately long to fairly short, straight or weakly concave and usually very strongly tapered to a sharp point. Feet are completely nonporous.

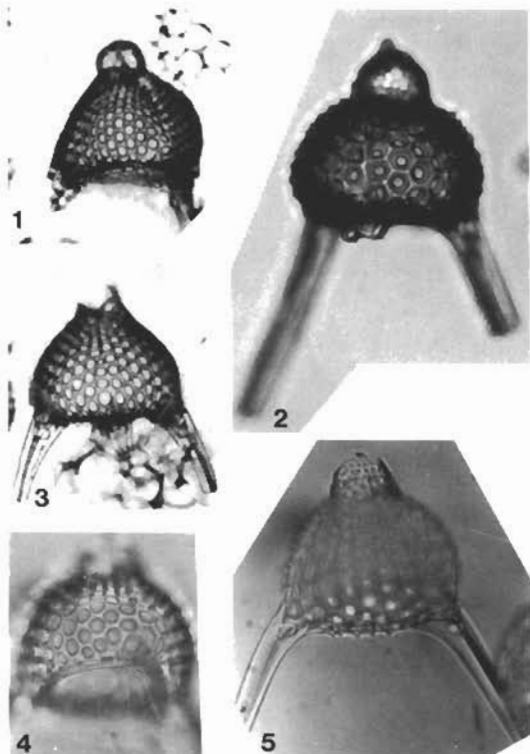


FIGURE 18—*Pterocanium korotnevi* and forms related to it. 1, specimen of *P. korotnevi* showing irregular hemispherical cephalis, circular pores (V20-105, 966 cm; thoracic width 85 micrometers). 2, more heavily silicified individual in the *P. korotnevi* group with hemispherical thorax, framed pores and heavy bars, long curved feet (thoracic width 75 micrometers). 3, montage of photographs from different planes of focus from the same specimen, illustrating base of feet and general thorax shape (V20-105, 966 cm; O11; thoracic width 90 micrometers). 4, specimen from focus on pores and bars of thorax (158-9-2, 50–51 cm; thoracic width 70 micrometers). 5, same as 4, focus on cephalis (broken at top), and feet.

*Distribution.*—A subtropical form, *P. audax* has been recorded as well in relatively low latitude sediments from the Indian Ocean and in the Eastern tropical Pacific (Figure 9). The early history of this lineage is not known, but extends well into the Miocene, for we have seen forms assignable to the same general type in early Late Miocene sediments from the Indian Ocean and other locations.

*Comments.*—Intermediate morphologies between *P. audax* and *P. c. trilobum* are en-

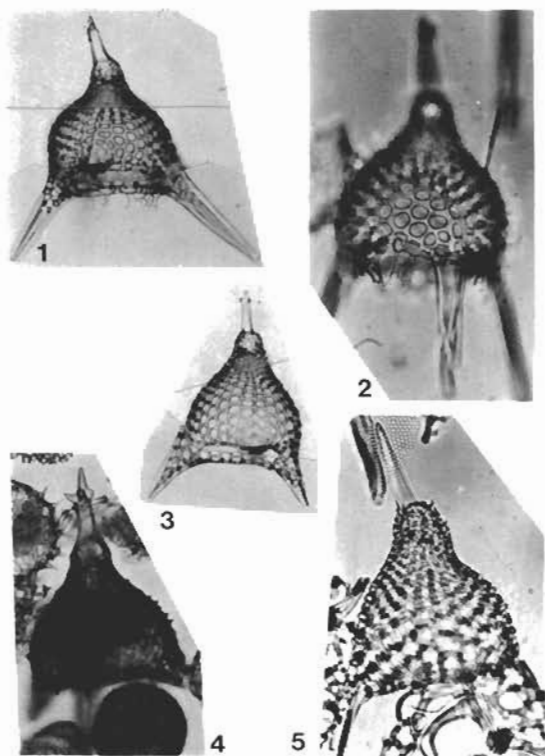


FIGURE 19—*Pterocanium audax*. 1, general view of a specimen (158-9-2, 50–51 cm; J27.1; thoracic width 125 micrometers). Tip of apical horn apparently broken in life and partially regrown. Montage of photographs from different focal planes. 2, Individual from 158-16-2, 49–51 cm (G38/9; thoracic width 145 micrometers). Focus on pores and bars of thorax, fragmentary abdominal veil. 3, intermediate between *P. audax* and *P. c. trilobum* (158-9-2, 50–51 cm; L11.1; thoracic width 115 micrometers). Note (relative to *P. audax*) thin bars, porous foot-bases, rudimentary development of thorns on apical horn. Montage of photographs from different focal planes. 4, early Pliocene individual from V19-169 showing rugose thorax, well developed thorns on apical horn (thoracic width 105 micrometers). 5, 'small form' of *P. audax*?, showing simple apical horn, very indistinct cephalic suture (158-16-2, 49–51 cm; H19.1; thoracic width 120 micrometers).

countered in early Pliocene and late Miocene samples from DSDP site 158, as noted earlier.

#### PHYLOGENY AND EVOLUTION OF *PTEROCANIUM*

Having defined a taxonomic framework for our study, we proceeded to reconstruct the

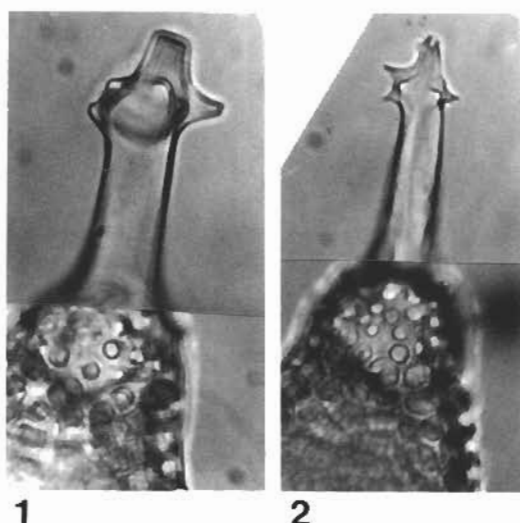


FIGURE 20—Cephalis and apical horns. 1, *P. audax* (158-9-2, 50–51 cm). 2, *P. audax*/*P. c. trilobum* intermediate of Figure 19.3. Montages from different focal planes.

phylogeny of the group by phenetic linkage of stratigraphically successive forms. An overview of the phylogeny of this group is given below, and is summarized in Figure 21.

Mid late Miocene populations were dominated by species in the *P. korotnevi* complex in higher latitudes, and by *P. c. trilobum*, *P. audax*, and morphological intermediates between these latter two in lower latitudes. *P. audax* in older samples seems to show little or no intergradation with *P. charybdeum* morphologies. Thus it may be possible to trace the morphologic ancestry of Pliocene *P. audax* to not one but two ancestral types, each a reasonably distinct morphospecies displaying a separate and characteristic morphologic unity, a separation which partially disappears in some samples in the late Miocene and early Pliocene.

In the latest part of the late Miocene, equatorial *Pterocanium* assemblages consist mainly of *P. c. allium*. This form is not only morphologically similar to *P. c. trilobum*, from which it arose, but also to both *P. prismatium* and to *P. p. eucolpum*. Morphologic fragmentation of the late Miocene *P. charybdeum* population is observed in samples covering the latest Miocene to early Pliocene (6 Ma to 4.0 Ma).

By the Early Pliocene, distinct differences



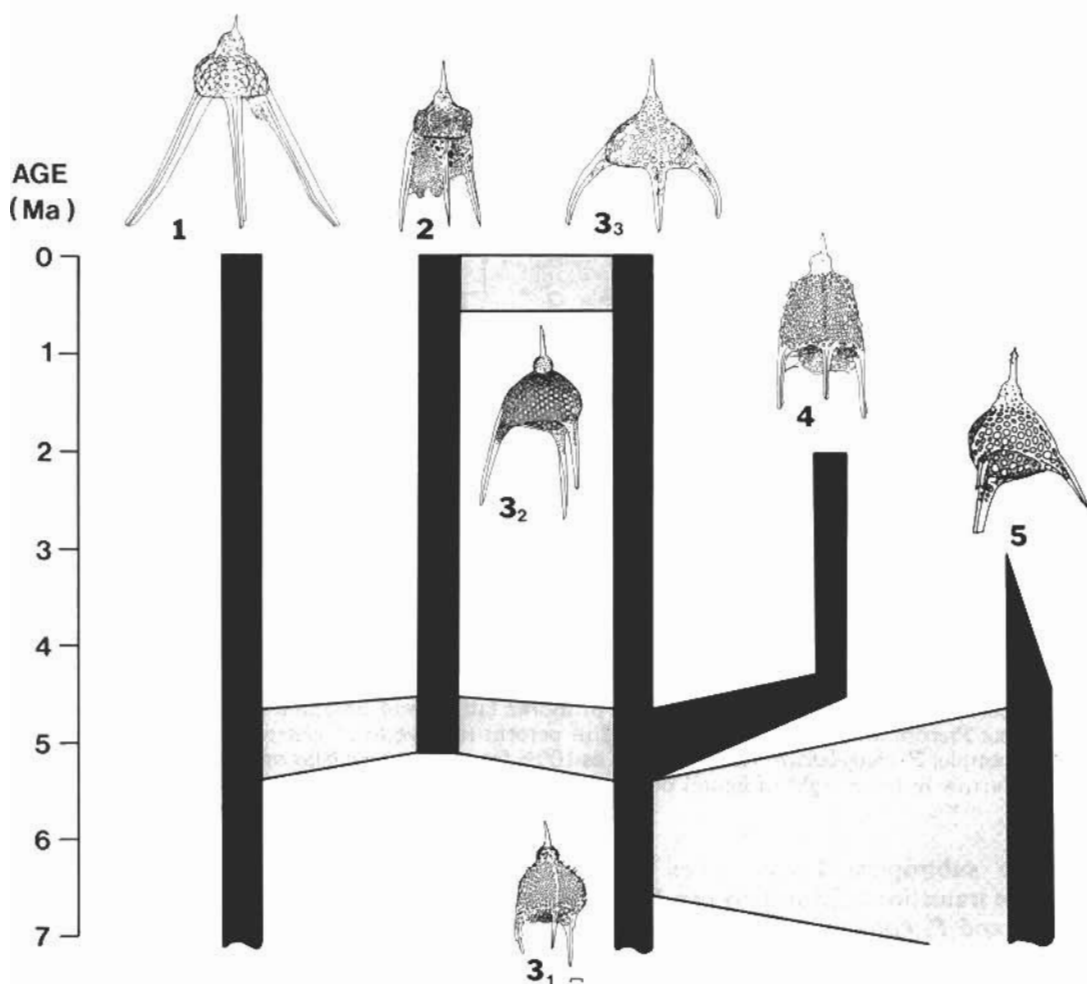


FIGURE 21—Phylogeny of late Neogene *Pterocanium*. Solid bars show main lineages, shaded intervals show zones of morphologic intergradation between lineages. Figure is diagrammatic, and vertical lines do not imply morphological stasis. Figured specimens drawn with a camera-lucida to the same scale (10 micrometer bar shown below 3.1). 1, *Pterocanium korotnevi* (V21-148, 20 cm: late Pleistocene), 2, *P. praetextum* (RC12-66, 0–2 cm: late Pleistocene), 3.1, *P. charybdeum allium* (RC12-66, 2555 cm: Late Miocene), 3.2, *P. c. charybdeum* (RC12-66, 0–2 cm), 3.3, *P. c. trilobum* (V19-169, 9–10 cm: late Pleistocene), 4, *P. prismatium* (RC12-66, 1,187 cm: mid-Pliocene), 5, *P. audax* (V19-171, 880 cm: mid-Pliocene). Core and depth information gives source of each figured specimen.

between equatorial Pacific and equatorial Indian Ocean faunas are apparent (Figure 9). *P. audax* is a common member of the equatorial Indian Ocean assemblage, but is absent from all but the easternmost tropical Pacific (DSDP site 158). *P. c. trilobum* is common in samples from the Indian Ocean, while *P. c. charybdeum* is relatively more common in the Pacific.

*P. praetextum* also seems to have evolved

from two ancestral forms near the Miocene–Pliocene boundary. Forms intermediate between *P. c. allium* (and/or *P. c. charybdeum*) and *P. p. euclpum* are particularly common in the earliest Pliocene (~4.5 Ma) in the equatorial Indian Ocean. By 4 Ma *P. p. euclpum* is a common member of the equatorial Indian Ocean assemblage, although it is less common in equivalent aged sediments from the Pacific. Late Miocene and early

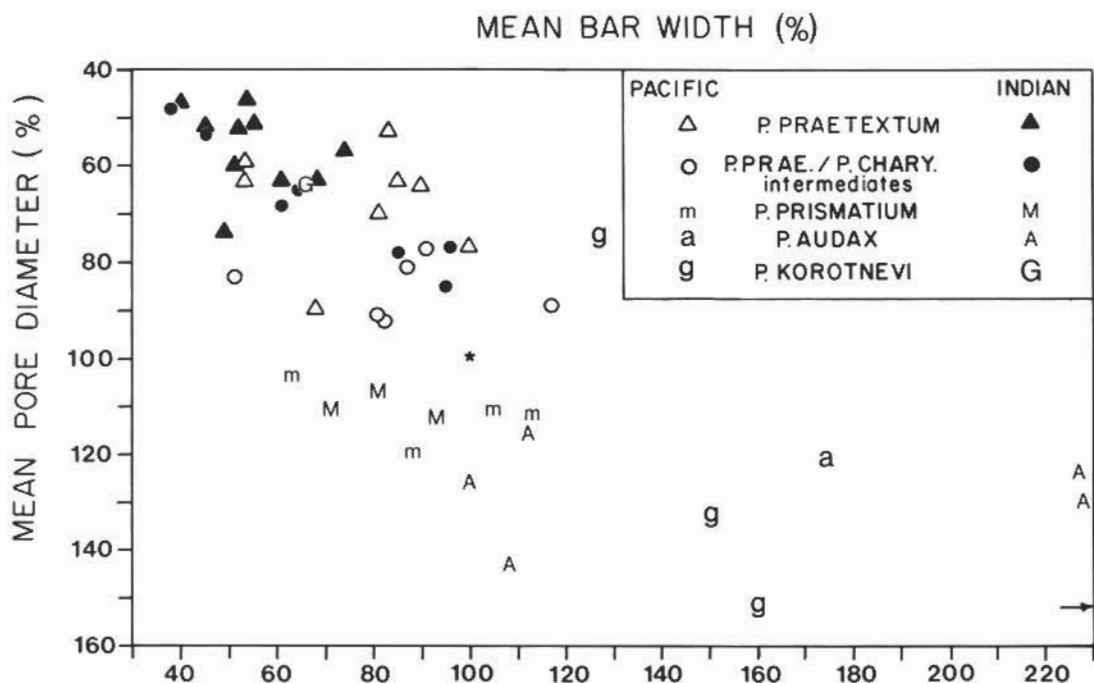


FIGURE 22—Scatterplot of population means of thorax lattice wall pore and bar dimensions for late Neogene *Pterocanium* taxa. Data expressed in percent relative to *P. charybdeum* means from the same sample. *P. charybdeum* values defined as 100% for each sample (star on plot). One *P. korotnevi* value (arrow in lower right of figure) plots off-scale at (152,395). Sample sizes listed in Appendix.

Pliocene subtropical Pacific cores record common transitional forms between *P. p. eucolpum* and *P. korotnevi*. These transitional forms become rarer in younger sediments.

*P. prismatium* evolved from *P. charybdeum* in the early Pliocene (Figure 9). Relatively rapid evolution of the lineage occurred from 4.4 Ma to 3.9 Ma.

By approximately 3.6 Ma, *P. p. eucolpum* became more common in Pacific sediments (Figure 9). Later evolution of *P. praetextum* in the equatorial Pacific and equatorial Indian Ocean involves the increasing dominance of the *P. p. praetextum* subspecies.

Later Pliocene samples from the Indian Ocean record the gradual disappearance of *P. audax*, which is last seen in the Gauss (~3 Ma, Figure 9). It has not been reported in Pleistocene sediments anywhere in the world.

*Pterocanium prismatium* became extinct at the Pliocene–Pleistocene boundary. The late Pleistocene is marked in the low latitudes by the reappearance of transitional morphologies between *P. praetextum* and *P. charybdeum*. Details of the Pleistocene evo-

lution of *P. korotnevi*, the other surviving lineage, are not known.

The phyletic relationships described above are presented in diagrammatic form in Figure 21. This figure represents our understanding of the timing and general topology of morphologic evolution in *Pterocanium*. Additional qualitative and quantitative data on morphologic characters are needed to document details of evolutionary trends or changes in phyletic rates of evolution. Although our few crude measures cannot show the many subtleties of *Pterocanium* evolution, they can be used, together with more qualitative observations, to demonstrate that significant differences exist between taxa, and that evolutionary change occurred in measurable characters in many of the lineages examined.

Pore diameter and bar width data are shown in Figure 22. Only sample means are shown, since for our pore and bar measurements the measurement error on an individual specimen is nearly as large as the measured value itself. This is a consequence of the small size of the characters being measured. Data of this

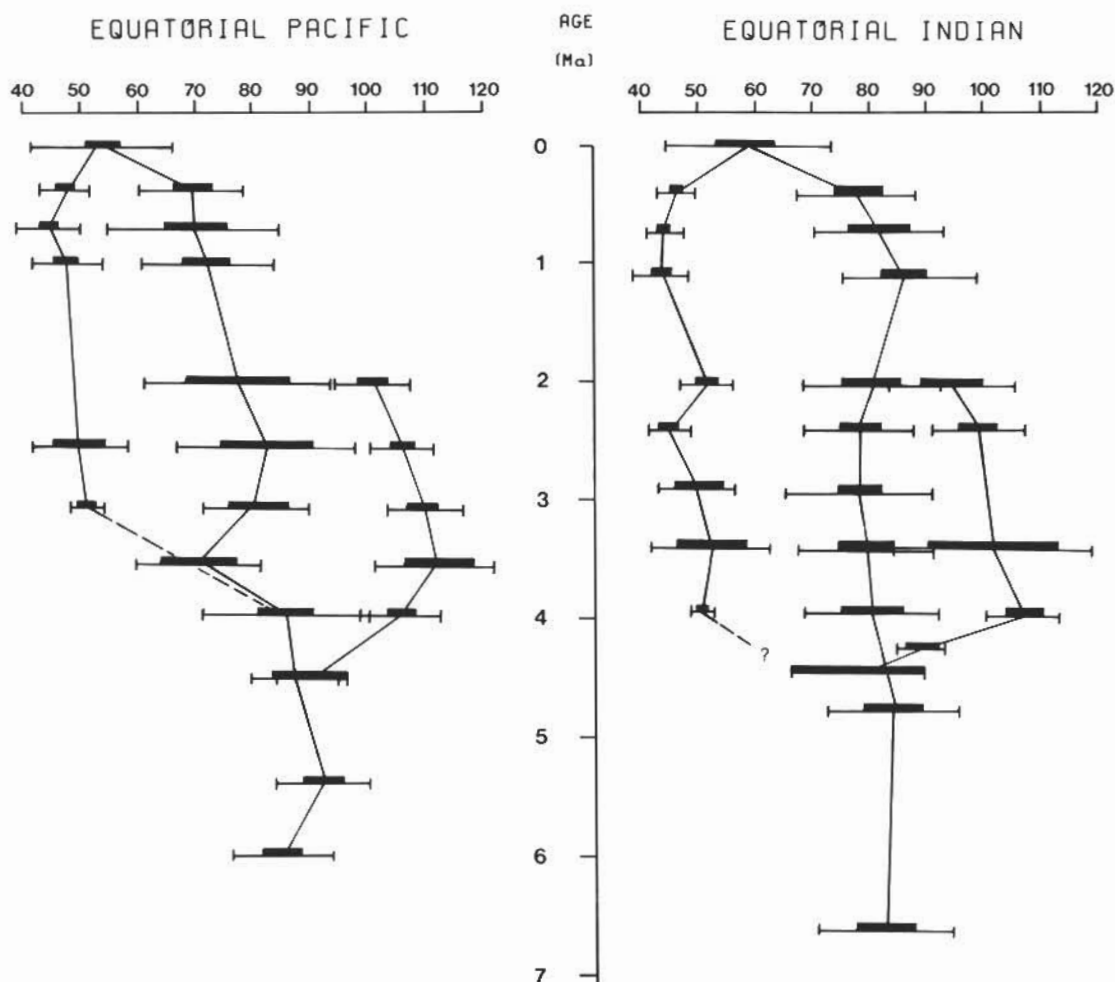


FIGURE 23—Rates of change in thorax length (in micrometers) in *Pterocanium praetextum*, *P. charybdeum*, and *P. prismatium*. Pacific and Indian Ocean data plotted separately. Left lineage in each plot is *P. praetextum*, middle lineage is *P. charybdeum*, and right lineage is *P. prismatium*. Thin lines in each sample mark  $\pm 1$  population standard deviation, heavy bars  $\pm 2$  standard errors for sample mean. Sample identifications shown in Figure 9, sample sizes in Appendix. Phylogeny from Figure 21. Latest Pleistocene sample plotted as a single population because of large number of intermediate forms.

sort, consequently, are also unusually sensitive to small systematic biases due to calibration errors, operator differences in measurement procedure, etc. To reduce this variance in data, all values for each sample have been normalized to that sample's mean values for *P. charybdeum*. While reducing systematic biases, normalized data, like all ratio data, magnify random measurement error. Nonetheless, the resulting scatterplot reveals significant differences between each lineage. *P. praetextum*, *P. prismatium*, and

*P. audax* are all reasonably well separated from *P. charybdeum* and from each other. *P. korotnevi* is not consistently separated from other taxa. The reason for this is not known. Data labeled "intermediates" will be discussed later. Because of the low resolution of our data on pore, and particularly bar dimensions, we have not attempted to use this information in an analysis of phyletic trends. These data, when viewed in conjunction with thorax length and width data, do serve, however, to objectively demonstrate that differ-

# Width of Thorax (in micrometers)

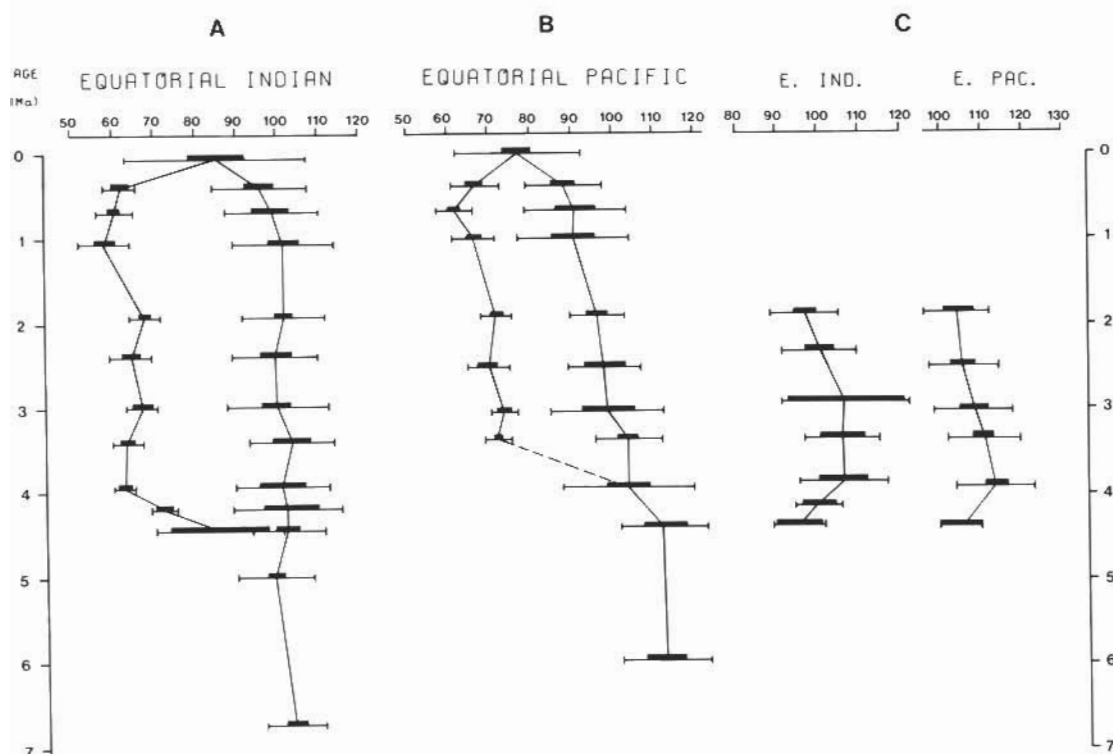


FIGURE 24—Rates of change in thorax width (in micrometers) in *Pterocanium praetextum*, *P. charybdeum*, and *P. prismatium*. Left lineage in A and B is *P. praetextum*, right is *P. charybdeum*. *P. prismatium* data overlap with *P. charybdeum* and is plotted separately (C). Plotting conventions as in Figure 23.

ences exist between taxa in more than just one or two characters.

Thoracic width and length data can distinguish between some, but not all, of the taxa in our study. Thoracic width most clearly differentiates between *P. praetextum* and *P. charybdeum*, while thoracic length discriminates not only *P. praetextum* from *P. charybdeum* (via size), but also *P. prismatium* from *P. charybdeum* (via the shape of the thorax). Therefore the quantified record of change in these characters should tell us something about the general rates of evolution of these lineages. Results of such a measurement program, representing several thousand individual measurements, are shown in Figures 23

and 24. Thorax size and shape are less important in distinguishing *P. korotnevi* and *P. audax* from the other lineages, nor can these characters be related to the evolutionary development of these taxa from their ancestors, since the ancestral forms are not known in either case. However, thorax width and thorax length trends in *P. korotnevi* and *P. audax* still serve as tests of stasis, and some data for these two species are shown in Figure 25. The development of each lineage is discussed separately below.

## PHYLETIC TRENDS

*Pterocanium charybdeum* lineage.—Evolution within the *P. charybdeum* lineage can

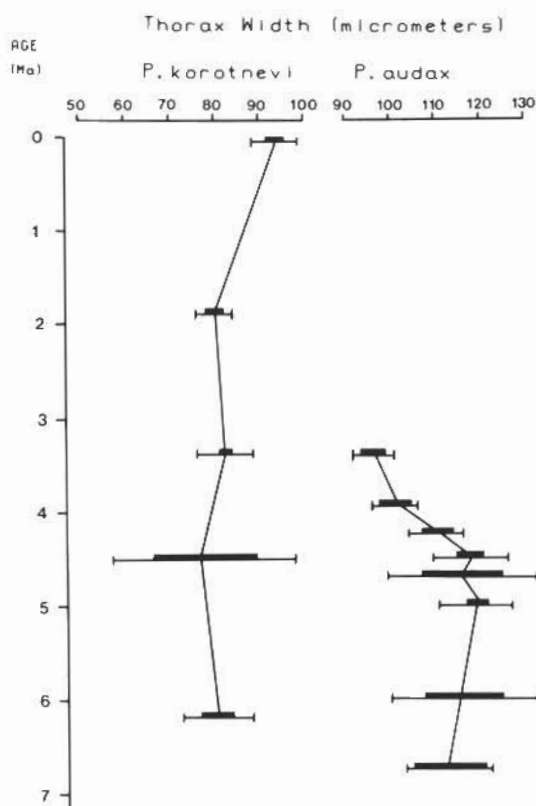


FIGURE 25—Rates of change in thorax width in *Pterocanium korotnevi* and *P. audax*. *P. korotnevi* data from North Pacific, *P. audax* data mostly from equatorial Indian and secondarily from DSDP site 158. Plotting conventions as in Figure 23.

be characterized by the persistence of an ancestral stock—*P. c. trilobum*—with the development of the additional subspecies *P. c. allium* and *P. c. charybdeum*. We did not investigate the history of *P. c. grandiporus*, and in our biometric work *P. c. grandiporus* was lumped with *P. c. trilobum*. In the later Miocene, *P. charybdeum* differentiates into a distinctive *P. c. allium* morphology, which dominates the lineage but does not extinguish *P. c. trilobum* entirely. Thus latest Miocene populations generally have more lightly silicified shells, shorter feet, smaller apical horns, etc. With the fragmentation of the *P. c. allium* population near the Mio-Pliocene boundary, the morphologic range within *P. charybdeum* once again becomes dominated by *P. c. trilobum* and *P. c. charybdeum*. The

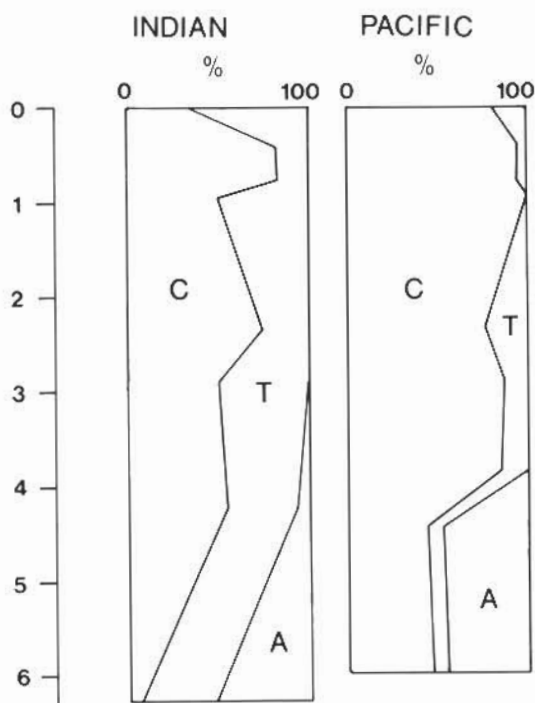


FIGURE 26—Changes in subspecies dominance within equatorial populations of *P. charybdeum*. A, *P. c. allium*; C, *P. c. charybdeum*; T, *P. c. trilobum*. Samples sizes and locations shown in Figure 9. History of *P. c. grandiporus* not investigated.

phyletic trends described here are beyond our ability to directly quantify, and a semi-quantitative approach must be used to document these changes. For each sample examined, individuals of *P. charybdeum* were assigned to one of the subspecies (other than *P. c. grandiporus*) formally recognized in our taxonomic section. This “binary” approach is somewhat artificial, since the phyletic change appears to have been continuous and gradual. It is also very subjective. Yet if the percent dominance of each end member is calculated, a reasonable approximation to the observed nature of the change is obtained. This is shown in Figure 26.

Long term trends in shell size (as measured by thorax width and thorax length) are seen in *P. charybdeum* (Figures 23 and 24). In the Indian Ocean, very little long term change is seen. The mean thoracic width fluctuates about a mean of ~105 micrometers, and the thorax length about a mean of ~80 micro-

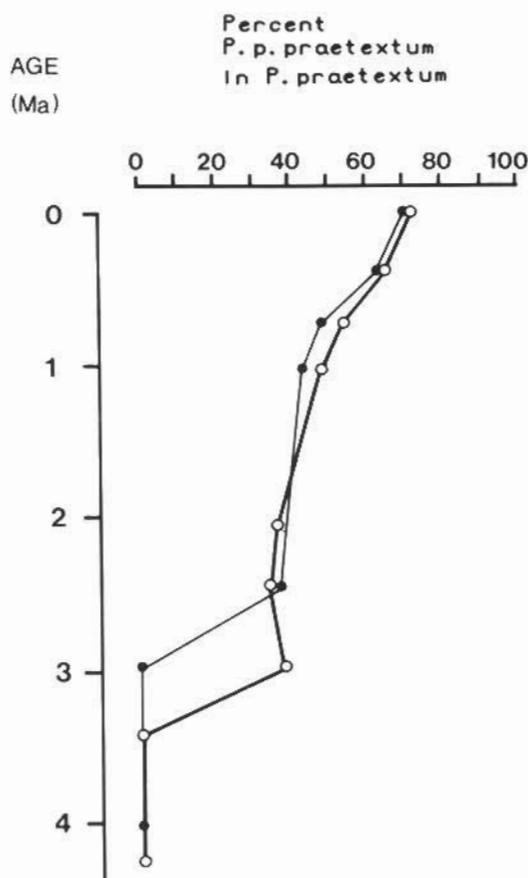


FIGURE 27—Phyletic increase in dominance of *P. p. praetextum* subspecies within the species *P. praetextum*. Solid dots, Pacific; open circles, Indian. Sample identifications in Figure 9, sample sizes in appendix.

meters. In the equatorial Pacific, however, long term phyletic change in thorax size is quite noticeable. Prior to 4 Ma, equatorial Pacific populations of *P. charybdeum* had significantly larger thorax widths than those of the equatorial Indian Ocean. Between 4 Ma and 3 Ma this differential disappeared, and by 2 Ma the equatorial Pacific populations had, in fact, become smaller than their Indian Ocean counterparts. The cause of this change is not known, but may be related to the initial absence and possible invasion of *P. praetextum* into the Pacific at approximately 3.5 Ma, and the subsequent convergence of *P. charybdeum* towards *P. praetextum*. Thorax length data show similar trends, although not so clearly as does thorax width.

*Pterocanium praetextum* lineage.—Trends

in *P. praetextum* were dominated by the gradual replacement of dominant *P. p. eucozum* morphology with *P. p. praetextum* morphology, and by the appearance of intermediate morphologies between *P. praetextum* and *P. charybdeum*. As shown in Figures 23 and 24, there is a slight, though significant, decrease in the width and length of the thorax in *P. praetextum* over the Pliocene–Pleistocene interval. As in the case of *P. charybdeum*, there is a consistent offset in thorax width and length measurements between the two regions, although not as large in *P. praetextum* as in *P. charybdeum*.

Documentation of the change within *P. praetextum* from *P. p. eucozum* to *P. p. praetextum* cannot be shown with thoracic width data, or for that matter any of the other measurable characters. We adopted, instead, the more subjective method described for *P. charybdeum*, of plotting subspecies dominance within the lineage through time. This is shown in Figure 27. The abundance of *P. p. praetextum* increases throughout the latter part of the Pliocene and all of the Pleistocene, and in a relatively gradual manner. There appears to be a significant difference in the morphologic state of the *P. praetextum* lineage between the two ocean basins at ~3.0 Ma, unlike the Pleistocene, when the two data sets are remarkably congruent. The Pacific data seems to lag that of the Indian Ocean, a finding consistent with the earlier development of substantial populations of *P. praetextum* in the Indian Ocean than in the Pacific Ocean.

*Pterocanium prismatium* lineage.—The evolution of *P. prismatium* is a distinctive event in the Pliocene radiolarian assemblage, as is its extinction near the Pliocene–Pleistocene boundary. Phyletic trends within the lineage are dominated by development of increasingly large, elongate, prismatic thoraxes, and by the associated development of elliptical pores in the thoracic lattice wall.

The phyletic evolution of *Pterocanium prismatium* was investigated previously by Kellogg and Hays (1975). They presented biometric data on the phyletic increase in thorax length in this lineage, based on samples taken from the same core (RC12-66) used in our study. In this earlier work, cladistic relationships of this species to other members of *Pterocanium* were not explicitly recognized. Thus, size data presented for *P. pris-*



*matium* in Kellogg and Hays (1975, fig. 4) actually represent two taxa in this study. Data from levels in the mid-Gilbert and younger, record evolutionary change in *P. prismatium*, as indicated. Below this level (~15 meters) the taxon measured is not *P. prismatium*, but rather *P. prismatium*'s ancestor, *P. charybdeum*. A more accurate representation of the evolution of *P. prismatium*, via speciation from *P. charybdeum*, is given in Figure 23, which includes data on thorax length for both *P. prismatium* and *P. charybdeum*. This figure, together with Kellogg and Hays (1975) data, shows the gradual nature of evolutionary divergence between these two lineages.

Measurements of thorax width in *P. prismatium* (Figure 24) differ from the pattern seen in measurements of thorax length. After an initial increase in width in the early Pliocene, stasis or slow decrease in thorax width is recorded. The pattern observed is largely the same in both the Pacific and Indian Oceans. As in other lineages, there is a persistent offset to the values between the two oceans. There is also some suggestion in the data that the decrease in thorax width in *P. prismatium* parallels decrease in the width of *P. charybdeum* populations, particularly in the equatorial Pacific. Confirmation of this, however, will require additional data on morphologic change in the two lineages.

The extinction of *P. prismatium* was a relatively sudden event whose synchronicity has been established by Hays (1971). A decrease in thorax length, shortly prior to extinction, has been observed in our data and by Kellogg and Hays (1975, fig. 4).

*Pterocanium audax* lineage.—The evolutionary history of *P. audax* is less well known than that of some of the other taxa in *Pterocanium*, as *P. audax* is usually common only in subtropical sites where our core coverage is weakest. Enough is known about this lineage to suggest significant amounts of evolution over the last few million years of its history, but details of this history still need to be worked out.

Early Late Miocene sediments contain a *Pterocanium* form that is sufficiently similar to the definition of *P. audax* given by Riedel (1953) that it may be conspecific. This morphology is characterized by a relatively small thorax, short feet, and an often smooth (not thorny) apical horn. In the later Miocene, specimens more typical of *P. audax* appear.

By the beginning of the Pliocene *P. audax* is well established in the equatorial Indian Ocean, and most specimens possess its characteristic robust thorax and thorny apical horn. However, this population soon becomes less common, and at the same time less distinctly different from *P. charybdeum*. The thorax size decreases (Figure 25), and development of thorns on the apical horn becomes less pronounced. These trends suggest renewed convergence towards *P. charybdeum* morphology, but unfortunately by this time the taxon has become so rare that the ultimate fate of the lineage has not been determined. The *P. audax* lineage became extinct in the Gauss.

*Pterocanium korotnevi* lineage.—The name *P. korotnevi*, as used in this study, encompasses a large group of forms whose evolutionary history is not well understood. Many morphotypes have been seen in the late Miocene and early Pliocene of the high latitudes, and the detailed history of this group may prove to be as complex as that of its lower latitude congeners. So far we have only been able to examine the relationships of the group as a whole to the other lineages studied.

*P. korotnevi* and *P. charybdeum* have been observed together in mid Late Miocene equatorial Pacific sediments, together with intermediate morphologies. Intergradation of this sort, by contrast, does not appear between the two taxa in later sediments. Intergradation between *P. korotnevi* and *P. praetextum* is seen instead.

As noted in the description of this group, in the Plio-Pleistocene, at least two morphotypes of *P. korotnevi* can be recognized, each distinct from late Miocene forms. Thus evolutionary changes occurred, as in the other lineages investigated. Because the characters involved in these changes were not primarily size related, we have not been able to adequately biometrically analyze these phyletic trends within *P. korotnevi*. The increase in mean thoracic width shown in Figure 25 suggests size-related evolution as well, although this must be confirmed by additional samples and a more refined taxonomic analysis.

#### RETICULATE PHYLOGENY AND POSSIBLE HYBRIDIZATION

In our analysis of *Pterocanium* we have noted several instances of possible phylogenetic reticulation and hybridization between



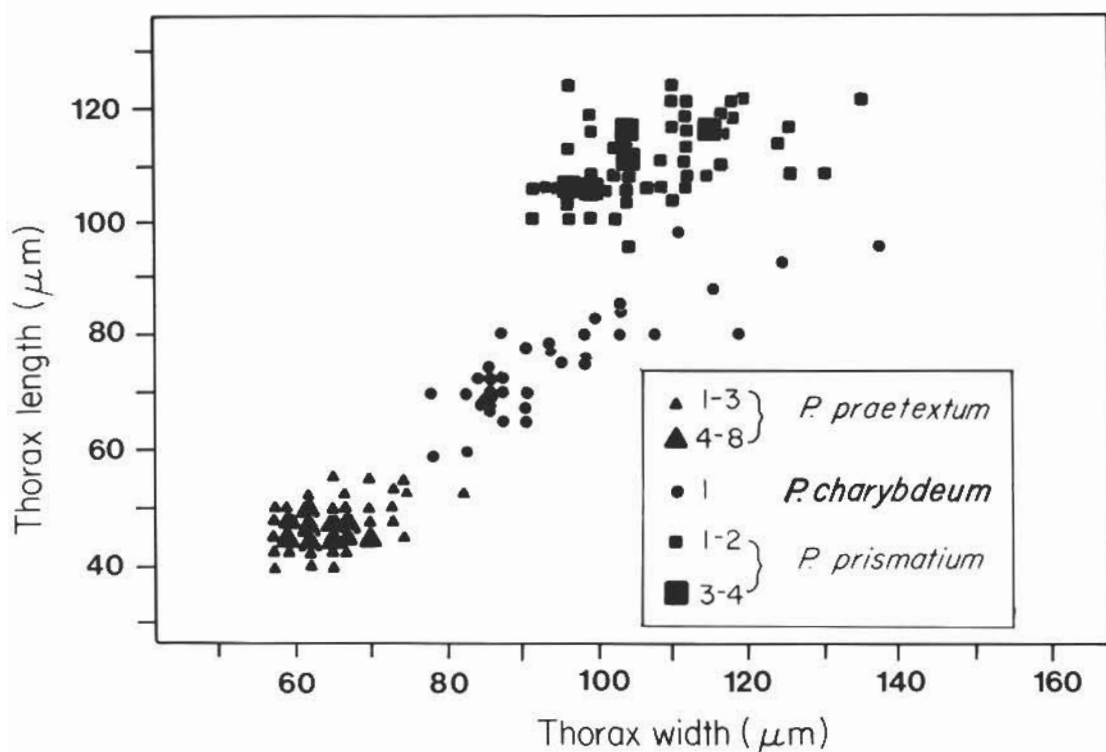


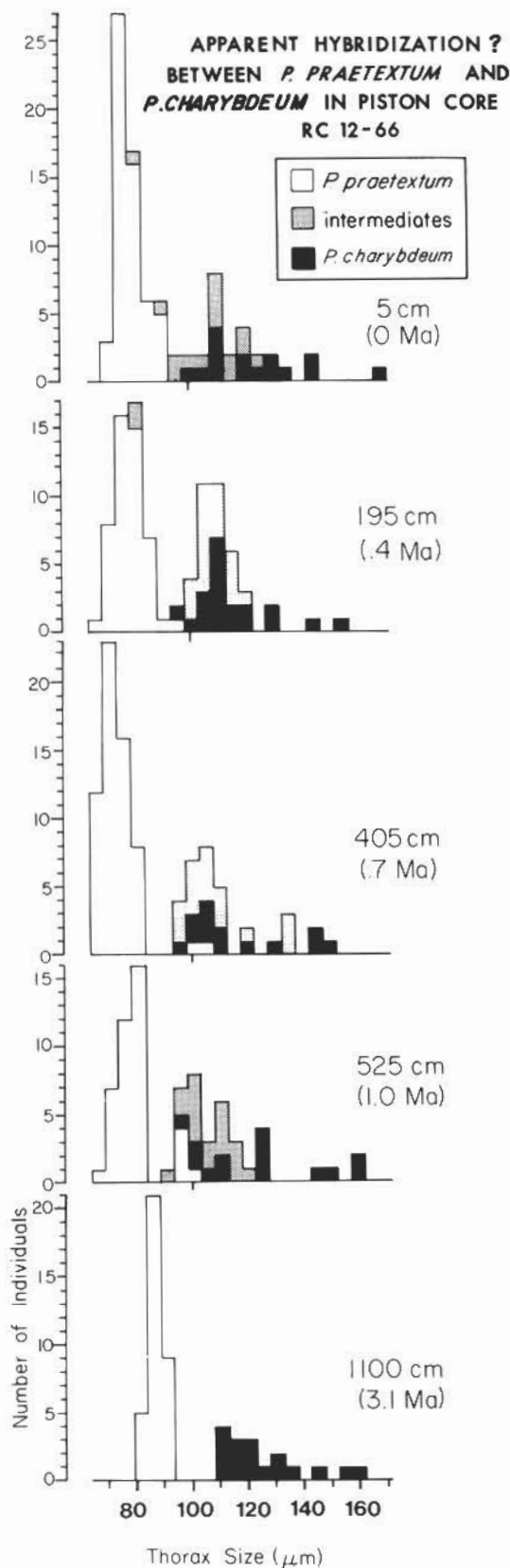
FIGURE 28—Scatterplot showing contrasting patterns of size and shape differentiation between equatorial Pacific populations of *P. praetextum*, *P. charybdeum*, and *P. prismatium*. Symbol sizes indicate number of individuals that plot in each unit area. Several samples have been combined to reflect the total range of variation in each species, although apparent hybrids and other problematic forms have been excluded. Data from RC12-66: 3–5 cm, 195 cm, 405 cm, 525 cm, and 1,100 cm.

lineages. Three occasions are particularly marked: between *P. charybdeum* and *P. audax* in the Late Miocene and earliest Pliocene; between *P. praetextum*, *P. korotnevi*, and *P. charybdeum* in the early Pliocene; and between *P. charybdeum* and *P. praetextum* in the late Pleistocene. These episodes of possible hybridization may have had substantial effects on the subsequent evolution of the lineages involved, and should be considered in any future model of evolutionary mechanisms in *Pterocanium*. We have concentrated on the morphologic convergence seen between *P. praetextum* and *P. charybdeum* in the late Pleistocene. Size is an important distinguishing character between these two lineages. As a result, thoracic width and length data can be used to investigate the history of this event.

The convergence between *P. charybdeum* and *P. praetextum* was followed in a series of samples from the equatorial Pacific. Tho-

racic width and length data are considered jointly in the scatterplot in Figure 28. The differentiating factor between the two lineages is primarily size, rather than shape, as the axis of between taxon differentiation is nearly isometric. "Size," calculated as the square root of thorax width times thorax length, was plotted as a sequence of histograms covering the late Pleistocene, and, for comparison, for a pre-Pleistocene sample as well (Figure 29).

Comparison of the mid-Pliocene level (3.1 Ma) to late Pleistocene samples indicates a reticulation event in thorax size data in the late Pleistocene. Middle Pliocene populations are clearly separated from each other, but are much less so in the latest Pleistocene. Different means still exist for the more or less arbitrarily defined end members, and each is still identified by a peak in the distribution. The interval between the two nodes however is populated by a nearly continuous spectrum



of intermediate valued individuals. The specimens comprising all of these populations were assigned to one of three taxonomic categories—*P. charybdeum*, *P. praetextum*, or “intermediate”—independently of, and prior to, measurement of any characters. Classification was based on the several other characters that differentiate the two end member lineages, e.g., foot length, foot shape, foot attachment angle, thorax outline, and development of abdominal veil (Table 1). The convergence of thoracic size data seems to coincide with the appearance of these taxonomically intermediate types. Further, “intermediate” morphologies, when measured, are intermediate in size. “Intermediates” also tend to be intermediate in pore and bar dimensions. This is shown in Figure 22.

#### DISCUSSION AND CONCLUSIONS

We have attempted to define the nature of evolutionary change in a representative group of deep-sea microfossils. Three features of the evolutionary patterns observed seem to us to be of particular importance:

1) In all lineages of *Pterocanium* that we have studied so far, morphologic evolution appears to be very gradual, though by no means uniform in rate or direction. Changes in subspecies dominance are gradual, quantitative rates of change in size measurements are gradual, and morphologic divergence of lineages is gradual. Complete stasis within a lineage is rare.

2) Complex patterns of geographic variation exist, which can be related to temporal records of morphologic evolution. Equatorial assemblages of Radiolaria differ significantly in the abundance of various specific and subspecific taxa of *Pterocanium*, and the temporal records of individual lineages occasionally differ between regions. Dramatic differences exist between low and high latitude faunas (e.g., *P. charybdeum* and *P. p. praetextum* in the tropics, *P. p. euclorum* in

FIGURE 29—Progressive convergence and apparent hybridization between *Pterocanium* lineages in the late Pleistocene. Horizontal scale for all plots is identical—100 micrometer mark shown on each for reference. Vertical spacing of plots not scaled to absolute age. Size is defined in text.

the subtropics, and *P. korotnevi* in the North Pacific), and these differences in some cases (e.g., *P. p. praetextum* vs. *P. p. euclpum*) mimic phylogenetic trends.

3) A seemingly reticulate phylogenetic pattern is perhaps the most surprising feature of our data. Possible intergradation between what were formerly two distinct lineages was observed in three instances—between *P. charybdeum* and *P. audax* in the latest Miocene and early Pliocene, between *P. korotnevi* or *P. charybdeum* and *P. praetextum* in the Pliocene, and between *P. charybdeum* and *P. praetextum* in the Pleistocene.

If we assume that the observed morphologic changes in *Pterocanium* reflect underlying changes in the genetic/developmental makeup of *Pterocanium*, what can we say about evolutionary processes in these planktonic protists? What additional information do we need to be able to test hypotheses of evolutionary pattern and mechanism against our data? The answers to these questions depend largely on the particular hypothesis being tested. We consider one widely debated one here: the "punctuated equilibrium" model of Eldredge and Gould (1972).

"Punctuated equilibrium" is actually a set of three hypotheses—two of mechanism and one of pattern derived from the mechanistic hypotheses. "Punctuated equilibrium" predicts that the pattern of species level evolution is one of saltation and stasis: lineages show little evolutionary change on either a short term or a long term basis, when compared to the rates and absolute amounts of change which occur during cladogenesis (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Stanley, 1979). The basis for this pattern of evolutionary change is in the nature of the processes that underlie speciation and control the subsequent fate of the lineage. Speciation is assumed to follow neontologic models of evolution that predict speciation occurring on time scales of one thousand years or so (Mayr, 1963) or even less (White, 1978). Established lineages are additionally presumed to be controlled by strong homeostatic mechanisms (Mayr, 1963, 1970), which limit further evolutionary change.

Our observations of both qualitative and quantitative morphologic change in *Ptero-*

*canium* suggests gradual phyletic evolution and equally gradual cladogenesis, rather than stasis and saltation. We conclude that the models of saltational speciation and subsequent homeostasis are not valid descriptors of evolution in our *Pterocanium* species. Other models must be considered that are more in accord with continuous, gradual rates of evolutionary change.

More knowledge is needed of the biology of *Pterocanium* and other deep-sea planktonic protists, to understand how such features as reproductive behavior affect long term evolutionary patterns. The possibility of hybridization in *Pterocanium* suggests that these effects may be substantial. Hybridization in plants, for example, has played a major role in their evolution (Grant, 1971), and hybridization in marine microfossil taxa, if widespread, would presumably have similar major effects (Goll, 1976, 1979; Lazarus, 1983).

Finally, many more quantitative analyses of evolutionary change are needed, in *Pterocanium*, in other marine microfossil groups, and for other types of fossils as well. More attention must be paid to studying geographic variation in morphology in conjunction with studies of local temporal change. This is necessary not only to detect potential biases in temporal records due to migration, but also to better understand the nature of biological variation which contributes to the evolution of species.

We believe that as these factors become better known, deep-sea microfossil sequences will provide significant new evidence on the nature of evolution through geologic time.

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## APPENDIX

Sample sizes (N), means (X) and standard deviations (S.D.) of biometric data for 4 characters in *Pterocanium*: thorax width (TW), thorax length (TL), thorax pore diameter (PORE), and thorax bar width (BAR). Values in micrometers. Pore and bar values listed separately for "intermediates" between *P. charybdeum* and *P. praetextum* (e.g., *P. charybdeum* convergent towards *P. praetextum*—see text). Thorax width and length data for "intermediates" combined with that of *P. charybdeum*. Asterisk denotes levels where extensive, continuous morphologic intergradation between *P. charybdeum* and *P. praetextum* exists and the two taxa are not separately distinguished (see text)—values given under *P. charybdeum* for both types, inclusive.

TABLE 2—*P. charybdeum*.

| Sample         | TW  |           |      | TL  |           |      | PORE |           |      | BAR |           |      |
|----------------|-----|-----------|------|-----|-----------|------|------|-----------|------|-----|-----------|------|
|                | N   | $\bar{x}$ | S.D. | N   | $\bar{x}$ | S.D. | N    | $\bar{x}$ | S.D. | N   | $\bar{x}$ | S.D. |
| PACIFIC        |     |           |      |     |           |      |      |           |      |     |           |      |
| RC12-66, 2,535 | 37  | 112.7     | 10.7 | 35  | 85.0      | 9.0  | 18   | 7.2       | 1.2  | 18  | 1.1       | 0.5  |
| RC12-66, 2,000 | —   | —         | —    | 23  | 92.7      | 9.6  | —    | —         | —    | —   | —         | —    |
| RC12-66, 1,595 | 23  | 112.3     | 10.7 | 20  | 87.5      | 7.6  | 23   | 8.2       | 1.3  | 23  | 1.6       | 0.7  |
| RC12-66, 1,395 | 44* | 103.4     | 16.0 | 41* | 88.5      | 11.9 | 11   | 5.9       | 1.4  | 11  | 2.2       | 1.0  |
| RC12-66, 1,187 | 48  | 103.6     | 8.4  | 20  | 70.4      | 13.6 | —    | —         | —    | 35  | 1.3       | 0.6  |
| RC12-66, 1,100 | 21  | 98.4      | 13.8 | 17  | 81.1      | 9.3  | 21   | 7.2       | 1.6  | 21  | 1.9       | 0.7  |
| RC12-66, 900   | 17  | 98.0      | 8.8  | 13  | 82.3      | 15.3 | 13   | 7.5       | 1.9  | 13  | 1.5       | 0.5  |
| RC12-66, 665   | 50  | 96.6      | 8.4  | 14  | 77.7      | 16.5 | 50   | 5.8       | 1.3  | 50  | 1.7       | 0.8  |
| RC12-66, 525   | 35  | 90.4      | 13.5 | 37  | 72.1      | 11.6 | 18   | 6.0       | 1.3  | 18  | 1.7       | 1.3  |
| RC12-66, 405   | 32  | 91.2      | 12.3 | 33  | 70.1      | 15.2 | 15   | 6.3       | 1.6  | 15  | 2.1       | 0.9  |
| RC12-66, 195   | 45  | 88.1      | 9.6  | 43  | 69.8      | 9.6  | 24   | 5.4       | 1.8  | 24  | 1.1       | 0.5  |
| RC12-66, top   | 91* | 76.7      | 15.8 | 87* | 54.2      | 12.7 | 17   | 7.7       | 1.2  | 17  | 1.9       | 0.7  |
| INDIAN         |     |           |      |     |           |      |      |           |      |     |           |      |
| RC12-335, bot  | 38  | 104.3     | 7.1  | 21  | 82.8      | 11.7 | 38   | 6.5       | 1.3  | 38  | 2.0       | 0.6  |
| V19-169, 1,120 | 103 | 99.7      | 9.5  | 18  | 84.1      | 11.1 | —    | —         | —    | —   | —         | —    |
| V19-169, 1,080 | 50  | 102.7     | 8.6  | —   | —         | —    | —    | —         | —    | —   | —         | —    |
| V19-169, 1,000 | 21  | 103.2     | 13.6 | —   | —         | —    | 26   | 7.0       | 1.7  | 26  | 1.6       | 0.6  |
| V29-40, 1,732  | 20  | 101.7     | 11.5 | 16  | 81.1      | 12.0 | 20   | 7.2       | 1.4  | 20  | 1.8       | 0.7  |
| V19-169, 656   | 24  | 103.9     | 10.6 | 20  | 80.2      | 11.7 | 24   | 7.2       | 1.6  | 24  | 1.7       | 0.7  |
| V29-40, 1,300  | 66  | 100.2     | 12.7 | 56  | 78.4      | 13.1 | 67   | 7.3       | 1.6  | 67  | 1.7       | 0.7  |
| V29-40, 1,130  | 40  | 100.5     | 10.6 | 36  | 78.3      | 10.0 | 40   | 6.7       | 1.2  | 40  | 1.8       | 0.7  |
| V19-171, 465   | 93  | 102.4     | 10.2 | 22  | 80.8      | 12.1 | 93   | 8.1       | 2.0  | 93  | 1.5       | 0.7  |
| RC14-22, 800   | 57  | 102.3     | 12.3 | 50  | 84.7      | 12.4 | 51   | 7.4       | 1.3  | 51  | 1.7       | 0.7  |
| RC14-22, 600   | 33  | 99.5      | 11.4 | 28  | 78.7      | 11.6 | 23   | 8.5       | 1.1  | 23  | 1.9       | 0.7  |
| RC14-22, 300   | 49  | 96.5      | 11.2 | 43  | 77.1      | 11.1 | 38   | 7.5       | 1.5  | 38  | 1.7       | 0.6  |
| V19-169, top   | 54* | 86.1      | 22.4 | 50* | 58.7      | 15.0 | 24   | 8.8       | 1.2  | 24  | 1.9       | 0.9  |

TABLE 3—*P. praetextum*.

| Sample         | TW |           |      | TL |           |      | PORE |           |      | BAR |           |      |
|----------------|----|-----------|------|----|-----------|------|------|-----------|------|-----|-----------|------|
|                | N  | $\bar{x}$ | S.D. | N  | $\bar{x}$ | S.D. | N    | $\bar{x}$ | S.D. | N   | $\bar{x}$ | S.D. |
| PACIFIC        |    |           |      |    |           |      |      |           |      |     |           |      |
| RC12-66, 1,395 | *  | —         | —    | *  | —         | —    | 5    | 4.2       | 0.6  | 5   | 1.8       | 0.7  |
| RC12-66, 1,187 | 61 | 71.5      | 3.3  | —  | —         | —    | 20   | 4.4       | 1.2  | 30  | 0.9       | 0.2  |
| RC12-66, 1,100 | 39 | 72.8      | 2.7  | 35 | 51.3      | 3.4  | 39   | 4.5       | 0.8  | 39  | 1.6       | 0.7  |
| RC12-66, 900   | 21 | 69.4      | 5.2  | 17 | 50.2      | 8.5  | 21   | 4.0       | 1.0  | 21  | 1.2       | 0.6  |
| RC12-66, 665   | 25 | 71.8      | 3.9  | —  | —         | —    | 25   | 5.2       | 0.8  | 25  | 1.1       | 0.4  |
| RC12-66, 525   | 44 | 66.4      | 5.6  | 41 | 47.9      | 6.2  | 44   | 3.8       | 0.8  | 44  | 1.6       | 0.8  |
| RC12-66, 405   | 61 | 61.4      | 4.8  | 59 | 44.7      | 5.9  | 61   | 4.0       | 0.7  | 61  | 1.1       | 0.5  |
| RC12-66, 195   | 50 | 66.0      | 6.2  | 51 | 47.6      | 4.6  | 51   | 4.2       | 0.8  | 51  | 1.1       | 0.6  |
| RC12-66, top   | *  | —         | —    | *  | —         | —    | 59   | 4.5       | 0.9  | 59  | 1.0       | 0.4  |
| INDIAN         |    |           |      |    |           |      |      |           |      |     |           |      |
| V19-169, 1,080 | 8  | 86.1      | 15.6 | —  | —         | —    | —    | —         | —    | —   | —         | —    |
| V19-169, 1,000 | 24 | 72.5      | 3.5  | —  | —         | —    | 21   | 4.0       | 0.6  | 21  | 1.2       | 0.4  |
| V29-40, 1,732  | 25 | 63.0      | 2.5  | 12 | 50.2      | 1.8  | 25   | 5.3       | 0.9  | 25  | 0.9       | 0.2  |
| V19-169, 656   | 26 | 63.7      | 3.8  | 13 | 52.7      | 10.3 | 26   | 4.5       | 1.3  | 26  | 1.0       | 0.3  |
| V29-40, 1,300  | 15 | 67.9      | 3.6  | 14 | 50.5      | 7.0  | 15   | 3.8       | 0.6  | 15  | 0.8       | 0    |
| V29-40, 1,130  | 23 | 65.0      | 5.2  | 19 | 45.2      | 3.7  | 21   | 4.0       | 0.4  | 21  | 0.9       | 0.2  |
| V19-171, 465   | 62 | 68.4      | 3.9  | 22 | 51.8      | 4.8  | 62   | 5.1       | 0.9  | 62  | 1.0       | 0.4  |
| RC14-22, 800   | 41 | 58.8      | 6.6  | 41 | 43.4      | 5.1  | 41   | 3.8       | 0.8  | 41  | 0.9       | 0.2  |
| RC14-22, 600   | 67 | 61.3      | 4.9  | 65 | 43.8      | 3.4  | 67   | 3.9       | 0.6  | 67  | 1.0       | 0.5  |
| RC14-22, 300   | 49 | 62.7      | 4.1  | 46 | 46.4      | 3.4  | 50   | 3.9       | 0.6  | 50  | 0.9       | 0.2  |
| V19-169, top   | *  | —         | —    | *  | —         | —    | 25   | 5.0       | 0.4  | 25  | 0.9       | 0.2  |



TABLE 4—*P. charybdeum*/*P. praetextum* intermediates.

| Sample         | TW |           |      | TL |           |      | PORE |           |      | BAR |           |      |
|----------------|----|-----------|------|----|-----------|------|------|-----------|------|-----|-----------|------|
|                | N  | $\bar{x}$ | S.D. | N  | $\bar{x}$ | S.D. | N    | $\bar{x}$ | S.D. | N   | $\bar{x}$ | S.D. |
| PACIFIC        |    |           |      |    |           |      |      |           |      |     |           |      |
| RC12-66, 1,395 | —  | —         | —    | —  | —         | —    | 19   | 4.8       | 1.5  | 19  | 1.1       | 0.2  |
| RC12-66, 900   | —  | —         | —    | —  | —         | —    | 9    | 6.1       | 1.5  | 9   | 1.3       | 0.6  |
| RC12-66, 525   | —  | —         | —    | —  | —         | —    | 21   | 5.5       | 1.0  | 21  | 1.4       | 0.5  |
| RC12-66, 405   | —  | —         | —    | —  | —         | —    | 19   | 5.7       | 1.0  | 19  | 1.7       | 0.7  |
| RC12-66, 195   | —  | —         | —    | —  | —         | —    | 22   | 4.8       | 0.8  | 22  | 1.3       | 0.5  |
| RC12-66, top   | —  | —         | —    | —  | —         | —    | 15   | 6.0       | 1.0  | 15  | 1.7       | 0.9  |
| INDIAN         |    |           |      |    |           |      |      |           |      |     |           |      |
| V19-169, 1,000 | —  | —         | —    | —  | —         | —    | 3    | 4.5       | 0.6  | 3   | 1.0       | 0    |
| V29-40, 1,300  | —  | —         | —    | —  | —         | —    | 2    | 3.9       | 0    | 2   | 0.8       | 0    |
| V29-40, 1,130  | —  | —         | —    | —  | —         | —    | 2    | 5.2       | 1.8  | 2   | 1.7       | 1.3  |
| RC19-22, 800   | —  | —         | —    | —  | —         | —    | 6    | 5.0       | 1.0  | 6   | 1.0       | 0.3  |
| RC19-22, 600   | —  | —         | —    | —  | —         | —    | 10   | 6.6       | 1.3  | 10  | 1.6       | 0.7  |
| RC19-22, 300   | —  | —         | —    | —  | —         | —    | 11   | 6.4       | 0.9  | 11  | 1.6       | 0.7  |
| V19-169, top   | —  | —         | —    | —  | —         | —    | 4    | 5.2       | 0    | 4   | 0.9       | 0.3  |

TABLE 5—*P. prismatum*.

| Sample         | TW |           |      | TL |           |      | PORE |           |      | BAR |           |      |
|----------------|----|-----------|------|----|-----------|------|------|-----------|------|-----|-----------|------|
|                | N  | $\bar{x}$ | S.D. | N  | $\bar{x}$ | S.D. | N    | $\bar{x}$ | S.D. | N   | $\bar{x}$ | S.D. |
| PACIFIC        |    |           |      |    |           |      |      |           |      |     |           |      |
| RC12-66, 1,595 | 4  | 105.0     | 4.6  | 4  | 91.7      | 5.4  | 4    | 8.6       | 0    | 4   | 1.0       | 0    |
| RC12-66, 1,395 | 50 | 113.7     | 8.1  | 42 | 106.7     | 7.2  | 51   | 7.1       | 1.1  | 51  | 2.0       | 0.8  |
| RC12-66, 1,187 | 66 | 110.7     | 9.1  | 15 | 112.7     | 10.8 | —    | —         | —    | —   | —         | —    |
| RC12-66, 1,100 | 36 | 108.6     | 9.8  | 36 | 111.0     | 6.8  | 37   | 8.0       | 1.7  | 37  | 2.0       | 0.7  |
| RC12-66, 900   | 39 | 105.5     | 8.8  | 39 | 107.0     | 5.8  | 41   | 8.4       | 1.5  | 41  | 1.6       | 0.6  |
| RC12-66, 665   | 25 | 104.2     | 8.2  | 15 | 101.3     | 6.6  | —    | —         | —    | —   | —         | —    |
| INDIAN         |    |           |      |    |           |      |      |           |      |     |           |      |
| V19-169, 1,080 | 2  | 96.2      | 3.6  | 2  | 79.3      | 12.9 | —    | —         | —    | —   | —         | —    |
| V19-169, 1,000 | 9  | 100.9     | 6.0  | 9  | 88.9      | 3.2  | 9    | 7.8       | 1.4  | 9   | 1.1       | 0.4  |
| V29-40, 1,732  | 17 | 107.1     | 10.9 | 13 | 107.7     | 6.4  | —    | —         | —    | —   | —         | —    |
| V19-169, 656   | 15 | 107.3     | 9.1  | 8  | 101.8     | 16.8 | —    | —         | —    | —   | —         | —    |
| V29-40, 1,300  | 7  | 107.7     | 16.8 | —  | —         | —    | 7    | 7.8       | 0    | 7   | 1.4       | 0.6  |
| V29-40, 1,130  | 34 | 101.6     | 9.4  | 33 | 99.4      | 8.4  | 34   | 7.5       | 0.8  | 34  | 1.0       | 0.6  |
| V19-171, 465   | 53 | 98.0      | 8.6  | 16 | 94.4      | 11.1 | —    | —         | —    | —   | —         | —    |

TABLE 6—*P. audax*.

| Sample         | TW |           |      | TL |           |      | PORE |           |      | BAR |           |      |
|----------------|----|-----------|------|----|-----------|------|------|-----------|------|-----|-----------|------|
|                | N  | $\bar{x}$ | S.D. | N  | $\bar{x}$ | S.D. | N    | $\bar{x}$ | S.D. | N   | $\bar{x}$ | S.D. |
| PACIFIC        |    |           |      |    |           |      |      |           |      |     |           |      |
| 158-16-2       | 16 | 116.5     | 16.1 | —  | —         | —    | —    | —         | —    | —   | —         | —    |
| 158-9-2        | 5  | 112.0     | 8.7  | —  | —         | —    | —    | —         | —    | —   | —         | —    |
| RC12-66, 1,395 | 2  | 104.0     | 3.7  | —  | —         | —    | 2    | 7.2       | 0.9  | 2   | 3.9       | 0    |
| INDIAN         |    |           |      |    |           |      |      |           |      |     |           |      |
| RC12-335, bot  | 7  | 113.3     | 10.0 | —  | —         | —    | 7    | 8.4       | 1.6  | 7   | 4.4       | 0.8  |
| V19-169, 1,120 | 90 | 120.0     | 8.6  | —  | —         | —    | —    | —         | —    | —   | —         | —    |
| V19-169, 1,080 | 49 | 118.1     | 8.6  | —  | —         | —    | —    | —         | —    | —   | —         | —    |
| V19-169, 1,000 | 19 | 110.8     | 6.6  | —  | —         | —    | 19   | 8.7       | 1.3  | 19  | 3.7       | 0.6  |
| V29-40, 1,732  | 12 | 101.2     | 5.7  | —  | —         | —    | 12   | 10.2      | 1.3  | 18  | 5.2       | 1.1  |
| V19-169, 656   | 13 | 96.8      | 4.6  | —  | —         | —    | 13   | 9.0       | 1.0  | 13  | 1.7       | 0.8  |
| V29-40, 1,300  | 2  | 97.5      | 9.2  | —  | —         | —    | 2    | 8.5       | 0.9  | 2   | 2.0       | 0.9  |

TABLE 7—*P. korotnevi*.

| Sample         | TW |           |      | TL |           |      | PORE |           |      | BAR |           |      |
|----------------|----|-----------|------|----|-----------|------|------|-----------|------|-----|-----------|------|
|                | N  | $\bar{x}$ | S.D. | N  | $\bar{x}$ | S.D. | N    | $\bar{x}$ | S.D. | N   | $\bar{x}$ | S.D. |
| PACIFIC        |    |           |      |    |           |      |      |           |      |     |           |      |
| RC12-66, 525   | 7  | 60.5      | 11.7 | —  | —         | —    | 7    | 9.1       | 1.8  | 7   | 2.8       | 0.9  |
| RC12-66, 405   | 3  | 56.3      | 6.5  | —  | —         | —    | 3    | 4.8       | 2.7  | 3   | 2.6       | 0    |
| RC12-66, 195   | 3  | 61.5      | 3.0  | —  | —         | —    | 3    | 8.2       | 1.5  | 3   | 4.3       | 0.8  |
| RC12-66, top   | 9  | 59.5      | 6.0  | —  | —         | —    | 9    | 10.2      | 2.8  | 9   | 2.9       | 1.1  |
| INDIAN         |    |           |      |    |           |      |      |           |      |     |           |      |
| V19-171, 465   | 3  | 79.7      | 4.0  | —  | —         | —    | 3    | 5.2       | 0    | 3   | 1.0       | 0.3  |
| V19-169, 1,120 | 3  | 83.4      | 4.0  | —  | —         | —    | —    | —         | —    | —   | —         | —    |
| 158-9-2, 50-1  | 2  | 76.7      | 12.8 | —  | —         | —    | 3    | 5.2       | 1.0  | 3   | 1.7       | 0.6  |
| V21-198, 20    | 21 | 93.8      | 5.2  | —  | —         | —    | —    | —         | —    | —   | —         | —    |
| V21-148, 630   | 30 | 79.8      | 6.4  | —  | —         | —    | 30   | 6.5       | 2.2  | 30  | 1.9       | 0.8  |
| V20-105, 466   | 39 | 82.1      | 6.0  | —  | —         | —    | 39   | 5.3       | 1.3  | 39  | 1.9       | 0.7  |
| V21-148, 940   |    |           |      |    |           |      |      |           |      |     |           |      |
| RC12-431-574   | 24 | 80.3      | 8.0  | —  | —         | —    | 26   | 5.4       | 1.5  | 26  | 1.9       | 0.6  |