EVOLUTION OF THE RADIALARIAN SPECIES-COMPLEX
PTEROCANUM: A PRELIMINARY SURVEY

DAVID LAZARUS; REED P. SCHERER AND DONALD R. PROTHERO
Department of Geological Sciences, Columbia University, New York 10027 and
LaMont-DeHaven Geological Observatory, Palisades, New York 10964;
Department of Geology, University of South Carolina, Columbia 29208 and
Department of Geology, Knox College, Galesburg, Illinois 61401

ABSTRACT—A global taxonomic and biometric study of the radialarian genus Pterocanium defines
5 major lineages over the last 6 million years: Pterocanium charbyldrum, P. praetextum, P. speci-
men, P. praeuman and P. audax. P. charbyldrum is divided into 4 subgroups: P. charbyldrum
charbyldrum (n. comb.), P. charbyldrum trilobum (n. comb.), P. charbyldrum praetextum (n. comb.),
and P. charbyldrum specimen (n. subsp.).

Symporphic or paraporphic speciation of P. praetextum and P. specimen from ancestral P. char-
byldrum was observed over a one-half million year interval in the latest Miocene and early Pliocene.
Measurements of biometric and qualitative observations suggest substantial, gradual phylo-
etic 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 im-
portance to this work, as nowhere else in the fossil record can be found such a combination of stratigraphic continuity, geographic con-
trol, and large sample sizes (Prothero and Lazarus, 1980; Lipp, 1981).

To use these unique records, we must un-
dersand certain factors. Geographic varia-
tion, for example, can make individual fossil
sequences difficult to interpret (Gould and Eldredge, 1977; Bookstein et al., 1978).

Taxonomic assumptions, stratigraphic reso-
olution, measurement techniques, and sam-
pling artifacts can also affect our ability to
use microfossil sequences to study evolution-
ary patterns. To assess the importance of these
factors in stratigraphic micropaleontology,
we have carried out an exploratory study of the late Neogene evolution of the radialarian
genus Pterocanium (Otheberg, 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 anal-
lysis. These data provide an unusually com-
plete 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 radialarian bio-
geographic 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 bio-
stratigraphic and magnetostratigraphic da-
tum levels to the standardized time scales
provided by Labrecque et al. (1977), Manki-
nen and Dalrymple (1979), Teytier and Haut-
mond (1974), Teytier et al. (1978), Harris and
Opdyke (1971) and Hayek (1979). More de-
tailed analysis was done on a subset of these
cores.

For each of 4 regional stratigraphic se-
cquences used in the detailed phase of this
project, several levels, spaced about 1.5 mil-
lion years apart, were sampled for initial
analysis. These levels were located at mag-
netic reversal datum levels and form globally

1 Present address: Woods Hole Oceanographic
Institute, Woods Hole, Massachusetts 02543.

Copyright © 1985, The Society of Economic
Paleontologists and Mineralogists and
The Paleontological Society.

183
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 these cores not mentioned elsewhere, see: DSDP 266, Hayes, Frakes et al. (1975); DSDP 278, Kennett, Hoatz, et al. (1975); DSDP 329, Barker, Dalziel, et al. (1977); DSDP 348, Talwani, Udintsev, et al. (1976); DSDP 314, Ludwig, Krasnennikov, et al. (1980). Stratigraphy of RCB-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), "S" 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-anomaly, 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 Pervencian 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 Thayer and Hammond (1974) and Thayer 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 Pervencian's evolutionary history in the equatorial Indian Ocean. Preservation of Pervencian specimens was generally good, although breakage sometimes made biometric analysis difficult. Late Pliocene 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 lowest 50 cm of RC12-335 contains abundant, well preserved radiolarians. The occurrence of the radiolarian stratigraphic indicator species Stichocorys delimantens, Didiemyris antependilum, Spongaster bermingianus, and Acrocyrtis tubularis, together with the absence of Trisolenia ommittatus and Diatrea Hughesi, indicate an age for this sediment of ~6.8 ± 0.2 Ma. Biostratigraphic data for DSDP sites 214 and 228 was taken from the relevant initial report volumes (Van 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 Pervencian diversity is thought to have taken place. Tropical Pacific.—The biostratigraphy (Saito et al., 1975) and magnetostratigraphy

---

**Figure 2**—Composite piston core set from the equatorial Indian Ocean. Bold numbers refer to the following radiolarian datum levels: 1, top Pervencian prominens; 2, top Stichocorys preproconsul; 3, top Spongaster prospect; 5, top Didiemyris antependilum; 6, top Spongaster bermingianus; 7, top Trisolenia ommittatus; 8, top Acrocyrtis tubularis. Smaller numbers associated with each datum level are depth to datum in core in centimeters. Histostratigraphic units (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 communication).
D. LAZARUS, R. P. SCHERER AND D. R. PROTHERO

EQUATORIAL INDIAN OCEAN
DSDP DRILL CORES

SITE 214

SITE 238

CLEMI

CORR DEPTH (METERS)

Fost, 1970) of piston cores RC12-65 and RC12-66 is well documented (Figure 4). Preservation of Peritetrath 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
rate of more than 4 cm/1000 years (Bukry, 1973; Dinkelman, 1973; Biscaye 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 V20-025. 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; Ketner, 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 micron 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-
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. Eye-piece micrometers on Wild M20 research microscopes (40× objectives and 10× oculars), and with a resolution of ±0.3 micrometers, were used for the majority of the measurements. A microcomputer digitizer system with a resolution of ±0.7 micrometers was used for a few of the most recently acquired measurements.

In order to define the higher level systematic hypothesis that delimits the range of ra-
diolarian lineages under investigation it was necessary to revise the genus *Pterocanium*. Although this revision was 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 summarized 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 genera and species were based on isolated specimens or were defined on the basis of single characters. In our conception, the generic morphologic type that embraces the lineages in question is a nasellarian with a small spherical cephalon and thorax possessing three thoracic ridges, 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 *Pterocanidi* skeletal type have been divided by Haeckel (1887) into some half dozen genera: *Lychnocanium*, *Theopodium*, *Neupodium*, *Lychnodicytum*, *Dicytophism*, *Pterocorys*, *Podocorys*, and *Pterocanium*. The artificial nature of most of these taxa can be seen immediately when compared, using more recent data on character variation. *Lychnodicytum*, for example, is distinguished from *Pterocanium* largely by the presence in the latter of an abdomen (Haeckel, 1887, p. 1329). In the context of pterocanid forms 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 *Lychnodicytum* 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. chaerhythmum*, we see a complete gradation between forms with well-developed lattice-work and forms with nearly solid foot bases.

Other problems arise because of inconsistences 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 *Dicytophism* fits the definition of "pteroanid" 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 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 penetration. We consider these two characters to be unrelated. The original 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 *Dicytophism*; 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
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 Haekel's work. For example, the structure of the cephalis was considered by Riedel (1967) to be of great importance in distinguishing the families Theopodidae and Pierocyrtihidae. *Pierocyrtis aquila* Haekel (1887) is, on the basis of his Plate 71, fig. 5, clearly assignable to the Theopodidae, and probably to *Pierocyrtis*, in our revised definition. Yet *Pierocyrtis campanula*—Plate 7, fig. 3—equally clearly belongs in the Pierocyrtihidae, 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 pterocyrtid generic taxa listed in Haekel, or at least revise generic definitions. Formal revision must however wait until more information is obtained on pterocyrtid stratigraphy and systematic characters. Until such information is available we formally restrict ourselves to revisiting just *Pierocyrtis*.

**Subgeneric taxa in Pierocyrtis.**—Taxonomic assignment within *Pierocyrtis* 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 integration 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 discreetness needed to be recognized as a species. Hence they are, at most, reference points in a morphologic continuum.

Whether our taxonomic species represent actual biologicai 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 knoegoes 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 systematics 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 *Pierocyrtis charybdeum* (with 4 subspecies), *P. praetextum* (with 2 subspecies), *P. karinevi, P. austral*, and *P. praetextum*. 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**

**GEOGRAPHY PTEROCYRTIS**

**Pierocyrtis EHRENBERG, 1847, p. 54.**

**Type species.**—*Podoscyrtis charybdeum* EHRENBERG, 1847, p. 492.

**Diagnosis.**—Radiolarians with spherical cephalis and more or less pyramidal thorn, possessing 3 typically 3-bladed feet extending from base of thorn and continuing to apex of thorn as thoracic ribs. Base of thorn terminated by distinct peristome. Abdomen, when present, thin and irregularly terminated. Proximal portion of feet often porous. Feet terminate distally in simple point. Ports of thorn 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 impoverished cephalis is relatively small, heavy walled, and covered with widely scattered
<table>
<thead>
<tr>
<th>No.</th>
<th>Category</th>
<th>Polymorphic end member usage</th>
<th>P. chartarum</th>
<th>P. trichoceras</th>
<th>P. torontianum</th>
<th>P. burti</th>
<th>P. p.</th>
<th>P. occidentale</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Apical spine length</td>
<td>long (0) to short (2)</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>Apical spine thorns</td>
<td>prominent (0) to absent (2)</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>Cornalia</td>
<td>sphere (0) to flattened (2)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>Thorax set</td>
<td>large (0) to small (2)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>Thorax scale shape</td>
<td>flat (0) to inflated (2)</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>Thorax rib shape</td>
<td>straight (1), sharply bent (2), simply curved (3), rounded (4)</td>
<td>11</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>7</td>
<td>Thorax porus size</td>
<td>large (0) to small (2)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>8</td>
<td>Thorax shape &amp; dist.</td>
<td>regular (0) to irregular (2)</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>9</td>
<td>Thorax spine width</td>
<td>narrow (0) to foated (2)</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>10</td>
<td>Thorax spine thickness</td>
<td>small (0) to absent (2)</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>11</td>
<td>Anterior body spines</td>
<td>long (0) to short (2)</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>12</td>
<td>Foot length</td>
<td>short (0) to thick (2)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>13</td>
<td>Foot thickness</td>
<td>thin (0) to thick (2)</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td>Foot shape</td>
<td>straight (0) to curved (2)</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>15</td>
<td>Foot stubness</td>
<td>small (0) to large (2)</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>16</td>
<td>Foot base</td>
<td>round (0) to hyaline (2)</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>17</td>
<td>Abdominal veil</td>
<td>prominent (0) to absent (2)</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>
pores, partially or more commonly nearly entirely filled with deposits of silicea. 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 "special" however, was not figured, has no known type material, and was described only in the vague manner. Rediscription 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 Petrushevskaia (1971) who considered the type species to be P. prosopodes, which we feel is a junior synonym of P. charbydaeum. P. charbydaeum is, to our knowledge, the oldest validly described species which has been associated by the author with the generic name Petrocunium.

Species such as Dicyopterinus inflabribractus 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 Petrocunium. Taxa previously assigned to Petrocunium by either authors and not directly mentioned here are retained in the genus, pending further work.

Reevaluation 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 Petrocunium is based on analysis of late Miocene to Recent material only. The taxonomic status of Paleogene forms with similar character suites is uncertain.

Petrocunium charbydaeum (Müller), 1855
Podocyrtis charbydae Müller, 1855, p. 492.
Petrocunium prosopodes Ehrenberg, 1838, p. 34-35.
Pterocanium charybdeum trilobum

Diagnosis:—Cephalis weakly silicified. The internal sepal ring at the collar structure 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. grandispora. 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. korotnevii, 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 subseries P. c. allum. P. c. trilobum shares several characteristics with P. audax, including a relatively heavy, coarse thorax and a weak collar structure. 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 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. undax. The occurrence of these morphological intermediates seems imply a close relationship between the two taxa. It also supports the synonymy of Pterocanium with Lyschnodicytum, the Haeckelian genus in which P. undax was originally assigned by Riedel (1953).

**Pterocanium charrybdeum charrybdeum**
Müller, n. comb.

Figures 11.1–11.4, 13.3

- (T)Dextrapodium trilobum Haeckel, 1862, p. 340, PI. 8, figs. 9–10.
- (T)Dextrapodium challenger Haeckel, 1878, p. 47, fig. 35.
- (T)Lyschnodicytum challenger (Haeckel), Haeckel, 1887, p. 123.
- (T)Pterocanium trilobum (Haeckel), (T)Haeckel, 1887, p. 1333; Ngorni (in part), 1967, p. 71–72; PI. 7, fig. 3b (only).

**Diagnosis.**—Heavily silicified cephalis is strongly constricted internally by well-developed septal ring at collar suture; (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 contains into base of feet. Abdominal veil weakly developed.

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

**Comments.**—P. c. charrybdeum is very similar to members of the P. praeextum lin.
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. charybdemum.

PTEROCANUM CHARYBDEMUM ALLIUM II. subsp. Figures 12.1-12.6

Diagnosis.—Cephalis moderately silicified, but usually "closed" at base (cf. diagnosis of P. c. charybdemum). Apical horn small. Thorax flared inflated cylinder, but not noticeably recurved. Sometimes weakly 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 "alliurn").

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, Florissant, Pliocene, and Pleistocene populations of P. charybdemum 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. charybdemum, P. praetextum, and P. prasinum. As noted earlier, P. c. allium was derived from earlier populations of P. c. trilobum by reduction in foTwo 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. charybdemum, P. praetextum, and P. prasinum.

PTEROQANUM CHARYBDEMUM (Müller) GRANDIFORIS Nigrini, n. comb. Figures 13.1, 13.2

Pterocanium grandiforius Nigrini, 1968, p. 57, Pl. 1, fig. 1.

Diagnosis.—Lightly silicified cephalis 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 distinctly 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, this, 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. grandiforus 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 the large size—are largely gradational with P. c. trilobum (Fig. 14). For this reason we do not feel that P. c. grandiforus 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.

PTEROQANUM PRAETEXTUM (Ehrenberg) 1872, Lychnocanium praetextum Ehrenberg, 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 range 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. exsulsum. This description is more in accord with the presence of common (though subordinate) P. p. exsulsum in contemporaneous samples of Radiolaria where P. p. praetextum dominates.
Pterocanium praetextum (Ehrenberg) Euclidum Haeckel, Nigrini, 1967

Figures 13-1-15A

Pterocanium praetextum (Ehrenberg) Euclidum Haeckel, Nigrini, 1967, p. 76, Pl. 7, fig. 2.

Pterocanium praetextum Euclidum Haeckel, 1887, p. 1332, Pl. 73, fig. 4.

Pterocanium bicornum Haeckel, 1887, p. 1332, Pl. 73, fig. 5.

Pterocanium praetextum (Ehrenberg) Euclidum Haeckel, 1887, p. 1331-1332, Pl. 73, fig. 1; Poysky, 1913, p. 392.

Pterocanium sp. Petushkovskaya, 1971, fig. 112, VII.

Pterocanium praetextum (Ehrenberg, Renz) in part, 1973, p. 186-187, Pl. 5, fig. 16a (only).

Diagnosis.—Cephalotheca is heavily silicified “closed” sphere (basal pore small), and is only slightly smaller than cephalotheca of P. charbydeum. Apical horn usually small. Thorax irregular hemispheric, much smaller than thorax of P. charbydeum. Thorax lateral 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. euclidum is widely distributed in temperate through tropical waters of the world ocean. This pattern has been typical throughout P. p. euclidum’s stratigraphic range, from its origin near the Miocene-Pliocene boundary to the present day.

Comments.—P. p. euclidum is the phylogenetically older of the two subspecies of P. praetextum, and morphologically more similar to its ancestor(s)—P. charbydeum and/or P. kovarini. Transitional series are noted in the descriptions of these two lineages. Pterocanium bicornum, as figured by Haeckel (1887, Pl. 73, apparently differs from his P. euclidum (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 percocamids with two apical horns (such as “Pterocanium sp.” Nigrieri and Moore, 1979) may still belong to different species, and are excluded from our synonomy.

Pterocanium praetextum (Ehrenberg) Euclidum Haeckel, Nigrini, 1967

Figures 16-1-16A


Pterocanium monopodium Poysky, 1913, p. 388.

Pterocanium praetextum Benson in part, 1966, p. 402-408, Pl. 27, fig. 3 (only).

Pterocanium praetextum (Ehrenberg) Benson, 1966, p. 408-410, Pl. 27, fig. 6; Pl. 28, fig. 1.

Pterocanium sp. Petushkovskaya, 1971, p. 530, fig. 114, II, III; Renz (in part) 1973, p. 186-187, Pl. 5, fig. 16b (only).

Pterocanium charbydeum (Müller), Petushkovskaya (in part), 1971, p. 228-229, fig. 113, III (only).

For additional synonomy see Nigrini, 1967.

---

Figure 12-1-16, Pterocanium charbydeum allium, n. subsp. 1, holotype displaying characteristic almost parallel thin feet; nearly nonporous foot-bases; circular, regular pores; and secondary spines on thorax. Inflated horn and necking of thorax at cephalotheca are not very well developed in this specimen (RC12-66, 1875 cm; 19, 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, portrait down showing variation in P. c. allium. All bar 2 are from same slide at holotype. 2, individual with short, thin parallel feet; inflated, “necked” thorax; and secondary spines on cephalotheca (D22, thoracic width 110 micrometers). 3, specimen from the late Miocene of the Indian Ocean displaying through-poor outline characteristic of P. c. allium (hatching and magnification unrecorded). 4, individual with prominent “neck” to apex of thorax (233-4, thoracic 125 micrometers). 5, specimen with unusually long feet (C15,3, thoracic width 125 micrometers). 6, example of thorax inflation (C15,4, thoracic width 125 micrometers). 7, Pterocanium of unknown species from early Pliocene with inflated thorax (left no “necking” of apex) and thin, parallel feet. Lack of necking and small size of thorax are reminiscent of P. praetextum euclidum (RC12-66, 2015 cm; F20, thoracic width 105 micrometers). Montage of photographs from different, focal planes. 8, Pterocanium charbydeum uncertain subspecies. Individual has P. c. allium-like thorax and cephalotheca, but feet (not shown) are strongly curved and more typical of P. c. triebium (RC12-66, 2,535 cm; D33-4; thoracic width 135 micrometers).
tremely common in modern equatorial as-
semblages 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. enucleatum was the most common
form of Pterocanium in tropical sediment
samples. P. p. praetextum is not found out-
side of the equatorial province, and may bear
a climatic relationship to the phylogenetically
older P. p. enucleatum, which dominates in
subtropical waters.

Pterocanium prismaticum Riedel, 1953
Figures 17.1-7.4
Pterocanium prismaticum RIEDEL, 1957, p. 87-88.
Pl. 3, figs. 4, 5.

Diagnosis.—Cephalis thick-walled, com-
plete sphere, apical horn small. Thorax very
large, consisting of an upper short tetrahe-
dron 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 mod-
erate thickness, and generally lack prominent
frames. Short flat triangular spines are often
found projecting from the upper thorax, par-
sicularly along thoracic ribs. Feet are mod-
erately 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 devel-
oped.

Distribution.—Pterocanium prismaticum
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 Pter-
ocanium in our study, P. prismaticum 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–Pleis-
tocene boundary, Hays (1971) has investi-
gated to detail the relationship between the
extinction of this lineage and the Olduvai
glacial event.
FIGURE 14—Comparison of thorax lattice wall pore and bar dimensions in *P. c. grandisporus* to those of other *P. charlesii* var. Measurements were made with an electronic digitizer and are accurate to approx. ±0.7 micrometers. Circles, *P. c. grandisporus*; solid dots, *uolgi P. charlesii*; bull’s-eyes, intermediate forms.

**Petrocamium korotnevi** (Dogiel), 1952

*Figures 18.1–18.5*

_Petrocamium korotnevi_ Dogiel, Dogiel and Remshak, 1952, p. 17, fig. 11.

(_Lithocamium stigmopodium_ Haekel, 1887, p. 1228, Pl. 61, fig. 15.

_Petrocamium prosperinum_ Benson (in par), 1966, p. 603–608, Pl. 27, fig. 5 (only).

_Petrocamium korotnevi_ (Dogiel, Nekrjas, 1970, Pl. 3, figs. 10, 11; Klung, 1973, p. 638, Pl. 4, figs. 1–4; Pl. 10, figs. 6–9.

_Lithocamium korotnevi_ (Dogiel), Petrushevskaya, 1971, fig. 111, 1.

_Lithocamium_ sp. cf. _L. sigmopodium_ Haekel, 1887, p. 185–186, Pl. 5, fig. 14.

_Lithocamium_ sp. cf. _L. grande_ Campbell and Clark, 1944, Klung, 1973, Pl. 4, figs. 9, 10.

_Reynolds, 1960, p. 766, Pl. 1, figs. 21, 22._

_Petrocamium philippianum_ (Haekel), Klung (in par), 1973, p. 638, Pl. 4, fig. 5 (only).

_Lithocamium_ sp. Sakai, 1980, Pl. 711, Pl. 9, figs. 1a, b.

**Diagnosis.**—Cephalis hemispherical, somewhat irregular, and relatively large. Apical spine small. Thorax small, hemispherical, very thick walled. Pores small, circular, surrounded by raised frames, bars corresponding thick. Feet moderately long and very robust, flared, straight or slightly concave, essentially unmodified even at base. No valve.

**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.

**Comment.**—Forms transitional in morphology between _P. korotnevi_ and _P. p. eucopipum_ are very common in the early Pliocene in cores located in transitional North Pacific–Subtropical locations. On morphologic grounds either _P. korotnevi_ or _P. charlesii_ could be ancestral to _P. p. eucopipum_—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-
Pterocanium praeextum eucolium. 1. Individual with flared legs and irregular thoracic outline (thoracic width 70 micrometers). 2. Individual with nearly complete, subparallel feet (thoracic width 60 micrometers). 3. Thoracic width 70 micrometers. 4. Thoracic width 60 micrometers. 5. Specimen intermediate between 1 and 2+3 (RC12-06, 15-87 cm; x14; thoracic width 80 micrometers).

Pterocanium praextum praextum. 1. Specimen showing spherical cephalis (thoracic width 60 micrometers). 2. Individual with subparallel lobes of thorax and intervening sunken rib areas (thoracic width 60 micrometers). 4. Equatorial Pacific individual (RC12-66, 0-2 cm; 237/8; thoracic width 75 micrometers), focus on pore structures.

The study 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 species' evolutionary history in more detail.

In recent sediments a more or less complete gradation exists between forms with small thoraxes, traditionally assigned to P. koroteni, and more robust forms which previously were assigned to Lychnocarina sp. or Lycnocarina 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 Lycnocarina grande in morphology exist in Pleocene 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. koroteni, 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

Lycnocarina audax Riedel, 1953, p. 810–811, Pl. 85, fig. 9; Sakai and Riedel, 1974, p. 1022–1023, Pl. 2, fig. 8; Sakai, 1980, p. 711, Pl. 2, figs. 1a, b.

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

**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-
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. koroneki 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. charadriusaeus 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. olisthum. This form is not only morphologically similar to P. c. trilobum, from which it arose, but also to both P. priscumatum and to P. p. excisum. Morphologic fragmentation of the late Miocene P. charadriusaeus population is observed in samples covering the latest Miocene to early Pliocene (6 Ma to 4.0 Ma).

By the Early Pliocene, distinct differences 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
between equatorial Pacific and equatorial Indian Ocean faunas are apparent (Figure 9). *P. eudoxus* 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. allum* (and/or *P. c. charybdeum*) and *P. p. eucolpus* are particularly common in the earlier Pliocene (~4.5 Ma) in the equatorial Indian Ocean. By 4 Ma *P. p. eucolpus* is a common member of the equatorial Indian Ocean assemblage, although it is still less common in equivalent aged sediments from the Pacific. Late Miocene and early
Pliocene subtropical Pacific cores record common transitional forms between *P. p. eucolpum* and *P. korotnevi*. These transitional forms become rarer in younger sediments. *P. prismatum* evolved from *P. charybdeum* in the early Pliocene (Figure 9). Rapidly evolving 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. *P. eucolpum* became extinct at the Pliocene–Pleistocene boundary. The late Pleistocene marked in the low latitudes by the reappearance of transitional morphologies between *P. praetextum* and *P. charybdeum*. Details of the Pleistocene evolution of *P. korotnevi*, the other surviving lineage, are not known.

The phylogenetic 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 *P. eucolpum*. 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 *P. eucolpum* 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
set, 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. praeextum, P. prismaticum, and P. audax are all reasonably well separated from P. charybdeum and from each other. P. keratium 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 differe-
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. pratense and P. charybdeum, while thoracic length discriminates not only P. pratense from P. charybdeum (via size), but also P. primitivum 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
be characterized by the persistence of an ancestral stock—P. c. trilobum—with the development of the additional subspecies P. c. altum 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. altum morphology, which dominates the lineage but does not extinguish P. c. trilobum entirely. Thus later Miocene populations generally have more lightly silicified shells, shorter feet, smaller apical horns, etc. With the fragmentation of the P. c. altum population near the Miocene-Pliocene boundary, the morphologic range within P. charybdeum once again becomes dominated by P. c. trilobum and P. c. charybdeum. The phylogetic 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 phylogetic 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-
in P. praetextum were dominated by the gradual replacement of dominant P. p. eu-
colium morphology with P. p. praetextum morphology, and by the appearance of inter-
mediate morphologies between P. praetex-
tum 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-Pleisto-
cene interval. As in the case of P. charyb-
drum, there is a consistent offset in thorax
width and length measurements between the
two regions, although not as large in P. praetex-
tum as in P. charybdeum.

Documentation of the change within P. praetextum from P. p. eucoleum 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 domi-
nance 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 lin-
eage 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 devel-
opment of substantial populations of P. praetex-
tum in the Indian Ocean than in the Pacific
Ocean.

Pterocanium prismatum lineage.—The
evolution of P. prismatum is a distinctive
event in the Pliocene radiolarian assemblage,
as is its extinction near the Pliocene-Pleis-
tocene boundary. Phyletic trends within the
lineage are dominated by development of in-
creasingly large, elongate, prismatic thoraxes,
and by the associated development of elip-
tical pores in the thoracic lattice wall.

The phyletic evolution of Pterocanium
prismatum was investigated previously by
Kellogg and Hays (1975). They presented
biometric data on the phyletic increase in
thorax length in this lineage, based on sam-
ples 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 recog-
nized. 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. prismaticum, as indicated. Below this level (∼15 meters) the taxon measured is not P. prismaticum but either P. prismaticum's ancestor, P. charbydem, or a more primitive form. A more accurate representation of the evolution of P. prismaticum, via speciation from P. charbydem, is given in Figure 23, which includes data on thorax length for both P. prismaticum and P. charbydem. 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. prismaticum (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. prismaticum parallels the decrease in width of P. charbydem 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. prismaticum 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 mor- phology 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. charbydem. The thorax size decreases (Figure 25), and development of thorns on the apical horn becomes less pronounced. These trends suggest renewed convergence towards P. charbydem 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 Quaternary.

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

As noted in the description of this group, in the Plioc-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 thorax 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
lineages. Three occasions are particularly marked: between *P. charybdeum* and *P. audax* in the late Miocene and earliest Pliocene; between *P. prae texts* and *P. korotnevi*, and *P. charybdeum* in the early Pliocene; and between *P. charybdeum* and *P. prae texts* 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 *Pericosmus*. We have concentrated on the morphologic convergence seen between *P. prae texts* 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. prae texts* was followed in a series of samples from the equatorial Pacific. Thoracic 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 near 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 retardation 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 modes, 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. praestatum, 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 fifth abdominal vein (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. praestatum* in the tropics, *P. p. eucolymn* in the north).

---

**Figure 29**—Progressive convergence and apparent hybridization between the common lineages in the low Pliocene. 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 subtopics, and \textit{P. korotnevii} in the North Pacific), and these differences in some cases (e.g., \textit{P. praetextatum} vs. \textit{P. p. eucalyptum}) 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 \textit{P. charbdream} and \textit{P. audax} in the latest Miocene and early Pliocene, between \textit{P. korotnevii} or \textit{P. charbdream} and \textit{P. praetextatum} in the Pliocene, and between \textit{P. charbdream} and \textit{P. praetextatum} in the Pleistocene.

If we assume that the observed morpho-

logic changes in \textit{Pterocanium} reflect underlying changes in the genetic/developmental makeup of \textit{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 in 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 \textit{Pterocan}ium suggest 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 \textit{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 \textit{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 \textit{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 (Goff, 1978, 1979; Lazarus, 1983).

Finally, many more quantitative analyses of evolutionary change are needed, in \textit{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.

Acknowledgments

We thank A. Pesanell for assistance in the biometric analysis, Lloyd Buckle and Neil Opdyke for access to unpublished data, Cathy Nigrini for the loan of her RIS material, and several reviewers whose comments have improved the manuscript: O. Roger Anderson, Jullian F. Finn, James D. Hays, Dave Johnson, Cathy Nigrini, and W. R. Riedel. Remaining errors, omissions, and crazy thinking are, of course, a product of the authors. D. Lazarus was supported by NSF grants OCE79-19692 and DEB81-18743. This is Lamon-Doherty contribution number 3727.
REFERENCES
Doyle, V. A. and V. V. Resheina. 1952. Materialiy po radiolitavraMy sevvero-pazdnom chasti tikhogo okeana. Izbedovaya Dalnoves-


```
```
sealarii v planktonne Mirovogo Okeana. Idaho-
dovannia flutru morei, Leningrad, 9177:5-487.
POPOVSKY, A. 1913. Die Nestelien des Wurm-
wassergetriebens. Deutsche Sibepolare Expedition,
Berlin, 14:217-416.
Planktonic microbassis and the recognition of
acecets. Systematic Zoology, 29:119-120.
REINZ, G. W. 1973. The distribution and ecology
of Radiolarians in the Central-Pacific plankton
and surface sediments. Unpubl. Ph.D. dissertation,
University of California, San Diego, p.1-250.
REYNOLDS, R. A. 1980. Radiolarians from the
western North Pacific, Leg 57, Deep Sea Drilling
Reports of the Deep Sea Drilling Project, 56,
57, Part 2. United States Government Printing
Office.
RIDDLE, W. R. 1953. Mesozoic and late Tertiary
Radiolaria of Benti. Journal of Paleontology, 27:
805-813.
—. 1957. Radiolaria: a preliminary stratigra-
phy. Reports of the Swedish Deep-Sea Expe-
—. 1957. Protosasa, class Acoela. p. 291-
298. In: The Fossil Record, a Symposium with
Documentation, Geological Society of London.
Late Miocene to Pliocene biostratigraphy of
equatorial Pacific sediments, p. 225-244. In: T.
Saito and L. Burkalle (eds), Late Neogene Epoch
Boundaries. American Museum of Natural His-
tory, Micropaleontology Press.
SAMA, J. 1980. Radiolarians from sites 434, 435,
and 436, Northwest Pacific, Leg 56, Deep Sea
Initial Reports of the Deep Sea Drilling Project,
56, 57, Part 2. United States Government Printing
Office.
SANTILEPO, A. and RIDDLE, W. R. 1974. Radi-
olaria from the west-central Indian Ocean and
Arabian Sea, DSDP Leg 24, p. 997-1036. In: R.
L. Fisher, E. T. Bucel, et al., Initial Reports of
STANLEY, S. M. 1979. Macroevolution, Pattern
Reports of the Deep Sea Drilling Project. Vol-
ume 38. United States Government Printing Of-
fice, p. 1-1226.
TREVES, F. and S. R. HAMMOND. 1974. Pale-
magnetic polarity sequence and radiolarian jux-
zones. Brushites to polarity epoch 20. Earth and
Paleomagnetic and geochronological calibration
of latest Oligocene to Pliocene radiolarians in the
equatorial Pacific. Marine Micropaleontology,
2:377-393.
VOCSET, E., J. S. KILLINGLY and W. H. BERGER.
1980. The magnetic Epoch 6 carbon shift: a
change in the ocean's 13C/12C ratio 6:2 m.y.
VON DER BÖNOT, C. C., J. G. SCALTER, et al.
Project, Volume 22. United States Government Printing
WHITE, M. J. D. 1978. Modes of Speciation, W.
MANUSCRIPT RECEIVED DECEMBER 30, 1982
REVISED MANUSCRIPT RECEIVED MAY 4, 1983
Minor author contributed $150 in support of
this article. Woods Hole Oceanographic Institute
contributed $300 in support of this article.

APPENDIX

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

Sample size
N
X
S.D.
Thorax Width (TW)
15
5.0
1.0
Thorax Length (TL)
15
35.0
5.0
Thorax Pore Diameter (PORD)
15
55.0
10.0
Thorax Bar Width (BAR)
15
15.0
3.0
## Table 3 - *P. chrysosomum*

<table>
<thead>
<tr>
<th>Sample</th>
<th>TW</th>
<th>TL</th>
<th>PORE</th>
<th>BAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>x</td>
<td>S.D.</td>
<td>N</td>
<td>x</td>
</tr>
<tr>
<td>PACIFIC</td>
<td></td>
<td></td>
<td>PACIFIC</td>
<td></td>
</tr>
<tr>
<td>RC12-66-2,535</td>
<td>37</td>
<td>112.7</td>
<td>10.7</td>
<td>35</td>
</tr>
<tr>
<td>RC12-66-2,200</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>RC12-66-1,555</td>
<td>23</td>
<td>112.3</td>
<td>10.7</td>
<td>20</td>
</tr>
<tr>
<td>RC12-66-1,555</td>
<td>44</td>
<td>103.6</td>
<td>10.0</td>
<td>41</td>
</tr>
<tr>
<td>RC12-66-1,187</td>
<td>48</td>
<td>103.6</td>
<td>8.4</td>
<td>80</td>
</tr>
<tr>
<td>RC12-66-1,100</td>
<td>21</td>
<td>98.4</td>
<td>13.8</td>
<td>17</td>
</tr>
<tr>
<td>RC12-66-900</td>
<td>17</td>
<td>98.0</td>
<td>8.8</td>
<td>13</td>
</tr>
<tr>
<td>RC12-66-663</td>
<td>30</td>
<td>96.6</td>
<td>8.4</td>
<td>14</td>
</tr>
<tr>
<td>RC12-66-525</td>
<td>35</td>
<td>97.2</td>
<td>13.5</td>
<td>37</td>
</tr>
<tr>
<td>RC12-66-403</td>
<td>32</td>
<td>91.2</td>
<td>12.3</td>
<td>33</td>
</tr>
<tr>
<td>RC12-66-195</td>
<td>45</td>
<td>81.1</td>
<td>9.6</td>
<td>43</td>
</tr>
<tr>
<td>RC12-66-top</td>
<td>91</td>
<td>76.7</td>
<td>15.8</td>
<td>87</td>
</tr>
</tbody>
</table>

## Table 3 - *P. pruinosa*

<table>
<thead>
<tr>
<th>Sample</th>
<th>TW</th>
<th>TL</th>
<th>PORE</th>
<th>BAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>x</td>
<td>S.D.</td>
<td>N</td>
<td>x</td>
</tr>
<tr>
<td>PACIFIC</td>
<td></td>
<td></td>
<td>PACIFIC</td>
<td></td>
</tr>
<tr>
<td>RC12-66-1,395</td>
<td>*</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>RC12-66-1,187</td>
<td>61</td>
<td>71.5</td>
<td>3.3</td>
<td>20</td>
</tr>
<tr>
<td>RC12-66-1,100</td>
<td>39</td>
<td>72.8</td>
<td>2.2</td>
<td>36</td>
</tr>
<tr>
<td>RC12-66-900</td>
<td>24</td>
<td>69.4</td>
<td>5.2</td>
<td>17</td>
</tr>
<tr>
<td>RC12-66-663</td>
<td>25</td>
<td>71.8</td>
<td>3.9</td>
<td>-</td>
</tr>
<tr>
<td>RC12-66-525</td>
<td>44</td>
<td>66.4</td>
<td>5.6</td>
<td>41</td>
</tr>
<tr>
<td>RC12-66-403</td>
<td>61</td>
<td>61.4</td>
<td>10.8</td>
<td>59</td>
</tr>
<tr>
<td>RC12-66-195</td>
<td>50</td>
<td>60.6</td>
<td>6.2</td>
<td>51</td>
</tr>
<tr>
<td>RC12-66-top</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

## Table 3 - *P. chrysophylax*

<table>
<thead>
<tr>
<th>Sample</th>
<th>TW</th>
<th>TL</th>
<th>PORE</th>
<th>BAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>x</td>
<td>S.D.</td>
<td>N</td>
<td>x</td>
</tr>
<tr>
<td>INDIAN</td>
<td></td>
<td></td>
<td>INDIAN</td>
<td></td>
</tr>
<tr>
<td>V16-169</td>
<td>1,120</td>
<td>103</td>
<td>99.7</td>
<td>9.5</td>
</tr>
<tr>
<td>V16-169</td>
<td>1,000</td>
<td>50</td>
<td>102.2</td>
<td>8.6</td>
</tr>
<tr>
<td>V16-169</td>
<td>1,000</td>
<td>21</td>
<td>103.2</td>
<td>13.6</td>
</tr>
<tr>
<td>V20-40</td>
<td>1,732</td>
<td>20</td>
<td>101.7</td>
<td>11.3</td>
</tr>
<tr>
<td>V20-49</td>
<td>1,156</td>
<td>24</td>
<td>103.9</td>
<td>10.6</td>
</tr>
<tr>
<td>V20-49</td>
<td>1,300</td>
<td>66</td>
<td>100.2</td>
<td>12.7</td>
</tr>
<tr>
<td>V29-40</td>
<td>1,130</td>
<td>40</td>
<td>100.5</td>
<td>10.6</td>
</tr>
<tr>
<td>V17-171</td>
<td>465</td>
<td>93</td>
<td>102.4</td>
<td>10.2</td>
</tr>
<tr>
<td>V17-22,400</td>
<td>57</td>
<td>102.3</td>
<td>2.3</td>
<td>50</td>
</tr>
<tr>
<td>V17-22,500</td>
<td>53</td>
<td>99.5</td>
<td>11.4</td>
<td>28</td>
</tr>
<tr>
<td>V14-22,300</td>
<td>49</td>
<td>96.5</td>
<td>11.2</td>
<td>43</td>
</tr>
<tr>
<td>V16-169</td>
<td>34</td>
<td>86.1</td>
<td>22.4</td>
<td>20</td>
</tr>
</tbody>
</table>
### Table 4 - P. chrysostoma / P. protostomum intermediates.

<table>
<thead>
<tr>
<th>Sample</th>
<th>TW</th>
<th>X</th>
<th>S.D.</th>
<th>TL</th>
<th>X</th>
<th>S.D.</th>
<th>PORE</th>
<th>X</th>
<th>S.D.</th>
<th>BAR</th>
<th>X</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>PACIFIC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 1,395</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>19</td>
<td>4.8</td>
<td>1.5</td>
<td>19</td>
<td>1.1</td>
<td>0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 530</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>21</td>
<td>5.5</td>
<td>1.0</td>
<td>21</td>
<td>1.4</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 525</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>19</td>
<td>5.7</td>
<td>1.0</td>
<td>19</td>
<td>1.2</td>
<td>0.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 405</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>22</td>
<td>4.8</td>
<td>0.8</td>
<td>22</td>
<td>1.3</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 565</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>15</td>
<td>6.0</td>
<td>1.0</td>
<td>15</td>
<td>1.7</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>INDIAN</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V19-169, 1,000</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>4.5</td>
<td>0.6</td>
<td>3</td>
<td>1.0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V29-40, 1,380</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>3.9</td>
<td>0</td>
<td>2</td>
<td>0.9</td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V29-40, 1,385</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>4.0</td>
<td>0</td>
<td>2</td>
<td>1.1</td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC19-22, 800</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6</td>
<td>5.0</td>
<td>1.0</td>
<td>6</td>
<td>1.0</td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC19-22, 600</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>10</td>
<td>6.8</td>
<td>1.3</td>
<td>10</td>
<td>1.6</td>
<td>0.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC19-22, 300</td>
<td>3</td>
<td>4.6</td>
<td>0.9</td>
<td>3</td>
<td>1.6</td>
<td>0.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V19-169, top</td>
<td>4</td>
<td>5.2</td>
<td>0</td>
<td>4</td>
<td>0.9</td>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Table 5 - P. parvioculus.

<table>
<thead>
<tr>
<th>Sample</th>
<th>TW</th>
<th>X</th>
<th>S.D.</th>
<th>TL</th>
<th>X</th>
<th>S.D.</th>
<th>PORE</th>
<th>X</th>
<th>S.D.</th>
<th>BAR</th>
<th>X</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>PACIFIC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 1,395</td>
<td>4</td>
<td>105.0</td>
<td>8.6</td>
<td>4</td>
<td>91.7</td>
<td>5.4</td>
<td>4</td>
<td>8.6</td>
<td>0</td>
<td>4</td>
<td>1.2</td>
<td>0</td>
</tr>
<tr>
<td>RC12-66, 1,235</td>
<td>50</td>
<td>113.7</td>
<td>8.1</td>
<td>42</td>
<td>106.7</td>
<td>7.3</td>
<td>31</td>
<td>7.1</td>
<td>1.1</td>
<td>1</td>
<td>2.0</td>
<td>0.8</td>
</tr>
<tr>
<td>RC12-66, 1,187</td>
<td>46</td>
<td>110.7</td>
<td>9.1</td>
<td>15</td>
<td>112.7</td>
<td>10.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>RC12-66, 1,100</td>
<td>36</td>
<td>108.6</td>
<td>9.8</td>
<td>36</td>
<td>111.0</td>
<td>6.8</td>
<td>37</td>
<td>8.0</td>
<td>1.7</td>
<td>37</td>
<td>2.0</td>
<td>0.7</td>
</tr>
<tr>
<td>RC12-66, 900</td>
<td>39</td>
<td>105.5</td>
<td>8.8</td>
<td>39</td>
<td>97.0</td>
<td>5.8</td>
<td>41</td>
<td>8.4</td>
<td>1.5</td>
<td>41</td>
<td>1.6</td>
<td>0.6</td>
</tr>
<tr>
<td>RC12-66, 665</td>
<td>23</td>
<td>104.2</td>
<td>8.2</td>
<td>15</td>
<td>105.3</td>
<td>6.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>INDIAN</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V19-169, 1,080</td>
<td>2</td>
<td>96.2</td>
<td>3.6</td>
<td>2</td>
<td>78.3</td>
<td>12.9</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>V19-169, 1,000</td>
<td>9</td>
<td>100.9</td>
<td>6.0</td>
<td>9</td>
<td>88.9</td>
<td>3.2</td>
<td>9</td>
<td>7.8</td>
<td>1.4</td>
<td>9</td>
<td>1.1</td>
<td>0.4</td>
</tr>
<tr>
<td>V29-40, 1,732</td>
<td>17</td>
<td>107.1</td>
<td>10.9</td>
<td>13</td>
<td>102.7</td>
<td>6.4</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>V19-186, 665</td>
<td>15</td>
<td>107.5</td>
<td>9.1</td>
<td>8</td>
<td>101.8</td>
<td>16.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>V29-40, 1,800</td>
<td>7</td>
<td>107.3</td>
<td>16.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>V29-40, 1,130</td>
<td>34</td>
<td>101.5</td>
<td>9.1</td>
<td>33</td>
<td>99.4</td>
<td>8.4</td>
<td>34</td>
<td>7.3</td>
<td>0.8</td>
<td>34</td>
<td>1.0</td>
<td>0.6</td>
</tr>
<tr>
<td>V19-171, 465</td>
<td>33</td>
<td>98.0</td>
<td>8.6</td>
<td>16</td>
<td>94.4</td>
<td>11.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

### Table 6 - P. saxifraga.

<table>
<thead>
<tr>
<th>Sample</th>
<th>TW</th>
<th>X</th>
<th>S.D.</th>
<th>TL</th>
<th>X</th>
<th>S.D.</th>
<th>PORE</th>
<th>X</th>
<th>S.D.</th>
<th>BAR</th>
<th>X</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>PACIFIC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>158-16-2</td>
<td>10</td>
<td>116.5</td>
<td>16.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>158-0-5</td>
<td>5</td>
<td>112.0</td>
<td>8.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>RC12-335, 1,395</td>
<td>2</td>
<td>104.0</td>
<td>3.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>INDIAN</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-335, top</td>
<td>2</td>
<td>112.3</td>
<td>10.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>V19-169, 1,120</td>
<td>90</td>
<td>120.5</td>
<td>8.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>V19-193, 2,280</td>
<td>49</td>
<td>118.1</td>
<td>8.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>V19-169, 1,200</td>
<td>40</td>
<td>108.4</td>
<td>5.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>V29-40, 1,732</td>
<td>17</td>
<td>101.8</td>
<td>5.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>V19-169, 966</td>
<td>13</td>
<td>96.8</td>
<td>4.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>V29-40, 1,300</td>
<td>7</td>
<td>97.5</td>
<td>9.2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>V29-40, 1,300</td>
<td>2</td>
<td>8.3</td>
<td>0.9</td>
<td>2</td>
<td>2.0</td>
<td>0.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sample</td>
<td>TW</td>
<td>S.D.</td>
<td>TL</td>
<td>S.D.</td>
<td>PORE</td>
<td>S.D.</td>
<td>BAR</td>
<td>S.D.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>------------</td>
<td>-----</td>
<td>------</td>
<td>-----</td>
<td>------</td>
<td>------</td>
<td>------</td>
<td>------</td>
<td>------</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 525</td>
<td>7</td>
<td>60.5</td>
<td>11.7</td>
<td>-</td>
<td>-</td>
<td>7</td>
<td>9.1</td>
<td>1.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 463</td>
<td>3</td>
<td>56.3</td>
<td>6.3</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>4.4</td>
<td>2.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, 195</td>
<td>3</td>
<td>61.3</td>
<td>3.0</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>8.2</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-66, top</td>
<td>9</td>
<td>59.5</td>
<td>6.0</td>
<td>-</td>
<td>-</td>
<td>9</td>
<td>10.2</td>
<td>2.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V19-171, 463</td>
<td>3</td>
<td>79.7</td>
<td>4.0</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>5.2</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V19-169, 1120</td>
<td>3</td>
<td>83.4</td>
<td>4.0</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>5.2</td>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V19-9-2, 30-1</td>
<td>2</td>
<td>76.7</td>
<td>12.8</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>5.2</td>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V21-148, 203</td>
<td>21</td>
<td>95.8</td>
<td>5.2</td>
<td>-</td>
<td>-</td>
<td>30</td>
<td>6.5</td>
<td>2.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V21-148, 850</td>
<td>30</td>
<td>79.8</td>
<td>6.4</td>
<td>-</td>
<td>-</td>
<td>39</td>
<td>5.3</td>
<td>1.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V21-148, 940</td>
<td>39</td>
<td>82.1</td>
<td>6.0</td>
<td>-</td>
<td>-</td>
<td>39</td>
<td>5.3</td>
<td>1.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC12-431 814</td>
<td>24</td>
<td>80.3</td>
<td>8.0</td>
<td>-</td>
<td>-</td>
<td>26</td>
<td>5.4</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>