# The genus *Pterocorys* (Radiolaria) from the tropical late Neogene of the Indian and Pacific Oceans

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**ABSTRACT:** An extensive study has been made of the radiolarian genus *Pterocorys* Haeckel in Neogene (< 8 Ma) sediments from the tropical Indian and Pacific Oceans. The detailed morphologies of eight species are described along with their geographic and stratigraphic ranges. Morphometric analysis has suggested certain phylogenetic lineages which are described in detail. Since there are numerous transitional forms, and since several species are apparently delicate and, therefore, rare, only 2 stratigraphically useful and easily recognizable Neogene datum levels (F.A.D. of *P. hertwigii* and L.A.D. of *P. campanula*, both between 0.6 and 1.1 Ma) based on *Pterocorys* can be identified and paleomagnetically dated. Stratigraphic events associated with the genus *Pterocorys* and their absolute ages are presented in tabular form.

## INTRODUCTION

In the search for reliable and easily recognizable radiolarian datum levels in the tropical Neogene of the Indian and Pacific Oceans (see Johnson and Nigrini 1985; Caulet 1979, 1986a), we found that the genus *Pterocorys* contains a number of distinctive species. Some of these species appeared to be related to each other phylogenetically; some seemed to be stratigraphically important. For this reason we undertook a detailed study of all commonly-occurring low latitude members of this genus and of their relationship to each other.

The eight species included in this report have all been previously described. Some of these descriptions have been reprinted herein. Other descriptions have been either rewritten or modified. Extensive, hopefully complete, synonymies have been compiled for each species in order to clarify some considerable confusion in the literature. Appendix I contains a list of species formerly ascribed by other authors to the genera *Pterocorys, Lithopilium* and *Theoconus,* but which do not conform with our definition of *Pterocorys.* In addition, we have given a concise statement of the "Distinguishing Characters" for each species and we have determined the tropical geographic and stratigraphic ranges of the species from our Indian and Pacific Ocean samples (tables 3–9). Additional range data from the literature have been incorporated where appropriate.

## MATERIAL STUDIED

This study was based on DSDP and piston core material from the tropical Indian and Pacific Oceans (table 1; text-fig. 1). Additional information about the French *Marion Dufresne* and *Kaiko* cores and dredge samples used may be found in Caulet et al. (1984). Samples range in age from the Recent to the upper part of the *Didymocyrtis antepenultima* Zone (~ 8.0 Ma).

## PALEOMAGNETIC STRATIGRAPHY AND BIOSTRATIGRAPHY

Those cores marked with an asterisk have indirectly derived paleomagnetic ages associated with them (Johnson and Nigrini 1985, figs. 3, 4, tables III, V; Nigrini 1985; Barron et al. 1985). The data for MD81-369 is based on direct measurements of core material. Additional unpublished work on MD81-369 has shown that our indirectly derived ages, at least for DSDP 214, are accurate. These ages are used to determine the synchroneity or time-transgressiveness of events. Table 10 summarizes the paleomagnetic ages we have determined for nine biostratigraphic events associated with the genus *Pterocorys* in the Indian Ocean, the western Pacific and the central Pacific.

In describing the stratigraphic ranges of various species, we have used the zonations of Nigrini (1971) and Caulet (1979) for the Quaternary and of Riedel and Sanfilippo (1978) for the Miocene and Pliocene. Although we have used traditional zonal boundaries on our range charts, the reader should be aware that the absolute ages of the zonal boundaries are not necessarily synchronous, because the defining radiolarian events are not always synchronous. In particular, the F.A.D. of *S. pentas,* which defines the lower boundary of the *S. pentas* Zone, has been shown to be diachronous by 1.3 Ma

TABLE 1
Location and depth of cores examined to determine stratigraphic ranges and morphology of described species. Cores marked with an asterisk have indirectly derived paleomagnetic ages associated with them (see text).

| Code | Core | Latitude | Longitude | Water Depth |
|---|---|---|---|---|
| *1 | DSDP Site 214 | 11°20.2′S | 88°43.1′E | 1671 m |
| 2 | MD77-157 | 04°48.2′S | 90°02.3′E | 4833 m |
| 3 | MD81-365 | 12°26.2′S | 83°36.8′E | 4487 m |
| 4 | MD81-367 | 06°59.1′S | 80°06′E | 4860 m |
| 5 | MD81-368 | 09°58.5′S | 79°26′E | 5300 m |
| 6 | MD81-369 | 10°02.6′S | 79°48′E | 5293 m |
| 7 | MD81-371 | 12°02.5′S | 79°04.5′E | 5347 m |
| 8 | MD81-374 | 12°48.0′S | 77°43′E | 5332 m |
| 9 | MD81-375 | 12°47.2′S | 77°45.8′E | 5279 m |
| *10 | DSDP Site 586 | 00°29.8′S | 158°29.9′E | 2208 m |
| 11 | LSDH 90P | 07°19′N | 175°28′W | 5190 m |
| 12 | AMPH 97P | 03°42′S | 157°40′W | 5228 m |
| *13 | DSDP Site 573 | 00°29.9′N | 113°18.6′W | 4301 m |

TABLE 2
Identification key comparing diagnostic characteristics of those species of *Pterocorys* described herein.

| *Pterocorys* | Length of Apical Horn | Shell Wall | Thoracic Shape | Thoracic Ribs | Wings/ Thorns | Ridges | Pores | Abdominal Shape |
|---|---|---|---|---|---|---|---|---|
| *campanula* | ≥ cephalis | thin | inflated conical | well developed | wings | on thorax only | small, uniform | cylindrical to inflated |
| *clausus* | < cephalis | thick | campanulate | poorly developed | thorns | no | large, very regular | cylindrical |
| *hertwigii* | ≥ cephalis | thin | campanulate | well developed | wings | on thorax and abdomen | small, uniform | inflated, cylindrical |
| *longicollis* | ≥ cephalis | rather thin | cupola-shaped | poorly developed | small wings | no | large, uniform | campanulate when present |
| *macroceras* | < cephalis | thin | conical | poorly developed | thorns | few | small, irreg. distally | usually incomplete |
| *minythorax* | < cephalis | thick | campanulate rel. small | poorly developed | thorns | no | large, uniform | conical |
| *sabae* | > cephalis | rather thin | sharply conical | very well developed | wings | no | large | conical when present |
| *zancleus* | ≥ cephalis | thin | campanulate | poorly developed | thorns | no | small, uniform | cylindrical |

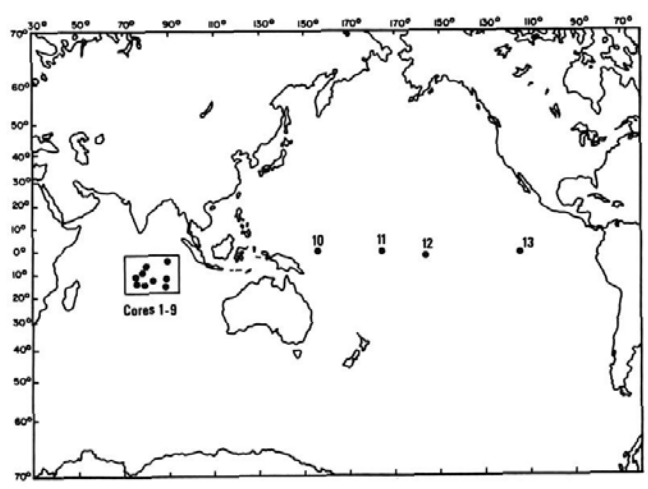
between the Indian and eastern Pacific Oceans (Johnson and Nigrini 1985, p. 501, table VIII).

## METHODS

Each core studied was sampled at regular intervals and strewn slides were prepared for Radiolaria. After noting the abundance and preservation of each assemblage, abundances for each species of *Pterocorys* were recorded in the following manner: A = more than 30 specimens; C = 10–30 specimens; F = 5–10 specimens; R = 2–5 specimens; + = 1 specimen; ? = doubtful identification (tables 3–9).

## SPECIATION AND EVOLUTION

Since classification of fossil Radiolaria is necessarily based on the shape of their skeletons, only morphologic changes can document speciation and evolution within a genus. Previous definitions of species used subjective assessments of morphologic characters rather than more elaborate biometric studies. For the most part, the former method has proved to be sufficient to distinguish between those species of Late Neogene *Pterocorys* which possess distinctive morphologic characters such as wings, ribs or ridges. However, biometric data are needed to distinguish between species with no peculiar morphology or between transitional forms. Our ability to quantify radiolarian morphology is still limited, but microcomputer digitizer systems can be used to investigate changes in the outline of the skeleton or variations in the distribution of pores. These data appear useful principally to document intraspecific changes correlated to climatic variations (Granlund 1986) or morphologic intergradations within evolutionary lineages (Lazarus et al. 1985). However, the determination of climatic variants and detailed phyletic changes in *Pterocorys* is not within the scope of this paper. In fact, for routine stratigraphic analysis of cores, complex measurements of large numbers of specimens are impractical.




TEXT-FIGURE 1
Location of cores used to determine stratigraphic ranges and morphology of described species (see table 1).

## MORPHOLOGICAL CHARACTERS SELECTED

Simple measurements of overall size and shape defined by the width and length of the three shell segments appear to be sufficient to recognize different species and intraspecific forms. An eyepiece micrometer on a Zeiss standard research microscope (× 25 objectives and × 12.5 oculars) with a resolution of ± 2 microns was used for the measurements.

Eight morphological characters were measured on 40 to 50 specimens of each species of *Pterocorys* treated herein. Two hundred specimens of the *P. clausus* group from the Late Miocene to the Recent were measured. Many characters proved to be non-diagnostic for general characterization of species, because of their uniformity within the whole genus, or because their variation was restricted to a single species.

The morphological characters measured are:

TABLE 3

Ranges and abundances of taxa, DSDP Site 214. Species abundances are recorded as follows: A = > 30 specimens; C = 10–30 specimens; F = 5–10 specimens; R = 2–5 specimens; + = 1 specimen. Assemblage abundances are recorded as follows: C = common; F = few; R = rare. Preservation is recorded as follows: G = good; M = moderate; P = poor.

| Core-Section | Abundance | Preservation | *P. campanula* | *P. clausus* | *P. hertwigii* | *P. longicollis* | *P. macroceras* | *P. minythorax* | *P. sabae* | *P. zancleus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0101 | F | M | — | R | — | — | R | — | R | — | *C. tuberosa* Zone |
| 0103 | C | G | — | R | — | — | F | — | R | — | *A. ypsilon* Zone |
| 01cc | C | G | — | F | — | — | C | — | F | + | |
| 0203 | C | G | R | F | — | — | C | — | — | — | *A. angulare* Zone |
| 02cc | C | M | + | R | — | — | F | — | — | R | |
| 0303 | C | G | — | + | — | — | R | — | — | — | *P. prismatium* Zone |
| 03cc | C | M | R | C | — | — | F | — | + | — | |
| 0403 | C | M | + | F | — | — | F | — | — | — | |
| 04cc | C | M | R | + | — | — | R | — | — | — | *S. pentas* Zone |
| 0503 | C | M | + | F | — | — | R | — | — | — | |
| 05cc | C | M | — | + | — | — | — | — | — | — | |
| 0603 | C | M | R | + | — | — | — | — | — | — | |
| 06cc | C | G | R | R | — | — | R | — | — | — | |
| 0703 | C | M | — | + | — | — | + | — | — | — | |
| 07cc | C | G | R | C | — | — | F | — | — | — | |
| 0803 | C | G | — | C | — | — | + | — | — | — | |
| 08cc | C | G | + | C | — | — | — | — | — | — | |
| 0903 | C | G | R | F | — | — | R | — | — | — | *S. peregrina* Zone |
| 09cc | C | G | — | F | — | — | R | — | — | — | |
| 1003 | C | G | + | C | — | — | — | — | — | — | |
| 10cc | C | G | — | C | — | — | + | — | — | — | |
| 1103 | C | G | — | C | — | — | R | — | — | — | |
| 11cc | C | G | — | C | — | — | R | — | — | — | |
| 1203 | C | G | — | C | — | — | R | — | — | — | |
| 12cc | C | G | — | F | — | — | R | — | — | — | |

1) *Length of apical horn:* The apical horn can be of very different sizes in individuals from the same species. A maximum apical horn length was measured on specimens of *P. longicollis* (50–60 μ), but many specimens of *P. zancleus* and *P. campanula* also have long apical horns (up to 50 μ). Two species are characterized by short apical horns. Typical specimens of *P. clausus* have horns 20–25 μ in length, and *P. macroceras* has an even shorter apical horn (15–22 μ). However, in both species this morphological character appears to have changed since the Middle Miocene. Apical horns were very short (12–15 μ) on early Pliocene specimens of *P. macroceras.* On the other hand, they were sometimes longer on *P. clausus* individuals (10–30 μ). Some transitional forms of the same species, with a broader abdomen and more pronounced ribs, are characterized by generally longer apical horns (30–40 μ).

2, 3) *Breadth and length of cephalis:* Cephalic dimensions appear to be rather stable. The cephalic breadth varies only between 25 and 29 μ within the whole genus. The cephalic

TABLE 4

Ranges and abundances of taxa, composite site of *Marian Dufresne* (French) cores. See caption of table 3 for explanation.

| Core-Section-Depth | Abundance | Preservation | *P. campanula* | *P. clausus* | *P. hertwigii* | *P. longicollis* | *P. macroceras* | *P. minythorax* | *P. sabae* | *P. zancleus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 81365-9-140 | C | G | C | C | — | — | A | R | F | — | *A. angulare* Zone |
| 81368-8-128 | C | G | F | F | — | — | C | R | — | — | *P. prismatium* Zone |
| 81371-9-138 | C | G | C | C | — | — | A | R | R | — | |
| 81374-10-142 | C | G | — | C | — | + | C | — | R | — | |
| 81367-8-140 | C | G | R | A | — | — | F | ? | — | — | *S. pentas* |
| 81375-12-87 | C | G | R | C | — | + | A | — | — | — | |
| 81369-12-140 | C | G | + | A | — | — | A | — | — | — | |
| 77157-3-30 | C | G | — | C | — | + | F | — | — | — | *S. peregrina* Zone |
| 77157-3-120 | C | G | — | A | — | + | F | — | — | — | |

length is more variable (25–35 μ), probably because the upper part of the cephalis extends into the apical horn, and it is not easy to recognize the cephalis-apical horn boundary. No species appears to have a cephalis that is markedly longer than the others.

4, 5) *Breadth and length of thorax:* Thoracic dimensions proved to be very useful morphological characters because they can be easily measured, even on individuals which are not fully developed, and particularly because they are relatively uniform within a given species (see below).

6, 7) *Breadth and length of abdomen:* Abdominal breadth was very useful in separating campanulate species from cylindrical ones. However, this character appears to have changed within species having a long stratigraphic range. Abdominal length appears to be an unreliable measure because almost all specimens are broken or not fully grown. Differences of 40 μ in length are commonly measured within the same species.

8) *Width of pores and bars:* Pores and bars have approximately the same width in many species and are close in size to the accuracy limits of our ocular micrometer; therefore, they were not found to be useful for distinguishing between species.

#### The *P. clausus-P. hertwigii* Lineage (text-fig. 3)

Evolution between *P. clausus* and *P. hertwigii* can be characterized by the persistence of an ancestral stock (*P. clausus*) along with the development of more ornate and campanulate forms (*P. campanula* and *P. hertwigii*) since the Late Miocene. In Middle Miocene populations, the genus *Pterocorys* is represented only by very rare individuals of *P. clausus* which appear to be the oldest well-known species of *Pterocorys* (text-fig. 3). The true ancestor of *Pterocorys* is probably to be found among some small, cylindrical and undescribed forms from the Late Eocene or Oligocene (A. Sanfilippo, personal communication). Those small forms seem to persist in Mid-Miocene populations from the North Pacific (pl. 1, fig. 1).

TABLE 5
Ranges and abundances of taxa, DSDP Site 586/586A. See caption of table 3 for explanation.

| Core-Section | Abundance | Preservation | *P. campanula* | *P. clausus* | *P. hertwigii* | *P. longicollis* | *P. macroceras* | *P. minythorax* | *P. sabae* | *P. zancleus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0101 | C | M | – | R | R | – | R | – | – | – | No zonation |
| 0201 | F | M | – | + | – | – | – | – | + | – | |
| 0203 | C | M | – | C | F | – | F | + | R | + | |
| 0206 | F | M | – | + | + | – | + | – | – | – | |
| 0303 | C | G | F | C | F | – | R | – | R | R | |
| 0306 | C | M | C | F | – | – | F | – | – | + | |
| 0403 | C | G | C | F | – | – | F | – | + | – | *A. angulare* Zone |
| 0406 | C | M | F | R | – | – | – | – | – | – | |
| 0503 | C | M | F | C | – | – | C | – | – | – | *P. prismatium* Zone |
| A0103 | C | G | C | C | – | – | R | – | – | – | |
| A0106 | C | G | C | – | – | – | – | – | – | – | |
| A0203 | C | G | C | R | – | – | R | – | – | – | |
| A0206 | F | P | R | – | – | – | + | – | – | – | |
| A0303 | C | G | C | – | – | – | – | – | – | – | *S. pentas* Zone |
| A0306 | C | G | + | R | – | – | – | – | – | – | |
| A0403 | C | G | R | R | – | – | + | – | ? | – | |
| A0406 | C | G | + | + | – | – | – | – | – | – | |
| A0503 | C | G | + | R | – | – | – | – | – | – | |
| A0506 | C | G | C | – | – | – | + | – | – | – | |
| A0603 | C | G | R | F | – | – | – | – | + | – | |
| A0606 | C | M | R | – | – | – | – | – | – | – | |
| A0703 | C | G | + | R | – | – | – | – | – | – | |
| A0706 | C | G | F | – | – | + | – | – | – | – | |
| A0803 | C | G | R | – | – | – | – | – | – | – | |
| A0806 | C | M | C | R | – | – | – | – | – | – | |
| A0903 | C | G | C | – | – | – | – | – | – | – | |
| A0906 | C | G | F | – | – | – | – | – | – | – | |
| A1003 | C | G | R | F | – | – | – | – | – | – | |
| A1006 | C | G | R | – | – | – | – | – | – | – | |
| A1103 | C | G | R | R | – | + | – | – | – | – | *S. peregrina* Zone |
| A1106 | C | G | – | R | – | – | – | – | – | – | |
| A1203 | C | G | – | R | – | + | – | – | – | – | |
| A1206 | C | M | + | F | – | – | – | – | – | – | |
| A1303 | C | G | – | C | – | – | – | – | – | – | |
| A1403 | C | G | – | C | – | – | – | – | – | – | |
| A1503 | C | G | – | R | – | – | – | – | – | – | |
| A1506 | C | G | – | – | – | – | – | – | – | – | |
| A1603 | C | G | – | F | – | – | – | – | – | – | |
| A1606 | C | G | – | R | – | – | – | – | – | – | |
| A1703 | C | G | – | R | – | – | – | – | – | – | |
| A1706 | C | G | – | R | – | + | – | – | – | – | |

Late Miocene and Early Pliocene populations of *Pterocorys* are dominated by *P. clausus.* The maximum thoracic breadth of *P. clausus* fluctuates between 60 and 80 $\mu$ in most typical specimens since the Late Miocene. The corresponding values of thoracic length are between 40 and 55 $\mu$, and the apical horn is always shorter than 30 $\mu$. The maximum abdominal breadth of these forms is never more than 100 $\mu$ (text-fig. 2). However, many individuals of this species may have different thoracic dimensions, longer apical horns, and broader abdomens, even when they have no ridges and poorly developed thoracic ribs. In these larger forms of *P. clausus* from the Late Miocene, the thorax is much broader (80–100 $\mu$) than long (50–60 $\mu$), and the apical horn is usually longer than 30 $\mu$. Slender individuals can have an abdominal breadth of less than 100 $\mu$, but most of the large *P. clausus* have broad abdomens (100–120 $\mu$) (text-fig. 2). The thoracic and abdominal dimensions of these atypical forms are identical to those of the first *P. campanula,* which appear in the latest Miocene (text-fig. 3). Only poorly developed thoracic ribs and ridges discriminate *P. campanula* from *P. clausus* in the Early Pliocene. Transitional forms with more or less ornamented shells have been observed, showing clearly that *P. clausus* is the ancestor of *P. campanula.*

Two subspecies of *P. campanula,* dissimilar only in size, were previously described by Caulet (1979). The slender forms were named *P. campanula variabilis* and the larger ones (abdominal breadth > 120 $\mu$), *P. campanula campanula.* Our new data show that all intermediate sizes occur between the subspecies, and that their stratigraphic ranges are nearly the same. *P. campanula campanula* appears to be more abundant in Late Pliocene populations, and seems to be restricted to equatorial waters. We have, herein, placed the two subspecies in synonymy.

By the Middle Pleistocene, *P. hertwigii* evolved from *P. campanula.* Transitional morphotypes with one or two ridges extending into the upper part of the abdomen (pl. 1, fig. 4) are very rare, and the relatively rapid evolution of the lineage occurred between 1.0 and 0.6 Ma. Thoracic and abdominal dimensions are identical for *P. hertwigii* and *P. campanula.*

*P. zancleus* evolved shortly before *P. hertwigii.* This species might be included in the *P. clausus-P. hertwigii* lineage because its thoracic dimensions are generally between those of *P. clausus* and *P. campanula* (text-fig. 2). If it were included, however, we would have two distinctly different forms evolving from *P. campanula*: one a larger, more ornamented form (*P. hertwigii*) and one reverting to a smaller, simpler form (*P. zancleus*). Since the tendency towards more and more ornamented forms is uniform in the *P. clausus-P. hertwigii* lineage, and since no transitional forms between contemporaneous specimens of *P. hertwigii* and *P. zancleus* can be found, *P. zancleus* appears not to be included in this lineage.

Previous studies have shown that *P. zancleus* is much more common in Mediterranean or mid-latitude sediments than in equatorial regions (Caulet 1974, 1986b). No biometric data are yet available for these temperate individuals, but they seem to be smaller than tropical specimens (Caulet, personal observations). Moreover, Early Pleistocene samples from the southern Indian Ocean show their gradual appearance among populations where the only other species of *Pterocorys* present is *P. clausus.* All these observations suggest that *P. zancleus* could have originated from *P. clausus* in mid-latitudes. More data are obviously needed to document this suggested new lineage.

#### The *P. clausus-P. sabae* Lineage (text-fig. 3)

Thoracic length clearly differentiates *P. sabae* from the *P. clausus-P. campanula* group (text-fig. 2). The three strong thoracic ribs characteristic of *P. sabae* can, however, be less developed in some individuals. Common in Pleistocene sed-

TABLE 6
Ranges and abundances of taxa, DSDP Site 586B. See caption of table 3 for explanation.

| Core-Section | Abundance | Preservation | *P. campanula* | *P. clausus* | *P. hertwigii* | *P. longicollis* | *P. macroceras* | *P. minythorax* | *P. sabae* | *P. zancleus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0101 | C | G | – | R | C | – | + | – | + | C | NR1 and NR2 = *B. invaginata* and upper *C. tuberosa* Zones |
| 0102 | C | G | – | C | R | – | C | + | F | C | |
| 0104 | F | G | – | F | C | – | C | + | R | R | |
| 0105 | C | G | – | F | R | – | R | – | + | F | |
| 0106 | F | P | – | – | + | – | – | – | – | – | NR3 = lower *C. tuberosa* Zone |
| 0201 | R | P | – | – | – | – | – | – | – | – | |
| 0203 | R | P | – | – | – | – | – | – | – | – | |
| 0204 | R | P | – | – | – | – | – | – | – | – | |
| 0205 | C | P | – | – | – | – | – | – | – | + | NR4 = *A. ypsilon* Zone |
| 0301 | F | P | – | – | – | – | – | – | – | – | |
| 0302 | C | P | R | R | – | – | – | – | R | – | |
| 0303 | C | P | – | – | – | – | – | – | – | – | |
| 0304 | R | P | – | – | – | – | – | – | – | – | |
| 0305 | R | P | – | – | – | – | – | – | – | – | |
| 0306 | R | P | – | – | – | – | – | – | – | – | NR5 = *A. angulare* Zone |
| 0401 | C | G | R | F | – | + | R | – | + | ? | |
| 0402 | C | G | C | C | – | + | R | – | – | ? | |
| 0404 | C | G | F | C | – | – | R | – | + | – | |
| 0405 | C | G | C | C | – | + | A | + | R | – | |
| 0406 | C | M | F | F | – | R | A | – | – | – | |
| 0501 | C | M | C | C | – | R | C | + | R | – | |
| 0502 | C | M | R | R | – | R | F | – | – | – | |
| 0503 | C | P | + | R | – | + | + | – | – | – | |
| 0504 | C | G | F | C | – | + | C | – | – | – | |
| 0505 | C | M | F | + | – | R | C | – | R | – | |
| 0506 | C | P | + | + | – | – | – | – | + | – | |
| 0601 | C | G | R | F | – | R | C | + | + | – | *P. prismatium* Zone |
| 0602 | F | M | R | R | – | + | F | – | R | – | |
| 0603 | C | M | R | + | – | – | R | – | + | – | |
| 0604 | C | M | F | – | – | – | – | – | – | – | |
| 0605 | C | M | – | – | – | + | – | – | – | – | |
| 0606 | C | M | F | – | – | – | – | – | – | – | |
| 0701 | C | G | R | F | – | + | C | + | R | – | |
| 0702 | F | M | + | – | – | – | – | – | – | – | |
| 0703 | C | M | R | – | – | – | – | – | – | – | |
| 0704 | F | M | + | – | – | – | – | – | – | – | |
| 0705 | C | M | + | – | – | R | – | – | – | – | |
| 0706 | C | P | – | – | – | – | – | – | – | – | |
| 0801 | C | P | – | – | – | + | – | – | – | – | |
| 0803 | C | M | – | – | – | – | – | – | – | – | |
| 0805 | C | M | R | F | – | – | R | – | – | – | |
| 1101 | C | P | – | R | – | – | – | – | – | – | |
| 1103 | C | P | – | + | – | – | – | – | – | – | *S. pentas* Zone |
| 1105 | C | P | – | R | – | – | + | – | – | – | |
| 1201 | C | P | – | + | – | – | + | – | – | – | |
| 1203 | C | P | R | + | – | – | + | – | – | – | |
| 1204 | F | P | – | F | – | – | R | – | – | – | |
| 1304 | F | P | – | – | – | – | – | – | – | – | |
| 1401 | C | G | R | C | – | R | R | – | – | – | |
| 1403 | C | M | – | + | – | – | – | – | – | – | |
| 1405 | C | M | + | R | – | – | – | – | – | – | |
| 1501 | C | M | – | – | – | – | – | – | – | – | |

TABLE 6 (*Continued*)

| Core-Section | Abundance | Preservation | *P. campanula* | *P. clausus* | *P. hertwigii* | *P. longicollis* | *P. macroceras* | *P. minythorax* | *P. sabae* | *P. zancleus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1503 | C | M | – | – | – | – | – | – | – | – | |
| 1505 | C | G | – | R | – | R | – | – | – | – | |
| 1601 | C | M | + | F | – | R | – | – | – | – | |
| 1603 | F | M | + | – | – | – | – | – | – | – | |
| 1605 | C | G | – | R | – | – | – | – | – | – | |
| 1702 | R | M | – | – | – | – | – | – | – | – | |
| 1703 | C | M | – | F | – | – | – | – | – | – | |
| 1801 | C | M | – | F | – | – | – | – | – | – | |
| 1804 | F | M | – | F | – | – | – | – | – | – | |
| 1901 | R | G | – | – | – | – | – | – | – | – | |
| 1903 | F | G | – | R | – | – | – | – | – | – | |
| 1905 | C | M | – | + | – | – | – | – | – | – | |
| 2001 | F | M | – | R | – | – | – | – | – | – | |
| 2003 | C | M | – | + | – | – | – | – | – | – | *S. peregrina* Zone |
| 2005 | C | M | – | R | – | – | – | – | – | – | |
| 2101 | F | M | – | + | – | – | – | – | – | – | |
| 2103 | F | P | – | + | – | – | – | – | – | – | |
| 2105 | F | M | – | – | – | – | – | – | – | – | |
| 2201 | R | G | – | – | – | – | – | – | – | – | |
| 2203 | F | P | – | – | – | – | – | – | – | – | |
| 2205 | F | M | – | – | – | – | – | – | – | – | |
| 2303 | F | P | – | C | – | – | – | – | – | – | |
| 2305 | F | G | – | – | – | – | – | – | – | – | |
| 2401 | C | G | – | F | – | – | – | – | – | – | |
| 2403 | C | G | – | C | – | – | ? | – | – | – | |
| 2405 | C | G | – | R | – | – | – | – | – | – | |
| 2501 | C | M | – | R | – | – | – | – | – | – | |
| 2505 | F | G | – | R | – | – | – | – | – | – | |

iments, *P. sabae* is very rare in the Pliocene (see tables 3–9). The first *Pterocorys* with a conical thorax and three strong ribs appeared in the Middle Pliocene. Very rare and sporadic occurrences of *Pterocorys* with incipient wings and a conical thorax (pl. 2, fig. 9) are found in Early to Middle Pliocene samples from both oceans. Their thoracic dimensions are similar to those of slender *P. clausus* specimens from the same age. However, the incipient wings which are located halfway along the thorax in *P. sabae* give it a very different shape. Thus, these forms appear to be transitional between typical *P. clausus* and *P. sabae.* Unfortunately, their occurrence is so rare that a detailed evolution in this lineage cannot be documented.

#### The *P. clausus-P. macroceras* Lineage (text-fig. 3)

*P. macroceras* also seems to have evolved from ancestral *P. clausus* forms near the Miocene-Pliocene boundary. Individuals intermediate between typical *P. clausus* and *P. macroceras* are very rare in the Late Miocene populations of the Indian Ocean (Early Pliocene in the Pacific Ocean). These transitional forms have the same thoracic dimensions as *P. clausus,* but have at least one smooth rib extending into the upper part of the abdomen. They are broader than Pleisto-

TABLE 7

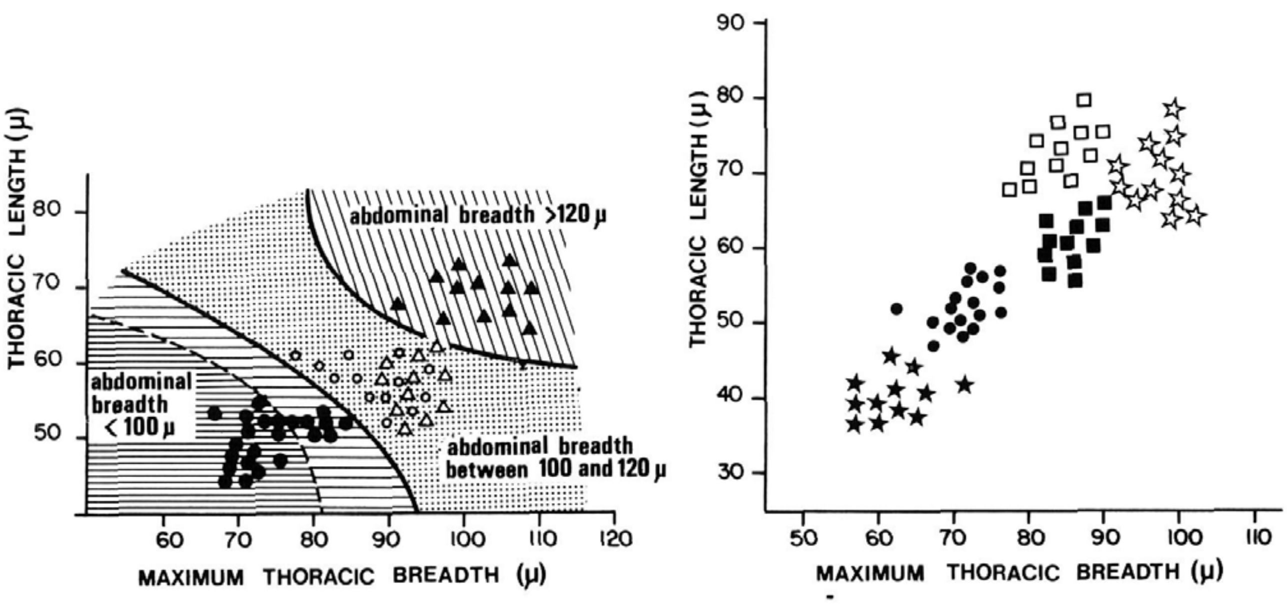
Ranges and abundances of taxa, LSDH 90P (Scripps Institution of Oceanography Lusiad Expedition). See caption of table 3 for explanation.

| Depth sampled (cm) | Abundance | Preservation | *P. campanula* | *P. clausus* | *P. hertwigii* | *P. longicollis* | *P. macroceras* | *P. minythorax* | *P. sabae* | *P. zancleus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0-3 | C | G | – | – | + | – | R | – | F | + | *C. tuberosa* Zone |
| 10-2 | C | G | F | R | – | – | C | – | F | – | |
| 25-7 | C | G | R | – | – | – | C | – | + | – | |
| 34-6 | C | G | C | R | – | – | C | – | F | ? | |
| 50-2 | C | G | F | R | – | – | F | – | + | – | |
| 74-6 | C | G | C | R | – | + | C | + | R | – | *A. angulare* Zone |
| 100-2 | C | M | F | – | – | – | R | – | – | – | |
| 124-6 | C | G | C | R | – | – | C | – | + | – | |
| 150-2 | C | M | R | – | – | – | R | – | + | – | |
| 174-6 | C | G | C | + | – | – | C | – | + | – | |
| 203-5 | C | G | C | R | – | – | F | – | – | – | |
| 251-3 | C | G | C | – | – | – | F | – | – | – | *P. prismatium* Zone |
| 300-2 | C | M | R | – | – | – | R | – | – | – | |
| 354-6 | C | G | F | ? | – | – | F | – | + | – | |
| 394-6 | C | G | F | – | – | – | R | – | – | – | |

TABLE 8

Ranges and abundances of taxa, AMPH 97P (Scripps Institution of Oceanography Amphitrite Expedition). See caption of table 3 for explanation.

| Depth Sampled (cm) | Abundance | Preservation | *P. campanula* | *P. clausus* | *P. hertwigii* | *P. longicollis* | *P. macroceras* | *P. minythorax* | *P. sabae* | *P. zancleus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 03-5 | C | G | – | ? | C | – | F | – | C | R | *C. tuberosa* Zone |
| 13-5 | C | G | – | R | F | – | F | – | C | R | *A. ypsilon* Zone |
| 23-5 | C | G | F | – | + | – | + | – | F | R | |
| 43-5 | C | G | C | + | – | – | R | – | R | – | |
| 63-5 | C | G | C | – | – | – | + | – | F | – | |
| 83-5 | C | M | F | – | – | – | R | – | + | – | |
| 103-5 | C | G | C | – | – | – | F | – | R | – | *A. angulare* Zone |
| 123-5 | C | G | C | + | – | – | F | – | + | – | |
| 143-5 | C | G | R | – | – | – | + | – | – | – | |
| 174-6 | C | G | C | – | – | – | R | – | R | – | |
| 199-201 | C | G | F | – | – | + | – | – | – | – | |
| 224-6 | C | M | F | – | – | – | + | – | – | – | |
| 249-51 | C | M | F | – | – | – | R | – | – | – | |
| 299-301 | C | M | F | – | – | – | R | – | – | – | *P. prismatium* Zone |
| 349-51 | C | M | F | – | – | – | – | – | – | – | |




a)— Evolution from *P. clausus* to *P. campanula* b)— Extant *Pterocorys* species

TEXT-FIGURE 2

a. Graphic comparison of thoracic breadth vs. thoracic length of forms showing the evolution from *P. clausus* to *P. campanula*. Each data point represents measurements on more than 1 specimen. ● typical *P. clausus*, ○ transitional *P. clausus-P. campanula*, △ slender *P. campanula*, ▲ broad *P. campanula*. Dashed line shows the division between forms having an apical horn length of < 30 μ (below dashed line) and > 30 μ (above dashed line). b. Graphic comparison of thoracic breadth vs. thoracic length of 5 extant species of *Pterocorys*. ★ *P. macroceras*, ● *P. clausus*, ■ *P. zancleus*, □ *P. sabae*, ☆ *P. hertwigii*.

TABLE 9
Ranges and abundances of taxa, DSDP Site 573. See caption of table 3 for explanation.

| Core-Section | Abundance | Preservation | *P. campanula* | *P. clausus* | *P. hertwigii* | *P. longicollis* | *P. macroceras* | *P. minythorax* | *P. sabae* | *P. zancleus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0101 | C | G | – | F | C | – | R | R | F | + | *B. invaginata* Zone |
| 01cc | C | G | – | C | C | – | R | R | R | – | *C. tuberosa* Zone |
| 0203 | C | G | – | C | C | – | + | F | R | – | |
| 02cc | C | G | – | C | C | – | – | F | F | R | *A. ypsilon* Zone |
| 0303 | C | G | C | F | – | – | + | F | F | R | |
| 03cc | C | G | C | R | – | – | – | + | R | – | *A. angulare* Zone |
| 0403 | C | G | F | F | – | – | – | – | + | – | *P. prismatium* Zone |
| 04cc | C | G | C | F | – | – | – | – | + | – | |
| 0503 | C | G | C | C | – | – | – | – | – | – | |
| 05cc | C | G | C | F | – | – | – | + | – | – | *S. pentas* Zone |
| 0603 | C | G | F | R | – | – | – | – | – | – | |
| 06cc | C | G | R | C | – | – | – | – | – | – | |
| 0703 | C | G | F | F | – | – | + | – | – | – | |
| 07cc | C | G | F | C | – | – | – | – | – | – | |
| 0803 | C | G | C | F | – | – | – | – | – | – | |
| 08cc | C | G | F | + | – | – | – | – | – | – | |
| 0903 | C | G | R | R | – | – | – | – | – | – | |
| 09cc | C | G | F | C | – | – | – | – | – | – | *S. peregrina* Zone |
| 1003 | C | G | + | R | – | – | – | – | – | – | |
| 10cc | C | G | + | C | – | – | – | – | – | – | |
| 1103 | C | G | – | F | – | – | – | – | – | – | |
| 11cc | C | G | – | F | – | – | – | – | – | – | |
| 1203 | C | G | – | F | – | – | – | – | – | – | |
| 12cc | C | G | – | C | – | – | – | – | – | – | |
| 1303 | F | G | – | + | – | – | – | – | – | – | |
| 1403 | C | G | – | C | – | – | – | – | – | – | *D. penultima* Zone |
| 1503 | C | G | – | C | – | – | – | – | – | – | |
| 15cc | C | G | – | C | – | – | – | – | – | – | |
| 1603 | C | G | – | C | – | – | – | – | – | – | |
| 16cc | C | G | – | C | – | – | – | – | – | – | *D. antepenultima* Zone |
| 1703 | C | G | – | C | – | – | – | – | – | – | |
| 17cc | C | G | – | C | – | – | – | – | – | – | |
| 1803 | C | G | – | C | – | – | – | – | – | – | |
| 1903 | C | G | – | C | – | – | – | – | – | – | |

cene specimens of *P. macroceras*. Their thoracic length is always longer than 38 $\mu$ (28–33 in Pleistocene specimens) and the maximum breadth of the thorax is between 62 and 72 $\mu$ (57–65 $\mu$ in Recent forms). However, the apical horn of these old *P. macroceras* is very small (12–15 $\mu$) compared to the apical horn of *P. clausus* (10–30 $\mu$). Detailed evolution between *P. clausus* and *P. macroceras* is not easy to understand because transitional forms are very rare.

### Origin of *P. longicollis* and *P. minythorax*

Very few data are available on the oldest occurrences of both these species and their origin remains unknown.

## SUMMARY

Our simple biometric data show that only two species of *Pterocorys* have diagnostic thoracic sizes: *P. macroceras* is the smallest *Pterocorys* and *P. sabae* is the longest. Other morphological characters are needed to distinguish between the remaining species. Thoracic size is helpful in recognizing the main lineages. The common ancestor of most Late Neogene forms is *P. clausus* whose thoracic dimensions have mean values. In all lineages morphologic evolution appears to be gradual, though not uniform in rate or direction. Morphologic divergence of lineages is also gradual.

From the ancestral form, *P. clausus*, three distinct descendant lineages can be recognized (text-fig. 3) in our material:

*1)* A decrease in thoracic size leads to the appearance of *P. macroceras* between 6 and 4 Ma.

*2)* Continuous increases in thoracic size, abdominal breadth and apical horn length can be seen between *P. clausus* and *P. campanula* from 5.5 to 4 Ma. At the same time, the thoracic ribs become more and more prominent. Ranges of transitional forms appear to be diachronous in Indian and Pacific Ocean sediments, but the appearance of the first true *P. campanula* is approximately synchronous at about 5 Ma. In the Pleistocene, thoracic ridges grow and extend from the thorax to the abdomen as *P. campanula* becomes *P. hertwigii* (0.6–1.0 Ma).

*3)* A third lineage (*P. clausus*-*P. sabae*) is characterized by a lengthening of the thorax and the development of thoracic wings. Transitional forms are very rare, however, and the first occurrence of *P. sabae* is not easily determined.

*P. longicollis* and *P. minythorax* are too rare to produce good morphometric data. Their origin is not yet recognized. Evolution of *P. zancleus* seems to be related to morphologic changes in middle or high latitude *P. clausus* populations.

Our data are not sufficient to prove hybridization between *Pterocorys* species, but some rare individuals show transitional characters, primarily in the *P. clausus*-*P. hertwigii* lineage. Finally, many more quantitative analyses are needed, particularly in temperate and cold populations. However, good samples will be hard to find because *Pterocorys* skeletons appear to be very fragile and easily broken in Middle and Late Miocene deposits.

## SYSTEMATICS

Family **PTEROCORYTHIDAE** Haeckel 1881 *emend.* Riedel 1967; Moore 1972

*Definition:* "Cephalis subdivided into three lobes by two obliquely downwardly directed lateral furrows arising from the apical spine, in the manner described for *Anthocyrtidium cineraria* Haeckel and *Calocyclas virginis* Haeckel by Riedel (1957)" (from Riedel 1967). Moore's emendation is simply a spelling correction.

Genus ***Pterocorys*** Haeckel

*Pterocorys* HAECKEL 1881, p. 435 (type sp. = *P. campanula* Haeckel 1887, p. 1316, pl. 71, fig. 3).
*Theoconus* HAECKEL 1887, p. 1399 (type sp. = *Eucyrtidium zanclaeum* Mueller 1855, p. 672; 1858, pl. 6, figs. 1–3).

TABLE 10
Summary tabulation of limits of stratigraphic ranges of species of *Pterocorys*. T = Last Appearance Datum; B = First Appearance Datum.

| Event | Indian Ocean | | Western Pacific | | Central Pacific | |
|---|---|---|---|---|---|---|
| | Core | Age (Ma) | Core | Age (Ma) | Core | Age (Ma) |
| B *Pterocorys hertwigii* | MD369 2.3 m | 0.9 | 586A-3-3 | 0.6 | 573-2-cc | 0.7 |
| | MD369 2.5 m | 1.0 | 586A-3-6 | 0.8 | 573-3-3 | 1.1 |
| T *Pterocorys campanula* | 214-1-cc | 0.6 | 586-3-3 | 0.6 | 573-2-cc | 0.7 |
| | 214-2-3 | 1.0 | 586-3-6 | 0.8 | 573-3-3 | 1.1 |
| B *Pterocorys zancleus* | 214-2-cc | 1.4 | 586A-3-6 | ·0.8 | 573-3-3 | 1.1 |
| | 214-3-3 | 2.0 | 586A-4-3 | 1.1 | 573-3-cc | 1.4 |
| T *Pterocorys longicollis* | too rare | | 586B-3-6 | 1.3 | absent | |
| | | | 586B-4-1 | 1.4 | | |
| B *Pterocorys minythorax* | present in MD81-371 | 1.6 | too rare | | 573-3-cc | 1.4 |
| | | 1.8 | | | 573-4-3 | 1.7 |
| B *Pterocorys sabae* | 214-3-cc | 2.3 | 586B-7-1 | 2.5 | 573-4-cc | 2.1 |
| | 214-4-3 | 2.5 | 586B-7-2 | 2.7 | 573-5-3 | 2.3 |
| B *Pterocorys macroceras* | below 214-12-cc | > 5.8 | 586B-14-1 | 4.1 | too rare | |
| | | | 586B-14-3 | 4.2 | | |
| B *Pterocorys longicollis* | too rare | | 586B-16-1 | 4.6 | absent | |
| | | | 586B-16-3 | 4.7 | | |
| B *Pterocorys campanula* | 214-10-3 | 4.7 | 586A-12-6 | 4.7 | 573-10-cc | 5.4 |
| | 214-10-cc | 5.1 | 586A-13-3 | 4.9 | 573-11-3 | 5.5 |

*Lithopilium* POPOFSKY 1913, p. 377 (type sp. = *Lithopilium macroceras* Popofsky 1913, p. 377, pl. 38, fig. 2, text-figs. 91–95).

*Original definition:* "*Theopilida* (vel *Tricyrtida triradiata aperta*) with three simple, free lateral wings arising from the sides of the thorax" (from Haeckel 1887, p. 1316).

*Definition:* Pterocorythidae with three segments, conical or cylindrical; tri-lobate cephalis, with the smaller paired lobes lateral to the larger unpaired lobe. Dorsal and lateral spines extend as ribs into the thorax and may project as thorns or wings. Single apical horn present. No differentiated peristome, terminal or subterminal teeth. The genus differs from *Lamprocyclas* by the presence of thoracic ribs and the absence of a differentiated peristome.

*Remarks:* Petrushevskaya (1971a, p. 232) believes that there is a tendency towards a saccular closing of the abdomen in species of *Pterocorys*. We have not observed this trend.

Members of this genus have three thoracic ribs and/or three wings projecting from the thorax (Sanfilippo, personal com-

PLATE 1

All figures × 225

1 ?*Pterocorys* sp., Kaiko 3.53.1 (Japan Trench), dredge sample, A-N39/0; *D. petterssoni* Zone.

2 *Pterocorys campanula* Haeckel with slender abdomen, DSDP 573-3-6, 130–131 cm, A-J44/0; *A. angulare* Zone.

3 *Pterocorys campanula* Haeckel with broad abdomen, MD81371 (Central Indian Basin), 13.8 m below sea floor, A-M38/0; *P. prismatium* Zone.

4 *Pterocorys campanula* Haeckel, form approaching *P. hertwigii*, MD85672 (Somalian Basin), 12.8 m below sea floor; *A. ypsilon* Zone.

5 *Pterocorys campanula* Haeckel, MD81365 (Central Indian Basin), 13.4 m below sea floor; *A. angulare* Zone.

6 *Pterocorys clausus* (Popofsky), focus on abdomen, MD73004 (Mascarene Plateau), 9.5 m below sea floor, A-X39/2; *C. tuberosa* Zone.

7 *Pterocorys clausus* (Popofsky), focus on cephalis, MD73004, 9.5 m below sea floor, A-X39/2; *C. tuberosa* Zone.

8 *Pterocorys clausus* (Popofsky), MD75072 (Crozet Basin), 11.1 m below sea floor; *A. ypsilon* Zone.

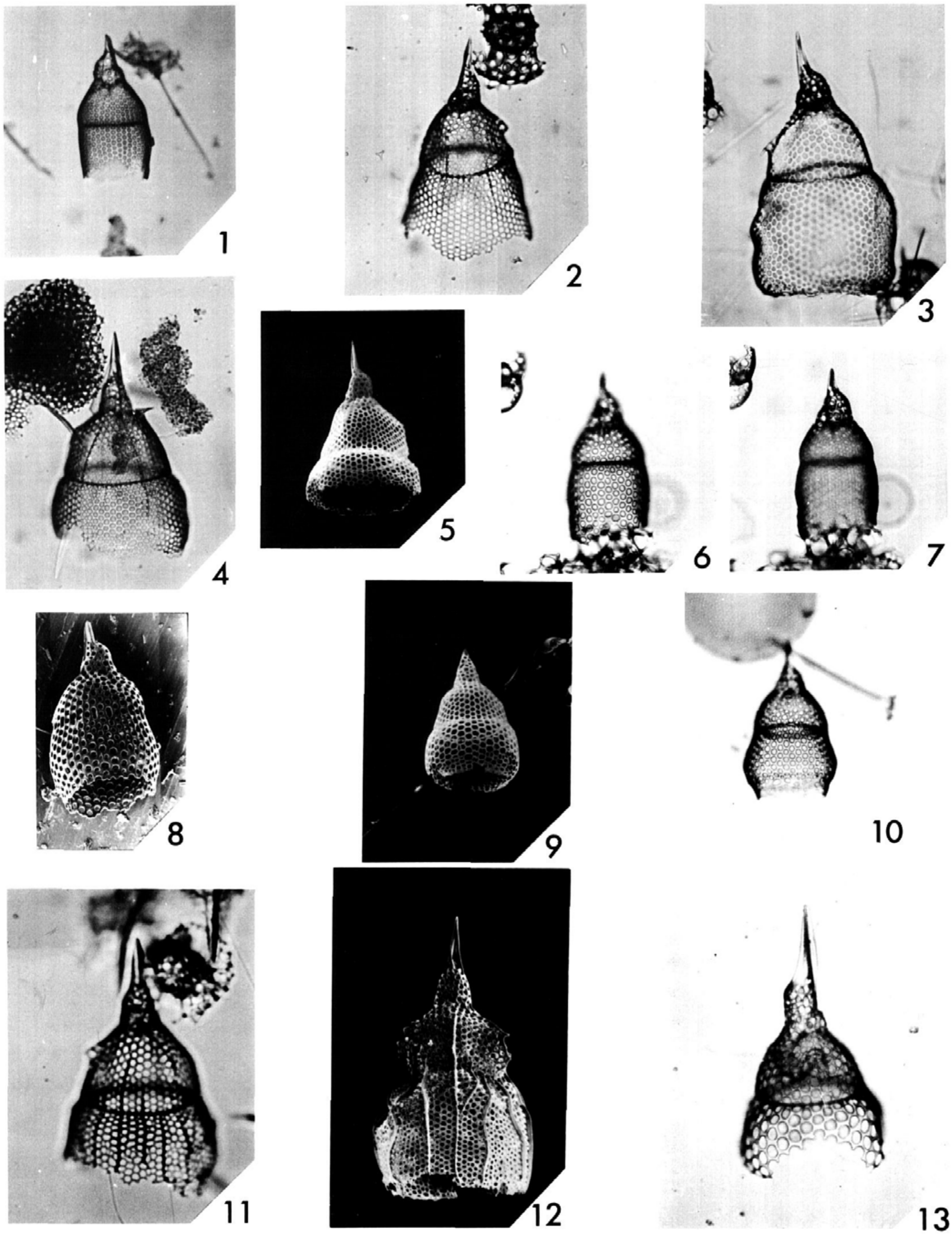
9 *Pterocorys clausus* (Popofsky) with small peristome, MD81375 (Central Indian Basin), 18.87 m below sea floor; *S. pentas* Zone.

10 *Pterocorys clausus* (Popofsky), form approaching *P. campanula*, with peristome, DSDP 573-8-cc, B-S27/0; *S. pentas* Zone.

11 *Pterocorys hertwigii* (Haeckel), MD85675 (Somalian Basin), top of core, A-Z12/4; *B. invaginata* Zone.

12 *Pterocorys hertwigii* (Haeckel), from surface plankton tow SMC72 (Central Indian Basin).

13 *Pterocorys longicollis* Caulet, DSDP 573-4-4, 130–131 cm, A-E53/4; *P. prismatium* Zone.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munication, April 10, 1986), but ribs are frequently very difficult to distinguish using a light microscope and can best be seen using an SEM.

Some specimens of *P. clausus* (Early Pliocene) may have an undifferentiated peristome.

***Pterocorys campanula*** **Haeckel**
Plate 1, figures 2–5

*Pterocorys campanula* HAECKEL 1887, p. 1316, pl. 71, fig. 3.
*Pterocorys campanula* Haeckel, PETRUSHEVSKAYA 1972a, pl. 1, fig. 9.—PETRUSHEVSKAYA 1976, pl. 3, fig. 5.
*Pterocorys* sp. aff. *P. hertwigii* (Haeckel), SANFILIPPO and RIEDEL 1974, pl. 4, fig. 1.
*Pterocorys campanula* Haeckel, CAULET 1979, p. 133, pl. III, figs. 2, 3, 5, 6 (includes subspecies *P. campanula campanula* and *P. campanula variabilis*).

*Description:* Shell conical to ovate, thin-walled, smooth except for longitudinal ridges at irregular intervals on the thorax. Rarely, there is a single ridge which is prolonged into the abdominal wall. Cephalis trilocular with numerous subcircular pores. Stout three-bladed apical horn about the same length as or a little longer than the cephalis. Primary lateral and dorsal spines aligned with three ribs in the thoracic wall.

Thorax inflated conical with subcircular to circular pores arranged in longitudinal rows, ornamented by irregular longitudinal ridges. In some specimens thoracic ribs project as small thorns or triangular, pored wings. Lumbar stricture distinct.

In Pacific Ocean sediments, early forms have a much inflated abdomen (> 120 $\mu$), broader than the thorax, but with similar pores. In later specimens the abdomen is less inflated (< 120 $\mu$), more cylindrical. In Indian Ocean sediments early forms have a rather narrow abdomen (< 120 $\mu$) and later forms are more inflated (> 120 $\mu$). Termination always ragged.

*Dimensions:* Total length (excluding apical horn) 139–217 $\mu$. Length of apical horn 28–43 $\mu$; of cephalis 26–37 $\mu$; of thorax 48–68 $\mu$; of abdomen 77–115 $\mu$. Maximum breadth of cephalis 24–29 $\mu$; of thorax 90–110 $\mu$; of abdomen 110–140 $\mu$.

*Distinguishing characters:* More than three longitudinal ridges on the thorax; very rarely a single ridge projects into the upper part of the abdomen.

*Stratigraphic range:* F.A.D. occurs in the upper part of the *S. peregrina* Zone at ~ 5.0 Ma. L.A.D. occurs in the Upper Pleistocene near the *A. angulare* (= NR5 of Caulet 1979)/*A. ypsilon* (= NR4 of Caulet 1979) zonal boundary between 0.6 and 1.1 Ma.

*Geographic range and abundance:* Common in both tropical Indian and tropical Pacific Ocean sediments. The form described by Caulet (1979) as *P. campanula variabilis* is rare to common in temperate latitudes.

*Phylogeny:* Evolved from *P. clausus* during the lowermost Pliocene (~ 4.0 Ma).

*Remarks:* The "surface" origin given by Haeckel (1887) for *Pterocorys campanula* cannot be reconciled with our observations that *P. campanula* becomes extinct in the Pleistocene, but his description seems to coincide with ours and so we have chosen to retain the name *campanula*.

Caulet (1979) described the two forms of *P. campanula* as follows: 1) *Pterocorys campanula campanula*: "*Pterocorys* with very pronounced wings which at the mid-point of the thorax project horizontally, but distally have a downward curve.

PLATE 2

All figures × 225

1 *Pterocorys macroceras* (Popofsky), Kaiko 3.53.6 (Japan Trench), dredge sample, A-P31/4; *P. prismatium* Zone.

2 *Pterocorys macroceras* (Popofsky), DSDP 573-1-1, 8–10 cm, A-Y26/1; *B. invaginata* Zone.

3 *Pterocorys macroceras* (Popofsky), DSDP 573-3-5, 130–131 cm, A-F45/1; *A. angulare* Zone.

4 *Pterocorys macroceras* (Popofsky) with peristome, MD85675 (Somalian Basin), 8.6 m below sea floor, B-D37/3; *B. invaginata* Zone.

5 *Pterocorys macroceras* (Popofsky), MD81375 (Central Indian Basin), 18.87 m below sea floor; *S. pentas* Zone.

6 *Pterocorys minythorax* (Nigrini), MD73004 (Mascarene Plateau), 9.04 m below sea floor, A-W44/4; *C. tuberosa* Zone.

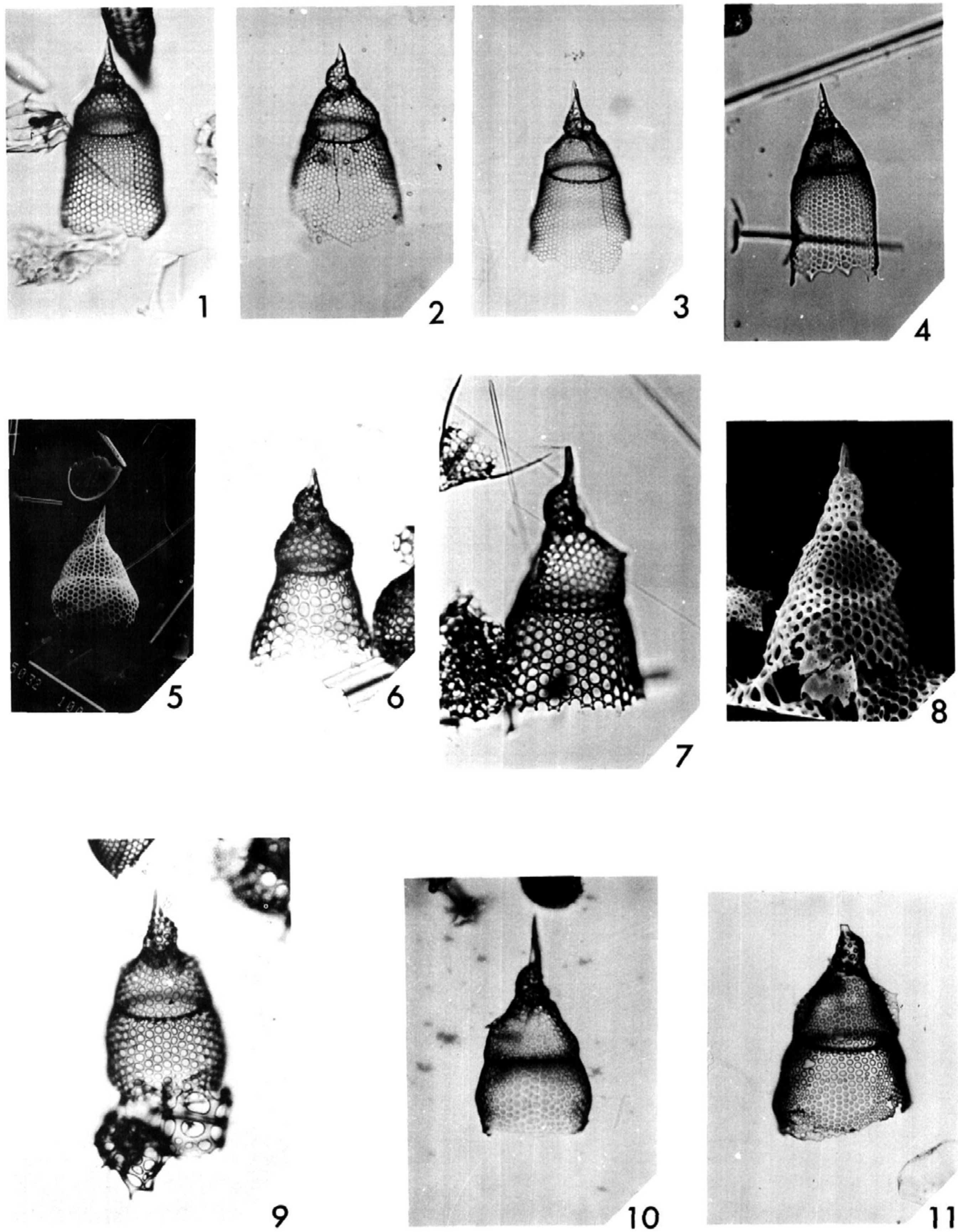
7 *Pterocorys sabae* (Ehrenberg), MD85675 (Somalian Basin), top of core, A-Y48/1; *B. invaginata* Zone.

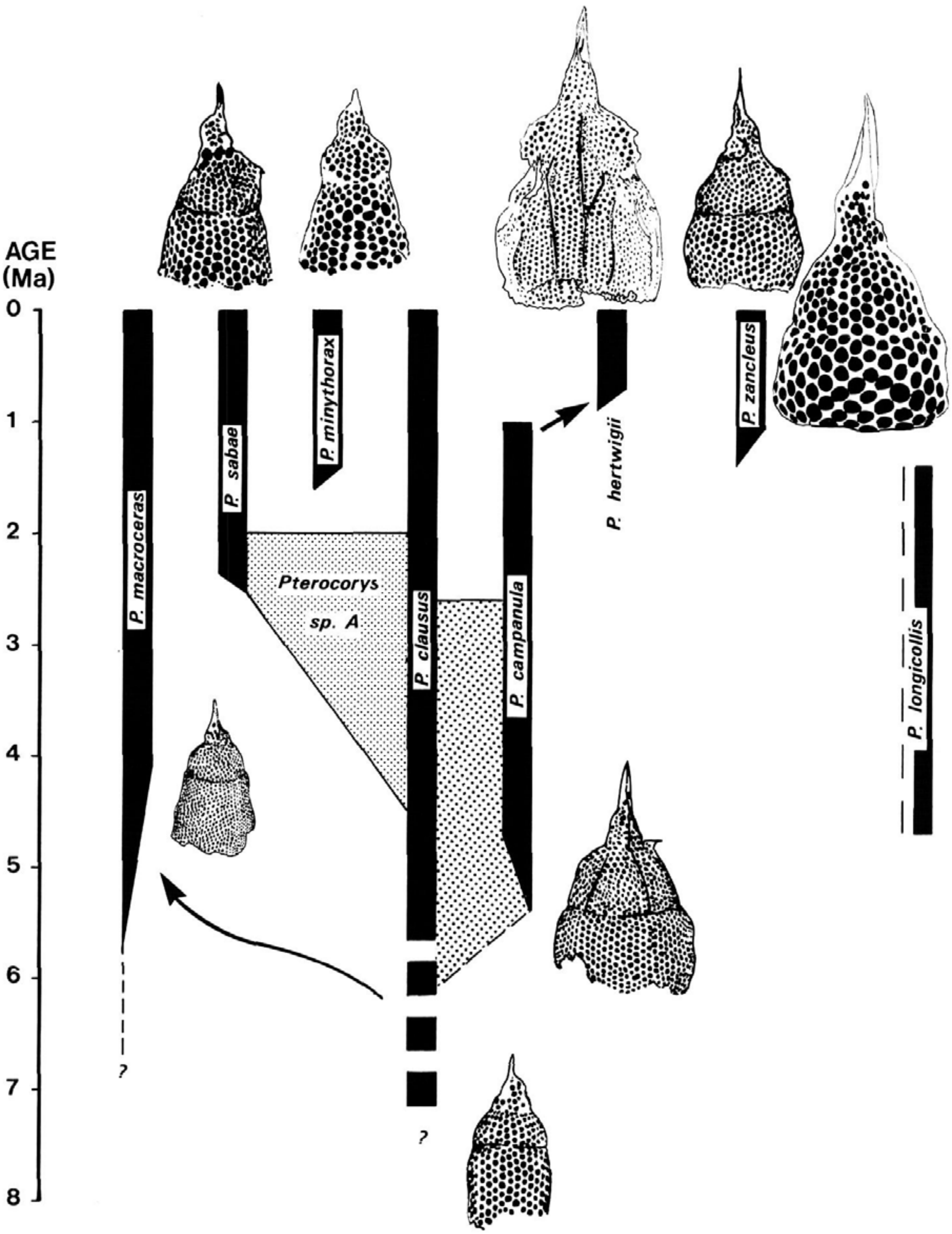
8 *Pterocorys sabae* (Ehrenberg), MD73004 (Mascarene Plateau), top of core; *C. tuberosa* Zone.

9 *Pterocorys* sp. A, DSDP 573-5-cc, A-Z48/0; *S. pentas* Zone.

10 *Pterocorys zancleus* (Mueller), MD73004 (Mascarene Plateau), 8.8 m below sea floor, A-C23/3; *C. tuberosa* Zone.

11 *Pterocorys zancleus* (Mueller), MD85675 (Somalian Basin), 10.1 m below sea floor, B-V33/2; *C. tuberosa* Zone.






TEXT-FIGURE 3
Summary range chart for the genus *Pterocorys*. Vertical bars show stratigraphic ranges of species with left side indicating Indian Ocean range and right side the Pacific Ocean range. Hatched areas indicate intervals in which transitional forms are found. All figures × 225.

"Abdomen very inflated just below the lumbar stricture. Rare ridges on the thorax" (translated from Caulet 1979, p. 133).
2) *Pterocorys campanula variabilis*: "Form more slender, more cylindrical than the former. The wings are less pronounced and project downwards almost to the lumbar stricture. The overall dimensions are smaller" (translated from Caulet 1979, p. 133).

In Caulet (1979), reference to Sanfilippo and Riedel (1974) should read fig. 1 for *P. campanula campanula* and fig. 2 for *P. campanula variabilis*.

Petrushevskaya (1972a) describes two different ranges for a "typical *P. campanula*" and an "atypical *P. campanula*". However, she does not figure the atypical form and so we are uncertain as to her meaning.

***Pterocorys clausus*** (Popofsky)
Plate 1, figures 6–10

*Lithornithium clausum* POPOFSKY 1913, p. 393, text-fig. 111 (*non* text-figs. 112–114).—PETRUSHEVSKAYA 1966, p. 231, fig. 6-6.
*Theoconus zancleus* (Mueller), POPOFSKY 1913, p. 397, pl. 38, figs. 6, 7.—KLING 1973, p. 639, pl. 5, figs. 9–11; pl. 12, figs. 7–9.
*Pterocorys clausus* group (Popofsky), PETRUSHEVSKAYA and KOSLOVA 1972, p. 545, pl. 36, figs. 16–18.—SAKAI 1980, p. 711, pl. 9, figs. 5, 6a, b.
*Pterocorys cranoides* (Haeckel), PETRUSHEVSKAYA 1972b, pl. 2, fig. 26.
*Pterocorys* sp. aff. *P. hertwigii* (Haeckel), RIEDEL, SANFILIPPO and CITA 1974, pl. 61, fig. 4.
*Theoconus junonis* Haeckel, RENZ 1976, p. 147, pl. 6, fig. 17.
*Pterocorys clausus* (Popofsky) *compressus*, PETRUSHEVSKAYA 1976, pl. 3, fig. I.
*Pterocorys zancleus* (Mueller), NIGRINI and MOORE 1979, pl. 25, figs. 11a, b.—MOLINA-CRUZ 1982, p. 996, pl. 5, figs. 2, 3.—MORLEY 1985, p. 411, pl. 3, fig. 4.—MORLEY and KOHL 1986, pl. 2, fig. 6.
*Pterocorys clausus* (Popofsky), KLING 1979, p. 311, pl. II, fig. 22.—BOLTOVSKOY and RIEDEL 1980, p. 127, pl. 5, fig. 19.
*Pterocorys* cf. *zancleus* (Mueller), NIGRINI and LOMBARI 1984, p. N167, pl. 30, fig. 3.
?*Pterocorys* sp. 2, PETRUSHEVSKAYA 1976, pl. 3, fig. B.
?*Pterocorys zancleus* (Mueller), TAKAHASHI and HONJO 1981, p. 154, pl. 10, figs. 1–3.—POLUZZI 1982, p. 64, pl. 26, fig. 4.

*Description:* Shell generally cylindrical, rarely conical, thick-walled, smooth. Cephalis trilocular with numerous subcircular pores. Stout three-bladed apical horn usually shorter than the cephalis. Primary lateral and dorsal spines aligned with three thoracic ribs which may be difficult to distinguish in transmitted light.

Thorax campanulate with subcircular to circular pores in regular longitudinal rows. Lumbar stricture distinct, somewhat constricted. Abdomen cylindrical with pores similar in shape and arrangement to those of the thorax, 12–14 on a half-equator. Termination usually ragged, but showing some distal constriction. Rarely, in older Pacific sediments (Early Pliocene) there is a short undifferentiated peristome with very small pointed teeth.

In the lowermost Pliocene, there are forms transitional to *P. campanula* in which the apical horn (30–42 $\mu$) becomes longer than the cephalis (28–33 $\mu$). In addition, there is an increase in thoracic breadth (86–92 $\mu$). This intermediate form is figured in Nigrini and Lombari 1984, pl. 30, fig. 3 and plate 1, figure 10 herein.

*Dimensions:* Total length (excluding apical horn) 130–154 $\mu$. Length of apical horn 28–42 $\mu$; of cephalis 24–33 $\mu$; of thorax 38–48 $\mu$; of abdomen 60–86 $\mu$. Maximum breadth of cephalis 24–28 $\mu$; of thorax 62–82 $\mu$; of abdomen 82–110 $\mu$.

*Distinguishing characters:* Shell generally cylindrical, thick-walled. Thoracic ribs indistinct. Pores relatively large in very regular longitudinal rows.

*Stratigraphic range:* Extant. F.A.D. not found in this study; it is, however, older than the *D. antepenultima* Zone.

*Geographic range and abundance:* Common in both tropical Indian and tropical Pacific Ocean sediments. Few to common in temperate and subarctic sediments.

*Phylogeny:* Appears to be the ancestral stock of the genus *Pterocorys* (see Sanfilippo and Riedel, in preparation).

*Remarks:* The specimens illustrated by Nakaseko and Nishimura (1982) as *Pterocorys* sp. (pl. 51, figs. 1–3; pl. 55, figs. 1, 2, 6–8) appear to be the high latitude form of *P. clausus.*

***Pterocorys hertwigii*** (Haeckel)
Plate 1, figures 11, 12

*Eucyrtidium hertwigii* HAECKEL 1887, p. 1491, pl. 80, fig. 12.—CASEY 1971, pl. 23.1, figs. 18, 20, ?fig. 19.—CASEY 1977, pl. 2, figs. 18–20.
*Theoconus hertwigii* (Haeckel), NIGRINI 1967, p. 73, pl. 6, figs. 4a, b.—RENZ 1974, pl. 19, fig. 16.—RENZ 1976, p. 146, pl. 6, fig. 22.—MOLINA-CRUZ 1977, p. 338, pl. 8, figs. 7, 8.
*Pterocorys hertwigii* (Haeckel), PETRUSHEVSKAYA 1971a, pl. 116, fig. 6.—PETRUSHEVSKAYA 1972a, pl. 1, fig. 10.—SANFILIPPO and RIEDEL 1974, p. 1023, pl. 3, figs. 12–14, *non* pl. 4, figs. 1, 2.—PETRUSHEVSKAYA 1976, pl. 3, fig. K.—RIEDEL and SANFILIPPO 1977, pl. 23, fig. 10.—RIEDEL and SANFILIPPO 1978, p. 72, pl. 9, fig. 2.—CAULET 1979, pl. 3, fig. 4.—NIGRINI and MOORE 1979, p. N85, pl. 25, fig. 9.—JOHNSON and NIGRINI 1980, p. 135, pl. IV, fig. 1, text-fig. 13c.—NISHIMURA and YAMAUCHI 1984, p. 63, pl. 38, fig. 7 (*non* fig. 6).—BOLTOVSKOY and JANKILEVICH 1985, pl. 5, fig. 5.
?*Eucyrtidium fatuosa* EHRENBERG 1872a, p. 309.—EHRENBERG 1872b, pl. 9, fig. 19.
*Phormocyrtis fatuosa* (Ehrenberg), BENSON 1966, p. 485, pl. 33, figs. 6, 7.

*Description:* "Shell conical to ovate, thin-walled, smooth except for longitudinal ridges at irregular intervals. Cephalis trilocular with numerous subcircular pores, heavier than rest of shell. Stout three-bladed apical horn usually about the same length or a little longer than cephalis. Primary lateral and dorsal spines aligned with three ribs in the thoracic wall.

"Thorax campanulate with subcircular to circular pores arranged in longitudinal rows. Lumbar stricture distinct. Abdomen broader than thorax, but with similar pores. In complete specimens abdomen slightly constricted distally with a smooth termination, but most specimens are incomplete.

"Both thorax and abdomen ornamented by poreless ridges which run more or less longitudinally, irregularly spaced and not necessarily continuous for entire shell length. On the thorax some of the ridges frequently bear 1 or 2 small spines" (from Nigrini 1967, p. 73).

*Dimensions:* "Total length (excluding apical horn) 119–191 $\mu$. Length of apical horn 9–45 $\mu$; of cephalis 23–32 $\mu$; of thorax 45–63 $\mu$; of abdomen up to 109 $\mu$. Maximum breadth of cephalis 27–32 $\mu$; of thorax 81–100 $\mu$; of abdomen 100–136 $\mu$" (from Nigrini 1967, p. 74).

*Distinguishing characters:* Wall of thorax and abdomen thin, with more than three thin longitudinal ridges, not necessarily continuous, throughout both thorax and abdomen.

*Stratigraphic range:* Extant. F.A.D. in the western and central tropical Pacific is between 0.6 and 1.1 Ma. In the tropical Indian Ocean the species is very rare, but the F.A.D. appears to be just below the L.A.D. of *Anthocyrtidium angulare* (0.9 to 1.0 Ma).

*Geographic range and abundance:* In the Indian Ocean "very sparsely distributed in low latitudes and does not occur in samples from south of 35°S" (from Nigrini 1967). See also Johnson and Nigrini (1980, p. 135; 1982, p. 258). Few to common in tropical Pacific sediments.

*Phylogeny:* Descendant of *Pterocorys campanula.*

*Remarks:* It is not clear if Sanfilippo and Riedel (1974, p. 67) have combined *P. hertwigii* and *P. campanula* in their examination of Late Tertiary Radiolaria from Crete.

If *E. fatuosum* were synonymous with *P. hertwigii, fatuosa* would be the senior synonym (*Eucyrtidium fatuosum* Ehrenberg 1872a, p. 309; 1872b, pl. 9, fig. 19). However, we are not able to determine the correct taxonomic position of the specimen figured by Ehrenberg.

According to Renz (1976) "some specimens lack ribs". We do not believe this to be true. By the original definition, *P. hertwigii* must have ribs and we concur with this description.

***Pterocorys longicollis*** Caulet
Plate 1, figure 13

*Pterocorys longicollis* CAULET 1986a, p. 850, pl. 4, figs. 4, 5.

*Description:* "Shell rather thin-walled. Three-lobed cephalis subdivided into two parts: *1)* upper portion, open, cylindrical, with circular pores, bearing a stout three-bladed apical horn, strong, with a great pore at its base; *2)* lower 'neck'*, formed by a very prominent dorsal lobe. Primary lateral and dorsal spines continue as ribs in the thoracic wall for about half its length. Sometimes, they are external, forming very small wings. Thorax is large, cupola-shaped with hexagonally framed, circular pores, quincuncially arranged and aligned longitudinally, 12–15 on a half-equator, 8–10 in a vertical series. Pronounced lumbar stricture. Abdomen campanulate. Distal end ragged; aperture never observed" (from Caulet 1986a, p. 850).

*Dimensions:* "Apical horn length: 50–60 $\mu$m. Total length of thorax 40–50 $\mu$m. Maximum width: 80 $\mu$m" (from Caulet 1986a, p. 850).

*Distinguishing characters:* Cephalis and neck elongated with pronounced bulging of the "D-lobe". Very strong apical horn up to twice the cephalic length.

*Stratigraphic range:* In Site 586B, F.A.D. occurs near the *S. pentas/S. peregrina* zonal boundary. L.A.D. occurs in the *A. angulare* (= NR5) zone. Specimens are extremely rare in our material. It seems likely that they are easily broken during slide preparation.

*Geographic range and abundance:* Very rare in both tropical Indian and tropical Pacific Ocean sediments.

*Phylogeny:* Unknown.

***Pterocorys macroceras*** (Popofsky)
Plate 2, figures 1–5

*Lithopilium macroceras* POPOFSKY 1913, p. 377, text-figs. 91–93 (*non* text-fig. 94).
*Lithornithium clausum* POPOFSKY 1913, p. 393, text-figs. 112–114 (*non* fig. 111).
*Pterocorys* sp. PETRUSHEVSKAYA 1968, p. 1305, fig. 2, XII.
*Pterocorys macroceras* (Popofsky), PETRUSHEVSKAYA 1971a, p. 234, fig. 120.
*Pterocorys clausus* (Popofsky), PETRUSHEVSKAYA 1972b, pl. 2, fig. 14.—PETRUSHEVSKAYA 1976, pl. 3, fig. H.
*Lamprocyclas cranoides* (Haeckel), MCMILLEN and CASEY 1978, pl. IV, figs. 13, 14.
*Pterocorys zancleus* (Mueller), TAKAHASHI 1981, pl. 42, figs. 1–4.

*Description:* Shell cylindro-conical, thin-walled, smooth. Cephalis trilocular with numerous subcircular pores, larger on either side of the apical spine. Three-bladed apical horn, almost triangular, usually shorter than the cephalis. Primary lateral and dorsal spines aligned with three thoracic ribs, some of which extend into the abdomen. Collar stricture not pronounced.

Thorax conical with subcircular to circular pores arranged in longitudinal rows. Pores adjacent to the ribs are larger. Abdomen usually incomplete, but in rare complete specimens it is cylindro-conical with a small undifferentiated peristome (pl. 2, fig. 4). Proximally subcircular to circular pores aligned longitudinally; distally pores are irregular in size and arrangement.

*Dimensions:* Total length (excluding apical horn) 90–145 $\mu$. Length of apical horn 12–20 $\mu$; of cephalis 20–29 $\mu$; of thorax 28–38 $\mu$; of abdomen 57–92 $\mu$. Maximum breadth of cephalis 24–33 $\mu$; of thorax 57–72 $\mu$; of abdomen 65–92 $\mu$.

*Distinguishing characters:* Shell very small, thin-walled. Cephalis short, basally enlarged with no distinct collar stricture. Up to three thoracic ribs, one of which is generally prolonged into the abdomen.

*Stratigraphic range:* Extant. F.A.D. occurs in the lower part of the *S. pentas* Zone in Site 586B (western tropical Pacific) at ~ 4.1 Ma. However, in our tropical Indian Ocean material, the F.A.D. is at least as old as 5.8 Ma, suggesting a strong diachroneity.

*Geographic range and abundance:* Rare to common in tropical Indian and western tropical Pacific sediments. Very rare in the central tropical Pacific.

*Phylogeny:* Uncertain, possibly arising from *P. clausus* in the Early Pliocene.

*Remarks:* Kling (1979) places Petrushevskaya's (1971a) description of *P. macroceras* (Popofsky) in synonymy with *P. clausus.* We do not agree with this action.

*The term "neck" here may be misleading and may cause some confusion with the type of "neck", narrower than the main part of the cephalis, which has been described for the genus *Theocorythium* (Nigrini 1967). *P. longicollis* has a cylindrical, elongated cephalis with a prominent dorsal lobe at the base.

*Eucyrtidium trochus* Ehrenberg 1872b, pl. 7, fig. 17 seems to be very similar to *P. macroceras*. It has the typical thorax with small pores and the typical cephalis of *P. macroceras*. However, the illustration is too poor for us to be certain.

***Pterocorys minythorax*** (Nigrini)
Plate 2, figure 6

*Theoconus minythorax* NIGRINI 1968, p. 57, pl. 1, fig. 8.—KLING 1977, p. 217, pl. 1, fig. 8.
*Theoconus zancleus* (Mueller), BENSON 1964, pl. 2, figs. 50, 51.—BENSON 1966, pl. 33, fig. 5 (*non* fig. 4).—CASEY 1971, pl. 23.3, fig. 15.
*Pterocorys zanguebaricus* (Ehrenberg), PETRUSHEVSKAYA 1972b, pl. 2, fig. 16.—PETRUSHEVSKAYA 1976, pl. 3, fig. G.
*Pterocorys zancleus* (Mueller), CASEY 1977, pl. 4, fig. 15.
*Pterocorys minythorax* (Nigrini), NIGRINI and MOORE 1979, p. N87, pl. 25, fig. 10.—MOLINA-CRUZ 1982, pl. 5, fig. 1.
*Theoconus minitorax* (*sic*) Nigrini, KRUGLIKOVA 1981, pl. 3, fig. 2.

*Description:* "Shell conical, rather thick-walled, smooth. Cephalis trilocular with relatively large subcircular pores and a short, three-bladed apical horn, usually about ½ of the cephalic length. Primary lateral and dorsal spines continue as ribs in the thoracic wall for more than ½ of its length and may project to form small, thornlike wings. Collar stricture not pronounced.

"Thorax small, campanulate; pores subcircular, 8–10 on a half-equator, aligned longitudinally with very narrow intervening bars. Lumbar stricture distinct.

"Abdomen slightly flared, up to 3 times as long as thorax. Pores similar to those on thorax, 9–10 on a half-equator. Termination always ragged, mouth wide open" (from Nigrini 1968, p. 57).

*Dimensions:* "Length of cephalis 27–36 $\mu$, of thorax 36–45 $\mu$, of abdomen 63–127 $\mu$. Maximum breadth of cephalis 18–27 $\mu$, of thorax 63–72 $\mu$, of abdomen 90–118 $\mu$ (from Nigrini 1968, p. 57). Indian Ocean specimens may have a broader thorax, up to 82 $\mu$; other dimensions are the same.

*Distinguishing characters:* Thorax very small and campanulate with elongated slightly flared abdomen.

*Stratigraphic range:* Extant. In Site 573 F.A.D. is in the *A. angulare* Zone (~ 1.5 Ma). Its presence in core MD81-391 in the tropical Indian Ocean indicates a similar F.A.D. there.

*Geographic range and abundance:* Very rare in tropical Indian Ocean and tropical western Pacific sediments. Rare in Site 573.

"Few to abundant in the regions of the North and South Equatorial and Peru Currents, but rare or absent in the region of the Equatorial Countercurrent" (from Nigrini 1968).

*Phylogeny:* Unknown.

*Remarks:* "This species differs from other members of the genus [*Pterocorys*] by its small thorax, relative to the size of its abdomen, and by its large pores. It was identified and described by Benson as *Theoconus zancleus* Mueller, but *T. zancleus* is apparently not synonymous with the species here described. Also, it is thought that Benson's description encompasses 2 species; the specimen shown on Plate 33, figure 5 appears to be the same as [*P.*] *minythorax*, but the one in Plate 33, figure 4 is not" (from Nigrini 1968).

***Pterocorys sabae*** (Ehrenberg)
Plate 2, figures 7, 8

*Pterocanium sabae* EHRENBERG 1872a, p. 319.—EHRENBERG 1872b, p. 299, pl. 10, fig. 17.
*Pterocorys sabae* (Eherenberg) HAECKEL 1887, p. 1317.—PETRUSHEVSKAYA 1972a, pl. 1, fig. 11.—PETRUSHEVSKAYA 1972b, pl. 2, fig. 2.—PETRUSHEVSKAYA 1976, pl. 3, figs. C, D.—JOHNSON and NIGRINI 1980, p. 150, pl. IV, fig. 2; pl. V, figs. 4, 5.
*Theoconus junonis* Haeckel, RENZ 1974, p. 798, pl. 19, fig. 27.
*Pterocorys zancleus* (Mueller), MCMILLEN and CASEY 1978, pl. IV, fig. 9.—NISHIMURA and YAMAUCHI 1984, pl. 38, figs. 3, 5 only.
*Pterocorys campanula* Haeckel, TAKAHASHI 1981, pl. 42, figs. 6, 7, ?8.—TAKAHASHI and HONJO 1981, p. 154, pl. 10, figs. 4, 5.—BOLTOVSKOY and JANKILEVICH 1985, pl. 5, fig. 4.—MORLEY and KOHL 1986, pl. 2, fig. 3.

*Description:* "Shell conical to ovate, quite smooth and rather thin-walled. Cephalis trilocular, the two secondary lobes beneath and somewhat lateral to the larger primary lobe; numerous subcircular pores; cephalis rather heavier than rest of shell. Stout three-bladed apical horn up to twice as long as cephalis. Collar stricture distinct.

"Thorax basically conical, but shape strongly influenced by three strong ribs which project as short wings about halfway along thoracic length. Pores subcircular, longitudinally aligned. Pores immediately adjacent to cephalis often enlarged. Lumbar stricture distinct.

"Abdomen broader than thorax, but with similar pores in more complete specimens. However, abdomen usually rudimentary and may have irregular pore arrangement. Termination always ragged. In high latitudes abdomen rarely present" (from Johnson and Nigrini 1980, p. 150).

*Dimensions:* "Length of cephalis and thorax 75–105 $\mu$m; of abdomen up to 127 $\mu$m. Maximum breadth of thorax 75–92 $\mu$m; of abdomen up to 127 $\mu$m" (from Johnson and Nigrini 1980, p. 150).

*Distinguishing characters:* Thorax sharply conical with shape strongly influenced by three strong ribs which project as short wings about halfway along the thoracic length. Thoracic pores immediately adjacent to cephalis often enlarged.

*Stratigraphic range:* Extant. F.A.D. occurs in the lowermost *P. prismatium* Zone (2.1 to 2.7 Ma).

*Geographic range and abundance:* "Present in most [western Indian Ocean] samples between 12°N and 40°S; abdomen rarely present in high-latitude specimens;" (from Johnson and Nigrini 1980, p. 135).

"Present in all [eastern Indian Ocean] samples north of about 32°S. Distribution pattern in the eastern Indian Ocean is similar to that found in the western Indian Ocean, except that the species ranges farther south (to about 40°S) in the western sector (from Johnson and Nigrini 1982, p. 258).

Few to common in tropical Pacific Ocean sediments.

*Phylogeny:* *P. sabae* appears to arise from a rare form, *Pterocorys* sp. A, transitional between *P. clausus* and *P. sabae* (pl. 2, fig. 9). This form has strong thoracic ribs, as does *P. sabae,* but they are directed outward, rather than downward, thus forming characteristic thoracic "shoulders". However, *Pterocorys* sp. A was found too rarely for us to be able to describe and measure it properly. It was observed in the *S. pentas* Zone and the lower part of the *P. prismatium* Zone.

***Pterocorys zancleus*** (Mueller)
Plate 2, figures 10, 11

*Eucyrtidium zanclaeum* MUELLER 1855, p. 672.—MUELLER 1858, p. 41, pl. 6, figs. 1–3.—HAECKEL 1862, p. 321.
*Eucyrtidium carinatum* HAECKEL 1862, pl. 7, figs. 4–7.
*Theoconus zancleus* (Mueller) HAECKEL 1887, p. 1399.—BENSON 1966, p. 482, pl. 33, fig. 4 (*non* fig. 5).
*Pterocorys carinata* (Haeckel) HAECKEL 1887, p. 1315.
*Pterocorys zancleus* (Mueller) PETRUSHEVSKAYA 1971a, p. 233, fig. 119, I–VII.—NIGRINI and MOORE 1979, p. N89, *non* pl. 25, figs. 11a, b.—POLUZZI 1982, p. 64, pl. 26, figs. 1, 3, ?2.—NISHIMURA and YAMAUCHI 1984, pl. 38, figs. 1, 4, 6 (*non* figs. 3, 5).—BOLTOVSKOY and JANKILEVICH 1985, pl. 5, fig. 6.
*Theoconus carinatus* (Haeckel) DUMITRICA 1973, p. 839, pl. 25, fig. 1; pl. 26, fig. 6.
*Pterocorys* sp. NISHIMURA and YAMAUCHI 1984, p. 64, pl. 38, fig. 2.
?*Pterocorys zancleus* (Mueller) NISHIMURA and YAMAUCHI 1984, pl. 56, fig. 9.
?*Pterocorys* cf. *zancleus* (Mueller) NIGRINI and LOMBARI 1984, p. N167, pl. 30, fig. 3.

*Description:* Structure of the cephalis including prominent dorso-lateral lobes, a straight dorsal face merging with a three-bladed apical horn, four collar pores, and the presence of three distinct thoracic ribs extending as short thorns above the base of the thorax. Cephalis closed at the top, with smooth surface and small, unequal to subequal, circular pores. Vertical spine indistinct but present; apical horn not robust. Thorax campanulate to truncate-conical, separated from the cephalis above by a change in contour and from the abdomen below by an indistinct lumbar stricture with an internal septal ring. Surface of thorax smooth. Thoracic pores circular to subcircular, in longitudinal rows. Abdomen smooth, ranging from subcylindrical with its distal portion tapering inward to truncate-conical with distal portion broader and not constricted and with equal (6–12 $\mu$), circular pores arranged hexagonally in longitudinal rows (modified herein from Benson 1966, p. 482).

See also Petrushevskaya 1971a, p. 233.

*Dimensions:* Length of apical horn 20–48 $\mu$; of cephalis 28–35 $\mu$; of thorax 39–58 $\mu$. Maximum breadth of cephalis 25–30 $\mu$; of thorax 72–94 $\mu$; of abdomen 86–120 $\mu$.

*Distinguishing characters:* Cylindro-conical shell; no pronounced change in contour between thorax and abdomen. No thoracic or abdominal ridges. No true wings.

*Stratigraphic range:* Extant. F.A.D. occurs near the *A. ypsilon* (= NR4)/*A. angulare* (= NR5) zonal boundary. Very rare.

*Geographic range and abundance:* Very rare in material used in this study from both the tropical Indian and tropical Pacific Oceans. It is more abundant in temperate sediments.

*Phylogeny:* Probably arises from *P. campanula* in temperate latitudes (Caulet 1986a).

*Remarks:* *E. aegaeum* Ehrenberg (1854, pl. 35A, XIXA, fig. 5) is probably synonymous with *P. zancleus,* but Ehrenberg's illustration (1854) and description (1858) are very poor. Hence, we prefer to retain the name *zancleus* and to use Mueller's good illustration (1858) and description (1855).

Petrushevskaya placed *P. sabae* in synonymy with *P. zancleus* in her 1971 paper, but on the same page she listed it with other species belonging to *Pterocorys.* She figured *P. sabae* in Petrushevskaya 1972a (pl. 1, fig. 11) and Petrushevskaya 1972b (pl. 2, fig. 2). Nishimura and Yamauchi (1984) apparently followed Petrushevskaya (1971a) and also placed *P. sabae* in synonymy with *P. zancleus.*

We are uncertain about the correct assignment for the specimen shown by Nishimura and Yamauchi (1984) on pl. 38, fig. 4—it could be transitional between *P. zancleus* and *P. campanula* gp.

**APPENDIX I**

We are uncertain of the correct assignment of the following published forms:

*Eucyrtidium zanguebaricum* Ehrenberg 1872a, p. 293; 1872b, pl. 9, fig. 22.
*Pterocorys sabae* (Ehrenberg) Petrushevskaya and Koslova 1972, p. 545, pl. 36, fig. 19.
*Pterocorys* sp. 1 Petrushevskaya 1976, pl. 3, fig. A.
*Pterocorys* sp. Boltovskoy and Riedel 1980, pl. 5, fig. 21.
*Pterocorys zancleus* (Mueller) Boltovskoy and Jankilevich 1985, pl. 5, fig. 6.
*Pterocorys* sp. Boltovskoy and Jankilevich 1985, pl. 5, fig. 7.

The following species have been described under the genera *Pterocorys, Lithopilium* or *Theoconus,* but do not conform to our definition of *Pterocorys*:

*Lithopilium hexacanthum* Popofsky 1913, p. 380, pl. 34, figs. 5, 6.
*Lithopilium reticulatum* Popofsky 1913, p. 379, pl. 35, figs. 4, 5.
*Lithopilium sphaerocephalum* Popofsky 1913, p. 380, pl. 35, figs. 2, 3.
*Pterocorys apsis* (Ehrenberg) Haeckel 1887, p. 1318.
*Pterocorys aquila* Haeckel 1887, p. 1317, pl. 71, fig. 5.
*Pterocorys barbadensis* (Ehrenberg) Haeckel 1887, p. 1318.
*Pterocorys carinata* (Haeckel) 1887, p. 1316.
*Pterocorys cassis* (Ehrenberg) Haeckel 1887, p. 1424.
NOTE: Petrushevskaya (1971a) includes *P. cassis* in *Pterocorys.* We think it might be more closely related to *Theocorythium,* but the original illustration is poor.
*Pterocorys columba* Haeckel 1887, p. 1317, pl. 71, fig. 2.
*Pterocorys falcifera* (Stöhr) Haeckel 1887, p. 1317.
*Pterocorys hirundo* Haeckel 1887, p. 1318, pl. 71, fig. 4.
*Pterocorys macroptera* Haeckel 1887, p. 1321.
*Pterocorys melitta* (Ehrenberg) Haeckel 1887, p. 1319.
*Pterocorys pipetta* Haeckel 1887, p. 1320.
*Pterocorys prismatica* Haeckel 1887, p. 1320.
*Pterocorys rhinoceros* Haeckel 1887, p. 1320, pl. 71, fig. 1.
*Pterocorys tricornis* Haeckel 1887, p. 1320.
*Pterocorys tubulosa* Haeckel 1887, p. 1319, pl. 68, fig. 6.
*Pterocorys turgida* (Ehrenberg) Haeckel 1887, p. 1319.
*Pterocorys zittelii* (Bütschli) Haeckel 1887, p. 1321.
*Pterocorys irregularis* Cleve 1899, pl. 4, fig. 1; Schroeder 1914, p. 119.

*Pterocorys amblycephalus* Jorgensen 1900, p. 87.
*Pterocorys gamphonyxos* Jorgensen 1900, p. 86, text-fig. 91.
*Pterocorys theoconus* Jorgensen 1900, p. 86.
*Pterocorys bicornis* Popofsky 1908, p. 288, pl. 34, figs. 7, 8.
*Pterocorys conica* Popofsky 1913, p. 374, text-fig. 90.
*Pterocorys longicornis* Popofsky 1913, p. 375, pl. 36, fig. 2.
*Pterocorys splendens* Campbell and Clark 1944, p. 46, pl. 6, figs. 19, 20.
*Pterocorys splendens* Campbell and Clark *albatrossensis* Riedel 1952, p. 7, pl. 1, fig. 2.
*Pterocorys bicornis* Dogiel, Dogiel and Reshetnyak 1952, p. 16, fig. 9.
*Pterocorys diplotriaena* Dogiel, Dogiel and Reshetnyak 1952, p. 15, fig. 8.
*Pterocorys korotnevi* Dogiel, Dogiel and Reshetnyak 1952, p. 17, fig. 11.
*Pterocorys schwiakowi* Dogiel, Dogiel and Reshetnyak 1952, p. 17, fig. 10.
*Pterocorys* sp. Nakaseko and Nishimura 1982, pl. 47, figs. 5, 10.
*Pterocorys killmari* (Renz) Benson 1983, p. 507.
*Theoconus amplus* (Ehrenberg) Haeckel 1887, p. 1402.
*Theoconus ampullaceus* (Ehrenberg) Haeckel 1887, p. 1402.
*Theoconus ficus* (Ehrenberg) Haeckel 1887, p. 1403.
*Theoconus jovis* Haeckel 1887, p. 1401, pl. 69, fig. 4.
*Theoconus junonis* Haeckel 1887, p. 1401, pl. 69, fig. 7.
*Theoconus longicornis* Haeckel 1887, p. 1401.
*Theocapsa lamarkii* Haeckel 1887, p. 1430, pl. 66, fig. 16.

NOTE: *T. lamarkii* is included in the genus *Pterocorys* by Petrushevskaya (1971a, p. 233), but we think it looks rather more like a *Theocorythium.*

*Eucyrtidium cranoides* Haeckel 1860, p. 838; 1862, p. 320, pl. VII, figs. 1–3.

NOTE: Benson (1966) places *E. cranoides* in synonymy with *P. zancleus.* We do not agree, but are uncertain of the correct generic assignment for this species.

The following species may belong to the genus *Pterocorys,* but since there is no illustration available, we cannot be certain of their correct generic assignment:

*Theoconus ariadnes* Haeckel 1887, p. 1402.
*Theoconus dionysius* (Ehrenberg) Haeckel 1887, p. 1402.
*Theoconus laterna* Haeckel 1887, p. 1403.
*Theoconus orthoconus* Haeckel 1887, p. 1400.

Finally, Petrushevskaya (1972a, pl. 2, fig. 13; 1976, pl. 3, figs. E, F) has illustrated, but not described, a temperate Plio-Pleistocene form, *Pterocorys ob,* which looks rather like an inflated *P. clausus.* Other references to this form may be found in Petrushevskaya (1981, p. 284) and Petrushevskaya (1971b, p. 115).

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