17. TIME-PROGRESSIVE MORPHOMETRIC CHANGES OF THE GENUS *GEPHYROCAPSA* IN THE QUATERNARY SEQUENCE OF THE TROPICAL INDIAN OCEAN, SITE 709[1]

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ABSTRACT

Stratigraphic variations in the morphometry of the genus *Gephyrocapsa* (calcareous nannoplankton) were quantitatively investigated in the Quaternary sequence of Hole 709C recovered from the tropical Indian Ocean. *Gephyrocapsa* can be roughly divided into groups of small and large *Gephyrocapsa,* mainly on the basis of their significant differences in coccolith size. Four lineages were recognized among the large *Gephyrocapsa,* and members of these lineages were tentatively named *Gephyrocapsa* sp. A, B, C, and D. These species are approximately 3 μm large at their incipient stages, and the latter three species become progressively larger thereafter. In the case of *Gephyrocapsa* sp. B and C, well-developed large forms disappeared abruptly, only to be succeeded by a new cycle of evolutionary size increase, respectively performed by *Gephyrocapsa* sp. C and D.

The first cycle observed in *Gephyrocapsa* sp. B occurred at the 16.02–12.02 mbsf interval (around 1.6–1.1 Ma), and *Gephyrocapsa* sp. A occurred simultaneously within this cycle. The second and third cycles, performed respectively by *Gephyrocapsa* sp. C and D, occurred at 9.62–6.02 mbsf (around 0.9–0.5 Ma) and above 5.62 mbsf (0.5 Ma to the present). The percentage abundance of large *Gephyrocapsa* species that showed an evolutional size increase conversely decreased with an increase in overall size. An interval lacking the large species that roughly corresponds to the "small *Gephyrocapsa* zone" was found between the first and second cycles, but changes in abundance of the small and large forms seem to be independent.

The appearance and disappearance of the large forms as well as their changes in overall size and abundance play major roles in the floral change throughout the Quaternary. The six nannoflora assemblages dividing the last 1.3 m.y. reported from the subtropical Pacific Ocean were also recognized in the tropical Indian Ocean. A new additional assemblage was identified in the basal part of the Pleistocene.

INTRODUCTION

Matsuoka and Okada (1989) studied time-progressive changes in the floral compositions and morphometries of major calcareous nannofossil taxa during the last 1.3 m.y. in the subtropical northwestern Pacific Ocean. They semiquantitatively measured the morphology of several placolith groups and demonstrated the existence of remarkable time-progressive changes in morphology as well as in the overall size of the *Gephyrocapsa* species. Because these measurements were conducted in a semiquantitative mode, details of the morphologic changes that have strong potential for paleoceanography as well as for improved Quaternary biostratigraphy are yet to be clarified.

A complete sequence of Quaternary sediment was retrieved from the tropical Indian Ocean at Hole 709C, and a set of high-resolution samples taken at 10-cm intervals was available to us for a quantitative study of Quaternary nannofossils. The purposes of this study were to investigate quantitatively the time-progressive changes in the morphometry of the genus *Gephyrocapsa* throughout the entire Quaternary period in the tropical Indian Ocean and to provide a base for the phylogeny of the genus and for the paleoceanography of this region. The results observed will also be examined for applicability to the improved biostratigraphy.

MATERIALS AND METHODS

Hole 709C is located in the western tropical Indian Ocean at 3°54.9'S and 60°33.1'E in a water depth of 3038.2 m. We iden-

tified the occurrence of the eight datum events, excluding the first occurrence (FO) of *Emiliania huxleyi,* under a light microscope in a full set of 10-cm-interval samples. The FO of *E. huxleyi* was determined under an electron microscope. The sedimentation rate obtained by plotting these datum events proved to be rather constant throughout the Quaternary at the average rate of 0.94 cm/k.y. (Fig. 1). We selected a set of 45 samples representative of the entire Quaternary sequence from Cores 115-709C-1H through -3H at 40-cm intervals to study the morphometry of the *Gephyrocapsa* complex (Table 1).

These samples were made into carbon replicas for detailed observation under a transmission electron microscope (TEM). The first 200 specimens of *Gephyrocapsa* species were measured for the overall size of the coccolith, the diameter of the central opening, and the angle of the central bridge vs. the long axis of the coccolith. The two lengths were measured to 0.1-μm precision. Because the bridge angle is difficult to measure precisely under a transmission microscope, it was classified into six categories: 0°, 15°, 15°–30°, 30°–45°, 45°–60°, 60°–75°, and 75°–90°. For those samples in which the small forms dominated the flora and the large forms were scarce, additional measurements were conducted exclusively for the large forms to obtain a sufficient data set. We also measured the composition of the flora, excluding the ubiquitous *Florisphaera profunda,* by identifying the first 200 coccoliths encountered. Advanced dissolution affects the preservation of nannofossils, and many fragmented specimens were observed in some samples. We identified and measured only reasonably well-preserved specimens.

CLASSIFICATION OF *GEPHYROCAPSA* TAXA

There are many extant or extinct species classified under the genus *Gephyrocapsa,* and the majority of these species are defined solely by morphologic characters to aid Quaternary biostratigraphy. The purpose of this investigation, on the other hand, is to study the time-progressive changes in morphometry
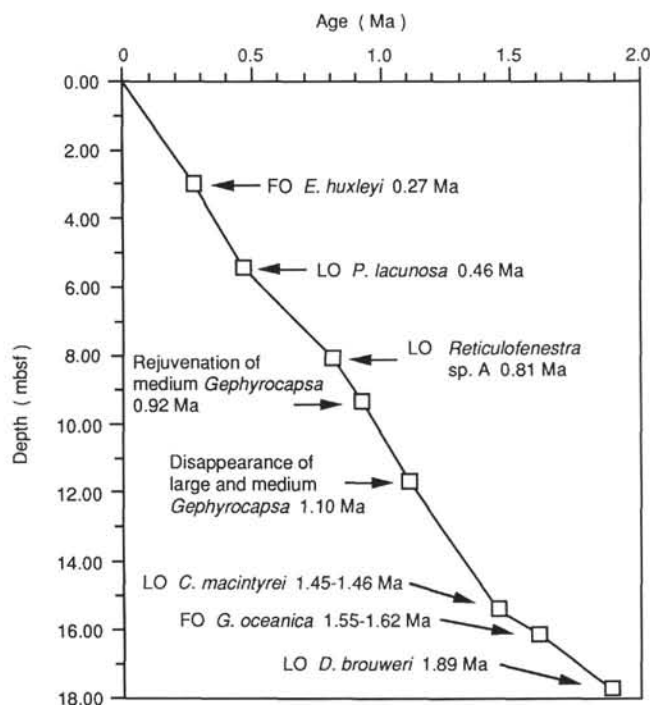
Figure 1. Depth-age relationship for the Quaternary sequence of Hole 709C. Biostratigraphic datum events are adopted from Matsuoka and Okada (1989) for the upper five events and from Rio et al. (in press) for the lower three events. The occurrences of datum events were determined by light microscopy except for the first occurrence of *Emiliania huxleyi*, which was determined under an electron microscope.

Table 1. List of studied samples.

Core, section, interval (cm)	Depth (mbsf)
115B-709C-	
1H-1, 2–3	0.02
1H-1, 42–43	0.42
1H-1, 82–83	0.82
1H-1, 122–123	1.22
1H-2, 12–13	1.62
1H-2, 52–53	2.02
1H-2, 92–93	2.42
1H-2, 132–133	2.82
1H-3, 22–23	3.22
1H-3, 62–63	3.62
1H-3, 102–103	4.02
1H-3, 142–143	4.42
1H-4, 32–33	4.82
1H-4, 72–73	5.22
1H-4, 112–113	5.62
2H-1, 22–23	6.02
2H-1, 62–63	6.42
2H-1, 102–103	6.82
2H-1, 142–143	7.22
2H-2, 32–33	7.62
2H-2, 72–73	8.02
2H-2, 112–113	8.42
2H-3, 2–3	8.82
2H-3, 42–43	9.22
2H-3, 82–83	9.62
2H-3, 122–123	10.02
2H-4, 12–13	10.42
2H-4, 52–53	10.82
2H-4, 92–93	11.22
2H-4, 132–133	11.62
2H-5, 22–23	12.02
2H-5, 62–63	12.42
2H-5, 102–103	12.82
2H-5, 142–143	13.22
2H-6, 32–33	13.62
2H-6, 72–73	14.02
2H-6, 112–113	14.42
2H-7, 2–3	14.82
2H-CC, 2–3	15.26
3H-1, 22–23	15.62
3H-1, 62–63	16.02
3H-1, 102–103	16.42
3H-1, 142–143	16.82
3H-2, 32–33	17.22
3H-2, 72–73	17.62

Note: Depth of samples is expressed in meters below sea floor (mbsf).

as well as in floral compositions of the *Gephyrocapsa* complex. During the course of our investigations, we have realized that various groups of the *Gephyrocapsa* complex underwent considerable size and morphologic changes in a successive manner. These groups, which were identified by forming clusters in a plot of overall size vs. proportion of central opening (Fig. 2), are actually evolutional lineages. Because the end members that occurred within each lineage are considerably different in size and morphology, biostratigraphers may have classified them into separate species.

Actually, most of the specimens observed in this investigation can be assigned to existing *Gephyrocapsa* species, and more than one existing species is recognized within each lineage. The classification of the genus *Gephyrocapsa* itself is, however, presently in disagreement among specialists, and some specimens that occur between different lineages are difficult to separate from each other. Because we consider these lineages to be independent species, and because it is almost impossible to apply the existing taxonomy to describe our species, we were forced to employ a completely different classification to describe our results. Thus, our principle scheme of classification is completely different from the usual taxonomic scheme used for biostratigraphy. We decided to name our species with alphabetic characters to avoid further confusion in this troublesome, yet biostratigraphically useful group of nannofossils.

Actually, we identified two groups, the small and large *Gephyrocapsa*, within the *Gephyrocapsa* complex. These two groups were easily separated in the plots of the overall size of coccolith vs. the diameter of the central opening in most of the samples, but they were mixed together and were inseparable within some intervals (Fig. 2). The boundary drawn between these groups is interdependent on the coccolith size and the size of the central

opening, and it ranges between 2.0 and 3.5 µm for the overall coccolith size (Fig. 2). Because the boundary is diagonal to the horizontal axis of Figure 2, which represents the overall coccolith size, the simple separation of these two groups by a predetermined overall size is impossible.

In practice, specimens <2.0 µm and >3.5 µm are automatically classified as small *Gephyrocapsa* and large *Gephyrocapsa*, respectively. Specimens with overall sizes that range between these boundary sizes are divided according to their position in the coccolith-size/central-opening-size plot as well as by their general appearance.

The small *Gephyrocapsa* group includes small forms with large central openings, and it may consist of several species, such as *Gephyrocapsa aperta*, *Gephyrocapsa ericsonii*, *Gephyrocapsa pelta*, *Gephyrocapsa protohuxleyi*, and *Gephyrocapsa sinuosa*. Because it is easy to identify and has biostratigraphic potential, *G. protohuxleyi* is the only species identified as a separate entity, and all other small *Gephyrocapsa* are lumped under the name of *Gephyrocapsa* spp. (small). As we will mention
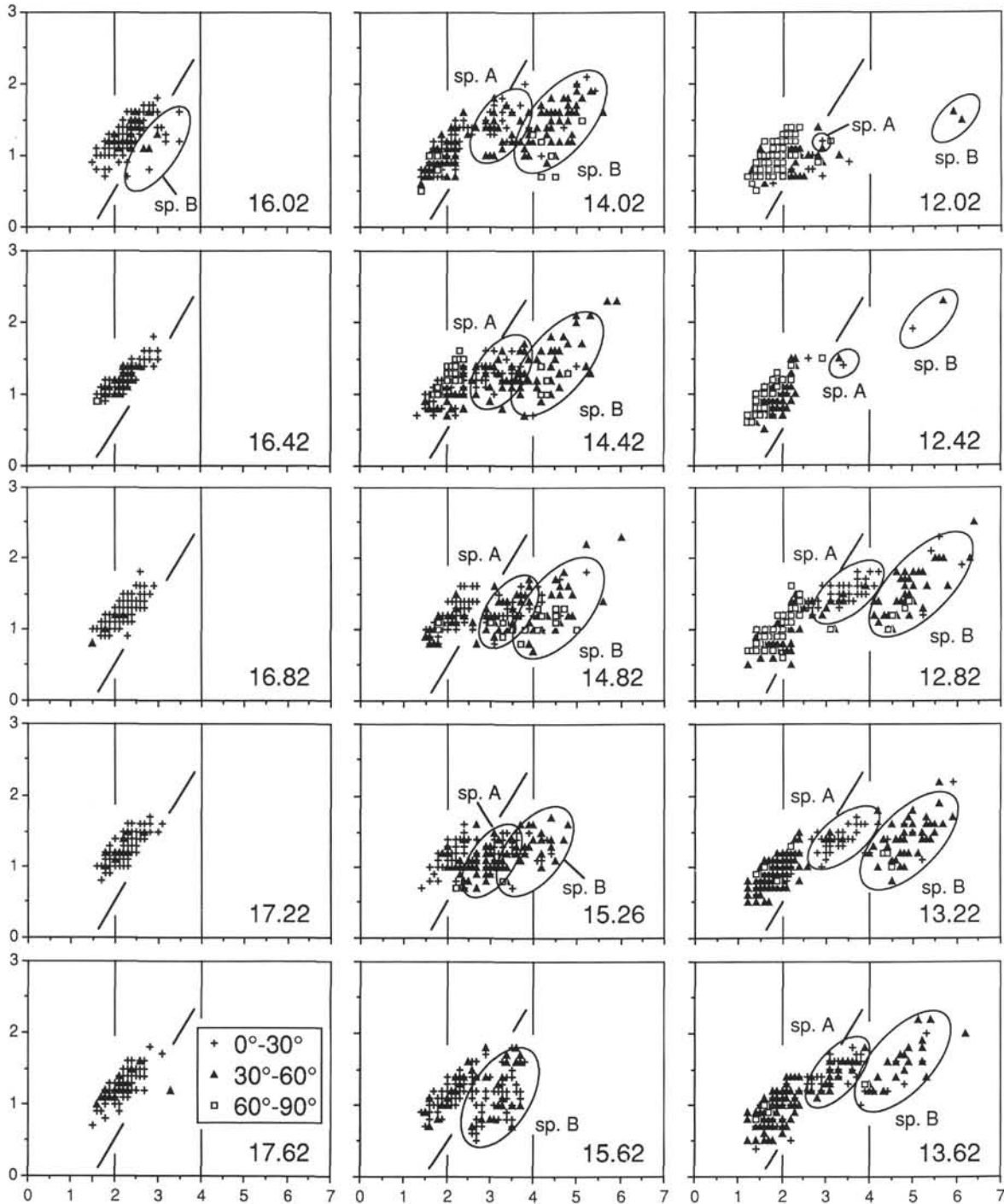
Figure 2. Plot of overall coccolith size (horizontal axis) vs. diameter of central opening (vertical axis) for the 200 specimens of *Gephyrocapsa* observed in the samples studied. Numerical values in the lower right-hand corner of each plot indicate sub-bottom depth (expressed in mbsf) of each sample. The horizontal and vertical scales are expressed in μm. The diagonal line indicates the boundary between small and large *Gephyrocapsa*. In the six samples between 14.82 and 12.82 mbsf, in which large *Gephyrocapsa* are rather scarce, additional plots of approximately 100 specimens were added to clarify the trend of the morphometric changes. The six categories of the bridge angle (15° interval), which denotes the inclination of the bridge vs. the long axis of the coccolith, were regrouped into three categories (30° interval) to make each plot identifiable in this figure. Crosses = specimens with low bridge angles (0°–30°); solid triangles = specimens with medium (30°–60°) bridge angles; open squares = specimens with high (60°–90°) bridge angles.
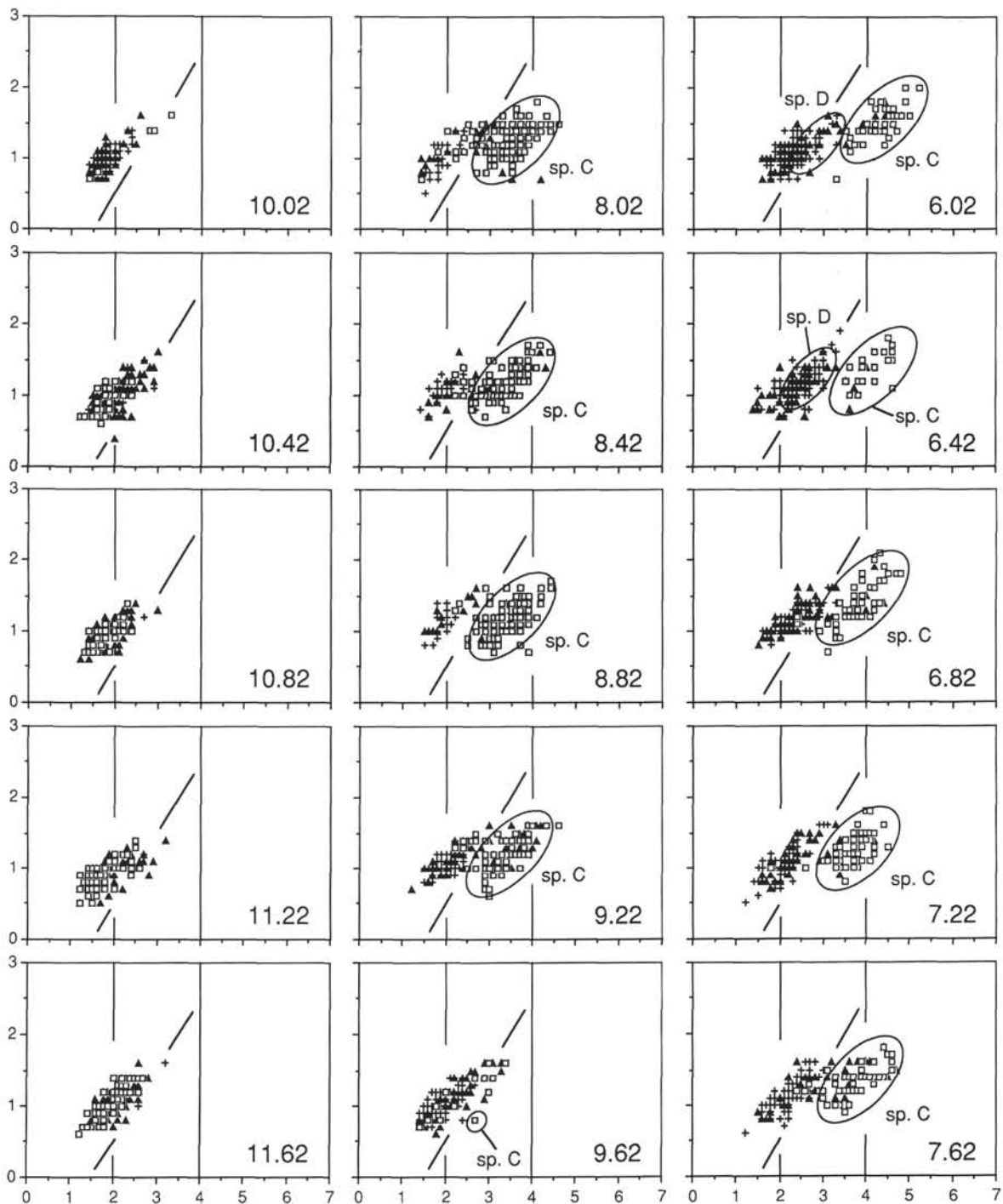
Figure 2 (continued).

later, a possible ancestral taxon of *G. protohuxleyi* was also identified, and hence, three taxa were identified within the small *Gephyrocapsa*.

In addition to the separation into small and large forms, Figure 2 shows that there are four clusters of large *Gephyrocapsa*. Although one lower cluster does not change its size throughout its existence, the three other clusters become time-transgressively larger and result in three evolutional cycles. Indeed, each of these cycles is mainly determined by the size increase of each corresponding type of large *Gephyrocapsa*, and the stratigraphic

ranges of these cycles do not overlap for the most part (Fig. 2) These clusters are interpreted as lineage, and members of each cluster are tentatively identified as *Gephyrocapsa* sp. A, B, C, and D: *Gephyrocapsa* sp. A for the cluster with no size increase; and *Gephyrocapsa* sp. B, C, and D for the members of the lower (first evolutional cycle), middle (second cycle), and upper (third cycle) clusters, respectively. Although there are other large *Gephyrocapsa* that are not members of these four lineages, these large *Gephyrocapsa*, identified as *Gephyrocapsa* spp. (large), are not important elements of the *Gephyrocapsa* complex be-
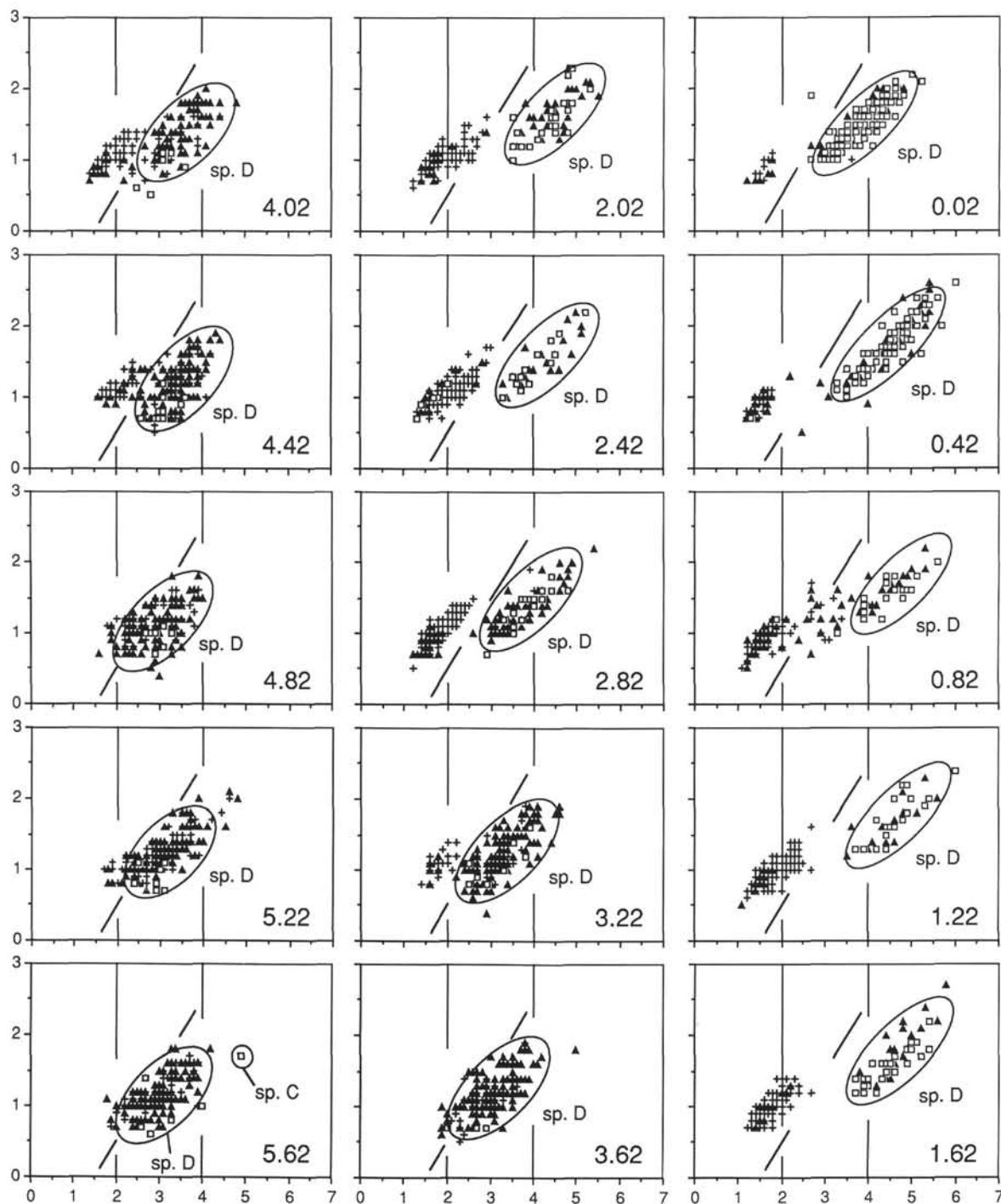
Figure 2 (continued).

cause of their rare occurrences. The classification and taxonomy we have employed are summarized in Table 2.

TIME-PROGRESSIVE CHANGE IN MORPHOMETRY OF *GEPHYROCAPSA*

Small *Gephyrocapsa* Group

The lowest interval of the sequence studied (between 17.62 and 16.42 mbsf) corresponds to the top of the Pliocene and the base of the Pleistocene. Although *Gephyrocapsa* spp. (small) dominate the assemblage of the *Gephyrocapsa* complex, the mor-

phologic diversity is low. Specimens that occur in this interval possess a low-angled (<30°) bridge and are fairly large in overall size for the small *Gephyrocapsa* (Fig. 3).

Overall size and bridge angle of *Gephyrocapsa* spp. (small) change markedly within the lower Quaternary sequence, which corresponds to the interval between 16.02 and 10.02 mbsf. At 1602 mbsf, most specimens have a low-angled (>30°) bridge and an average overall size of 2.2 μm (Fig. 3). Specimens with moderate bridge angles (30°–60°) occur abundantly at 13.62 mbsf, and the average coccolith size is reduced to 1.8 μm. At 12.02 mbsf, the majority of small *Gephyrocapsa* show high

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Table 2. Classification of *Gephyrocapsa* complex employed in this study.

Small forms of *Gephyrocapsa*

G. protohuxleyi —————*G. protohuxleyi* (s. str.)
                                G. protohuxleyi var. A
Gephyrocapsa spp. (small)

Large forms of *Gephyrocapsa*

Gephyrocapsa sp. A
Gephyrocapsa sp. B
Gephyrocapsa sp. C
Gephyrocapsa sp. D
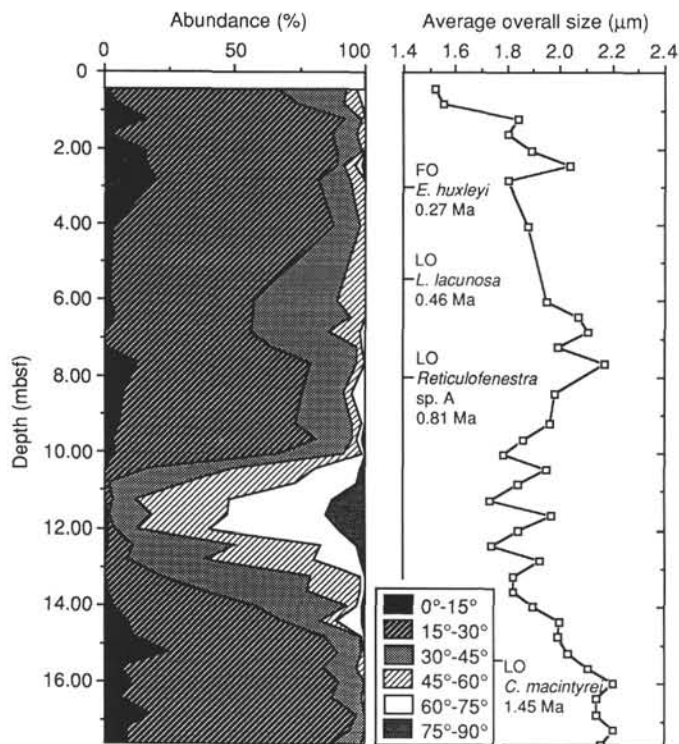*Gephyrocapsa* spp. (large)

Figure 3. Stratigraphic changes in the percentage abundance of the six categories of *Gephyrocapsa* spp. (small) divided by bridge angles (left column) and in average coccolith size of the *Gephyrocapsa* spp. (small) (right column). *Gephyrocapsa protohuxleyi* is excluded from the plot, and samples in which *Gephyrocapsa* spp. (small) do not occur in large numbers are also omitted.

(>60°) bridge angles. In the two top samples of the lower sequence (10.42 and 10.02 mbsf), specimens with high bridge angles disappeared rather abruptly, and specimens with low (<30°) bridge angles again showed up abundantly.

A small *Gephyrocapsa* that Matsuoka and Okada (1989) identified as *Gephyrocapsa protohuxleyi* var. A occurs between 11.62 and 6.02 mbsf, and typical *Gephyrocapsa protohuxleyi* occurs in small amounts between 2.42 and 0.82 mbsf. These two taxa are not differentiated in Figure 2, and their occurrence is discussed below.

Gephyrocapsa spp. (small) is less abundant between 9.22 and 3.22 mbsf, and specimens with low bridge angles are common in this interval (Figs. 2 and 3). Small *Gephyrocapsa* with rather large coccolith sizes and low (<30°) bridge angles are abundant in the upper interval between 2.82 and 1.22 mbsf (Fig. 3). In the

topmost sequence (0.82–0.02 mbsf), *Gephyrocapsa* spp. (small) are extremely small (1.0–2.0 μm) and decline noticeably in the total nannoflora (Figs. 2 and 3).

Large *Gephyrocapsa* Group

As previously mentioned, four species of large *Gephyrocapsa* and three evolutional cycles were recognized through the entire Quaternary.

The First Cycle

Gephyrocapsa sp. A, which has a robust low-angled (<30°) bridge and a large central opening, and *Gephyrocapsa* sp. B, characterized by a slim bridge span at moderate angles (30°–60°), a fairly small central opening, and an obscure central collar, are components of the first cycle, which was recognized between 16.02 and 12.02 mbsf (Figs. 2 and 4). *Gephyrocapsa* sp. A does not change in coccolith size significantly, and it is generally smaller as well as morphologically more diverse than *Gephyrocapsa* sp. B.

The FO of large *Gephyrocapsa*, the cluster of early *Gephyrocapsa* sp. A and B, was recognized at 16.02 mbsf; its average coccolith size is approximately 3 μm (Fig. 4). The large *Gephyrocapsa* started to diverge into *Gephyrocapsa* sp. A and B at 15.26 mbsf, but it is difficult to draw an exact boundary between these two taxa at this level (Fig. 2). The clusters of these two taxa were distinguishable above 13.62 mbsf, and both taxa simultaneously disappeared at 12.02 mbsf. Because the average overall size of *Gephyrocapsa* sp. B increases to >5 μm, this species is conspicuous under a light microscope. Specimens that are about 3 μm in overall size and have a small central opening appeared abruptly at 12.02 mbsf (Fig. 2). These specimens are classified as *Gephyrocapsa* spp. (large).

Large *Gephyrocapsa* scarcely occur in the interval between 11.62 and 10.02 mbsf. The very rare large *Gephyrocapsa* observed here are fairly small and are also classified as *Gephyrocapsa* spp. (large).

The Second Cycle

Gephyrocapsa sp. C is the main constituent of the second cycle, which was identified between 9.62 and 6.02 mbsf (Fig. 4). A high bridge angle (>60°) characterizes this species (Fig. 5). It first appeared at 9.62 mbsf and became abundant in the interval between 9.22 and 8.02 mbsf. It was conversely reduced in abundance as the overall size increased (Fig. 4). The average coccolith size in this cycle is 3.2 μm at 9.22 mbsf, which increased to 4.2 μm at 6.02 mbsf. The last occurrence (LO) of *Gephyrocapsa* sp. C is marked by a single specimen that occurred at 5.62 mbsf.

A group of specimens clustering along the boundary between large and small *Gephyrocapsa* at 6.42 and 6.02 mbsf was easily distinguishable from *Gephyrocapsa* sp. C (Fig. 2). This group exhibited transitional features between *Gephyrocapsa* sp. C and *Gephyrocapsa* spp. (small) and was tentatively included into *Gephyrocapsa* sp. C.

The Third Cycle

Gephyrocapsa sp. D undergoes significant bridge angle changes throughout its stratigraphic range. It forms a main cluster in the third cycle in the upper Quaternary sequence above 5.62 mbsf.

The acme of *Gephyrocapsa* sp. D occurs between 5.62 and 3.22 mbsf (Fig. 4). The specimens observed in this interval are fairly small, the bridge angle is low (<45°), and the proportion of the central opening vs. the coccolith length varies greatly (25%–55%) (Fig. 5). This species became larger in the higher interval between 2.82 and 1.22 mbsf, and specimens with higher (>45°) bridge angles as well as a narrow range in the proportion of the central opening (30%–45%) are more common (Fig.
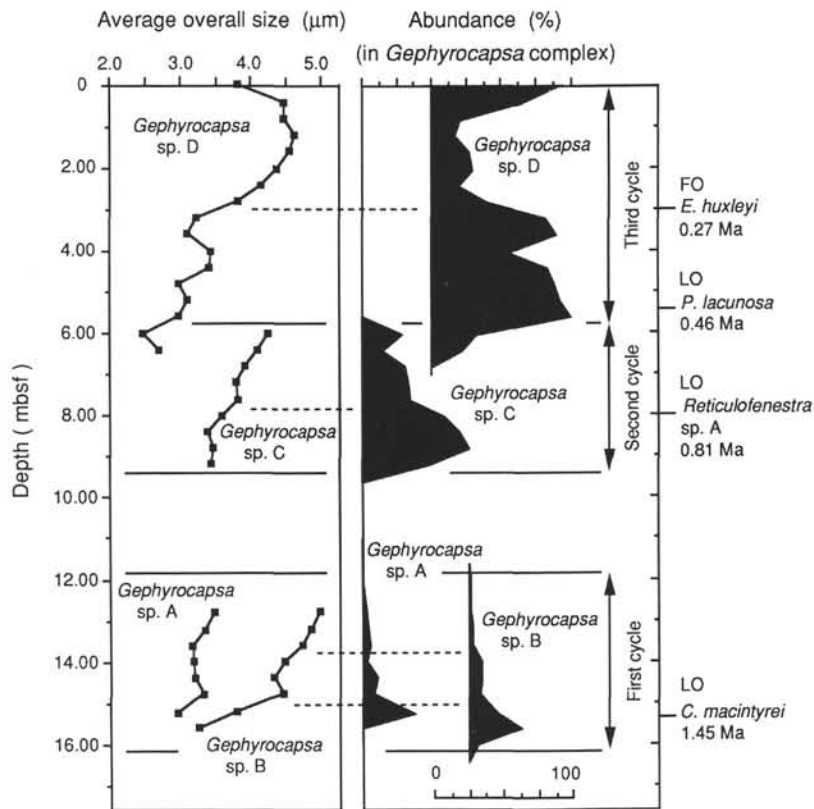
Figure 4. Stratigraphic changes in the average coccolith size (left column) and in percentage occurrence within the *Gephyrocapsa* complex (right column) of the four species of large *Gephyrocapsa*. The percentage abundance indicates the value within the total *Gephyrocapsa* complex. Dashed lines indicate the "transitional phases" of *Gephyrocapsa* sp. B, C, and D that showed evolutional size increase. Because large *Gephyrocapsa* are scarce in some samples, additional measurements were conducted to maintain the minimum amount of data. The minimum number of specimens measured for this plot is 50 for *Gephyrocapsa* sp. B and 100 for *Gephyrocapsa* sp. C and D. Samples in which large *Gephyrocapsa* are exceedingly scarce were omitted in this figure.

5). This species became smaller and regained its abundance in the higher interval between 0.82 and 0.02 mbsf (Fig. 4). This change probably correlates with the simultaneous acme of *E. huxleyi,* and it is somewhat questionable to include these smaller specimens into *Gephyrocapsa* sp. D.

Specimens with an overall size of approximately 3 μm and a small central opening appeared abruptly at 0.82 mbsf (Fig. 2); they were classified as *Gephyrocapsa* spp. (large). This is an event similar to the one observed at 12.02 mbsf (Fig. 2); these two events took place immediately above the climax in size increase of *Gephyrocapsa* sp. B and *Gephyrocapsa* sp. D, respectively (Fig. 4).

Common Features of the Evolutional Cycles

The observations mentioned in the sections on the first, second, and third cycles have revealed several common features among the morphometric changes of the three large *Gephyrocapsa* species, *Gephyrocapsa* sp. B, C, and D. These features are:

1. The early specimens of each species are fairly small, and clusters tend to overlap with small *Gephyrocapsa* in the coccolith-size/central-opening-size plot, resulting in a single large cluster (Fig. 2).

2. As each species becomes larger in an upward direction, the overlapping large cluster diverges into two separate clusters:

large *Gephyrocapsa* and small *Gephyrocapsa* (Fig. 2). In the first and third cycles, small *Gephyrocapsa* decreased in average size while the sizes of *Gephyrocapsa* sp. B and D increased (Figs. 3 and 4).

3. The evolutional development of *Gephyrocapsa* sp. B, C, and D can be divided into early and late stages by abrupt changes in overall size as well as in abundance (Fig. 4). Each of the three species are smaller and generally more numerous within the *Gephyrocapsa* complex during the early stages than in the late stages. This boundary is hereafter to be called the "transitional phase." The transitional phases of *Gephyrocapsa* sp. B, C, and D are located at 15.26–14.82, 8.02–7.62, and 3.22–2.88 mbsf, respectively (Fig. 4). In the case of *Gephyrocapsa* sp. B, an additional transitional phase was observed within the late stage between 14.02 and 13.62 mbsf.

4. The proportion of the central opening vs. coccolith size was constant within each cycle, measuring 31%, 34%, and 37% for *Gephyrocapsa* sp. B, C, and D, respectively, and became larger in the later cycles (Fig. 6).

5. The coccolith size of each species always starts at approximately 3 μm in its evolutional size increase, and the early small forms of each cycle are clearly distinguished from the large forms of *Gephyrocapsa* spp. (small) (Figs. 2 and 4). This observation may indicate that each species of large *Gephyrocapsa* always evolved from a common ancestral stock with an overall approximate size of 3 μm.
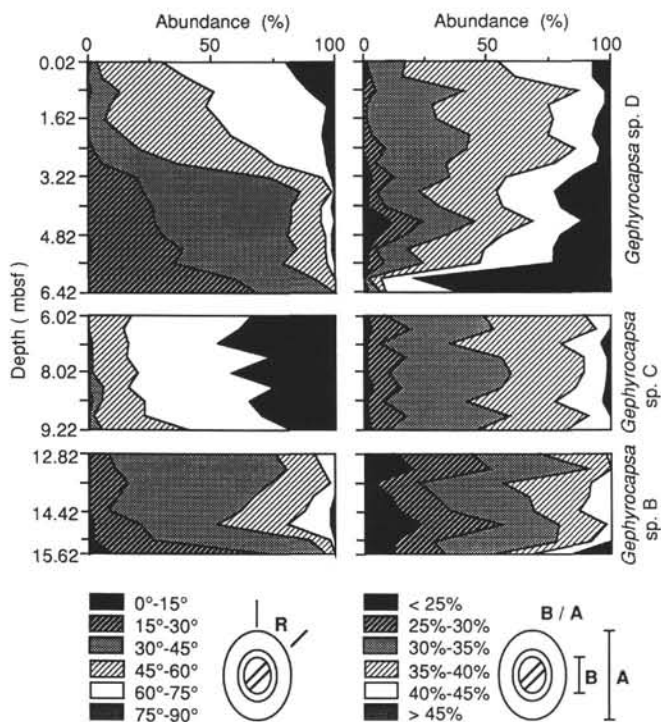
Figure 5. Stratigraphic changes in percentage abundances of the bridge angles (left column) and the proportion of central openings vs. cocco-lith sizes (right column) for the three large *Gephyrocapsa* species that showed time-progressive size increases.

Figure 6. Stratigraphic changes in the averaged proportion of the central openings of the four large *Gephyrocapsa* species.

CORRELATION OF THE DATA OBSERVED TO THE EXISTING TAXONOMY AND BIOSTRATIGRAPHIC SCHEME

Gephyrocapsa protohuxleyi Complex

Because its minute size makes it difficult to distinguish under a light microscope, morphometric variations and the stratigraphic occurrence of *G. protohuxleyi* had not been investigated in detail. In his original description of the species, McIntyre (1970) mentioned its phylogenic status as a transitional link between *Emiliania huxleyi* and the *Gephyrocapsa* complex. He identified its stratigraphic range from 0.095 to 1.20 Ma and reported its abundant occurrences at near the Brunhes/Matuyama boundary as well as at a level close to the first appearance of *E. huxleyi*. Samtleben (1980) did not list *G. protohuxleyi* among his 11 *Gephyrocapsa* species. Matsuoka and Okada (1989) confirmed the prominent acme of *G. protohuxleyi* near the Brunhes/Matuyama boundary. Because the distal shield of *G. protohuxleyi* observed in this interval is formed with robust elements that lack the T-shaped configuration of a typical *G. protohuxleyi* that occurs in higher horizons, Matsuoka and Okada called this type "*G. protohuxleyi*" var. A.

As observed in Matsuoka and Okada (1989), the occurrence of *G. protohuxleyi* is also concentrated in two stratigraphic sequences at Hole 709C: in the interval between 11.62 and 6.02 mbsf where *G. protohuxleyi* var. A occurs, and in the interval between 2.42 and 0.82 mbsf where *G. protohuxleyi* (s. str.) occurs (Fig. 7). *Gephyrocapsa protohuxleyi* var. A, which seems unrelated to the evolution of *E. huxleyi*, is further subdivided into two morphotypes: (1) a type with high bridge angles and a large central opening that occurs in the interval between 11.62 and 7.62 mbsf, and (2) another type with low bridge angles that occurs in the level between 7.22 and 6.02 mbsf (Fig. 7). The
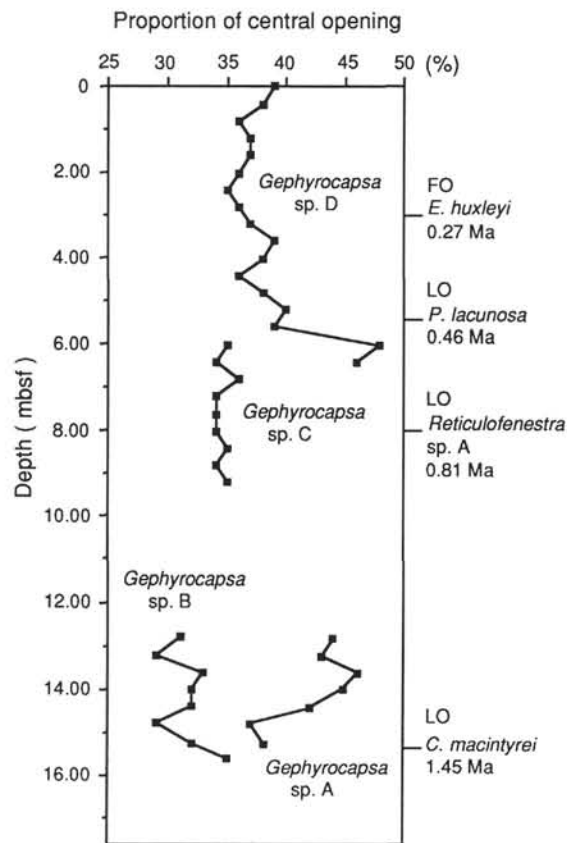
acme of the latter type is consistent with that found by Matsuoka and Okada (1989) (Fig. 8).

Specimens with no slits on the distal shield and a notched periphery occur between 7.22 and 6.02 mbsf. These specimens are similar to *G. protohuxleyi* var. A except for the absence of slits on the distal shield. Because their occurrence exactly corresponds with that of *G. protohuxleyi* var. A, these specimens are probably a variation of *G. protohuxleyi* var. A. *Gephyrocapsa protohuxleyi* (s. str.) is morphologically similar to *E. huxleyi* except for the presence of a bridge. Since its stratigraphic occurrence is very close to the evolutional development of *E. huxleyi* (Fig. 8), there is little doubt regarding the direct phylogenic relations between these two taxa.

Slits on the distal shield are also found among the large forms of *Gephyrocapsa*. These large slitted forms were not differentiated from the usual types of large *Gephyrocapsa* in the previous discussions. The exclusive plot of the slitted large forms exhibits two peaked occurrences that correspond to the incipient stages of *Gephyrocapsa* sp. B and C (Figs. 7 and 8). The reason why these slits develop is unknown, but evidence indicates a morphologic instability in the *Gephyrocapsa* complex during the early stages of its evolutional cycles.

Gephyrocapsa caribbeanica Complex

The classification of *G. caribbeanica* is in considerable confusion, and two contradicting definitions have been commonly used. These criteria identify the species by (1) the presence of a small central opening that often shows irregular periphery or (2) a low bridge angle. In Hole 709C, specimens assignable to the four large *Gephyrocapsa* species that fit the first criterion mainly occur in three intervals (Fig. 7). These intervals seem to corre-
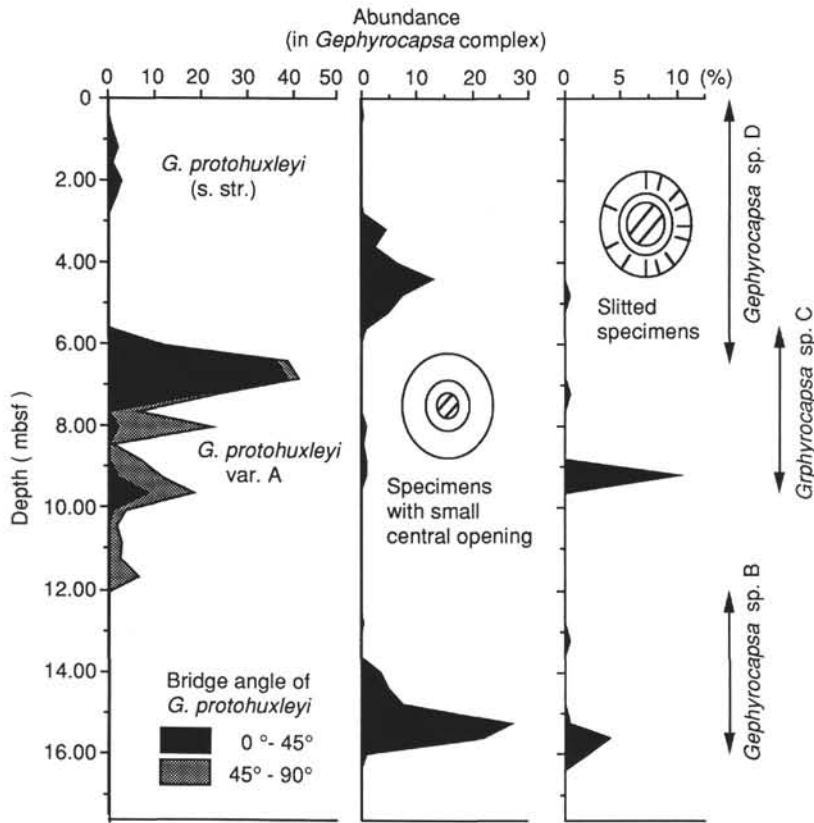
Figure 7. Stratigraphic occurrences of *Gephyrocapsa protohuxleyi* (left column), large *Gephyrocapsa* with a very small central opening (center column), and large *Gephyrocapsa* with slits on the distal disc (right column). Plots are expressed in percentage abundances in the total *Gephyrocapsa* complex. These specimens were included in the normal specimens of the respective categories in other figures.

spond to the early stages of the three evolutional cycles as well as to the acme of the large *Gephyrocapsa* that has slits on its distal discs (Figs. 4 and 7). In this interpretation, *G. caribbeanica,* as defined by the first criterion, is an end member of the morphometric variations developed during the early stages of the evolutional cycles. Specimens identifiable as *G. caribbeanica,* according to the second criterion (i.e., bridge angle), occur in most of the intervals. In particular, almost all *Gephyrocapsa* sp. B and early forms of *Gephyrocapsa* sp. D would fit into this category.

No matter which criterion we adopt, there are many intermediate forms with no clear breaking points. Therefore, it is extremely difficult to differentiate *G. caribbeanica* as an independent taxon in quantitative analyses of the *Gephyrocapsa* complex. Accordingly, the FO of *G. caribbeanica,* which was defined as the base of Subzone CN13b (Bukry, 1973; Okada and Bukry, 1980), should correspond to the beginning of the first evolutional cycle.

As mentioned in Matsuoka and Okada (1989), the original definition (Bukry, 1973) of the Zone CN13/CN14 boundary corresponds to the rejuvenation of *G. oceanica,* which occurred at the top of the Jaramillo Event. This is the same event discussed here as the start of the second cycle, although no magnetic data are available for Hole 709C.

The "Small *Gephyrocapsa* Zone"

Gartner (1977) identified a biostratigraphically useful middle Pleistocene event in which small *Gephyrocapsa* predominate the nannoflora. The "small *Gephyrocapsa* zone" of Gartner was

defined as an interval between the last appearance datum (LAD) of *Helicosphaera sellii* and the end of the small *Gephyrocapsa* acme. Because *H. sellii* is rare and sporadic in many sections, a common practice for many biostratigraphers in identifying the "small *Gephyrocapsa* zone" is to substitute the original definition by the almost complete absence of large *Gephyrocapsa*.

In Hole 709C, we made the following observations:

1. The acme of small *Gephyrocapsa* occurs at several intervals throughout the Pleistocene, although the most significant one did occur during the later part of the early Pleistocene (Fig. 9).

2. The most significant acme of small *Gephyrocapsa* does not precisely correspond to the temporal disappearance of large *Gephyrocapsa* (Fig. 9). The exact beginning of this acme is difficult to pinpoint, but its top was observed in the interval between 10.42 and 10.02 mbsf. The base of the almost complete temporal disappearance of large *Gephyrocapsa,* which corresponds to the LO of *Gephyrocapsa* sp. B, is detected at 12.02 mbsf, whereas its top, the FO of *Gephyrocapsa* sp. C, is identifiable at 9.62 mbsf.

3. This significant acme of small *Gephyrocapsa* is also characterized by the abundant occurrence of high-bridge-angled small *Gephyrocapsa,* which are totally absent or rare in other intervals (Fig. 9).

It is not yet clear what caused the peculiar flora of the "small *Gephyrocapsa* zone." Gartner (1988) hypothesized that it was an intensified equatorial upwelling caused by a sudden change
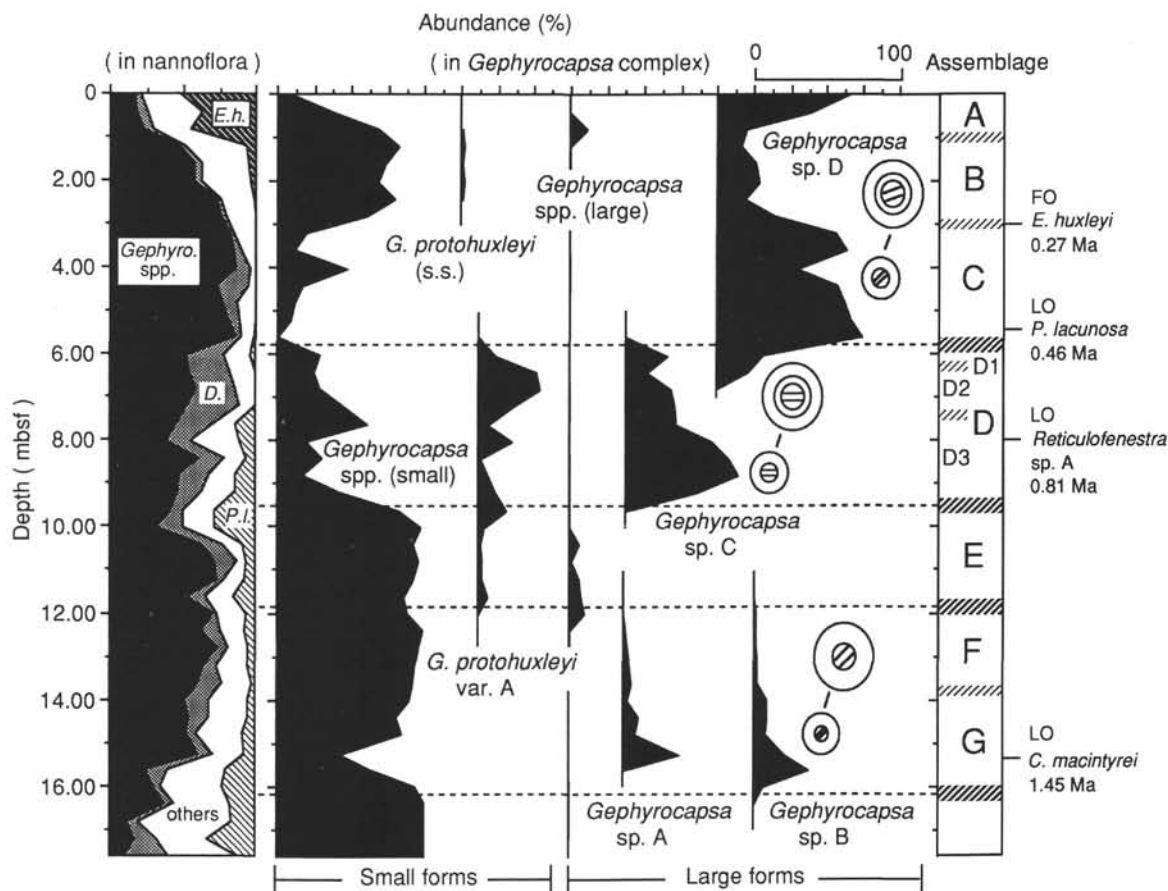
Figure 8. Stratigraphic change of nannoflora and the percentage abundance of each *Gephyrocapsa* taxon within the total *Gephyrocapsa* complex. *E.h.* = *Emiliania huxleyi*, *D.* = *Dictyococcites* spp., and *P.l.* = *Pseudoemiliania lacunosa*.

in ocean circulation. The occurrence of large forms at Site 709C is similar to the one observed in the northwestern Pacific Ocean (Matsuoka and Okada, 1989). We have observed in both oceans that the decline of small *Gephyrocapsa* is not always accompanied by an increase of large *Gephyrocapsa* or vice versa (Fig. 9). This observation implies mutually independent causes for the changes in abundance of small and large *Gephyrocapsa*.

Relationship to Previously Defined Taxa of *Gephyrocapsa*

The main criteria for the classification of *Gephyrocapsa* are (1) the overall size of the coccolith, (2) the proportion of the central opening, and (3) the shape and angle of the central bridge. Observations throughout this investigation have revealed the continuous morphologic development of the *Gephyrocapsa* taxon and the existence of morphologically diverse variations within the *Gephyrocapsa* complex. It is difficult, therefore, to correlate precisely some of the existing taxa to the various forms observed here. The following are examples of possible correlations between some important taxa and the quantitatively identified forms.

Early forms of *Gephyrocapsa* sp. B, C, and D that showed evolutional size increase were not morphologically distinct, and they were probably identified as *G. oceanica*, *Gephyrocapsa caribbeanica*, or small *Gephyrocapsa*, depending upon who the observers were. Well-developed late forms of *Gephyrocapsa* sp. B, C, and D can be assigned to the existing taxa. The late form of *Gephyrocapsa* sp. B corresponds to *Gephyrocapsa lumina* Bukry (1973), *G. oceanica* sp. 1 and sp. 2 of Rio (1982), and *G.*

oceanica (large) and *G. caribbeanica* (large) of Takayama and Sato (1986). *Gephyrocapsa* sp. C, which has high bridge angles, can be identified as *G. oceanica rodela* Samtleben (1980), *Gephyrocapsa omega* Bukry (1973), and *G. oceanica* sp. 3 of Rio (1982). *Gephyrocapsa parallela* of Takayama and Sato (1986) corresponds to *Gephyrocapsa* sp. C and the late forms of *Gephyrocapsa* sp. D. The original *G. parallela* Hay and Beaudry (1973) is likely to correspond to the late forms of *Gephyrocapsa* sp. D.

Most researchers separate small forms from large forms within the *Gephyrocapsa* complex, but there is no common criterion for the exact boundary between them. Matsuoka and Okada (1989), Gartner (1988), Rio (1982), and Takayama and Sato (1986) set the boundaries at 2.5, 3, 3.5, and 4 μm, respectively. For biostratigraphic studies that use light microscopes, 3 μm is easier to apply than 2.5 μm as the cut-off point. As shown in Fig. 2, numerous specimens range from 3 to 4 μm in overall size, and, therefore, a boundary of 3.5 or 4.0 μm seems unfitted to identify the large forms. A minimal size of 4 μm for large forms, meanwhile, is useful for biostratigraphy because specimens that are larger than 4 μm occur only in limited intervals.

TIME-PROGRESSIVE CHANGES IN QUATERNARY NANNOFLORA

Matsuoka and Okada (1989) identified six floral assemblages (Assemblages A–F) within the last 1.3 m.y. in the subtropical northwestern Pacific Ocean. These assemblages are mainly based on relative abundances of various morphotypes within the *Ge-*
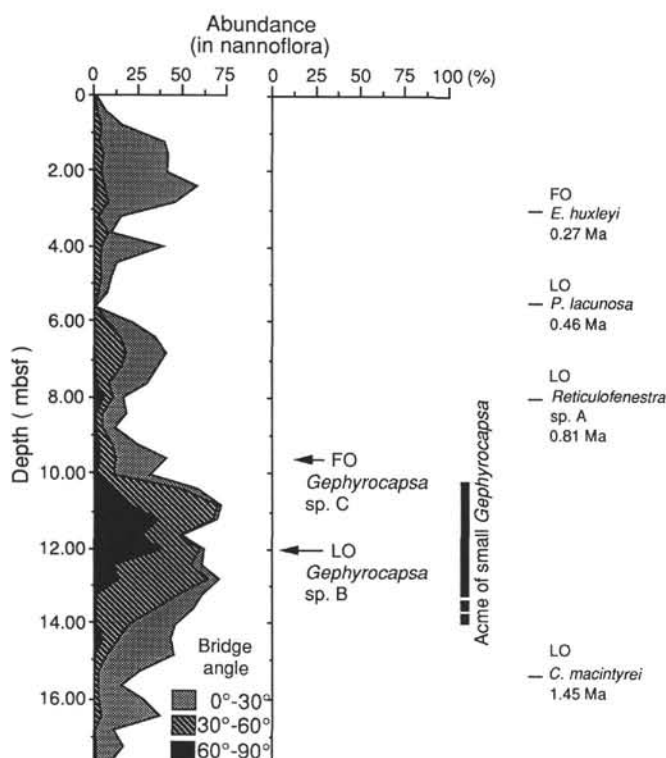
Figure 9. Stratigraphic occurrences in the abundance of all small *Gephyrocapsa* (left column) and of *Gephyrocapsa* sp. A, B, C, and D combined (right column). Data are expressed as percentage abundances within the total nannoflora. Small *Gephyrocapsa* were subdivided into three categories according to the bridge-angle difference; the legend for the filled patterns is exclusively for small *Gephyrocapsa*.

Figure 10. Correlation of assemblage zones with the stratigraphic ranges of the three large *Gephyrocapsa* species that showed evolutional size increase.

penetration for the sample they studied, Matsuoka and Okada (1989) could not observe this assemblage. The assemblage, which is newly identified as Assemblage G, is characterized by the absence of very large *Gephyrocapsa* and by the abundant occurrence of medium-sized *Gephyrocapsa* with moderate bridge angles (Fig. 9). Specimens with small central openings are also abundant in this new assemblage. The basal occurrence of Assemblage G is marked by the first appearance of *Gephyrocapsa* sp. B.

The boundaries between the floral assemblages defined by Matsuoka and Okada (1989) correspond well to the incipient and terminal phases as well as to the "transitional phases" of the three specimens of large *Gephyrocapsa* (Figs. 4 and 10). Because boundary criteria for the floral assemblages and the evolutional phases are defined by the significant changes in the *Gephyrocapsa* complex, this finding is no surprise. However, it does indicate that stratigraphic changes in the *Gephyrocapsa* complex occurred in a similar mode between the tropical Indian Ocean and the subtropical northwestern Pacific Ocean.

Although the succession of floral assemblages are similar, some differences in floral composition were noticed between these two oceans. First, small forms of *Gephyrocapsa* (excluding *G. protohuxleyi*) are more abundant throughout the Quaternary sequence in Hole 709C than in the Pacific core. In addition, several reports have been given that imply environmental controls over the morphology of *Gephyrocapsa* species (i.e., Bukry, 1973; Geitzenauer et al., 1976, 1977; Roth and Coulbourn, 1982). In these reports, specimens with high-angled bridges were found abundantly in low latitudes, whereas specimens with low-angled bridges were more common in high latitudes. Furthermore, the time intervals in which *Gephyrocapsa* with high-angled bridges occur abundantly (around 0.9–0.5 Ma and 0.3 Ma to the Present) are much longer than the glacial-interglacial cycle, which is the most likely controlling factor of ocean environment. Aside from the possible influence of intensified upwelling resulting in Assemblage E (flora of the "small *Gephyrocapsa* zone"), the time-progressive morphological changes observed in this investigation are likely to be evolutional events.

phyrocapsa complex, and the defining criteria for these assemblages are convertible to the modified classification employed here (Fig. 10).

Assemblage A, defined by the dominant occurrence of *Emiliania huxleyi*, occurs in the top three samples taken at 0.02, 0.42, and 0.82 mbsf (Fig. 8). Assemblage B, characterized by the common occurrence of *E. huxleyi* and various forms of *Gephyrocapsa*, was identified between 1.22 and 2.82 mbsf, which corresponds to the middle upper part of the range of *Gephyrocapsa* sp. D (Fig. 8). Assemblage C, characterized by the dominant occurrence of medium-sized *G. oceanica*, occurs between 3.22 and 5.62 mbsf and corresponds to the early stage of *Gephyrocapsa* sp. D.

The presence of Subassemblage D1, in which large *Gephyrocapsa* with high bridge angles are dominant, is rather obscure in Hole 709C. The flora observed at 6.02 mbsf probably corresponds to this subassemblage. Subassemblage D2, defined by the dominant occurrence of *G. protohuxleyi* var. A, is identifiable in the interval between 6.42 and 7.22 mbsf. Subassemblages D1 and D2 correspond to the upper range of *Gephyrocapsa* sp. C. Subassemblage D3, characterized by abundant *Gephyrocapsa* with medium sizes and high bridge angles, was observed between 7.62 and 9.62 mbsf. This subassemblage corresponds to the lower range of *Gephyrocapsa* sp. C. Assemblage E, distinguished by the almost complete absence of large *Gephyrocapsa*, is identified between 10.02 and 11.62 mbsf. Assemblage F, characterized by the common occurrence of very large *Gephyrocapsa*, corresponds to the interval between 12.02 and 13.62 mbsf.

An additional floral assemblage was observed between 14.02 and 16.02 mbsf (Figs. 8 and 10). Because of the lack of core

SUMMARY

The purpose of the present investigation was to study quantitatively the time-progressive changes in morphometry and floral composition of the *Gephyrocapsa* complex. The present classification of the *Gephyrocapsa* complex, which was established mainly from the biostratigraphic viewpoint and has proven to be

useful for that purpose, cannot be used to describe our species, which represent evolutional lineages. Consequently, only one established species (*Gephyrocapsa protohuxleyi*) that is easily identifiable without any confusion was employed, and four large species (*Gephyrocapsa* sp. A, B, C, and D) were newly created to describe our results. The results of our investigation of the Quaternary sequence of Hole 709C into the morphometric changes in the *Gephyrocapsa* complex as well as into the stratigraphic changes in the nannoflora can be summarized as follows:

1. Small and large *Gephyrocapsa* were recognizable within the *Gephyrocapsa* complex, but we demonstrated that separation of *Gephyrocapsa* specimens into these groups by coccolith size alone is not pragmatic for a phylogenetic study of this complex.

2. The small *Gephyrocapsa* were further subdivided into groups of *Gephyrocapsa protohuxleyi* and all other small *Gephyrocapsa*. The former species was subdivided into two varieties that occupy completely isolated stratigraphic ranges. The earlier variety showed good potential for biostratigraphy.

3. Four species, *Gephyrocapsa* sp. A, B, C, and D, were identified within the large *Gephyrocapsa*, and the latter three were found to become progressively larger.

4. *Gephyrocapsa* sp. B and C disappeared abruptly after reaching their maximum sizes. Thus, three cycles of morphologic development were distinguishable. These cycles occurred in the following time intervals: the first cycle was found in *Gephyrocapsa* sp. B around 1.6–1.1 Ma; the second cycle was found in *Gephyrocapsa* sp. C around 0.9–0.5 Ma; and the third cycle was found in *Gephyrocapsa* sp. D from 0.5 Ma to the present.

5. The abundance of *Gephyrocapsa* sp. B, C, and D in each evolutional cycle decreased as their overall sizes increased, and the stratigraphic ranges of each species can be divided into early and late intervals based on changes in their overall sizes and relative abundance.

6. Six assemblages (Assemblages A–F) identified in the subtropical Pacific Ocean can be applied to the Quaternary nannoflora of Hole 709C in the tropical Indian Ocean, and a new assemblage (Assemblage G) was proposed in the lowest Pleistocene below Assemblage F.

ACKNOWLEDGMENTS

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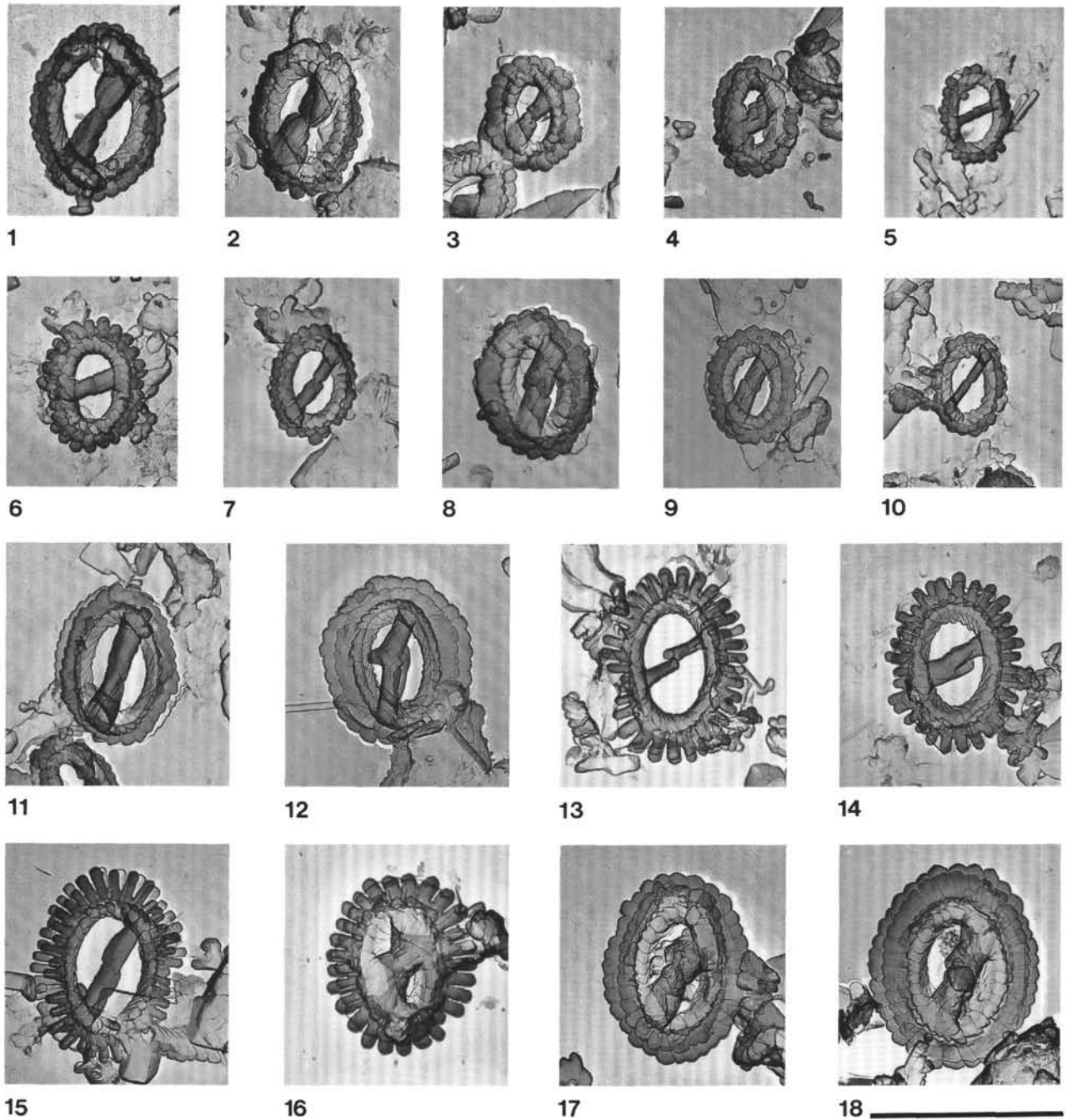
Plate 1. Transmission electron micrographs. All figures have the same magnification. The scale bar in the lower right corner represents 3 μm. **1–12.** *Gephyrocapsa* spp. (small). 1 and 2, Sample 115-709C-3H-1, 142–143 cm (16.82 mbsf); 3 and 4, Sample 115-709C-2H-5, 142–143 cm (13.22 mbsf); 5 and 6, Sample 115-709C-2H-4, 132–133 cm (11.62 mbsf); 7, Sample 115-709C-2H-3, 42–43 cm (9.22 mbsf); 8, Sample 115-709C-2H-1, 62–63 cm (6.42 mbsf); 9, 11, and 12, Sample 115-709C-1H-2, 92–93 cm (2.42 mbsf); and 10, Sample 115-709C-1H-1, 122–123 cm (1.22 mbsf). **13–16.** *Gephyrocapsa protohuxleyi* var. A. 13, Sample 115-709C-2H-3, 42–43 cm (9.22 mbsf); 14, Sample 115-709C-2H-2, 72–73 cm (8.02 mbsf); 15, Sample 115-709C-2H-1, 102–103 cm (6.82 mbsf); 16, Sample 115-709C-2H-1, 22–23 cm (6.02 mbsf). **17–18.** *Gephyrocapsa* sp. A. Sample 115-709C-2H-6, 32–33 cm (13.62 mbsf).
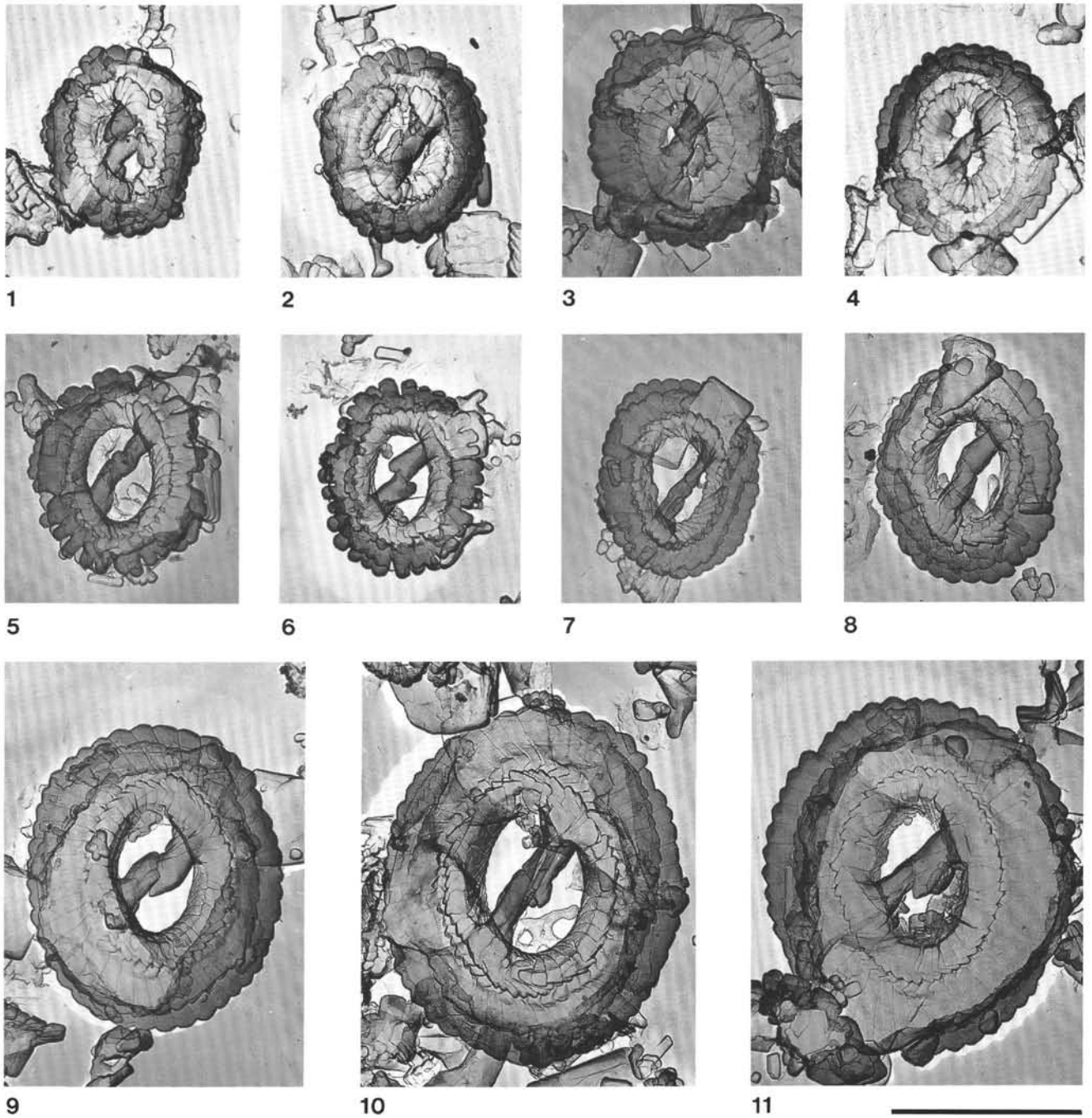
Plate 2. Transmission electron micrographs. All figures have the same magnification. The scale bar in the lower right corner represents 3 μm. **1–11.** *Gephyrocapsa* sp. B. 1–4, Sample 115-709C-3H-1, 22–23 cm (15.62 mbsf); 5 and 6, slitted specimen, Sample 115-709C-3H-1, 22–23 cm (15.62 mbsf); 7 and 8, Sample 115-709C-2H-7, 2–3 cm (14.82 mbsf); 9 and 10, Sample 115-709C-2H-6, 32–33 cm (13.62 mbsf); and 11, Sample 115-709C-2H-5, 62–63 cm (12.42 mbsf).
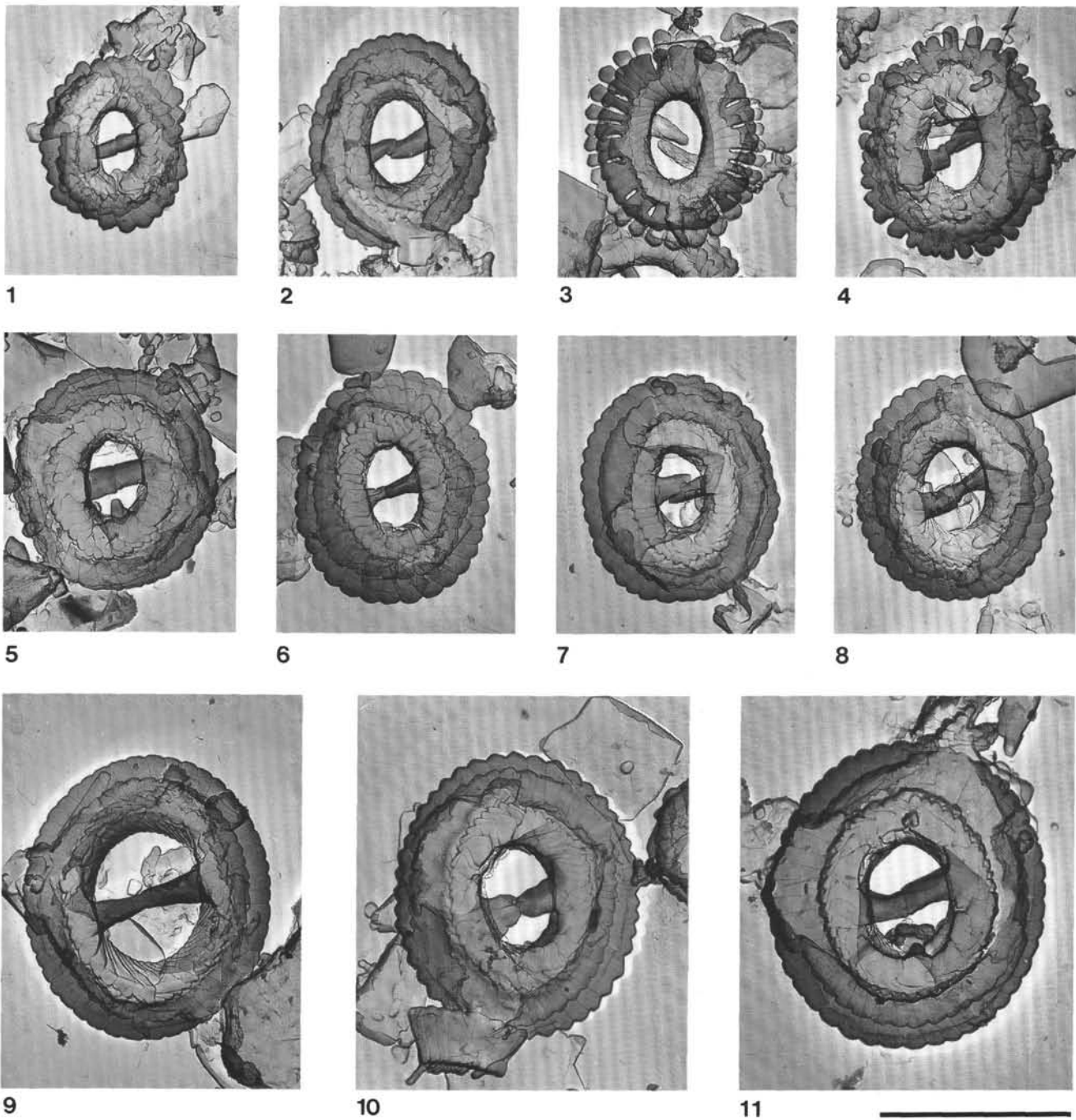
Plate 3. Transmission electron micrographs. All figures have the same magnification. The scale bar in the lower right corner represents 3 μm. **1-11.** *Gephyrocapsa* sp. C. 1, 2, and 5, Sample 115-709C-2H-3, 42–43 cm (9.22 mbsf); 3 and 4, slitted specimen, Sample 115-709C-2H-3, 42–43 cm (9.22 mbsf); 6–8, Sample 115-709C-2H-2, 72–73 cm (8.02 mbsf); 9, Sample 115-709C-2H-1, 102–103 cm (6.82 mbsf); 10, Sample 115-709C-2H-1, 62–63 cm (6.42 mbsf); 11, Sample 115-709C-2H-1, 22–23 cm (6.02 mbsf).
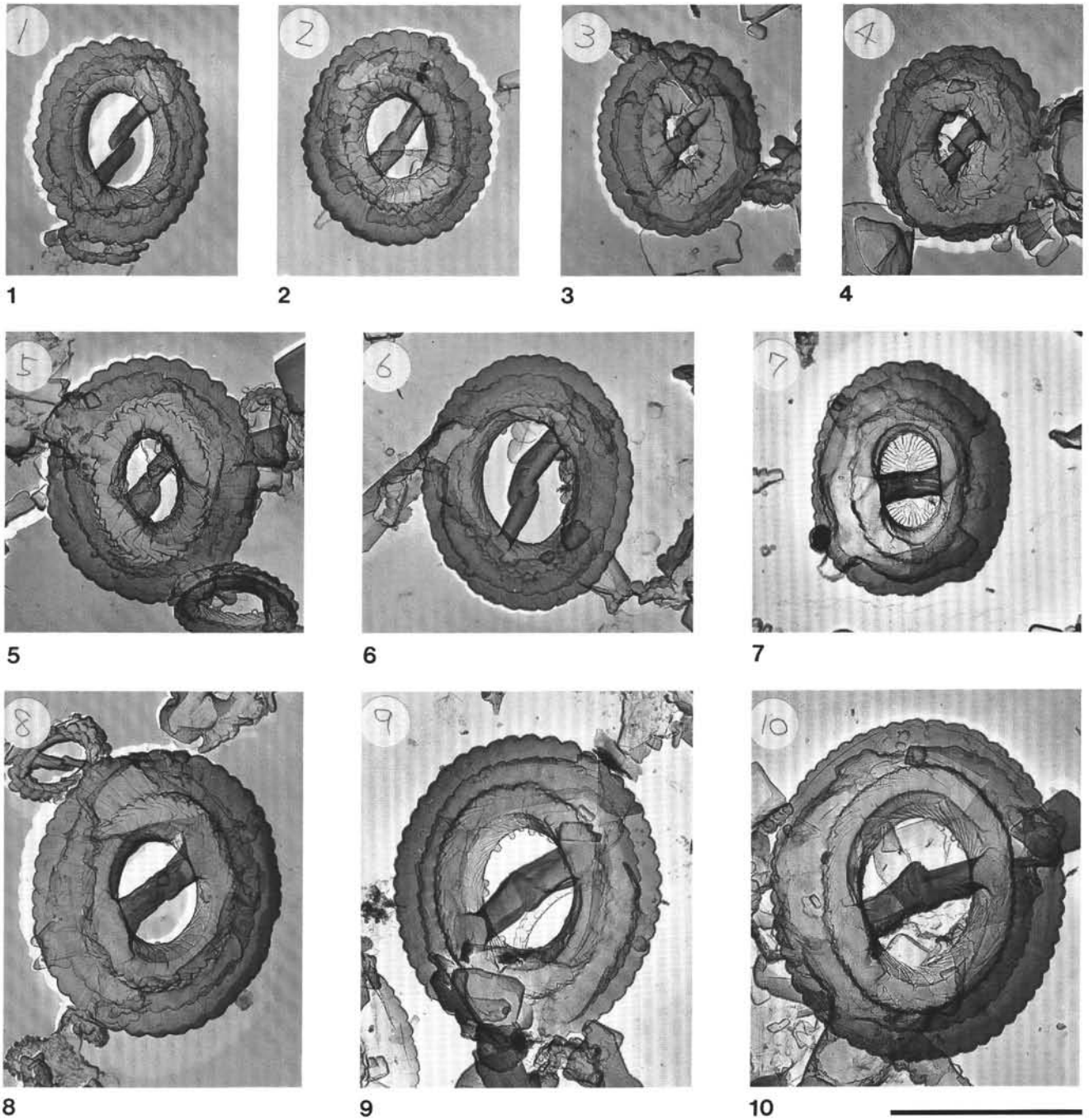
Plate 4. Transmission electron micrographs. All figures have the same magnification. The scale bar in the lower right corner represents 3 μm. 1-10. *Gephyrocapsa* sp. D. 1 and 2, Sample 115-709C-1H-4, 112–113 cm (5.62 mbsf); 3 and 4, Sample 115-709C-1H-4, 32–33 cm (4.82 mbsf); 5 and 6, Sample 115-709C-1H-3, 102–103 cm (4.02 mbsf); 7, Sample 115-709C-1H-1, 2–3 cm (0.02 mbsf); 8, Sample 115-709C-1H-2, 52–53 cm (2.02 mbsf); 9 and 10, Sample 115-709C-1H-1, 42–43 cm (0.42 mbsf).