

11. LATE QUATERNARY POLYCYSTINE RADIOLARIANS AND SILICOFLAGELLATES OF A DIATOMACEOUS SAPROPEL FROM THE EASTERN MEDITERRANEAN, SITES 969 AND 971¹

Taniel Danelian² and Dimitris Frydas³

ABSTRACT

Well-preserved radiolarians and silicoflagellates discovered in the diatomaceous Sapropel S5 were studied and quantitatively analyzed. The silicoflagellate assemblage is almost exclusively composed of warm-water *Dictyocha* species. The radiolarian assemblage is very diverse and dominated by the counting-group *Arachnocorallium*, an indicator of eutrophication. Paleocological evaluation of the fauna indicates that polycystin radiolarians occupied various ecological niches. Radiolarian taxa, known to be abundant in association with a subsurface layer of chlorophyll- α maxima are much better represented in the sapropel S5 than above it, suggesting that this deep layer of primary productivity was much stronger and better developed during accumulation of the sapropel. Deep-dwelling, detritivore radiolarians are also present and well-represented in the sapropel, contrary to the assemblage that is above it, in which these taxa appear to be absent. In the latter sample, surface-dwelling, symbiont-bearing radiolarians are the dominant group.

If the Nile river was the main cause of eutrophication in the Eastern Mediterranean, excessive riverine discharge would have supplied abundant nutrients (in particular, phosphorus and silica) to sustain the bloom of the siliceous phytoplankton (diatoms and silicoflagellates). Eutrophication would have encouraged radiolarians to occupy ecological niches at various depths of the water column. Excessive export of biogenic silica (diatom shells in particular) diminished the corrosive action of the Mediterranean sea water and preserved siliceous microfossils. After the decrease of riverine discharge, which brought an end to the formation of Sapropel S5, silica was probably not available in sufficient quantities to sustain siliceous phytoplankton growth far beyond the coasts of Egypt, and settling of organic matter would have been reduced to levels below the critical values necessary for the sustenance of the detritivore radiolarian niches. This change in eutrophication did not affect the surface-dwelling radiolarians, whose needs are substantially supported by their symbionts.

INTRODUCTION

The occurrence of siliceous microfossils, such as radiolarians (zooplankton), silicoflagellates and diatoms (phytoplankton), is generally very scarce in the Pliocene-Quaternary sediments of the Eastern Mediterranean, which is largely dominated by carbonate-rich sediments. However, opal assemblages are exceptionally well-preserved in some organic-rich levels, known as sapropels (Dumitrica, 1973a, 1973b; Schrader and Matherne, 1981; Riedel et al., 1985; Anastasakis and Filippas, 1990). High accumulation rates of biogenic silica are regarded as a good fossil indicator of eutrophication (Brasier, 1995) and there is a general association in the geological record of organic carbon-rich sediments and abundant biogenic silica. Having been the main siliceous planktonic group for most of pre-Cenozoic times, radiolarians are often associated with hydrocarbon source rocks and, given the presence of lipids in their living representatives (Anderson, 1983), they themselves may well have been significant contributors to the accumulation of organic-rich sediments (Ormiston, 1993).

In order to understand the paleoceanographic and depositional processes that led to the accumulation and preservation of sapropels in the Eastern Mediterranean (a main topic of the ODP Leg 160; Emeis and Shipboard Scientific Party, 1996) scientific interest has focused on their age and cyclicity, sedimentology, mineralogy and geochemistry and their fauna/flora. The latter are the subject of the present paper. Sapropel accumulation in the Eastern Mediterranean sediments has the character of a synchronous event and it is widely

regarded as the result of climate-driven external forcing. More particularly, a temporal correlation has been observed between the accumulation of sapropels and the precessional cycle of earth's orbit. Furthermore, a link has been established between the sapropels and (1) intensifications of the African monsoons, which affected the discharge of the Nile river (Rossignol-Strick, 1983) and (2) increased activity of Mediterranean depressions followed by enhanced humidity in the northern borderlands of the Eastern Mediterranean (Rohling, 1994). Geochemical evidence indicates that sapropel formation has been promoted by increased productivity (Calvert et al., 1992; Howell and Thunell, 1992). However, agreement has not yet been reached concerning the mechanism(s) that conveyed sapropel accumulation, and more especially their preservation, onto the Mediterranean seafloor (Pedersen and Calvert, 1990).

In recent years paleocological information from the fauna and flora included in the Pliocene-Quaternary sediments has provided new insights to the puzzling question of sapropel formation in the Eastern Mediterranean, a basin reputed to be "a nutrient desert in a nutrient desert" (Emeis and Shipboard Scientific Party, 1996). More particularly, paleocological analysis of planktonic foraminifers (Rohling and Gieskes, 1989) and calcareous nannofossils (Castradori, 1993) from the sapropels has brought forward new and elaborated models concerning the depths and intensity of primary paleo-productivity. Contrary to calcareous plankton, the siliceous plankton preserved in the sapropels have not yet been well-explored, mainly because of their sparsity in the sedimentary record.

Among the many sapropel layers discovered to date in the Pliocene-Quaternary sediments of the Eastern Mediterranean, the Late Pleistocene Sapropel S5 is of particular importance. Abundant and well-preserved opal assemblages were studied by Schrader and Matherne (1981), although these authors focused their study on diatoms and reported only a few silicoflagellates. The abundant biogenic silica preserved in the Sapropel S5 seems to cover a significantly extensive area of the Eastern Mediterranean south of Crete (Fig. 1), and

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²Department of Geology and Geophysics, The University of Edinburgh, West Mains Road, Edinburgh EH9 3JW, United Kingdom. Taniel.Danelian@ed.ac.uk

³Patras University, Department of Geology, Section for Physical-Marine Geology and Geodynamics, GR-26110, Patras, Greece.

during ODP Leg 160, well-preserved siliceous assemblages from this sapropel were encountered at Site 971 (Shipboard Scientific Party, 1996b, p. 435). The radiolarian and silicoflagellate assemblages from this level are discussed and extensively documented here for the first time. Moreover, radiolarians discovered a few centimeters above the Sapropel S5 at Site 969 provide a good opportunity to observe the long-term changes incurred by radiolarian populations during and just after the accumulation of the Sapropel S5.

MATERIAL AND METHODS

Sites 969 and 971 are close to each other and are both situated at depths of 2100–2200 m on the Mediterranean Ridge, south of Crete (Fig. 1). No radiolarian or silicoflagellate specialist was included in the shipboard party of Leg 160; therefore, this investigation is based on samples selected on the ship by other specialists. Radiolarians were studied by T. Danelian and silicoflagellates by D. Frydas. Sample 160-971B-2H-CC comes from the 30-cm-thick diatom-rich sapropel S5, which was drilled in the center of a moat situated at the southeastern edge of the Napoli mud volcano (Robertson et al., 1996). In this sample, radiolarians are very well preserved and diverse. The studied sample is of late Pleistocene age (younger than 0.26 Ma) and is situated between Subzone MNN 21a and Zone MNN 20 of the calcareous nannofossils (Shipboard Scientific Party, 1996b). More precisely, Sapropel S5 accumulated during the warm isotopic stage 5e, at approximately 125 Ka (Rossignol-Strick, 1983). Sample 160-969A-1H-3, 65–67 cm, comes from a level situated a few centimeters above the same sapropel (S5) and is of late Pleistocene age too (Zone MNN21, Shipboard Scientific Party, 1996a). At the time of receipt this sample was already washed and sieved and the residue contained radiolarians of moderate preservation, but no silicoflagellates were encountered in it. Sample 160-971B-2H-CC was washed under a 45- μ m sieve and slides were prepared according to Goll and Björklund (1989).

RADIOLARIAN RESULTS AND SYSTEMATICS

Radiolarians from the Mediterranean plankton and sediments were the subject of the very first classical works on this group (Müller, 1858; Ehrenberg, 1858; Haeckel, 1860a, 1860b). However, despite this early interest and substantial efforts during the seventies

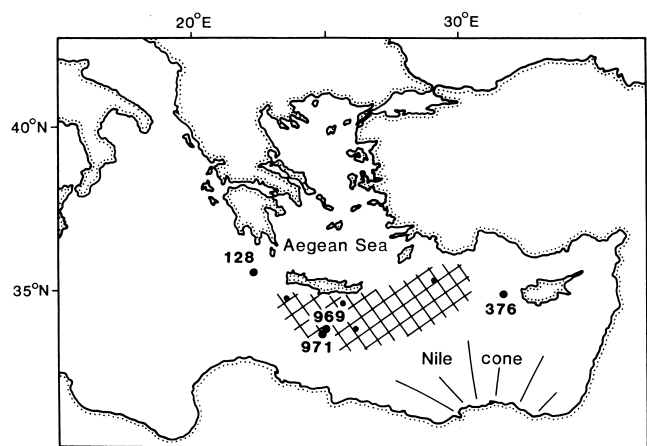


Figure 1. Eastern Mediterranean DSDP Sites 128 and 376 and ODP Sites 969 and 971 with Quaternary radiolaria. The hatched area indicates the inferred distribution of siliceous microfossil occurrence in sapropel S5 (after Schrader and Matherne, 1981). Small black circles without site numbers indicate study cores in which the above authors found diatoms.

to document the Late Cenozoic radiolarian assemblages of the Mediterranean (Sanfilippo, 1971; Dumitrica, 1973a; Sanfilippo et al., 1973; Caulet, 1974; Riedel et al., 1974; Sanfilippo and Riedel, 1975) our knowledge is still far from complete. This is especially true for the Pliocene–Quaternary sediments, in which radiolarians are very sparse, but their presence is even more important, because it may have had a particular paleoenvironmental/paleoceanographic significance (e.g., increased biological productivity; Riedel et al., 1985). Despite the rarity of radiolarian assemblages in the sedimentary record, differences in their structure at family level were noticed and appeared to provide ground for paleoecological interpretations (Sanfilippo, 1971). Riedel et al. (1985) examined quantitatively a number of late Neogene radiolarian samples from the Eastern Mediterranean with a paleoenvironmental perspective in mind. Two of their samples are of Quaternary age and come from the west of Crete (128-3-5) and Cyprus (376-1-4; see Fig. 1). These authors successfully introduced the “counting-group” approach, at the approximate level of genera, to describe the composition of their studied radiolarian assemblages.

To explore the paleoenvironmental significance of the radiolarian assemblages from samples from ODP Leg 160, the approach of Riedel et al. (1985) was adopted. We therefore quantified the composition of radiolarian assemblages on the basis of ~500 specimens encountered on traverses of strewn-slide preparations. The numbers in Table 1 refer to the taxa studied by Riedel et al. (1985, see their table 23.1 for comparison).

Radiolarian Systematics

For each taxon mentioned herein there is at least one reference in the synonymy list that contains appropriate descriptions and illustrations. As data on Quaternary Radiolaria from the Eastern Mediterranean are sparse, this list links observations of the present study with previous findings. In order to investigate dominant counting-groups in our material (indicated in bold), the taxonomic scheme of Riedel et al. (1985) was followed in this study and, therefore, only a few taxa are dealt with at species level. In general, each counting-group is identified as “spp.” or “group.” The former was used when the above authors had reason to believe that there was more than one species present, and “group” when they did not know whether there was more than one species (W. Riedel, pers. comm., 1996).

Subclass RADIOLARIA
Superorder POLYCYSTINA
Order SPUMELLARIA

Family COLLOSPHAERIDAE Müller, 1858
Collosphaerid group
(Pl. 2, Figs. 1–2)

Collosphaerid group; Riedel et al., 1985, p. 504, pl.1, fig.1a–d.

Acrosphaera spinosa (Haeckel) group?
(Pl. 2, Fig. 1)

Polysolenia spinosa (Haeckel); Dumitrica, 1973a, p. 832, pl. 18, fig. 2.
Acrosphaera spinosa (Haeckel); Van de Paverd, 1995, p. 49, pl. 5–7.
Acrosphaera spinosa (Haeckel) group?; Boltovskoy, in press, fig. 15.18.

Solenosphaera chierchiai Brandt
(Pl. 2, Fig. 2)

Otosphaera polymorpha Haeckel; Nigrini and Moore, 1979, p. S9, pl. 1, fig. 5.
Solenosphaera chierchiai Brandt; Boltovskoy, in press, fig. 15.22.

Family ACTINOMMIDAE Haeckel, 1862; emend. Riedel, 1967b

Table 1. Radiolarian assemblages.

Counting group	Sample	Sample
	160-969A-1H-3, 65-67 cm	160-971B-2H-CC
(1) Collosphaerid group	1.96	0.37
(5) <i>Cladococcus</i> group	0.20	?
(6-7) <i>Hexacontium</i> group	1.76	10.97
(8) <i>Thecosphaera</i> spp.	0.20	+
(9) Other actinommids	20.35	2.23
(11) <i>Didymocyrtis</i> spp.	?	0.19
(12) <i>Dictyocoryne</i> group	-	1.30
(13) <i>Hymeniastrum</i> group	+	+
(14) <i>Porodiscus</i> group A	0.20	1.86
(15) <i>Porodiscus</i> group B	0.20	1.12
(14-15) <i>Porodiscus</i> group	0.78	3.53
(17) <i>Spongaster</i> spp.	+	0.56
(18) <i>Spongocore</i> spp.	-	0.19
(19) <i>Spongodiscus</i> group	-	0.74
(20) Pyloniid group	17.42	1.30
(21) Tholoniid group	-	0.37
(23) <i>Larospira</i> group	0.39	0.37
(25) <i>Pylospira</i> group	1.17	1.49
(26) <i>Acanthodesmia</i> group	20.94	1.30
(27) <i>Ceratospyrus</i> group A	1.37	1.30
(28) <i>Ceratospyrus</i> group B	-	0.19
(29) <i>Ceratospyrus</i> group C	1.37	0.93
(30) <i>Despospyris</i> group	0.20	+
(31) <i>Nephrospyris</i> spp.	1.17	1.12
(32) <i>Tholospyris</i> group	0.59	+
(35) <i>Zygocircus</i> group	0.20	0.93
(37) <i>Arachnocorys</i> group	0.78	2.23
(38) <i>Arachnocorallium</i> group	2.15	21.75
(39) <i>Ceratocyrtis</i> group	0.39	0.19
(40) <i>Lophophaena</i> group	7.24	12.27
(42) <i>Pseudodictyophimus</i> group	-	0.37
(43-44) Sethophormin group	+	0.37
(45) Other plagoniids	-	1.12
(46) <i>Cornutella</i> spp.	-	1.49
(47) <i>Eucecryphalus</i> group	-	3.16
(49) <i>Eucyrtidium punctatum</i> group	+	2.23
(48, 50) Other eucyrtidium	0.39	4.28
(53) <i>Litharachnium</i> group	-	0.56
(55) <i>Pterocanium</i> group	0.98	1.30
(57) <i>Theocorys</i> group	0.39	0.93
(58) Other theoperids	-	0.37
(59) <i>Carpocanistrum</i> group A	5.68	1.49
(61) <i>Anthocyrtidium</i> group	0.39	0.37
(62) Three-segmented pterocorythids	0.78	1.67
(63) <i>Botryostrobos</i> group	0.39	1.12
(64) <i>Phormostichoartus</i> group	?	0.56
(65) <i>Siphocampe</i> group	0.19	0.19
(66) <i>Spirocorytis</i> group	0.19	1.30
(67) Cannobotryid group	-	5.20
(68) <i>Carpocanarium</i> group	0.59	?
Not identified	9.20	6.50
Total number of specimens counted	511	538

Note: The abundance of each taxon is expressed as a percentage. If a specimen was not identifiable because it was broken and incomplete, it was not counted. On the other hand, if a specimen was complete but its identification was hampered because of taxonomic uncertainties or inappropriate position in the slide, the specimen was counted but classified as "not identified." + = presence of very rare taxa that were not found during the counting; - = these taxa were not observed; ? = identification is uncertain.

Cladococcus group

Cladococcus group; Riedel et al., 1985, p. 505, pl. 1, fig. 5.

Hexacontium group

(Pl. 1, Fig. 1; Pl. 2, Figs. 3-4)

Hexacontium group A; Riedel et al., 1985, p. 505, pl. 1, fig. 6a-c.

Hexacontium group B; Riedel et al., 1985, p. 505, pl. 1, fig. 7a-c.

Remarks: Although both of the groups distinguished by Riedel et al. (1985) were encountered in our material, for most of the specimens it was difficult to count the number of pores across the half equator.

Thecosphaera spp.

(Pl. 2, Fig. 5)

Thecosphaera spp.; Riedel et al., 1985, p. 505, pl. 1, fig. 8.

Thecosphaera inermis (Haeckel)

(Pl. 2, Fig. 5)

Thecosphaera inermis (Haeckel); Boltovskoy, in press, fig. 15.38.

Other actinommids

(Pl. 1, Fig. 2; Pl. 2, Figs. 6-7)

Other actinommids; Riedel et al., 1985, p. 505, pl. 1, fig. 9a-d.

Remarks: The majority of morphotypes encountered in Sample 160-969A-1H-3, 65-67 cm looks very similar to *Hexacontium*, but they do not display any medullary shell.

Family COCCODISCIDAE Haeckel, 1862; emend. Sanfilippo and Riedel, 1980

Didymocyrtis spp.

(Pl. 2, Fig. 8)

Ommatartus spp.; Dumitrica, 1973a, p. 834, pl. 6, fig. 6; pl. 11, fig. 7, 9.

Peripanartium sp.; Sanfilippo et al., 1978, p. 756, pl. 1, fig. 6.

Didymocyrtis spp.; Riedel et al., 1985, p. 505, pl. 1, fig. 11a-e.

Family SPONGODISCIDAE Haeckel, 1862; emend. Riedel, 1967b

Dictyocoryne group

(Pl. 1, Figs. 3, 4; Pl. 2, Figs. 9-12)

Rhopalastrum spp.; Dumitrica, 1973a, p. 835, pl. 9, fig. 1, 3; pl. 11, fig. 4.

Dictyocoryne group; Riedel et al., 1985, p. 505, pl. 2, fig. 1a-b.

Dictyocoryne profunda Ehrenberg

(Pl. 2, Fig. 9)

Dictyocoryne profunda Ehrenberg; Boltovskoy, in press, fig. 15.68.

Dictyocoryne truncatum (Ehrenberg)

(Pl. 1, Fig. 4; Pl. 2, Fig. 10)

Dictyocoryne truncatum (Ehrenberg); Boltovskoy, in press, fig. 15.69.

Hymeniastrum group

(Pl. 2, Figs. 13-15)

Hymeniastrum group; Riedel et al., 1985, p. 506, pl. 2, fig. 2a-b.

Hymeniastrum regulare (Haeckel)

(Pl. 2, Fig. 13)

Trigonastrum regulare Haeckel; Dumitrica, 1973a, p. 835, pl. 10, fig. 1-4; pl. 11, fig. 1, 3, 5, 8

Trigonastrum regulare Haeckel; Sanfilippo et al., 1978, p. 757, pl. 1, fig. 11.

Remarks: It is worth noting that Dumitrica (1973a) found this species only in a very restricted interval of Site 128-3-6, 80-100 cm (west of Crete). In order to elucidate the occurrence of this very distinctive species, it has been searched for in many late Neogene samples by Sanfilippo et al. (1978), but found only in Core 376-1 (west of Cyprus). This species is very rare and found only in sample 160-971B-2H-CC.

Hymeniastrum virchowii (Haeckel)

(Pl. 2, Fig. 14)

Amphirhopalum virchowii (Haeckel); Dumitrica, 1973a, p. 835, pl. 9, fig. 2, 4; pl. 11, fig. 6; pl. 21, fig. 2-13.

Porodiscus group
(Pl. 1, Fig. 5; Pl. 3, Figs. 1–4)

Porodiscus spp.; Dumitrica, 1973a, p. 835, pl. 8, fig. 1–6; pl. 9, fig. 6.

Remarks: Included are both groups A and B of *Porodiscus* described by Riedel et al. (1985). No morphotypes of group C have been encountered in our material.

Porodiscus group A
(Pl. 3, Fig. 1)

Porodiscus group A; Riedel et al., 1985, p. 506, pl. 2, fig. 3a–b.

Porodiscus group B
(P. 3, Figs. 2, 3)

Porodiscus group B; Riedel et al., 1985, p. 506, pl. 2, fig. 4.

Spongaster spp.
(Pl. 1, Fig. 6; Pl. 3, Figs. 5–8)

Spongaster spp.; Riedel et al., 1985, p. 506, pl. 2, fig. 6a–c.
Spongaster sp (p); Sanfilippo et al., 1978, p. 756, pl. 1, fig. 7–9.

Spongocore spp.
(Pl. 3, Figs. 10–13)

Spongurus cylindricus Haeckel; Dumitrica, 1973a, p. 834, pl. 11, fig. 2; pl. 18, fig. 23.
Spongocore spp.; Riedel et al., 1985, p. 506, pl. 2, fig. 7.
Spongurus cylindricus Haeckel; Van de Paverd, 1995, p. 149, pl. 40, fig. 1–9.

Spongocore puella Haeckel
(Pl. 3, Figs. 10, 11)

Spongocore puella Haeckel, 1887, p. 347, pl. 48, fig. 6.
Spongocore sp.; Riedel et al., 1985, pl. 2, fig. 7.
Spongocore puella Haeckel; Björklund and De Rooter, 1987, fig. 3.15–16.

Spongodiscus group
(Pl. 3, Fig. 9)

Spongodiscus spp.; Dumitrica, 1973a, p. 834, pl. 9, fig. 5; pl. 10, fig. 5–6.
Spongodiscus group; Riedel et al., 1985, p. 506, pl. 2, fig. 8.

Family PYLONIIDAE Haeckel, 1881
Pyloniid group
(Pl. 1, Fig. 7; Pl. 3, Fig. 14)

Tetrapyle (?) sp.; Dumitrica, 1973a, pl. 6, fig. 5.
Pyloniid group; Riedel et al., 1985, p. 506, pl. 2, fig. 9a–b.

Family THOLONIIDAE Haeckel, 1887
Tholoniid group
(Pl. 3, Fig. 15)

Cubotholus sp.; Dumitrica, 1973a, pl. 7, fig. 3.
Tholoniid group; Riedel et al., 1985, p. 506, pl. 2, fig. 10.

Amphitholus metallasson (Haeckel)
(Pl. 3, Fig. 15)

Cubotholus sp.; Dumitrica, 1973a, pl. 7, fig. 3.
Amphitholus metallasson (Haeckel); Van de Paverd, 1995, p. 184, pl. 53, fig. 9–10, 12.

Family LITHELIIDAE Haeckel, 1862
Larcospira group

Larcospira group; Riedel et al., 1985, p. 506, pl. 2, fig. 12.

Pylospira group
(Pl. 3, Figs. 16–18)

Pylospira group; Riedel et al., 1985, p. 509, pl. 2, fig. 14a–b.

Pylospira octopyle Haeckel
(Pl. 3, Fig. 16)

Pylospira octopyle Haeckel; Boltovskoy, in press, fig. 15.90.

Order NASSELLARIA

Family SPYRIDAE Ehrenberg, 1847

Acanthodesmia group
(Pl. 1, Fig. 8)

Acanthodesmia group; Riedel et al., 1985, p. 507, pl. 3, figs. 1a–b.

Acanthodesmia vinculata (Müller)
(Pl. 1, Fig. 8)

Acanthodesmia vinculata (Müller); Dumitrica, 1973a, p. 841, pl. 28, figs. 1, 2.

Ceratospyris group A
(Pl. 4, Fig. 1)

Ceratospyris group A; Riedel et al., 1985, p. 507, pl. 3, fig. 2a–c.

Ceratospyris group B
(Pl. 4, Figs. 2, 3)

Ceratospyris (?) sp.; Dumitrica, 1973a, pl. 28, fig. 10.
Ceratospyris group B; Riedel et al., 1985, p. 507, pl. 3, figs. 3a–b.

Ceratospyris group C
(Pl. 4, Figs. 4, 5)

Ceratospyris (?) spp.; Dumitrica, 1973a, p. 841, pl. 27, figs. 5, 6.
Ceratospyris group C; Riedel et al., 1985, p. 507, pl. 3, fig. 4.

Desmospyris group
(Pl. 4, Fig. 6)

Desmospyris group; Riedel et al., 1985, p. 507, pl. 3, figs. 5a–c.

Nephrospyris spp.
(Pl. 4, Fig. 7)

Nephrospyris spp.; Riedel et al., 1985, p. 507, pl. 3, fig. 6.

Nephrospyris renilla Haeckel
(Pl. 4, Fig. 7)

Nephrospyris renilla Haeckel; Dumitrica, 1973a, p. 841, pl. 28, fig. 8.

Tholospyris group

Tholospyris group; Riedel et al., 1985, p. 507, pl. 3, figs. 7a–b.

Zygocircus group
(Pl. 4, Figs. 8, 9)

Zygocircus group; Riedel et al., 1985, p. 507, pl. 3, figs. 10a–b.

Zygocircus productus productus (Hertwig)
(Pl. 4, Fig. 8)

Zygocircus productus (Hertwig); Dumitrica, 1973a, pl. 27, fig. 7 (only)
Zygocircus productus productus (Hertwig); Goll, 1979, p. 382, pl. 2, fig. 3.
Zygocircus productus forma *productus* (Hertwig); Van de Paverd, 1995, p. 201, pl. 62, fig. 14.

Zygocircus productus piscicaudatus Popofsky
(Pl. 4, Fig. 9)

Zygocircus productus (Hertwig); Dumitrica, 1973a, pl. 27, fig. 8 (only).

Zygocircus productus piscicaudatus Popofsky; Goll, 1979, p. 382, pl. 2, figs. 1, 2.

Zygocircus productus forma *piscicaudatus* Popofsky; Van de Paverd, 1995, p. 202, pl. 62, figs. 11,13.

Family PLAGONIIDAE Haeckel, 1881; emend. Riedel, 1967b

Arachnocorys group
(Pl. 4, Fig. 10)

Arachnocorys group; Riedel et al., 1985, p. 508, pl. 3, figs. 12a, b.

Arachnocorys circumtexta Haeckel
(Pl. 4, Fig. 10)

Arachnocorys circumtexta Haeckel, 1862, p. 304, pl. 6, figs. 9–11.

Arachnocorallium group
(Pl. 4, Figs. 11–15)

Arachnocorallium group; Riedel et al., 1985, p. 508, pl. 3, figs. 13a–c.

Ceratocyrtis group
(Pl. 4, Fig. 17)

Ceratocyrtis group; Riedel et al., 1985, p. 508, pl. 3, figs. 14a–c.

Lophophaena group
(Pl. 4, Figs. 18–21)

Lophophaena group; Riedel et al., 1985, p. 508, pl. 3, figs. 15a–c.

Pseudodictyophimus group
(Pl. 4, Fig. 22)

Pseudodictyophimus group; Riedel et al., 1985, p.508, pl. 3, figs. 17a, b.

Sethophormin group
(Pl. 4, Fig. 23)

Sethophormin group A; Riedel et al., 1985, p. 508, pl. 4, figs. 1a, b.
Sethophormin group B; Riedel et al., 1985, p. 508, pl. 4, figs. 2a, b.

Other plagoniids
(Pl. 4, Fig. 24)

Other plagoniids; Riedel et al., 1985, p. 508, pl. 4, figs. 3a–c.

Clathrocorys teuscheri Haeckel
(Pl. 4, Fig. 24)

Clathrocorys teuscheri Haeckel; Bjørklund and De Ruiter, 1987, fig. 6.21.
Clathrocorys teuscheri Haeckel; Boltovskoy, in press, fig. 15.112.

Family THEOPERIDAE Haeckel, 1881; emend. Riedel, 1967b

Cornutella spp.
(Pl. 5, Figs. 1–3)

Cornutella spp.; Riedel et al., 1985, p. 509, pl. 4, fig. 4.

Cornutella profunda Ehrenberg
(Pl. 5, Figs. 2, 3)

Cornutella profunda Ehrenberg; Boltovskoy, in press, fig. 15.127.

Eucecryphalus group
(Pl. 1, Figs. 9, 10; Pl. 5, Figs. 4, 5)

Eucecryphalus group; Riedel et al., 1985, p. 509, pl. 4, figs. 5a–b.

***Eucyrtidium punctatum* (Ehrenberg) group**
(Pl. 5, Figs. 6–8)

Stichopterygium anomalum (Haeckel); Dumitrica, 1973a, p. 838, pl. 27, fig. 11.

Eucyrtidium anomalum (Haeckel); Sanfilippo et al., 1978, p. 756, pl. 1, figs. 1, 2.

Eucyrtidium punctatum (Ehrenberg) group; Sanfilippo et al., 1978, p. 756, pl. 1, fig. 3.

Eucyrtidium punctatum (Ehrenberg) group; Riedel et al., 1985, p. 509, pl. 4, fig. 7.

Other Eucyrtidium
(Pl. 1, Fig. 11; Pl. 5, Figs. 9–11)

Eucyrtidium spp.; Dumitrica, 1973a, p. 839, pl. 27, figs. 1, 2.

Other *Eucyrtidium*; Riedel et al., 1985, p. 509, pl. 4, figs. 8a, b.

Eucyrtidium cienkowskii Haeckel group; Riedel et al., 1985, p. 509, pl. 4, fig. 6.

Eucyrtidium acuminatum (Ehrenberg)
(Pl. 1, Fig. 11; Pl. 5, Fig. 9)

Eucyrtidium acuminatum (Ehrenberg); Nigrini and Moore, 1979, p. N61, pl. 24, figs. 3a–b.

Eucyrtidium acuminatum (Ehrenberg); Bjørklund and De Ruiter, 1987, fig. 4.20–23.

Eucyrtidium acuminatum (Ehrenberg); Boltovskoy, in press, fig. 15.137

Litharachnium group
(Pl. 5, Fig. 12)

Litharachnium group; Riedel et al., 1985, p. 509, pl. 4, fig. 11.

Pterocanium group
(Pl. 1, Fig. 12)

Pterocanium group; Riedel et al., 1985, p. 509, pl. 4, fig. 13.

Theocorys group

Theocorys group; Riedel et al., 1985, p. 510, pl. 4, fig. 15.

Other theoperids
(Pl. 1, Fig. 13; Pl. 5, Figs. 13, 14)

Other theoperids; Riedel et al., 1985, p. 510, pl. 5, fig. 1a–3.

Lithostrobos hexagonalis Haeckel
(Pl. 5, Fig. 13)

Lithostrobos hexagonalis Haeckel; Boltovskoy, in press, fig. 15.141.

Lipmanella bombus (Haeckel)
(Pl. 1, Fig. 13)

Lipmanella bombus (Haeckel); Boltovskoy, in press, fig. 15.133.

Lipmanella dictyoceras Haeckel
(Pl. 5, Fig. 14)

Lipmanella dictyoceras Haeckel; Boltovskoy, in press, fig. 15.134.

Family CARPOCANIIDAE Haeckel, 1881; emend. Riedel, 1967b

Carpocanistrum group A
(Pl. 5, Figs. 17, 18)

Carpocanistrum group A; Riedel et al., 1985, p. 510, pl. 5, fig. 2.

Family PTEROCORYTHIDAE Haeckel, 1881; emend. Riedel, 1967b

Anthocyrtidium group
(Pl. 5, Fig. 15)

Anthocyrtidium group; Riedel et al., 1985, p. 510, pl. 5, fig. 5.

Three-segmented pterocorythids
(Pl. 1, Figs. 14, 15; Pl. 5, Fig. 16)

Lamprocyclus group; Riedel et al., 1985, p. 510, pl. 5, figs. 6a, b.

Family ARTOSTROBIIDAE Riedel, 1967a

Botryostrobus group

(Pl. 5, Figs. 19, 20)

Botryostrobus group; Riedel et al., 1985, p. 510, pl. 5, fig. 7.

Phormostichoartus group

(Pl. 5, Figs. 21, 22)

Phormostichoartus group; Riedel et al., 1985, p. 510, pl. 5, figs. 10a, b.

Siphocampe group

(Pl. 5, Figs. 23, 24)

Siphocampe group; Riedel et al., 1985, p. 510, pl. 5, figs. 8a, b.

Spirocyrtis group

(Pl. 5, Figs. 25, 26)

Spirocyrtis group; Riedel et al., 1985, p. 511, pl. 5, fig. 9.

Family CANNOBOTRYIDAE Haeckel, 1881; emend. Riedel, 1967b

Cannobotryid group

(Pl. 5, Figs. 27–30)

Cannobotryid group; Riedel et al., 1985, p. 511, pl. 5, figs. 11a, b.

INCERTAE CEDIS

Carpocanarium group

Carpocanarium group; Riedel et al., 1985, p. 511, pl. 5, figs. 4a, b.

SILICOFLAGELLATE RESULTS AND SYSTEMATICS

The results of extensive stratigraphic research on silicoflagellates from the islands of Crete, Milos, and Aegina (Aegean Sea, Greece) have been recently published by Frydas (1996). Seven new Neogene acme-subzones and a new Pleistocene acme-subzone (*Octactis pulchra*) were defined therein. The exact position of the upper boundary of the latter acme-subzone has not yet been defined in these areas because of the absence of suitable outcrops of middle late Pleistocene age.

Three hundred silicoflagellate specimens were counted from the sample 160-971B-2H-CC. The relative abundance (%) of existing species is as follows, where A: Abundant (16–20%), C: Common (11–15%), F: Frequent (4–10%), R: Rare (1–3%):

- Dictyocha aculeata aculeata* (A),
- D. calida ampliata* (C),
- D. delicata* (C),
- D. fibula* (F),
- D. messanensis* (F),
- D. perlaevis perlaevis* (F),
- D. stapedia aspinosa* (C),
- D. stapedia stapedia* (C),
- Distephanus octogonus* (R)

The assemblage is assigned to the *Dictyocha aculeata aculeata* Zone, which is defined as the interval following the last occurrence of *Bachmannocena quadrangula* (middle late Pleistocene, Bukry, 1981, 1995). The type horizon of this zone is correlated with the following middle late Pleistocene biozones of calcareous nannoplankton: NN20/21 of Martini (1971), CN14b/15 of Okada and Bukry (1980) and MNN20/21 of Rio et al. (1990). The *Dictyocha aculeata aculeata* Zone can be correlated to:

1. The *D. aculeata* Zone of Dumitrica (1973b, 1973c), from the Mediterranean Sea and the southwestern Pacific Ocean;

2. The homonymous Zone of Bukry (1979, 1980), from the Site 397 off northwest Africa and from the Leg 54, in the eastern Equatorial Pacific;
3. The *D. messanensis aculeata* Zone of Martini (1990), Leg 112, from the eastern Pacific off Peru;
4. The *D. messanensis aculeata* Zone of Locker (1995), from off southern Chile.

Silicoflagellate Systematics

Genus DICTYOCHA Ehrenberg, 1837

Dictyocha aculeata aculeata (Lemmermann, 1901)

(Pl. 6, Figs. 7–16)

- 1901: *Dictyocha aculeata aculeata* Lemmermann, p. 261, pl. 11, figs. 1, 2.
 1935: *Dictyocha fibula* var. *aculeata* Lemmermann; Frenguelli, pl. 13, figs. 1–9.
 1968: *Dictyocha epidon* Ehrenberg; fide Loeblich et al., p. 90, fig. 15.
 1970: *Dictyocha aculeata* var. *aculeata* Lemmermann; Ling, p. 91, pl. 18, figs. 11–13.
 1973b: *Dictyocha aculeata* (Lemmermann); Dumitrica, p. 907, pl. 9, figs. 5–10.
 1973c: *Dictyocha aculeata* (Lemmermann); Dumitrica, p. 849, pl. 4, figs. 9–11.
 1973: *Dictyocha epidon* Ehrenberg; Bukry and Foster, p. 826, pl. 2, figs. 7–8.
 1974: *Dictyocha epidon* Ehrenberg; Locker, p. 634, pl. 1, figs. 1, 4, 5, 7, 8.
 1975: *Dictyocha aculeata* (Lemmermann); Perch-Nielsen, p. 686, pl. 5, figs. 3, 4.
 1976: *Dictyocha epidon* Ehrenberg; Poelchau, p. 170, pl. 1, figs. e, f; pl. 4, figs. 7, 8.
 1977: *Dictyocha aculeata* (Lemmermann); Bukry, p. 921.
 1980: *Dictyocha aculeata aculeata* (Lemmermann); Bukry, pp. 549–552, pl. 1, figs. 1–3.
 1986: *Dictyocha messanensis* ssp. *aculeata* (Lemmermann) f. *aculeata*; Locker and Martini, p. 904, pl. 3, figs. 11, 12.
 1990: *Dictyocha messanensis* ssp. *aculeata* (Lemmermann) f. *aculeata*; Martini, p. 169, fig. 2.
 1995: *Dictyocha messanensis* ssp. *aculeata* (Lemmermann); Locker, p. 233, fig. 2.
 1995: *Dictyocha aculeata aculeata* (Lemmermann); Bukry, p. 4, fig. 4(B)

Remarks: This important Quaternary warm-water species is characterized by the additional basal horns between the lateral bars and the sustaining spines, as well as by the presence of further additional spines on the basal ring and apical apparatus (Dumitrica, 1973b; Bukry, 1995). Two varieties of *D. aculeata aculeata* can be distinguished in our material, the large variety being almost one and a half times as large as the small one. In addition to these two varieties one pentagonal form was also observed (Pl. 1, fig. 15). According to Dumitrica (1973b) this taxon seems to occur exclusively in the Quaternary.

Dictyocha calida ampliata Bukry, 1979

(Pl. 6, Figs. 1–6)

1979: *Dictyocha calida ampliata* n. subsp.; Bukry, p. 982–983, pl. 2, figs. 1, 2, 9.

Remarks: According to Bukry (1979) *D. calida ampliata* is distinguished from *D. calida calida* by more extreme elongation of the portals. The ratio of the external width of the ring (X1) to the width of apical structure (X2) as measured perpendicularly to the bar allows a proportional comparison of elongation of portals between *D. calida calida* Poelchau (1976) and *D. calida ampliata* (Bukry, 1979). The ratio X1/X2 of *D. calida ampliata* in our material varies from 2.50 to 2.71, based on measurements made on 20 specimens, whereas the same ratio for Poelchau's *D. calida calida* varies from 2.07 to 2.39. *D. calida ampliata* is known to date from upper Pliocene to Holocene sediments only (Perch-Nielsen, 1985).

Dictyocha delicata (Bukry, 1982)

(Pl. 7, Figs. 4–6)

1976: *Dictyocha perlaevis delicata*; Bukry, p. 724, pl. 1, figs. 5–10.

1982: *Dictyocha delicata* (Bukry); Bukry, p. 432, pl. 2, fig. 7.

1994: *Dictyocha delicata* (Bukry); Frydas, p. 486, pl. 1, fig. 8.

Remarks: *Dictyocha delicata* is found in smaller numbers near Heraklion (Crete) in the locality of Gournes (Frydas, 1994). The silicoflagellate assemblages from the section Gournes belong to the *Dictyocha neonautica* acme-Subzone of Piacenzian age (Frydas, 1996). The stratigraphic distribution of *D. delicata* extends from the upper Pliocene through the Quaternary. It is most common in the lower Quaternary levels of Sites 157 and 321 (southeastern Pacific), but it is rare in the upper Quaternary levels of Site 321 (Bukry, 1976).

Dictyocha fibula Ehrenberg, 1839
(Pl. 7, Figs. 18, 19)

1839: *Dictyocha fibula* Ehrenberg; fide Loeblich et al., 1968, p. 90, pl. 9, figs. 7–12.

1973b: *Dictyocha fibula* Ehrenberg; Dumitrica, p. 906, pl. 3, figs. 7, 9; pl. 4, fig. 8; pl. 5, figs. 1–5, 8; pl. 6, figs. 1, 2, 4, 5, 7, 8; pl. 9, fig. 1.

1973: *Dictyocha fibula* Ehrenberg; Bukry and Foster, p. 826–827, pl. 2, fig. 9; pl. 3, figs. 1, 12.

1990: *Dictyocha fibula* Ehrenberg; Frydas, p. 96, pl. 1, fig. 13.

Remarks: According to Dumitrica (1973b), the Quaternary forms possess a squarish or slightly rhombic basal ring, with rounded corners, rather long blunt radial horns, and short sustaining spines. Locker's (1974) taxonomy for *D. fibula* is not accepted herein.

Dictyocha messanensis Haeckel in Peters, 1860
(Pl. 6, Figs. 17, 18)

1860: *Dictyocha messanensis* Haeckel in Peters; fide Loeblich et al., 1968, p. 103–104, pl. 17, figs. 24–27.

1972: *Dictyocha fibula* Ehrenberg var. *messanensis* (Haeckel); Ling, p. 161, pl. 25, figs. 18, 19.

1973b: *Dictyocha messanensis* Haeckel; Dumitrica, p. 907, pl. 8, figs. 8–13; pl. 9, figs. 2–4.

1973c: *Dictyocha messanensis* Haeckel; Dumitrica, p. 849, pl. 4, figs. 7, 75, 6, 7, 8; ?pl. 3, figs. 13–15.

1975: *Dictyocha messanensis* Haeckel; Perch-Nielsen, p. 686, pl. 5, figs. 13, 14.

1976: *Dictyocha messanensis* Haeckel; Martini, p. 443, pl. 1, fig. 9; pl. 2, figs. 2a, b.

1986: *Dictyocha messanensis aspinosa* (Bukry); Locker and Martini, p. 904, pl. 3, figs. 3–5; pl. 12, fig. 2.

1986: *Dictyocha messanensis messanensis* fa. *aspinosa* (Bukry);

Locker and Martini, p. 904, pl. 3, figs. 1, 9.

1995: *Dictyocha messanensis* Haeckel; McCartney et al., p. 147, pl. 3, figs. 12, 13.

Remarks: *Dictyocha messanensis* is a polytypic and polymorphic species. It can be distinguished from *D. aculeata* not only by the lack of additional basal horns, but also by its smaller size. *D. messanensis* is the most frequent species in the Quaternary of Sites 127 and 128 (Eastern Mediterranean) and is regarded as a warm-water species (Dumitrica, 1973b). Small, rhomboidal, more delicate forms were found in the material studied, which according to Dumitrica (1973c), probably indicate a great amount of sapropel. Species without apical or sustaining spines are known from Pleistocene and Holocene sediments (Perch-Nielsen, 1975).

Dictyocha perlaevis perlaevis Frenguelli, 1951
(Pl. 7, Figs. 20, 21)

1951: *Dictyocha perlaevis* Frenguelli, p. 279, figs. 4b, c.

1973: *Dictyocha fibula* Ehrenberg; Bukry and Foster, p. 826, pl. 3, fig. 1.

1975: *Dictyocha fibula perlaevis* (Frenguelli); Bukry, p. 855, pl. 3, fig. 5.

1978: *Dictyocha perlaevis* Frenguelli; Stradner and Bachmann, p. 806, pl. 1, figs. 5, 6, 9–11.

1979: *Dictyocha perlaevis perlaevis* Frenguelli; Bukry, p. 984, pl. 3, figs. 6–11.

1986: *Dictyocha messanensis* ssp. *stapedia* (Haeckel) f. *stapedia*; Locker and Martini, p. 905, pl. 3, figs. 6, 7.

1990: *Dictyocha perlaevis perlaevis* Frenguelli; Frydas, p. 97, pl. 1, fig. 14.

Remarks: *D. perlaevis perlaevis* is a warm-water species most commonly found in Pliocene and Quaternary assemblages. *D. perlaevis perlaevis* differs

from *D. fibula* by the long size of the basal ring and the pentals of the minor axis. *D. perlaevis perlaevis* is present in lesser numbers in our material.

Dictyocha stapedia aspinosa Bukry, 1976
(Pl. 7, Figs. 1–3, 7–10)

1976: *Dictyocha stapedia aspinosa*; Bukry, p. 724 (in part), pl. 2, figs. 7, 8.

1990: *Dictyocha stapedia aspinosa*; Frydas, p. 97, pl. 1, figs. 15, 16.

Remarks: The most significant criterion by which to distinguish *D. stapedia aspinosa* from *Dictyocha messanensis* is the distinctive basal spikes, which were also used by Haeckel (1887) to distinguish the two species. *D. stapedia* is widespread in all warm seas (Bukry, 1976). Its stratigraphic range extends from upper Pliocene to the Holocene.

Dictyocha stapedia stapedia Haeckel, 1887
(Pl. 7, Figs. 14–17)

1887: *Dictyocha stapedia*; Haeckel, p. 1561, pl. 101, figs. 10–12.

1887: *Dictyocha rhombus*; Haeckel, p. 1562.

1901: *Dictyocha rhombus* Haeckel; Lemmermann, pl. 11, fig. 3.

1976: *Dictyocha stapedia stapedia* Haeckel; Bukry, p. 724, pl. 3, figs. 1–7.

1986: *Dictyocha messanensis* Haeckel; Frydas, p. 8, pl. 5, fig. 4.

Remarks: *D. stapedia stapedia*'s longer radial spines along the major axis distinguish it from *D. stapedia aspinosa*. *D. messanensis* differs from *D. stapedia stapedia* in having a short apical bar. *D. stapedia stapedia* is a species with a wide geographic distribution whose range extends from the upper Pliocene to the Holocene.

Genus *DISTEPHANUS* Stohr, 1880
Distephanus octogonus (Ehrenberg, 1843)
(Pl. 7, Figs. 11–13)

1843: *Mesocena? octogona* Ehrenberg; fide Loeblich et al., 1968, p. 129, pl. 27, fig. 6).

1846: *Mesocena binonaria* Ehrenberg; fide Loeblich et al., 1968, p. 127, pl. 27, fig. 1.

1846: *Mesocena bioctonaria* Ehrenberg; fide Loeblich et al., 1968, p. 127, pl. 27, fig. 2.

1973b: *Distephanus octogonus* (Ehrenberg); Dumitrica, p. 908, pl. 12, fig. 16–19.

1974: *Octactis? bioctonaria* (Ehrenberg); Locker, p. 636, pl. 2, fig. 5–7.

1978: *Distephanus octogonus* (Ehrenberg); Stradner and Bachmann, p. 807, pl. 2, fig. 16.

1990: *Distephanus bioctonarius* f. *binonarius* (Ehrenberg) nov. comb; Martini, p. 166–167, pl. 3, figs. 5, 6.

1990: *Distephanus bioctonarius* f. *bioctonarius* (Ehrenberg) nov. comb; Martini, p. 167, pl. 3, figs. 3, 4.

Remarks: Eight-rayed forms of *D. octogonus* (Pl. 7, Fig. 13) are the common morphotypes in our material. Only two specimens with nine spines were found (Pl. 7, Figs. 11, 12). According to Dumitrica (1973b), *D. octogonus* appears to be restricted to the Quaternary (DSDP Sites 127 and 128 of the Eastern Mediterranean). This species occurs rarely in the Quaternary sediments of the Eastern Pacific (Bukry and Foster, 1973).

RADIOLARIAN PALAEOECOLOGICAL INTERPRETATION

The radiolarian assemblage in Sapropel S5 records an abundant, well-preserved and diverse fauna, which reflects accumulation below eutrophic waters (Casey, 1993). More particularly, it is dominated by *Arachnocorallium* gr. (22%), a counting-group that was correlated by Riedel et al. (1985) to *Peridinium spinipes* Haeckel, as studied by Casey et al. (1979a, 1979b). In peak abundances of polycystine radiolarians, which occur at depths between 100 and 200 m in the oligotrophic, open ocean Sargasso Sea, this species was found to be dominant. The same species was also found to be dominant in much more eutrophic waters, such as the southern Californian and the Gulf

Stream where the densities of living radiolarians peak in the upper 100 m of the water column (Casey et al., 1979a, 1979b). According to Casey et al. (1979a) the abundance of *Peridinium spinipes* in sediments can be regarded as an indicator of high productivity in the overlying waters. High primary production during accumulation of Sapropel S5 is independently supported by geochemical studies. Among the nine youngest sapropels of the Eastern Mediterranean, the lightest values of nitrogen isotope ratios were measured in this particular sapropel (Calvert et al., 1992). High productivity resulted in significantly high flux of organic matter in the S5 sapropel; this is recorded in the highest levels of organic carbon content preserved in it (Ten Haven et al., 1987; Fontugne and Calvert, 1992).

Ecological studies of living radiolarians suggest that many are restricted to certain depths or ecological niches. These are mainly feeding niches, reflecting different feeding strategies, but it is clear that some radiolarians may be involved in more than one feeding activity (Casey et al., 1979a; Anderson, 1983, 1993). Most radiolarian species prefer shallow-water niches and diversity decreases with depth (McMillen and Casey, 1978), but radiolarians have been reported living in waters as deep as 5000 m (Takahashi and Honjo, 1981). Shallow-water niches are mainly occupied by polycystines with symbiotic zooxanthellae (algae). Many of the near-surface-dwelling radiolarians contain algal symbionts in their cytoplasm, which to a large extent could provide the radiolarians' food requirements (Anderson, 1983, 1993). Among the taxa identified in our material, the colosphaerid group, *Hexacontium* gr., other actinommids, pyloniid gr., *Acanthodesmia* gr., *Dictyocoryne* gr., and *Spongaster* spp. would fall in this group (the latter two are more abundant in subsurface waters, see below). They represent a significant part of the radiolarian assemblage in the sapropel S5 (18%), but they form almost two thirds of the assemblage (62.5%) in Sample 160-969A-1H-3, 65–67 cm.

Depth profiles of radiolarian densities in the North Pacific and equatorial Atlantic (Kling, 1979; Dworetzky and Morley, 1987) establish that although many species are restricted to discrete depth zones (which is an indication of preferred habitats for those species) peak abundances of polycystines as a whole would in general coincide with a chlorophyll-maximum zone occurring at subsurface depths (50–100 m). This niche would be mainly occupied by herbivorous polycystines involved in the grazing food chain and fed essentially upon the micro- and nanophytoplankton. According to Casey et al. (1979a), *Arachnocorallium* gr. would belong to this niche. The presence of a deep chlorophyll-maximum layer is a characteristic feature of most oceanic waters, which may be stratified, and has also been detected in the Eastern Mediterranean (Abdel-Moati, 1990). More particularly, vertical profiles of chlorophyll- α and biogenic silica (diatoms) measured off the Egyptian coast displayed positive peaks during early summer, at depths of approximately 100 m, at the base of the euphotic zone.

Despite the limited amount of data relevant to the vertical distribution of radiolarians in the water column, some ecological information can be drawn for a certain number of them. Radiolarians such as *Eucecryphalus* gr., *Litharachnium* gr., *Phormostichoartus* gr., *Dictyocoryne* gr., *Spongodiscus* gr., *Ceratospyrus* gr. A, *Spongaster* spp., *Didymocyrtes* spp., *Larcospira* gr., *Anthocyrtydium* gr., and *Spongocore* spp. are known to be present in peak abundances at or near (above or below) the level of chlorophyll- α maxima (Kling, 1979; Dworetzky and Morley, 1987). They represent more than 9% of the radiolarian assemblage in Sapropel S5 and only 2.15% in Sample 160-969A-1H-3, 65–67 cm.

Deep-water habitats were also occupied during the accumulation of sapropel S5, as indicated by the significant abundance of deep-dwelling radiolarians (*Cornutella* spp., 1.5%). These habitats belong to the detritivore niche of polycystines—which feed upon suspended and settling dead or detrital material—and would be represented by *Eucecryphalus* gr., *Cornutella* spp., and *Litharachnium* gr. in our ma-

terial (Casey et al., 1979a). Radiolarians of this niche are absent from above the sapropel S5, but they are well-represented in the sapropel itself (5.2%).

All the above would suggest that during accumulation of Sapropel S5 radiolarians occupied ecological niches at various depths of the water column. The composition of the radiolarian assemblages indicates much stronger and better developed subsurface chlorophyll-maxima during accumulation of the sapropel S5. These results are in agreement with the paleoecological information yielded by planktonic foraminifers and calcareous nanofossils from this sapropel, which point to increased primary production confined to a chlorophyll maximum during its accumulation (Rohling and Gieskes, 1989; Castradori, 1993). However, after the end of the period of eutrophication (sapropel S5) the spectrum of radiolarian habitats was substantially reduced. This is reflected in the relative abundance of near-surface dwelling polycystines, whose energy needs are substantially supported by their symbionts (Anderson, 1993).

DISCUSSION AND CONCLUSIONS

Finding abundant and well-preserved siliceous microfossil assemblages in the Mediterranean sediments has a double importance: (1) in terms of biological productivity and (2) in terms of silica preservation on the seafloor and in the sediments.

Dissolution of diatom and radiolarian tests is a common phenomenon in seawater because of its undersaturation in silica (Berger, 1968; Schrader, 1971). This phenomenon appears to be much more intense in the Mediterranean Sea because of its very low silica content (Krom et al., 1991a). SEM observations of radiolarian tests from the surface of the Mediterranean seafloor display clear indications of dissolution (Caulet, 1972). Normally, in the Mediterranean, silica dissolution is very active in the upper 30 cm of the surface sediments; radiolarian tests have not been observed under this depth, apart from their exceptional preservation in some sapropel layers (Caulet, 1974). However, recent studies in small anoxic basins of the Eastern Mediterranean did establish that radiolarian preservation is very good in sediments that accumulated in the anoxic and hypersaline waters of these small protected basins (Bjørklund and De Ruiter, 1987). Similarities could be drawn to explain the exceptional preservation of opal assemblages in the S5 sapropel of Site 971 (Holes B and C; Shipboard Scientific Party, 1996b, Fig. 8), which accumulated in the moat of the Napoli mud volcano. However, the protection provided by this depression can only account for silica preservation to a certain extent. Siliceous microfossils have not been reported from the sediments in the same holes overlying the sapropel S5, not even in the well-expressed S1 layer. Hence, biogenic silica preserved in S5 has recorded a real event of particular significance.

It is possible that this particular event was the result of excessive discharge of the Nile river, which provided abundant nutrients for the Eastern Mediterranean. In present times, phosphorus appears to be the main biolimiting nutrient in the Eastern Mediterranean (Krom et al., 1991b). Also, because of the low values of silica in the Mediterranean, the limited availability of this element important for the healthy growth of diatoms (Ludwig and Volcani, 1986) and sili-coflagellates (Lipps, 1970) would certainly limit the bloom of siliceous phytoplankton. Both phosphorus and silica could have been supplied in excess by the Nile river, after the monsoonal precipitations in eastern Africa.

Excessive bloom of diatom mats and their high rate of accumulation (Sancetta, 1994) would not only preserve the organic matter, but would also preserve biogenic silica from dissolution. Indeed, within areas of high productivity, especially of excessive diatom production with their subsequent export flux onto the seafloor, dissolution of sil-

ica is substantially reduced, as deep waters become successively enriched in this element (Caulet, 1977; Qiu et al., 1993).

Radiolarian shell construction appears not to be limited by low levels of silica availability in the seawater. Moreover, symbiont-bearing radiolarians may be more competitive in absorbing silica even if it is available in very low quantities, since part of the substantial source of energy required may be supplied by the symbiont primary productivity (Anderson, 1996). The absence of preserved siliceous phytoplankton and the relative abundance of symbiont-bearing radiolarians above the sapropel S5, therefore, could be interpreted as the result of a drastic reduction in silicic acid and other biolimiting nutrients provided by the Nile into the Mediterranean.

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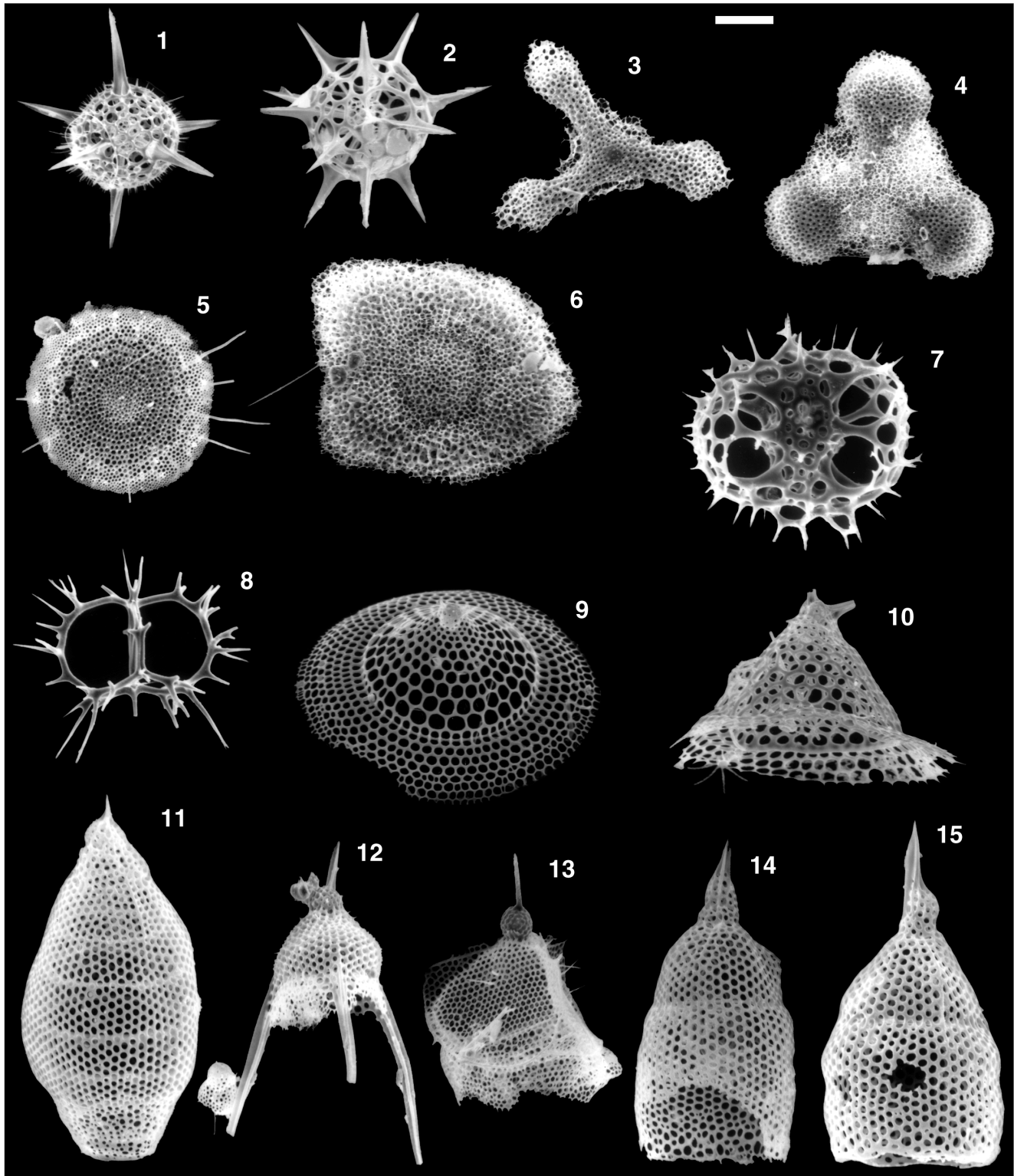


Plate 1. Scanning electron micrographs of radiolarians from Sample 160-971B-2H-CC. Numbers in μm in all figures refer to the same scale bar (upper right). **1.** *Hexacantium* group, 67 μm ; **2.** Other actinommids, 48 μm ; **3–4.** *Dictyocoryne* group: (3) 72 μm ; (4) *D. truncatum*, 75 μm ; **5.** *Porodiscus* group, 97 μm ; **6.** *Spongaster* sp., 67 μm ; **7.** Pyloniid group, 45 μm ; **8.** *Acanthodesmia vinculata*, 76 μm ; **9–10.** *Eucecryphalus* group: (9) 45 μm , (10) 43 μm ; **11.** *Eucyrtidium acuminatum*, 32 μm ; **12.** *Pterocanium* group, 53 μm ; **13.** Other theoperids: *Lipmanella bombus*, 43 μm ; **14–15.** Three-segmented pterocorythid: (14) 43 μm , (15) 44 μm .

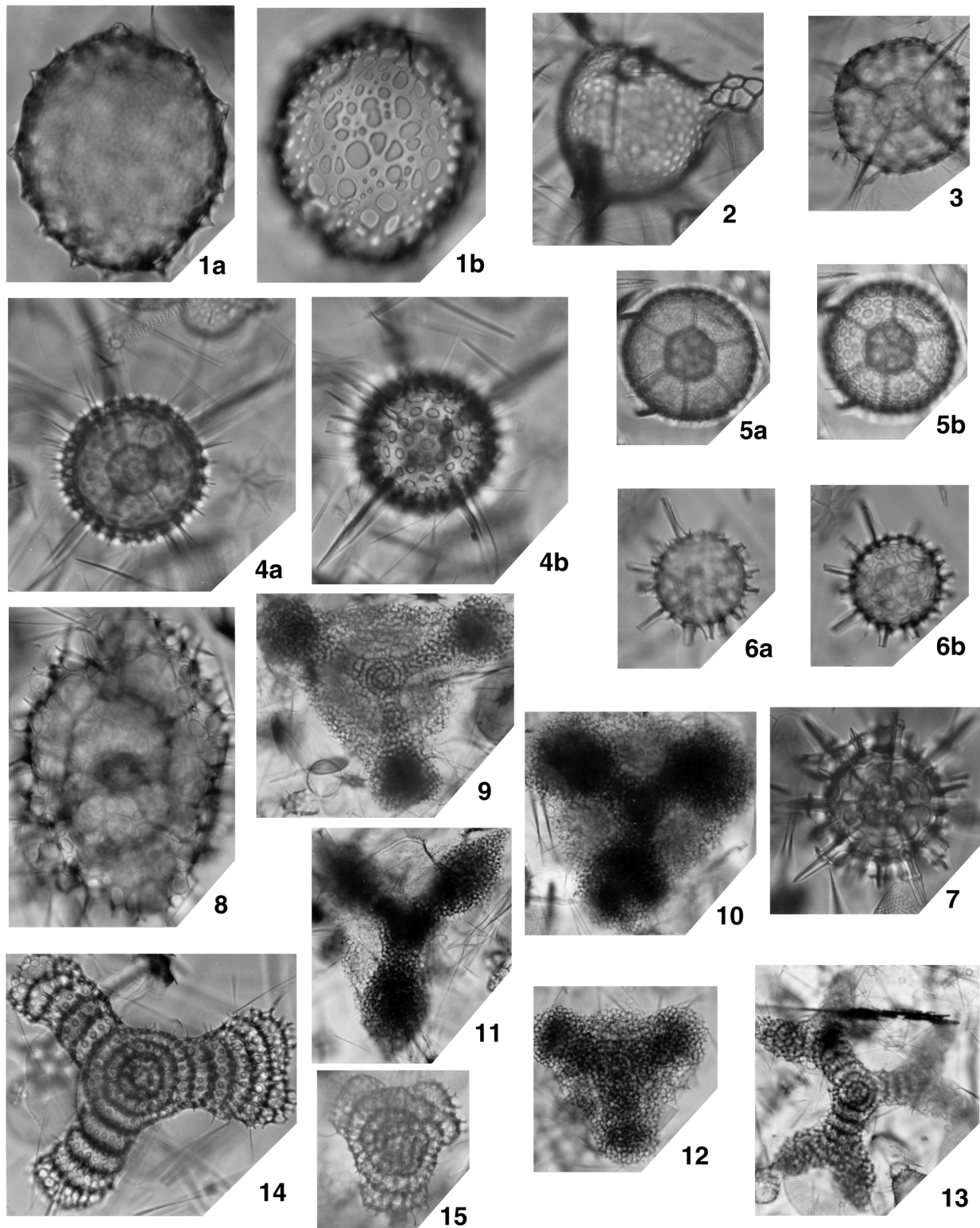


Plate 2. Radiolarians from Sample 160-971B-2H-CC. Magnification 240× for all figures apart from 9 to 13 (120×). 1–2. Collosphaerid group: (1) *Acrosphaera spinosa* group?; (2) *Solenosphaera chierchiai*; 3–4. *Hexacontium* group; 5. *Thecosphaera inermis*; 6–7. Other actinommids; 8. *Didymocyrtis* sp.; 9–12. *Dictyocoryne* group: (9) *D. profunda*; (10) *D. truncatum*; 13–15. *Hymeniastrum* group: (13) *H. regulare*; (14) *H. virchowii*.

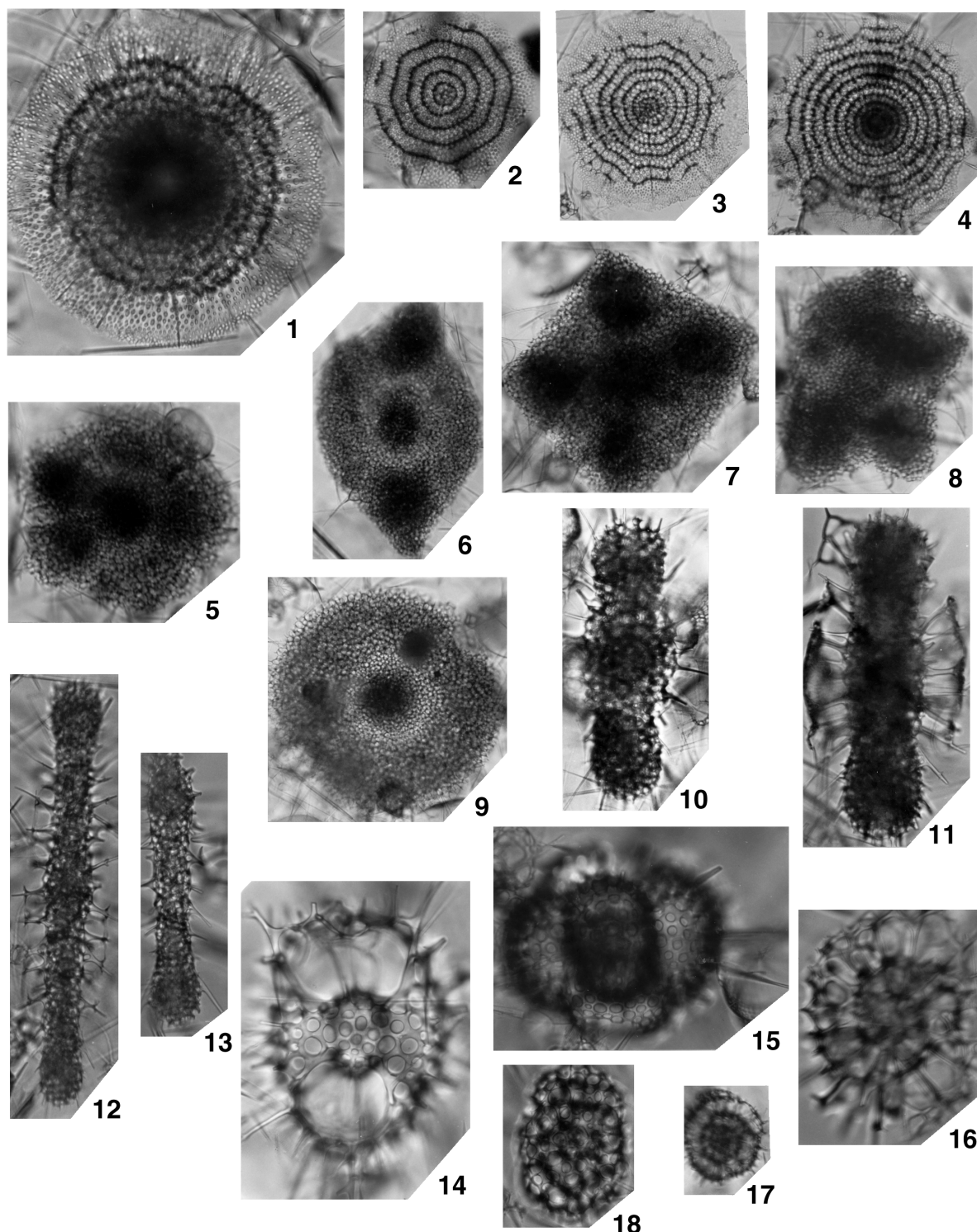


Plate 3. Radiolarians from Sample 160-971B-2H-CC. Magnification 120× for Figures 2–9, 17 and 240× for Figures 1, 10–16, 18. **1–4.** *Porodiscus* group: (1) *Porodiscus* group A; (2–3) *Porodiscus* group B; **5–8.** *Spongaster* spp.; **9.** *Spongodiscus* group; **10–13.** *Spongocore* spp.: (10–11) *Spongocore puella*; **14.** Pyloniid group; **15.** Tholoniid group: *Amphitholus metallasson*; **16–18.** *Pylospira* group, (16) *P. octopyle*.

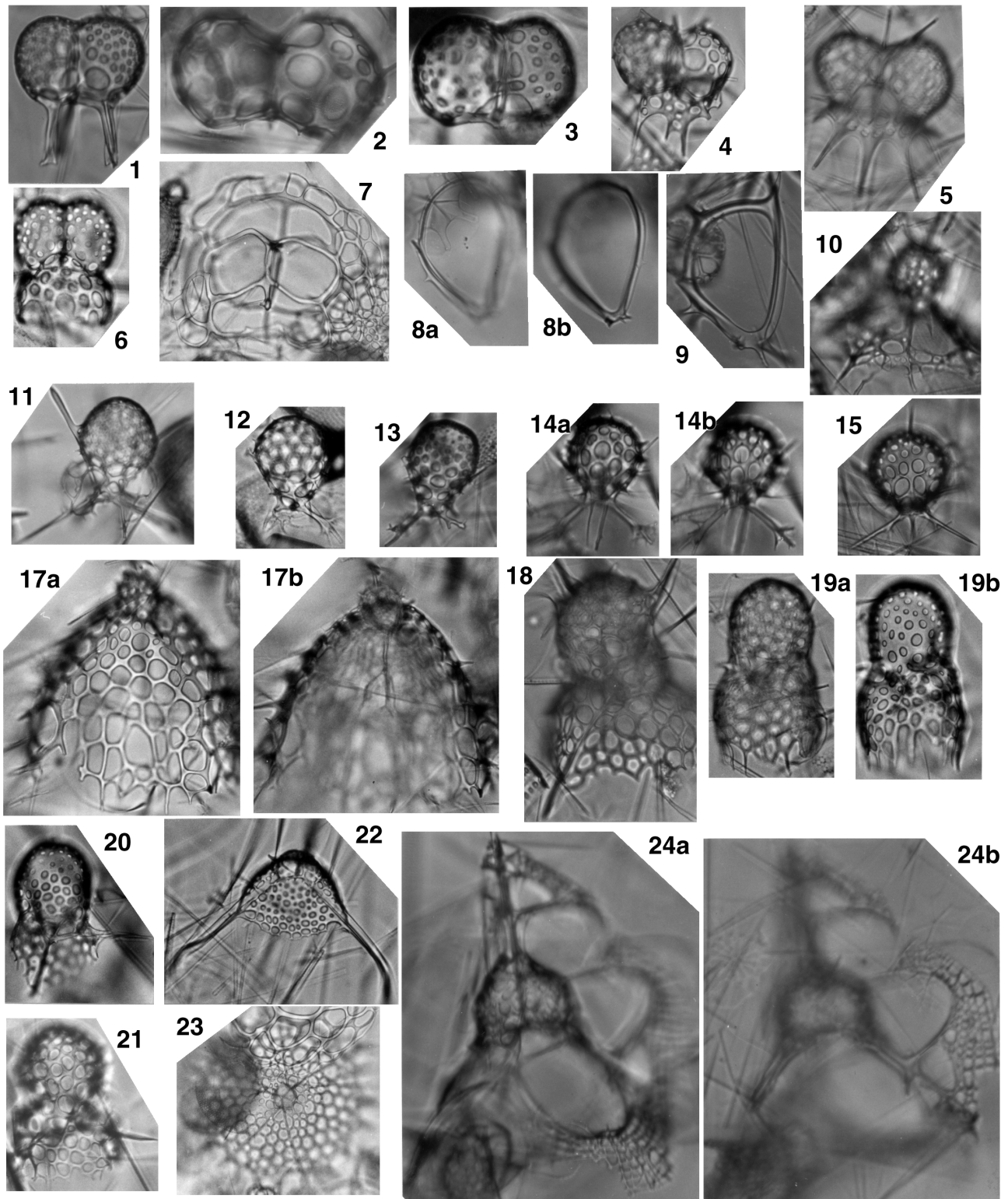


Plate 4. Radiolarians from Sample 160-971B-2H-CC. Magnification 300× for all figures apart from 7 and 22 (150×). **1.** *Ceratospyris* group A; **2–3.** *Ceratospyris* group B; **4–5.** *Ceratospyris* group C; **6.** *Desmospyris* group; **7.** *Nephrospyris renilla*; **8–9.** *Zygocircus* group: (8) *Z. productus productus*; (9) *Z. productus piscicaudatus*; **10.** *Arachnocorys circumtexta*; **11–15.** *Arachnocorallium* group; **17.** *Ceratocyrtis* group; **18–21.** *Lophophaena* group; **22.** *Pseudodictyophimus* group; **23.** Sethophormin group; **24.** Other plagoniids: *Clathrocorys teuscheri*. Note that there is not a Figure 16.

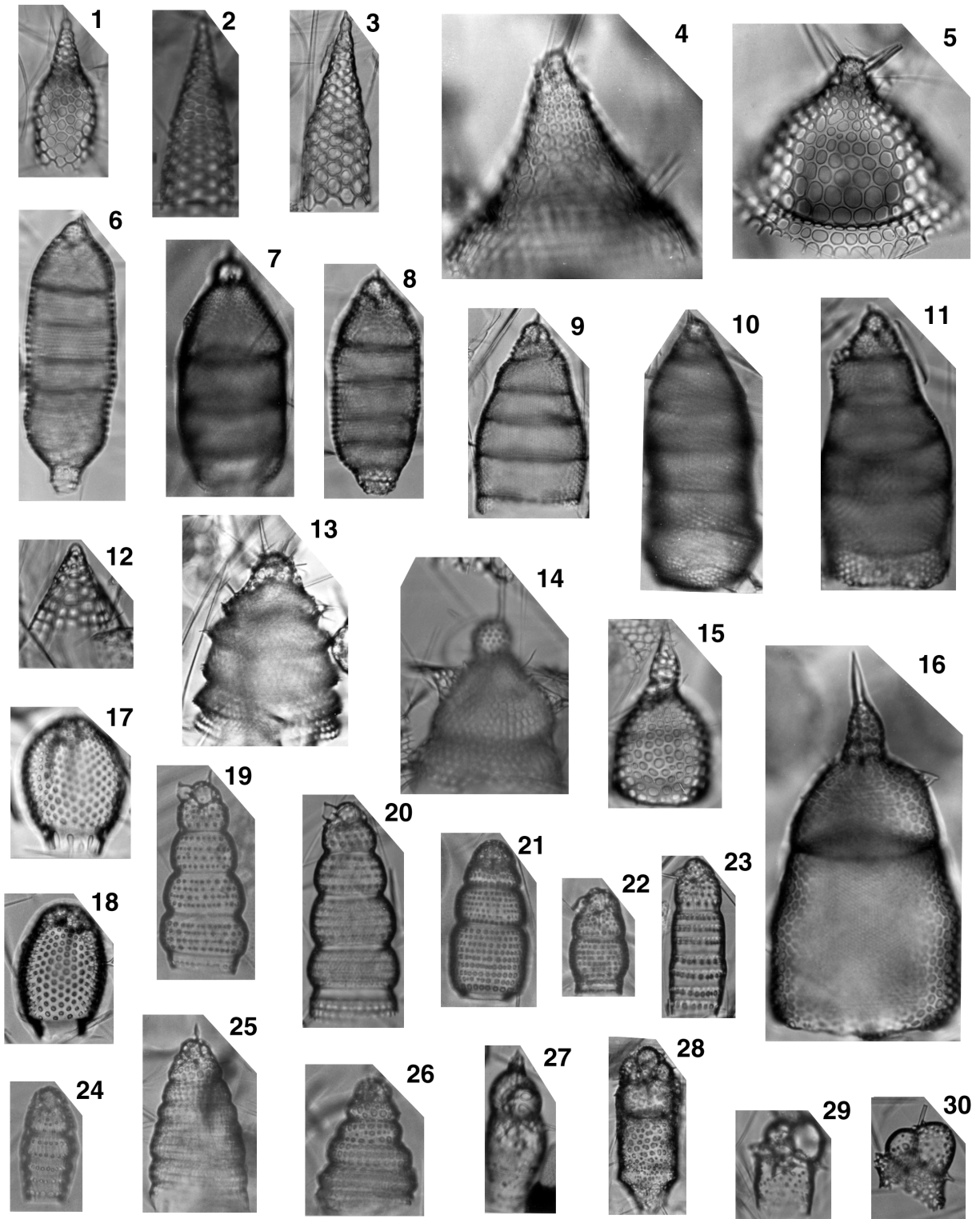


Plate 5. Radiolarians from Sample 160-971B-2H-CC. Magnification 240× for all figures. 1–3. *Cornutella* spp.: (2–3) *Cornutella profunda*; 4–5. *Eucecryphalus* group; 6–8. *Eucyrtidium punctatum* group; 9–11. Other *Eucyrtidium*: (9) *E. acuminatum*; 12. *Litharachnium* group; 13–14. Other theoperids: (13) *Lithostrobos hexagonalis*; (14) *Lipmanella dictyoceras*; 15. *Anthocyrtidium* group; 16. Three-segmented pterocorythid. 17–18. *Carpocanistrum* group A; 19–20. *Botryostrobos* group; 21–22. *Phormostichoartus* group; 23–24. *Siphocampe* group; 25–26. *Spirocyrtis* group; 27–30. Cannobotryid group.

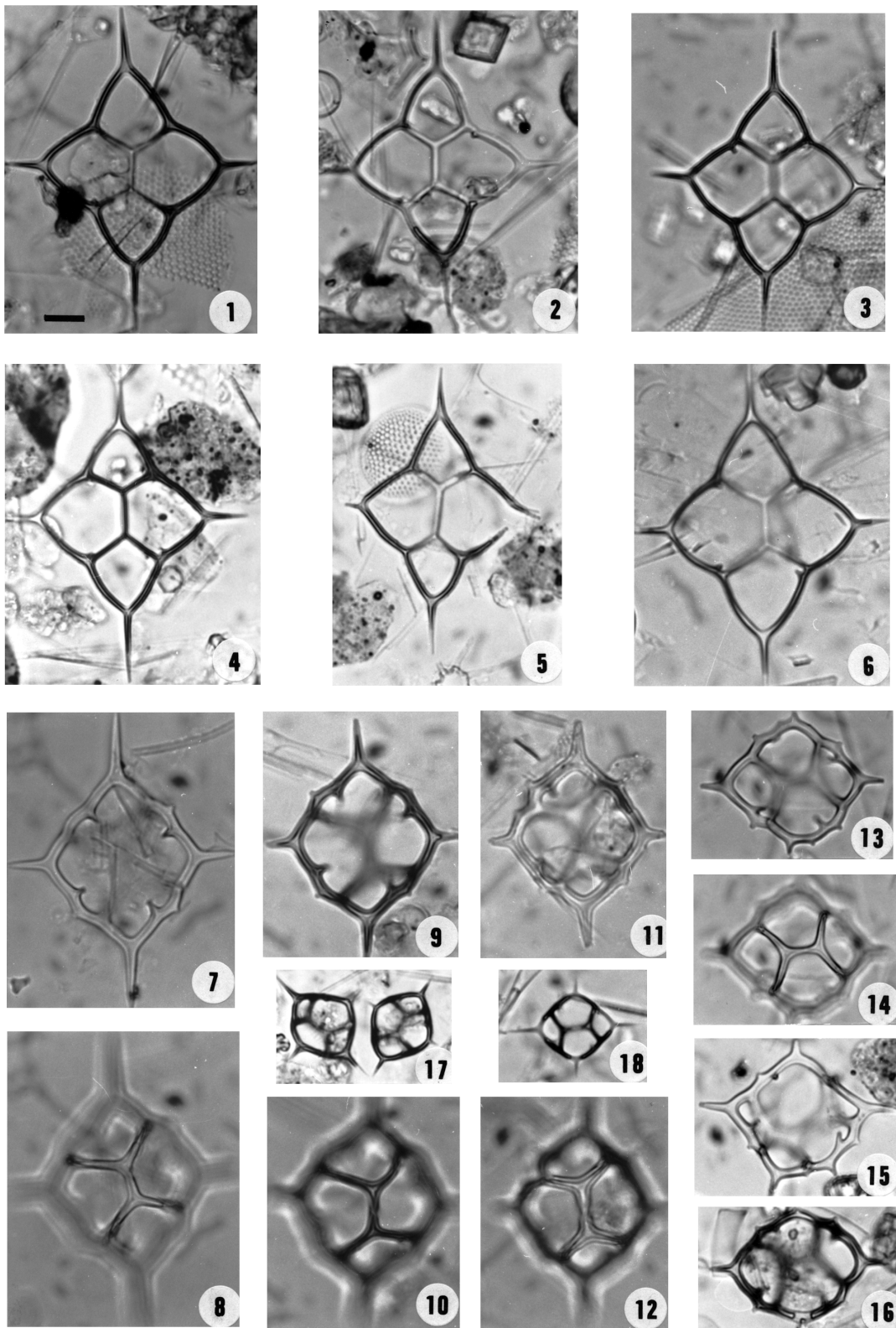


Plate 6. Silicoflagellates from Sample 160-971B-2H-CC. Magnification 600 \times for all figures; scale bar equals 10 μm . **1–6.** *Dictyocha calida ampliata*: (1–4, 6) normal forms; (5) irregular form; **7–16.** *D. aculeata aculeata*: (7–12) large forms; (13–16) small forms; (7, 9, 11, 13, 15, 16) focused on basal ring; (8, 10, 12, 14) focused on apical bar; (15) pentagonal specimen; **17–18.** *D. messanensis*, small rhomboidal forms.

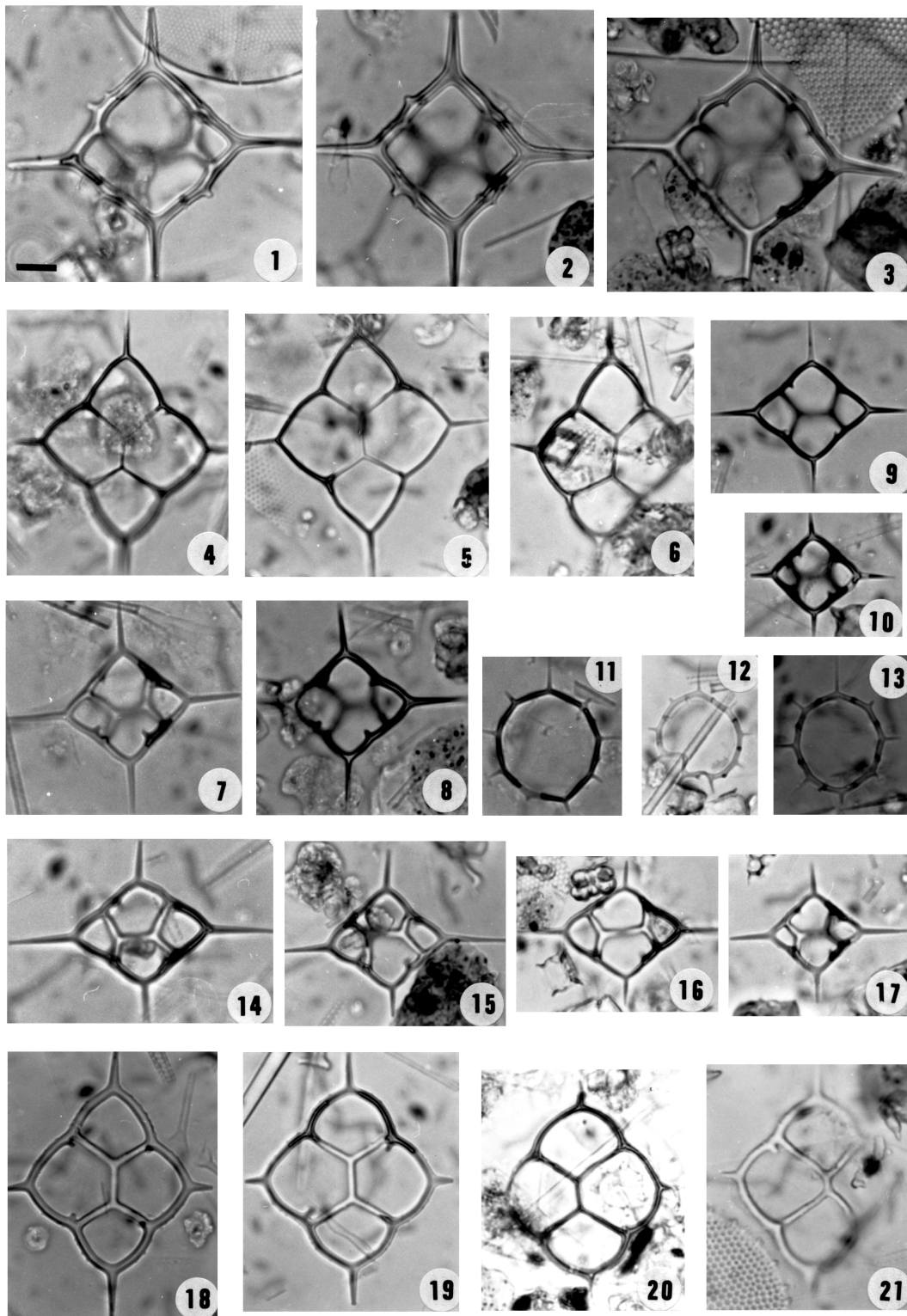


Plate 7. Silicoflagellates from Sample 160-971B-2H-CC. Magnification 600× for all figures; scale bar equals 10 μm. 1–3, 7–10. *D. stapedia aspinosa*: (1–3) large forms, focused on basal ring; (7–10) small forms, focused on basal ring; 4–6. *D. delicata*: 4–6 fibuloid forms with small apical bar. 11–12. *Distephanus octogonus*, nine-rayed forms; 13. *D. octogonus*, eight-rayed form. 14–17. *Dictyocha stapedia stapedia*, rhomboidal forms with long radial spines in the major axis. 18–19. *D. fibula*; 20–21. *D. perlaevis perlaevis*; asperoid forms.