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Radiolarians in the Adriatic Sea plankton (Eastern Mediterranean)

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Samples for the study of radiolarians in the Southern Adriatic were collected during five cruises at three stations along the Dubrovnik transect (stations S-100 to S-1000) from April 1993 through February 1995. Moreover, samples were collected during 21 cruises at the deepest station, S-1000/1200, from June 2001 through December 2009. Samples were taken in 2 to 8 vertical layers with a Nansen net 53 µm equipped with a closing system. In the central part of the southern Adriatic Pit, a total of 95 radiolarian taxa were recorded: 32 species of spumellaria, 46 species of nassellaria and 17 species of phaeodaria. The present research added 49 taxa to the known radiolarian fauna of the Adriatic Sea. The most common species were the phaeodarian Challengeria xiphodon*, the spumellarian* Stylodictya multispina *and the nassellarian* Cornutella profunda*, which were present in 99% of the vertical series. Radiolarians were rarely present in coastal areas and in the central Adriatic, whereas the highest abundances were recorded in the deepest parts of the south Adriatic Pit. Phaeodaria represented 20-86 % of the total average abundance. As a rule, very low abundances were noted in the euphotic layer except during October 2001, when a maximum of 169 ind. m^{-3} was recorded. Juvenile forms of the species* Eucyrtidium acuminatum *represented 98 % of the total number in these samples. In most cases, the maximum abundances were found in layers between depths of 200-300 m. The populations of most species were renewed by incoming eastern Adriatic currents from the Ionian Sea.*

Key words: Radiolaria, diversity, vertical distribution, indicator species, water masses, Adriatic Sea

INTRODUCTION

Radiolarians are non-motile holoplanktonic protozoans. Their special morphological structure is adapted to flotation. The skeleton is composed of amorphous silica. Solitary forms are from 30 µm to 2 mm in diameter, whereas colonial forms can be tens of centimetres in length. They are found in all seas and climatic zones, from the surface to the greatest depths. HAECKEL (1887) described an imposing figure of >3,000 species from material collected during the “Challenger” expedition. Many species are described on the basis of one occurrence. Most of these single occurrences are fossil forms. A partial revision has been made on the basis of comparative morphology and taxonomy (NIGRINI & MOORE, 1979; HOLLANDE & ENJUMENT, 1960; ANDERSON, 1983; BOLTOVSKOY, 1999; KLING & BOLTOVSKOY, 1999). In general taxonomy has accepted the division of radiolarians into Polycystina (Spumellaria and Nassellaria) and Phaeodaria (ANDERSON, 1983). Acantharia have been excluded from this division due to the chemical composition of the skeleton and the species *Sticholonche zanclea,* which is included under Taxopods according to CACHON & CACHON (1978).

Due to the number of species, radiolarians represent numerous group of plankton. TAKAHASHI (1991) has noted 420 radiolarian taxa. However, the life cycle is still not completely known, and quantitative and ecological data are rare. An increase in radiolarian numbers in the northern Atlantic occurs with an increase in sea temperatures, and the highest values occur in tropical waters (BOLTOVSKOY & RIEDEL, 1979). Research on recent radiolarians has intensified. These studies investigate radiolarians as hydrographic indicators. They also investigate the qualitative-quantitative and spatial distribution of radiolarians in oceanic waters (MOLINA-CRUZ *et al*., 1999; OKAZAKI *et al*., 2005; ISHITANI & TAKAHASHI, 2007; ZHANG *et al.,* 2009).

Almost all of the authors who worked at the «Zoological Station in Trieste» at the beginning of the 20th century reported data on the species *Stoholonche zanclea* and on a number of Acantharia species, including radiolarians, in their annual reports published in the «Zoologische Anzeiger». In the eastern part of the northern Adriatic, the radiolarian species *Lithomelissa thoracites* (ZACHARIAS, 1906; ISSEL, 1922) was first mentioned. The discovery of a juvenile form of *Dictyophimus* was also reported. During two cruises with the M/V «Rudolf Virchow» in 1907 and 1909 along the eastern coast of the Adriatic to Dubrovnik, STIASNY (1911) recorded 21 species, of which only 8 were valid radiolarian species. The greatest diversity was noted at a deep station south of Dubrovnik. At this station, the most common species were *Spongosphaera streptacantha* and *Lithomelissa thoracites.*

During 10 cruises with the «Andrija Mohorovičić» in the central part of the Southern Adriatic, a total of 53 radiolarian species were found from October 1985 through May 1990. The highest diversity, 50 species, was found during the October 1985 cruise alone (KRŠINIĆ, 1998). The population structure of radiolarians in the Strait of Otranto and their dependence on various types of water masses was investigated by KRŠINIĆ & GRBEC (2002). According to their study, radiolarians are the least known holoplanktonic organisms in the Adriatic Sea. The current paper presents the first complete data on the quantitative features of solitary-living radiolarians in the Adriatic Sea. Almost all species are documented by original photomicrographs. Special attention was given to their spatial and temporal distribution at one station in the central and deepest part of the Adriatic Sea. This information is particularly considerable because it is based on many years of research (2001-2009)

MATERIAL AND METHODS

In the open waters of the South Adriatic, samples were taken in vertical layers with a Nansen net 53-μm equipped with a closing system. The net was 45 cm in diameter and 250 cm in length. The hauling speed of the net was 0.5 m s^{-1}. The samples were collected in the following layers: A (0-50), B (50-100), C (100-200), D (200-300), E (300-400), F (400-600), G (600-800), H (800-1000) or (800-1200) from 2003. Samples were taken during five cruises (20-21 April 1993, 16-17 September 1993, 25-26 November 1993, 17-18 June 1994 and 21-22 February 1995), aboard the R/V *Bios* of the Institute of Oceanography and Fisheries, Split. Three stations were sampled along the Dubrovnik transect (S-100) to the deepest part of the South Adriatic (S-1000). Multi-annual investigations were conducted to collect samples from the deepest part of the South Adriatic during 21 cruises at stations S1000/1200 from June 2001 through December 2009 (Fig. 1), also with R/V Bios.

The organisms were counted by means of an inverted microscope (Olympus IMT-2) at magnifications of 100x and 400x. The samples were counted in a glass cell (7 x 4.5 x 0.5 cm). The analysis included the entire sample. Photomicrographs were made with an Olympus BX51 differential interference contrast microscope and a Cambridge 600 scanning electron microscope at the former Chemical Research and Development Centre RO Chromos, Zagreb. Specimens were measured using an ocular micrometer.

Vertical temperature and conductivity profiles were measured with a Sea Bird Electronic (SBE), CTD multi-parameter probe. The non-parametric Sperman's correlation coefficient (Rs) was used to test for correlations abundance of radiolarians between layers.

Radiolarians were identified on the basis of skeletal morphology using taxonomic references (HAECKEL, 1887; BORGERT, 1906, 1911; NIGRINI & MOORE, 1979; PETRUŠEVSKAJA, 1981; TAKAHASHI & HONJO, 1981; BOLTOVSKOY & JANKILEVICH, 1985; BOLTOVSKOY & RIEDL, 1987; BJÖRKLUND & de RUITER, 1987; BOLTOVSKOY, 1999; KLING & BOLTOVSKOY, 1999).

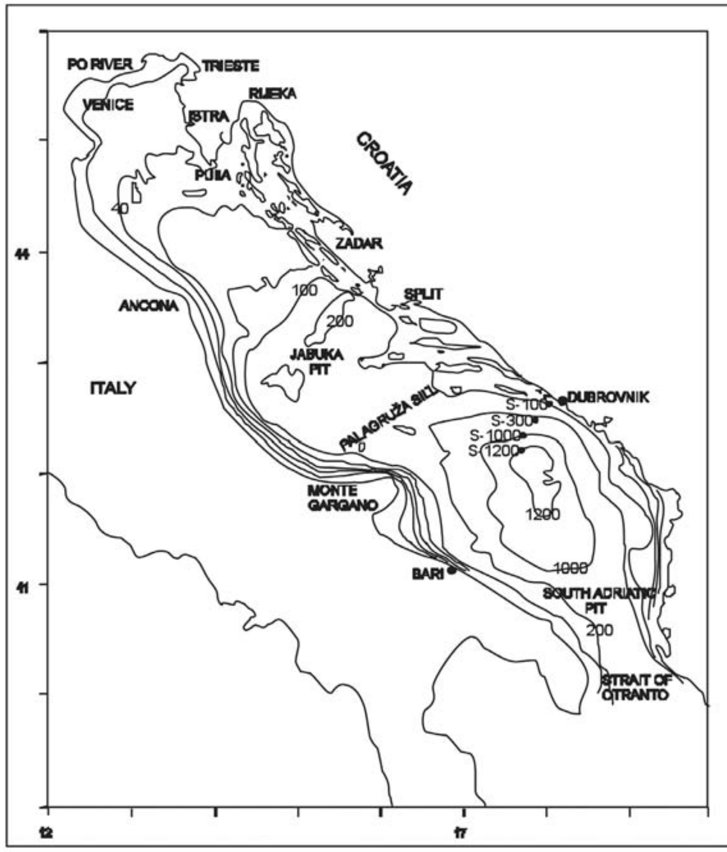

Fig. 1 Map showing the sampling stations in the southern Adriatic

RESULTS

Environmental conditions

In the study area along the Dubrovnik transect, the temperature varies from the surface to a depth of 80 m. During February 1995, isothermia was observed with temperatures ranging from 13.41 to 13.38°C. The highest temperatures of 22.0°C, were recorded during September 1993. In these layers, salinity values range from 38.0 to 38.65. However the lowest value of salinity, 37.66, was recorded during April 1993. Below 100 m depth, the temperature ranges from 13 to 14°C, and the salinity from 38.5 to 38.6. According to BATISTIĆ *et al.* (2004), the oxygen saturation ranged from 0.79 to 1.21 at the deepest station, S-1000, and Chl *a* concentrations ranged from 0.001 to 0.230 mg.m^{-3} with a maximum in April 1993. In the period from 2001 through 2009, the thermohaline characteristics at the deep stations were similar to those observed during an earlier period. Thermoclines formed in the surface layers from depths of 20 to 40 m during the summer. In August 2003, a maximum temperature of 25.5°C was recorded at the surface. Below depths of 150 m, the variability in water temperatures was low, ranging from 13.64 to 14.43°C. The variability in salinity below 100 m was also low. Occasionally, increased values of salinity were noted in the layers from 100 to 200 m in August 2002, during all cruises in 2004, and in August 2006, when maximum salinities ranging from 38.88 to 38.91 were recorded.

Radiolarian diversity

In the central part of the southern Adriatic Pit, a total of 95 living radiolarian taxa were recorded. These taxa included 30 solirary and 2 colonial forms of Spumellaria, 46 of Nassellaria and 17 of Phaeodaria (Table 1, Plate I-X).

Table 1. List of species (Bold, new taxa for the radiolarian Fauna in the Adriatic Sea)

Subclass RADIOLARIA Müller, 1858
Superorder POLYCCSTINA (Ehrenberg, 1838)
Order SPUMELLARIA Ehrenberg, 1875
Family COLLOSPHAERIDAE Müller, 1858
Collosphaera huxleyi Müller, 1855
Solenosphaera chierchiae Brandt, 1905

Family ACTINOMMIDAE Haeckel, 1862
Acanthosphaera actinota (Haeckel, 1860)
Actinomma borealis (Ehrenberg, 1861)
Actinomma leptoderma Jörgensen, 1900
Actinomma sol Cleve, 1900
Arachnosphaera myriacantha Haeckel, 1862
Astrosphaera stellata Haeckel, 1887
Carposphaera acanthophora (Popofsky, 1913)
Cenosphaera spp. group
Cladococcus abietinus Haeckel, 1887
Cladococcus cervicornis Haeckel, 1860
Cladococcus scoparius Haeckel, 1887
Hexacontium armatum Cleve, 1900
Hexacontium armatum group
Hexacontium laevigatum Haeckel, 1860
Hexacontium pachydermum Jörgensen, 1900
Plegmosphaera exodictyon Haeckel, 1887
Plegmosphaera lepticali Renz, 1976
Spongosphaera streptacantha Haeckel, 1862
Thecosphaera inermis (Haeckel, 1860)
Xyphosphaera tesseractis Dreyer, 1913

Family SPONGODISCIDAE Haeckel, 1862
Amphirhopalum ypsilon Haeckel, 1887
Dictyocoryne truncatum (Ehrenberg, 1861)
Spongurus cylindrica Haeckel, 1860
Spongurus sp.
Stylochlamydium asteriscus Haeckel, 1887
Stylodictya multispina Haeckel, 1860

Family COCCODISCIDAE
Didymocyrtis tetrathalamus Haeckel, 1887

Family LITHELIIDAE Haeckel, 1862
Larcopyle buetschlii Dreyer, 1889

Family PYLONIIDAE Haeckel, 1861
Tetrapyle octacantha Müller, 1858
Octopyle stenozona Haeckel, 1887

Order NASSELLARIA Ehrenberg, 1875
Family SPYRIDAE Ehrenberg, 1847
Acanthodesmia vinculata Müller, 1857
Amphispyris reticulata (Ehrenberg, 1872)
Lophospyris pentagona pentagona (Ehrenberg, 1872)
Lophospyris/Phormospyris spp.
Tholospyris baconiana baconiana (Haeckel, 1887)
Tholospyris tripodiscus Haeckel, 1887
Tholospiris *spp*. group
Zygocircus productus (Hertwig, 1879)

PLAGONIIDAE Haeckel, 1881
Arachnocorys circumtexta Haeckel, 1862
Arachnocorallium sp. group
Arachnospirys umbelifera Haechel, 1862
Clathrocorys teuscheri Haeckel, 1887
Enneaphormis rotula (Haeckel, 1887)
Lithomelissa thoracites Haeckel, 1862
Neosemantis distephanus (Haeckel, 1887)
Pseudocubus obeliscus Heackel, 1887
Tetraphormis dodecaster (Haeckel, 1887)

Family THEOPERIDAE Haeckel, 1881
Artobotrys borealis (Cleve, 1899)
Artostrobus annulatus (Bailey, 1856)

Cornutella profunda Ehrenberg, 1858
Corocalyptra elisabethae (Haeckel, 1887)
Cycladophora davisiana (Haeckel,)
Dictyophimus crisiae Ehrenberg, 1854
Dictyophimus sp.
Eucyrtidium acuminatum (Haeckel, 1887)
Eucyrtidium anomalum (Haeckel, 1860)
Lampromitra danaes (Haeckel, 1887)
Lipmanella dictyoceras (Haeckel, 1860)
Litharachnium tentorium Haeckel, 1860
Lithostrobus hexagonalis Haeckel, 1887
Pseudodictyophimus gracilipes (Bailey, 1856)
Pterocanium praetextum (Haeckel, 1887)
Pterocanium trilobum (Haeckel, 1860)
Theocorys veneris (Haeckel, 1887)
Theopilium tricostatum Haeckel, 1887
Tricolocapsa papillosa (Ehrenberg, 1872)
Tripodospiris sp.

Family CARPOCANIIDAE Haeckel, 1881
Carpocanistrum spp. group

Family PTEROCORYTHIDAE Haeckel, 1881
Anthocyrtidium ophirense (Ehrenberg, 1872)
Anthocyrtidium zanguebaricum (Ehrenberg, 1872)
Pterocorys minythorax (Nigrini, 1968)
Pteroscenium pinnatum Haeckel, 1887
Theocorythium trachelium (Ehrenberg, 1872)

Family ARTOSTROBIIDAE Riedel, 1967
Botryostrobus auritus/australis (Ehrenberg, 1844)

Family CANNOBOTRYIDAE Haeckel, 1881
Acrobotrys sp. group
Botryocephalina armata Petrushevskaya, 1965

Superorder PHAEODARIA Haeckel, 1879
Family AULOSPHAERIDAE Haeckel, 1862
Aulatractus fusiformis Haeckel, 1887

Family AULACANTHIDAE Haeckel, 1862
Aulacantha scolymantha Haeckel, 1860

Family LIRELLIDAE Ehrenberg, 1872
Lirella bullata (Stadum & Ling, 1969)
Lirella melo (Cleve, 1899)

Family CHALLENGERIDAE Murray, 1876
Challengeranium diodon (Haeckel, 1887)
Challengeria tritonis Haeckel, 1887
Challengeria xiphodon Haeckel, 1887
Challengeron channeri Murray, 1885
Challengeron willemoesii Haeckel, 1887
Entocannula circularis (Haeckel, 1887)

Family MEDUSETTIDAE Haeckel, 1887
Euphysetta lucani Borgert, 1892
Euphysetta pussilla Cleve, 1900
Medusetta rara (Borgert, 1902)

Family COELODENDRIDAE Haeckel, 1862
Coelodendrum ramosissimum Haeckel, 1860

Family CONCHARIDAE Haeckel, 1879
Conchophacus diatomeum (Haeckel, 1887)

Family POROSPATHIDIDAE Borgert, 1901
Porospathis holostoma (Cleve, 1899)

Family PHAEODINIDAE Haeckel, 1879
Phaeodina loricata Borgert, 1901

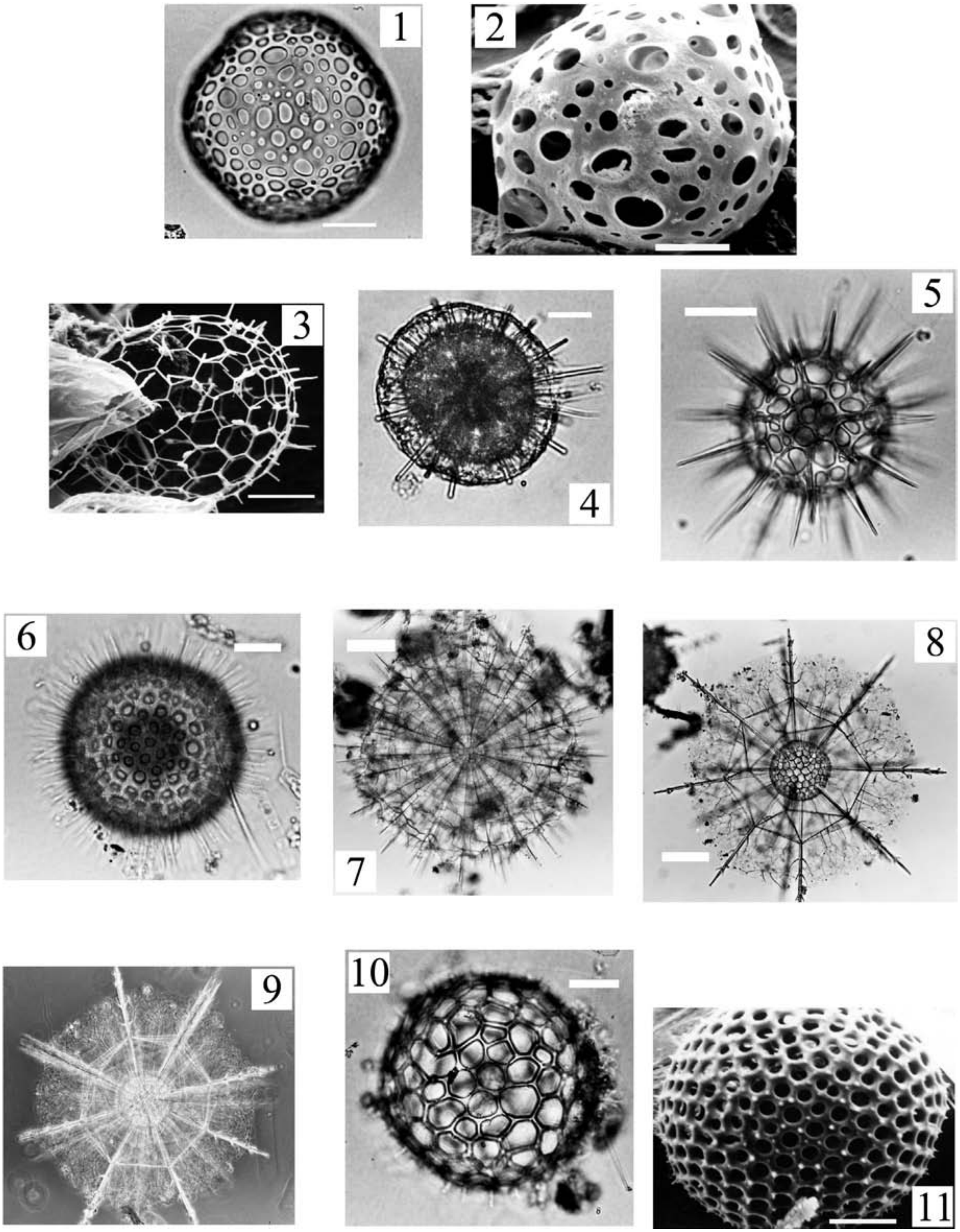

Plate I. 1. *Collosphaera huxleyi* (s.b.=35 μm), 2. *Solenosphaera chierchiae* (s.b.=20 μm), 3. *Acanthosphaera actinota* (s.b.=20 μm), 4. *Actinomma borealis* (s.b.=40 μm), 5. *Actinomma leptoderma* (s.b.=50 μm), 6. *Actinomma sol* (s.b.=30 μm), 7. *Arachnosphaera myriacantha* (s.b.=100 μm), 8,9. *Astrosphaera stellata* (s.b.=40 μm), 10. *Carposphaera acanthophora* (s.b.=40 μm), 11. *Cenosphaera* spp. group (s.b.=20 μm)

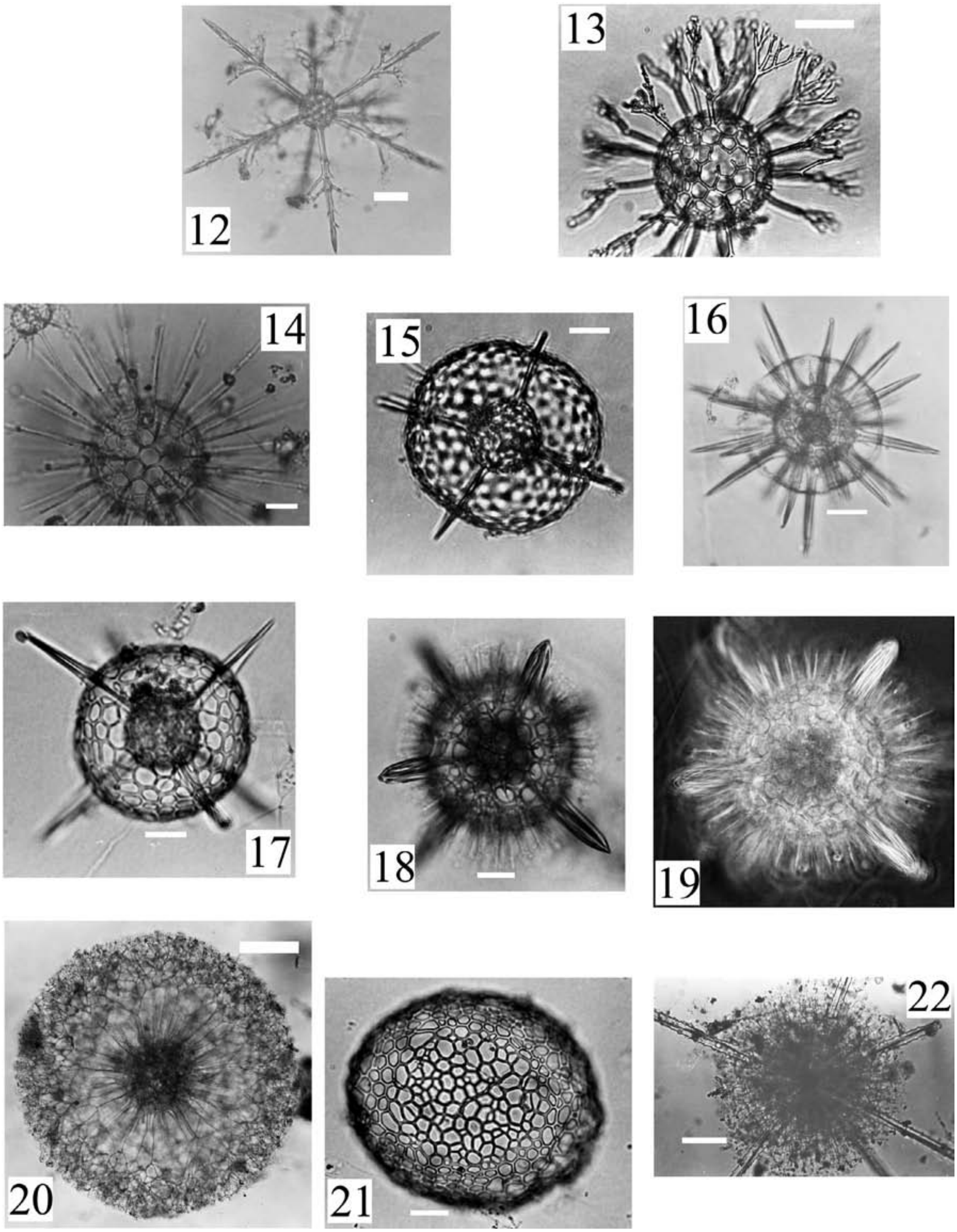

Plate II. 12. *Cladococcus abietinus* (s.b.=50 µm), 13. *Cladococcus cervicornis* (s.b.=45 µm), 14. *Cladococcus scoparius* (s.b.=50 µm), 15. *Hexacontium armatum* (s.b.=20 µm), 16. *Hexacontium armatum group* (s.b.=40 µm), 17. *Hexacontium levigatum* (s.b.=20 µm), 18, 19. *Hexaconthium pachydermum* (s.b.=25 µm), 20. *Plegmosphaera exodictyon* (s.b.=150 µm), 21. *Plegmosphaera lepticali* (s.b.=25 µm), 22. *Spongosphaera streptacantha* (s.b.=50 µm)

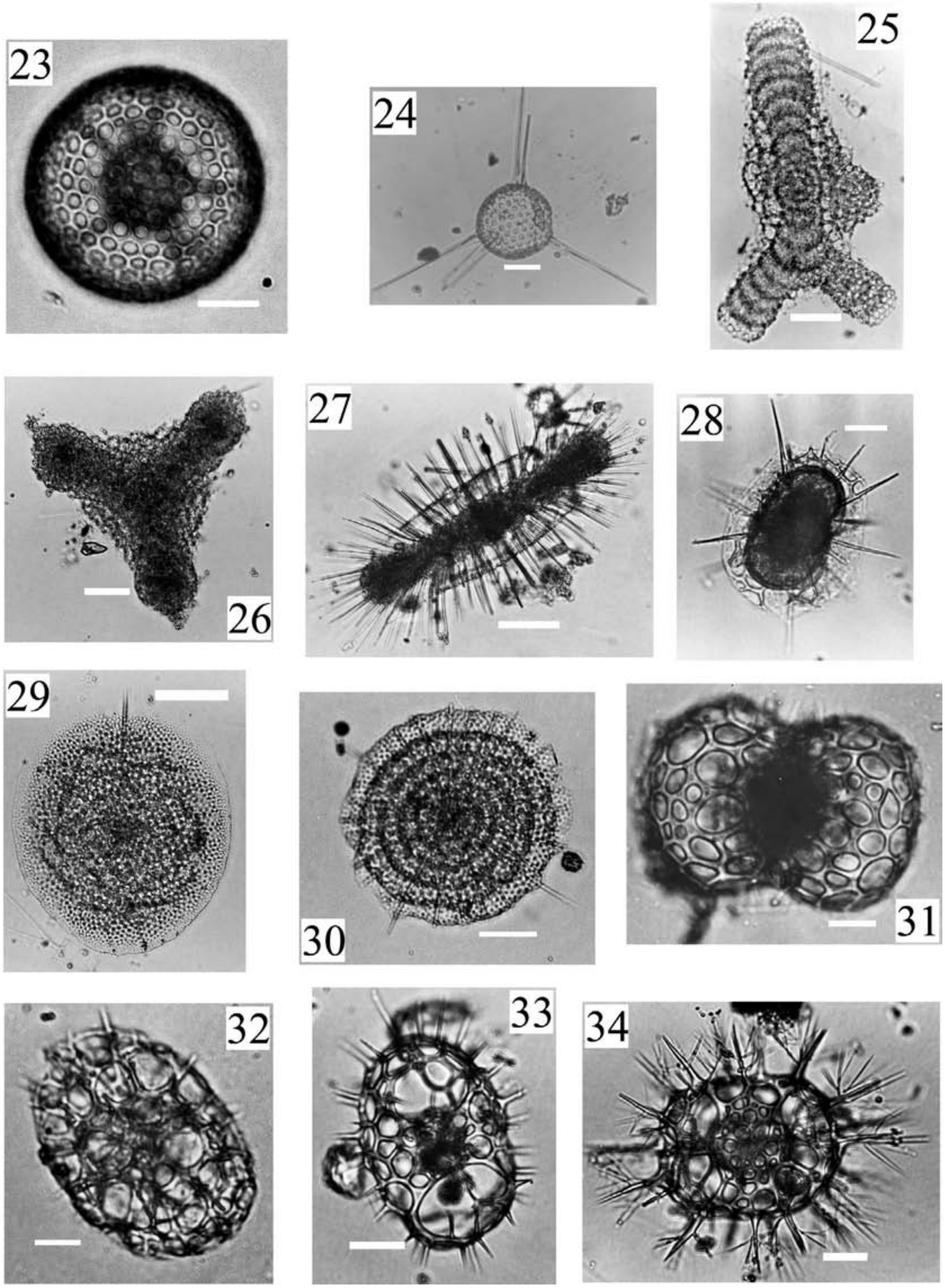

Plate III. 23. *Thecosphaera inermis* (s.b.=25 µm), 24. *Xyphosphaera tesseractis* (s.b.=40 µm), 27. *Amphirhopalum ypsilon* (s.b.=50 µm), 26. *Dictyocoryne truncatum* (s.b.=50 µm), 27. *Spongurus cylindrica* (s.b.=50 µm), 28. *Spongurus* sp. (s.b.=30 µm), 29. *Stylochlamydium asteriscus* (s.b.=60 µm), 30. *Stylodictya multispina* (s.b.=50 µm), 31. *Didymocyrtis tetrathalamus* (s.b.=25 µm), 32. *Larcopyle buetschlii* (s.b.=30 µm), 33. *Tetrapyle octacantha* (s.b.=30 µm), 34. *Octopyle stenozona* (s.b.=45 µm)

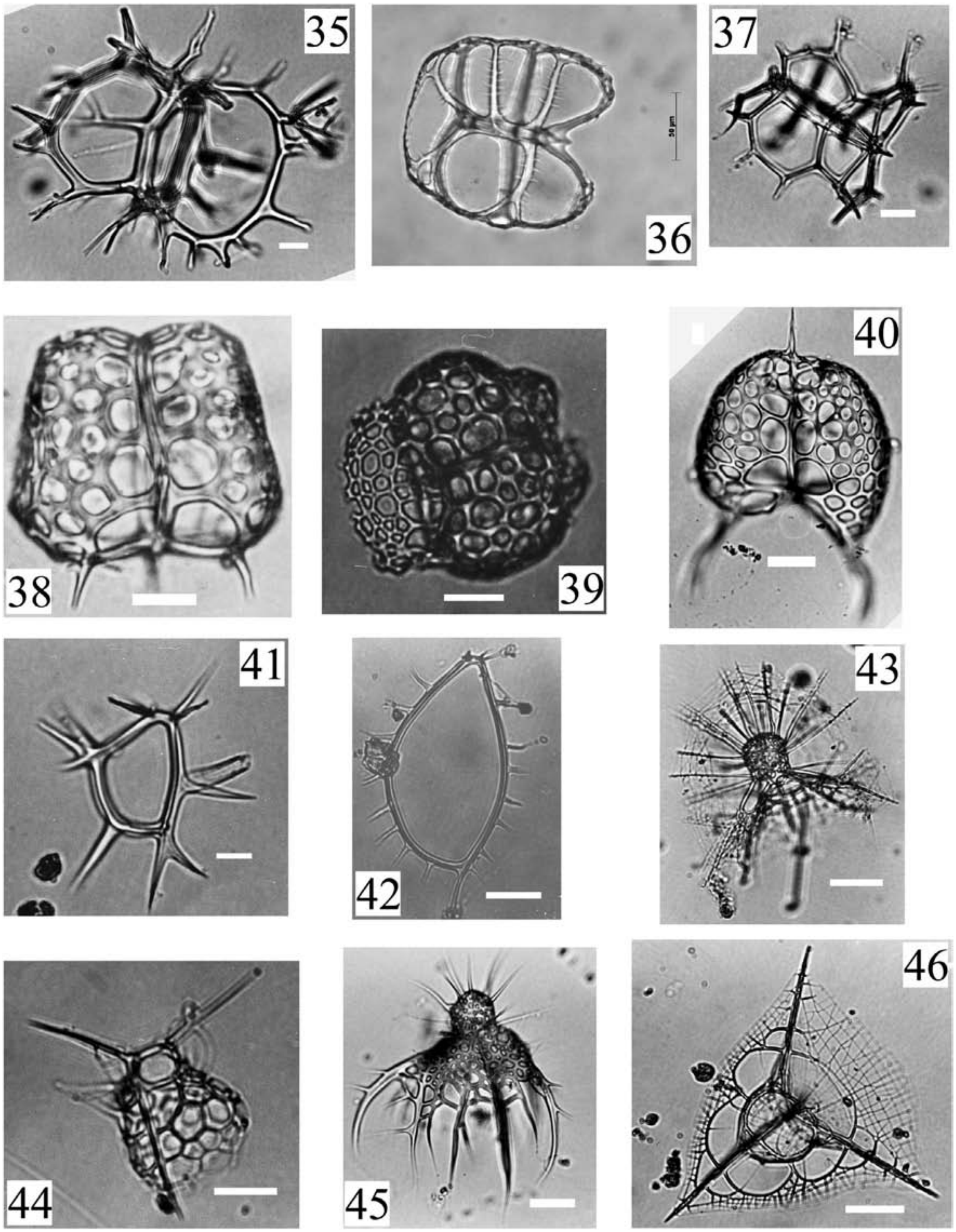

Plate IV. 35. *Acanthodesmia vinculata* (s.b.=30 µm), 36. *Amphispirys reticulata* (s.b.=50 µm), 37. *Lophospyris pentagona pentagona* (s.b.=20 µm), 38. *Lophospyris/Phormospyris* spp. (s.b.=20 µm), 39. *Tholospyris baconiana baconiana* (s.b.=25 µm), 40. *Tholospyris tripodiscus* (s.b.=40 µm), 41. *Tholospyris* spp. group (s.b.=25 µm), 42. *Zygocircus productus* (s.b.=40 µm), 43. *Arachnocorys circumtexta* (s.b.=25 µm), 44. *Arachnocorallium* spp. group (s.b.=30 µm), 45. *Arachnospirys umbelifera* (s.b.=30 µm), 46. *Clathrocorys teuscheri* (s.b.=25 µm)

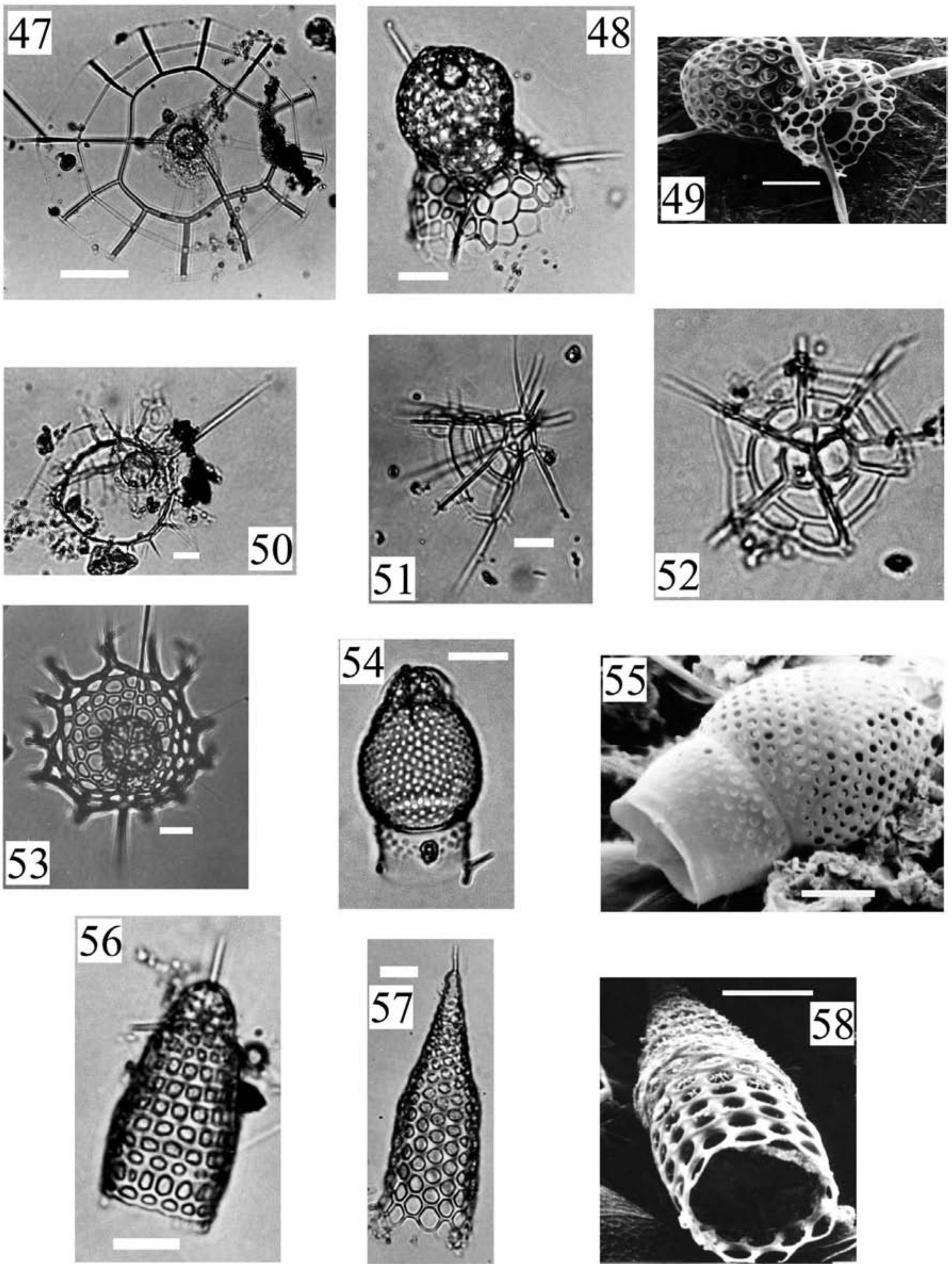

Plate V. 47. *Enneaphormis rotula* (s.b.=50 μm), 48, 49. *Lithomelissa thoracites* (s.b.=20 μm), 50. *Neosemantis distephanus* (s.b.=20 μm), 51, 52. *Pseudocubus obeliscus* (s.b.=25 μm), 53. *Tetraphormis dodecaster* (s.b.=50 μm), 54, 55. *Artobotrys borealis* (s.b.=20 μm, scan=10 μm), 56. *Artostrobus annulatus* (s.b.=25 μm), 57, 58. *Cornutella profunda* (s.b.=20 μm)

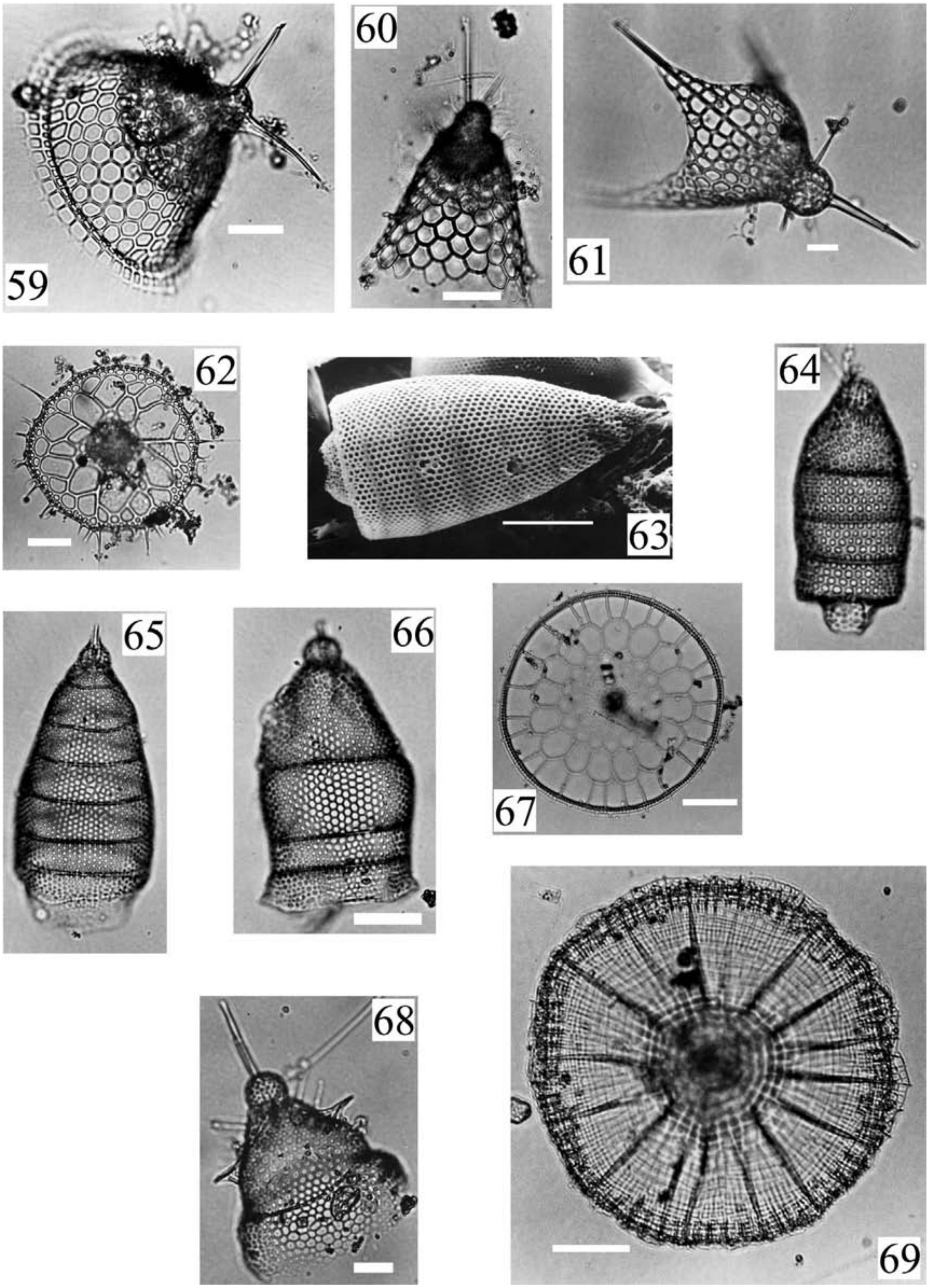

Plate VI. 59. *Carocalyptra elisabethae* (s.b.=25 µm), 60. *Cycladophora davisiana* (s.b.=50 µm), 61. *Dictyophimus crisiae* (s.b.=30 µm), 62. *Dictyophimus* sp. (s.b.=50 µm), 63,64,65. *Eucyrtidium acuminatum* (s.b.=40 µm), 66. *Eucyrtidium anomalum* (s.b.=50 µm), 67. *Lampromitra danaes* (s.b.=50 µm), 68. *Lipmanella dictyoceras* (s.b.=50 µm), 69. *Litharachnium tentorium* (s.b.=50 µm)

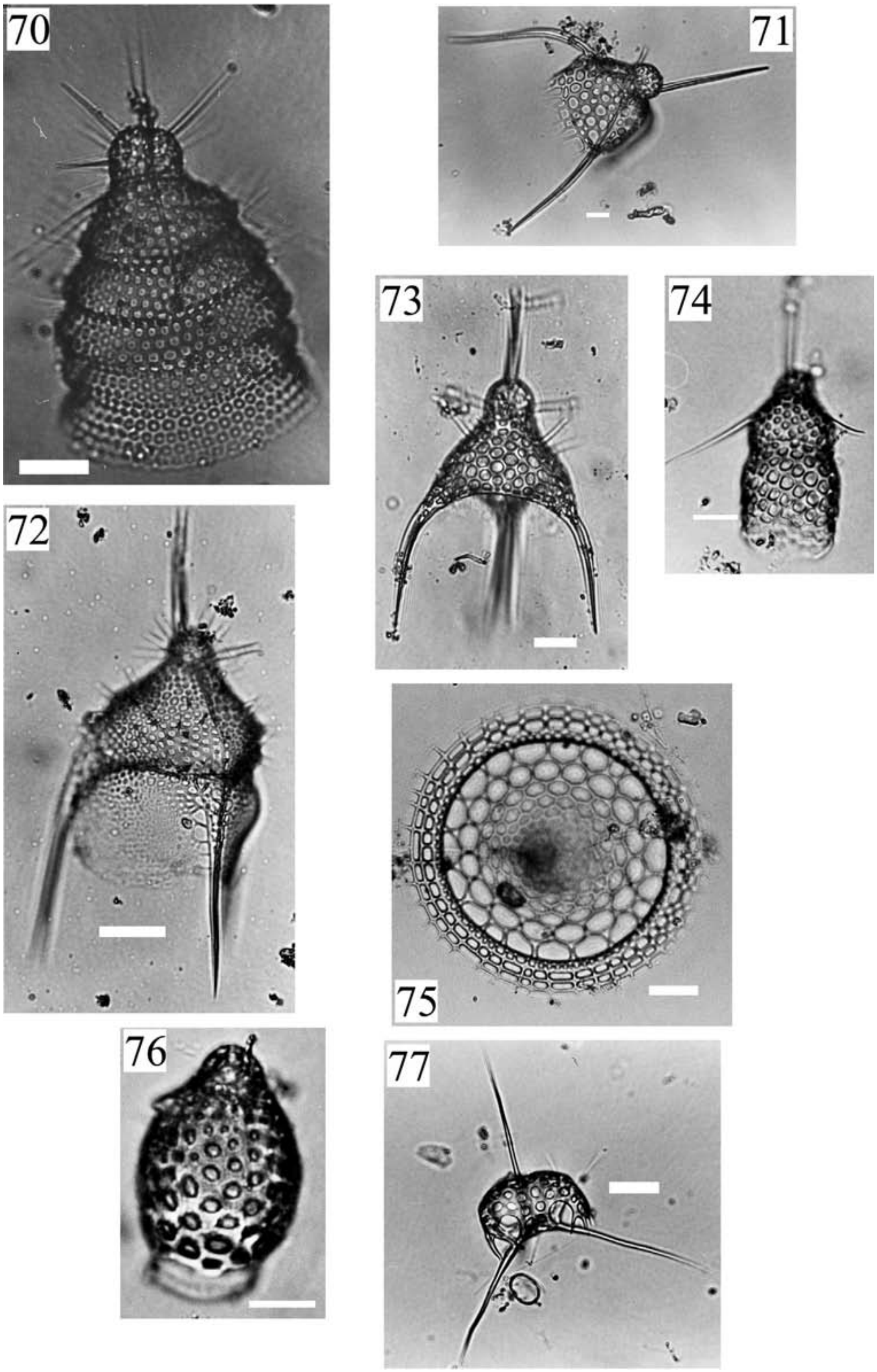

Plate VII. 70. *Lithostrobus hexagonalis* (s.b.=30 µm), 71. *Pseudodictyophimus gracilipes* (s.b.=30 µm), 72. *Pterocanium praetextum* (s.b.=25 µm), 73. *Pterocanium trilobum* (s.b.=30 µm), 74. *Theocorys veneris* (s.b.=20 µm), 75. *Theopilium tricostatum* (s.b.=50 µm), 76. *Tricolocapsa papillosa* (s.b.=20 µm), 77. *Tripodospiris* sp. (s.b.=20 µm)

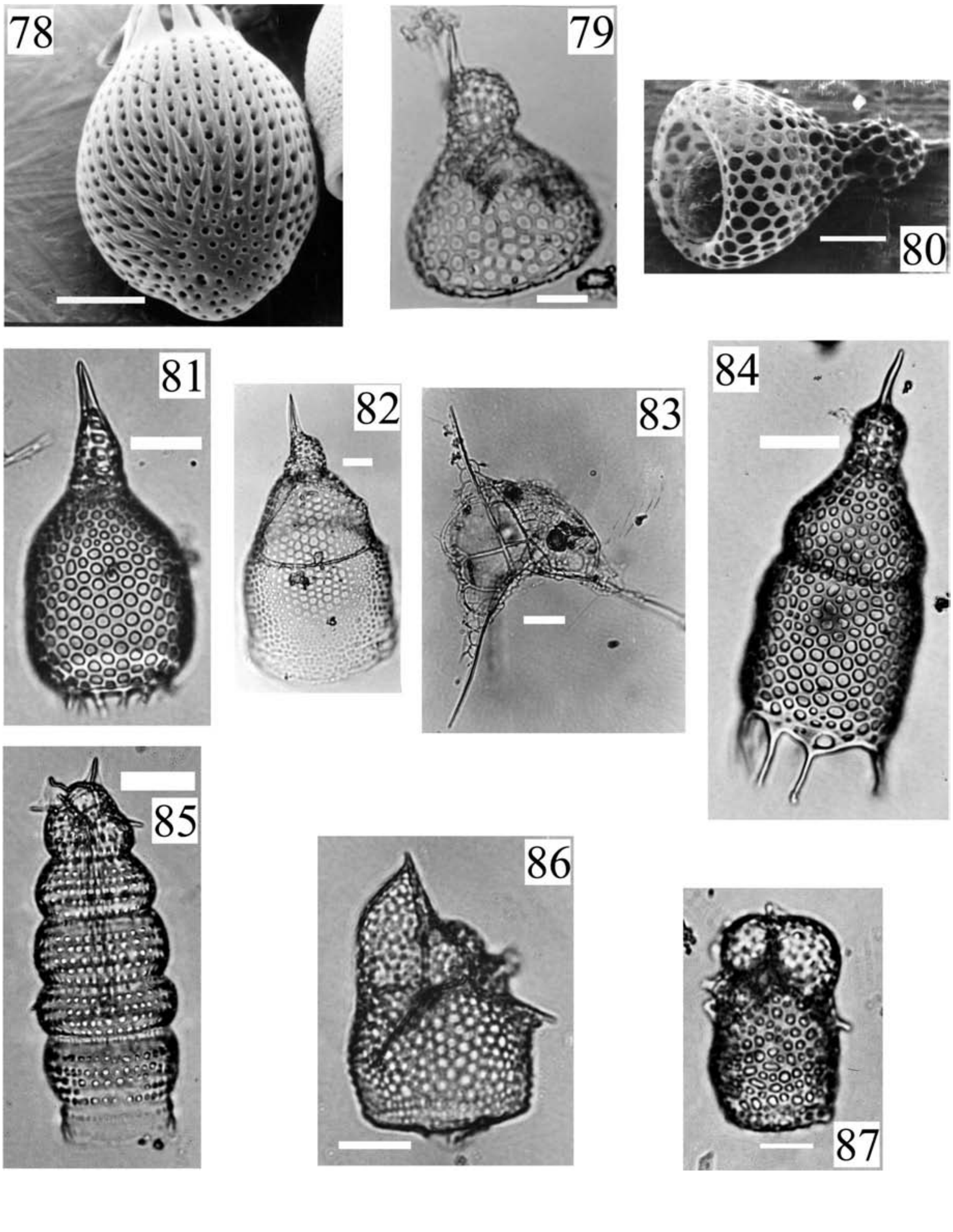

Plate VIII. 78. *Carpocanistrum* spp. group (s.b.=20 µm), 79,80. *Anthocyrtidium ophirense* (s.b.=20 µm), 81. *Anthocyrtidium zanguebaricum* (s.b.=40 µm), 82. *Pterocorys minythorax* (s.b.=20 µm), 83. *Pteroscenium pinnatum* (s.b.=30 µm), 84. *Theocorythium trachelium* (s.b.=40 µm), 85. *Botryostrobus auritu/ australis* (s.b.=30 µm), 86. *Acrobotrys* spp group. (s.b.=25 µm), 87. *Botryocephalina armata* (s.b.=20 µm)

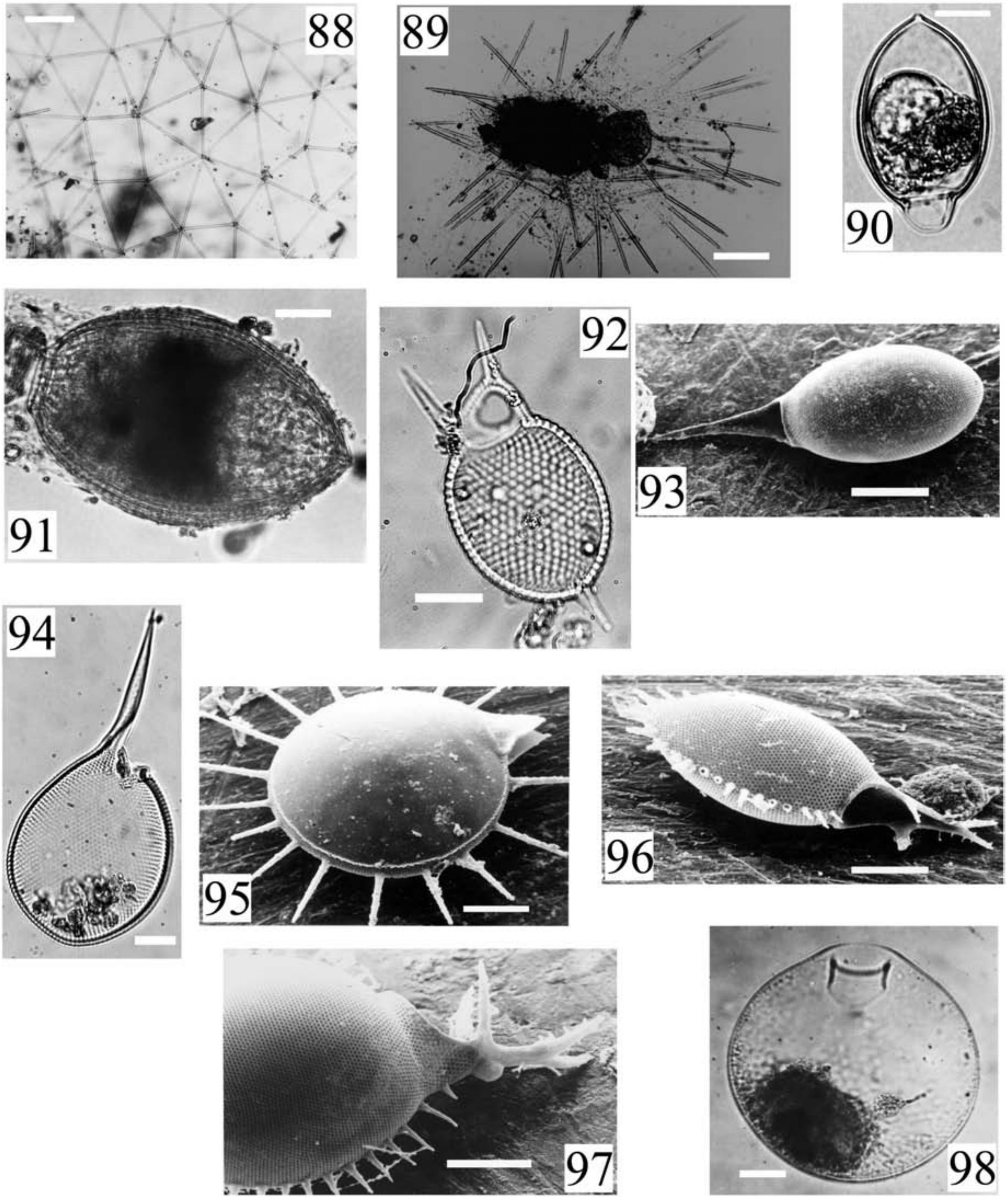

Plate IX. 88. *Aulatractus fusiformis* (s.b.=100 µm), 89. *Aulacantha scolymantha* (s.b.=200 µm), 90. *Lirella bullata* (s.b.=20 µm), 91. *Lirella melo* (s.b.=30 µm), 92. *Challengeranium diodon* (s.b.=20 µm), 93. *Challengeria tritonis* (s.b.=40 µm), 94. *Challengeria xiphodon* (s.b.=25 µm), 95. *Challengeron channeri* (s.b.=40 µm), 96,97. *Challengeron willemoesii* (s.b.=40 µm), 98. *Entocannula circularis* (s.b.=40 µm)

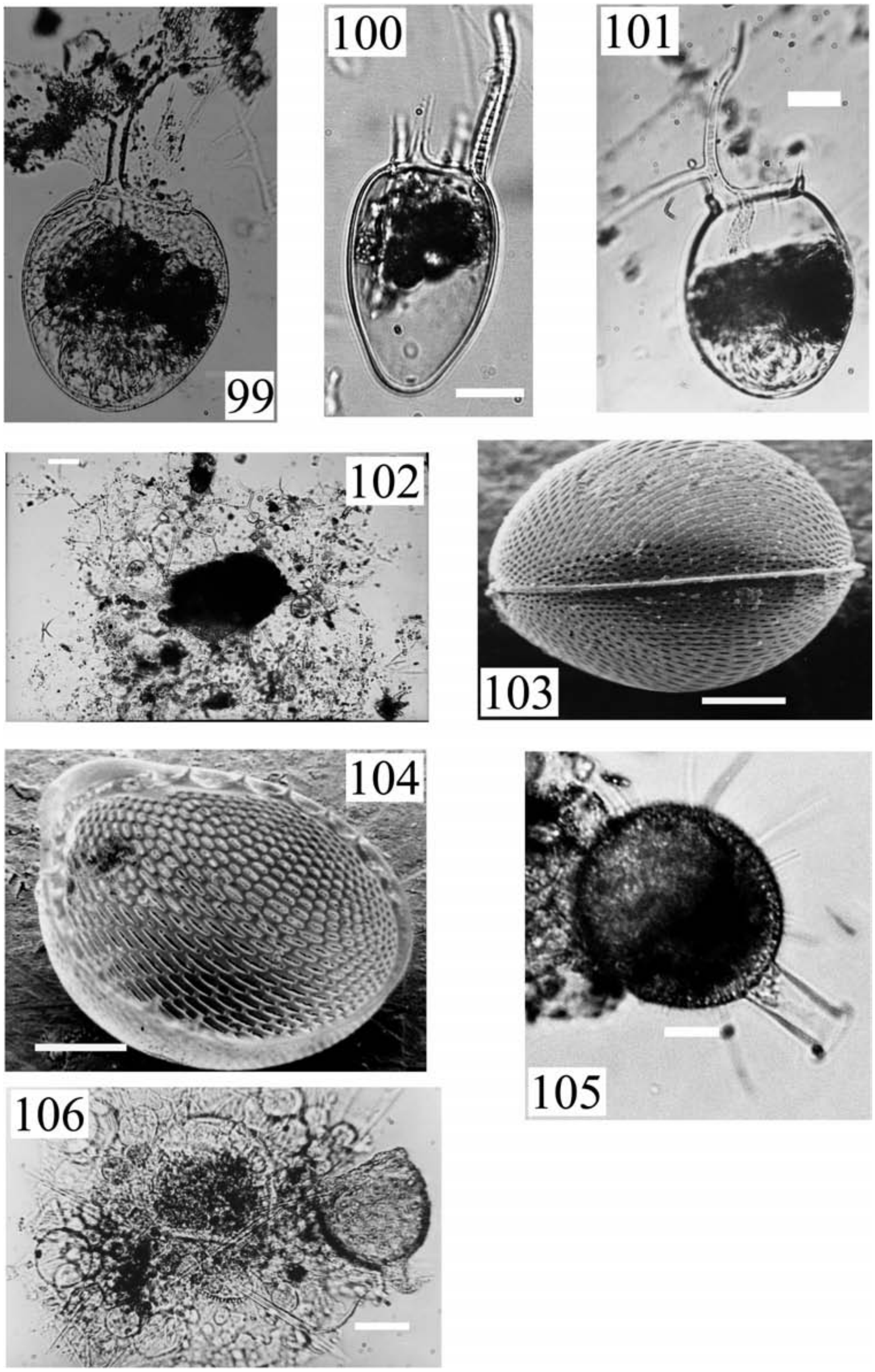

Plate X. 99. *Euphysetta lucani* (s.b.=30 μm), 100. *Euphysetta pussilla* (s.b.=30 μm), 101. *Medusetta rara* (s.b.=30 μm), 102. *Coelodendrum ramosissimum* (s.b.=200 μm), 103,104. *Conchophacus diatomeum* (s.b.=40 μm), 105. *Porospathis holostoma* (s.b.=20 μm), 106. *Phaeodina loricata* (s.b.=40 μm)

A total of 74 species were recorded during research along the transect from S-100 to S-1000, from April 1993 through February 1995. The species *Aulacantha scolymantha*, *Challemgeranium diodon*, *Challengeria xiphodon* and *Challengeron willemoesii* were recorded during all cruises and at stations S-300 and S-1000. Radiolarians were rarely present at the station closest to the coast, S-100. As a rule, the largest numbers of species were found at station S-1000 (Fig. 2). The number of species varied from 21 in February 1995 to 38 in November 1993. At station S-300, the number of species was significantly lower.

During the research period from 2001 through 2009, 80 species of radiolarians were recorded. From May 2002 through June 2006, the average number of species in the vertical column ranged from 12 to 20 species. The greatest diversity of species occurred from August 2006 through the end of the research. During this period, the average number of species in the water column ranged between 30 and 37 species (Fig. 3). The most common species were the phaeodarian *Challengeria xiphodon*, the spumellarian *Stylodictya multispina* and the

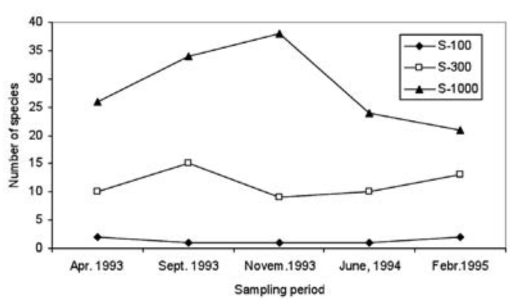

Fig. 2. Variations in the number of radiolarian species at three stations from April 1993 through February 1995

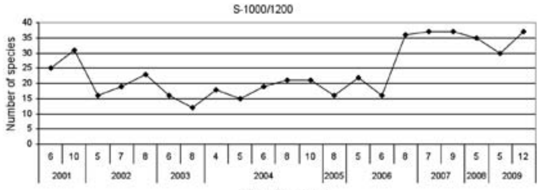

Fig. 3. Variations in the number of radiolarian species at station S1000/1200 from 2001 through 2009

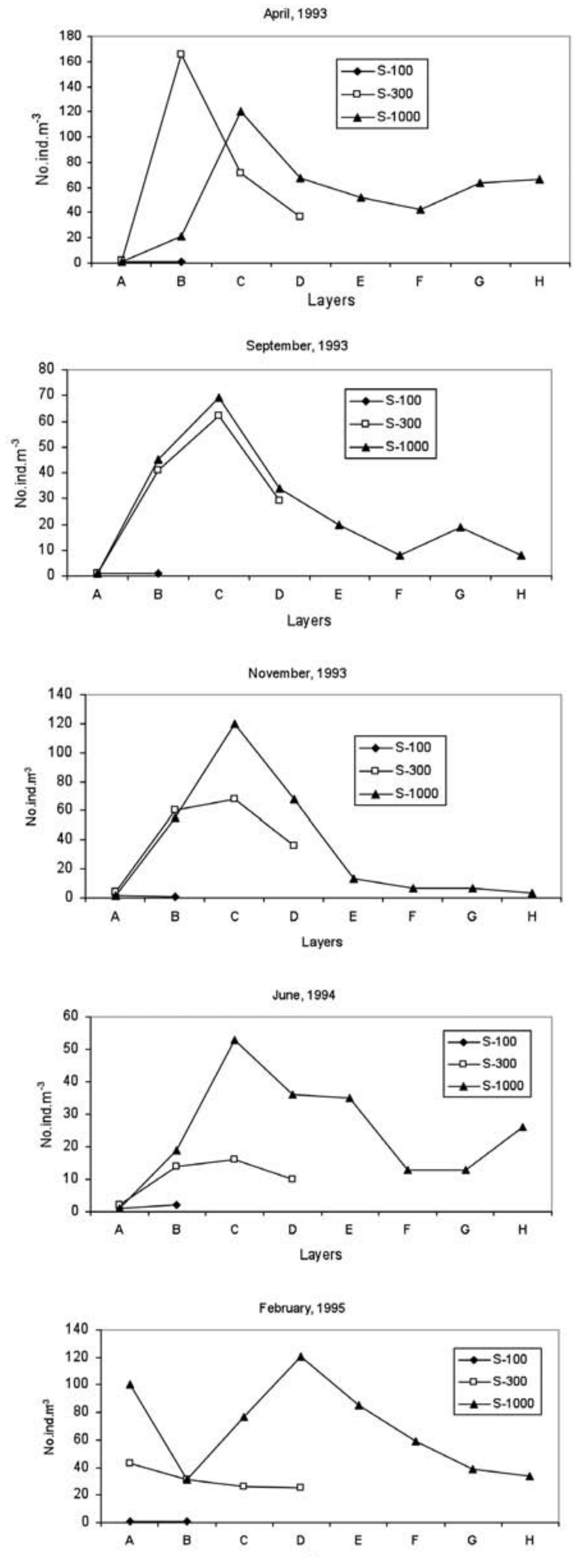

Fig. 4. Variations in total radiolarian abundance at three stations

nassellarian *Cornutella profunda,* which were present in 99% of the series. Common species that appeared at frequencies ranging from 76-85 % in the water column were *Hexaconthium pachydermum*, *Actinomma sol*, *Chellengeranium diodon* and *Botryostrobus auritus/australis*. As many as 37 species were rare and appeared only 1 to 3 times. Characteristic species in the euphotic layer were juvenile specimens of *Theocorythium trachelium*, *Eucyrtidium acuminatum* and *Stylodictya multispina* were also found occasionally in the euphotic layer. In layers at depths greater than 600 m, more species were present, but the only characteristic species was *Challengeria tritonis*. The highest diversity of species was found between depths of 100 and 400 m, where almost all species were present except for certain species characteristic of the euphotic layer.

Abundance of radiolaria on the Dubrovnik transect

The abundance of solitary-living radiolaria in vertical layers from the surface to the bottom at 3 stations during 5 periodic cruises is shown in Figure 4. The abundance of radiolarians at station S-100 was always very low. In general, the highest abundance values were recorded at the deepest station, S-1000, except in April 1993 (Fig. 4a), when a maximum value of 166 ind. m^{-3} was recorded in the sub-surface layer at station S-300. The species *Challengeria xiphodon* represented 67% of the overall number of radiolarians. The highest values were most frequent at both deep-sea stations at 100 to 200 m. At station S-1000, the lowest values were in the surface layer. The bulk of the population was at a depth of 100-300 m. The abundance decreased towards the bottom. During April 1993 and June 1994, however, higher values of abundance were recorded at the greatest depths.

Multi-annual vertical distribution of radiolarian abundance

Between 2001 and 2009 (Fig. 5), the representation of solitary spumellaria in the total average number of radiolarians ranged from 3.9% in May 2009 to 52% in June 2003 and August 2004. The representation of nassellaria ranged from 10% in May 2006 to 62% in October 2004, and the representation of phaeodaria ranged from 20% in June 2001 to 86% in June 2006.

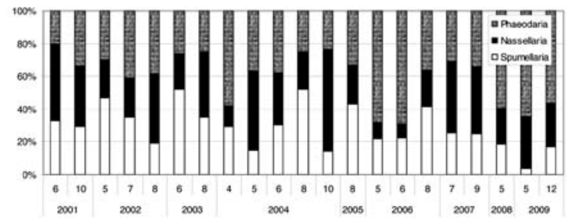

Fig. 5. Percentages of spumellaria, nassellaria and phaeodaria abundance at station S1000/1200 from 2001 through 2009

To characterise the multi-annual variability of abundance at the deep-sea stations in the southern Adriatic, we separately analysed the euphotic, mesopelagic and deep-sea zones. We can identify three well-characterised periods within the multi-annual span of the research. The first period, from October 2001 through April 2004, was characterised by a maximum abundance of radiolarians in the euphotic layer and a low percentage of phaeodaria in the entire water column (Fig. 5). The second period from May 2004 to May 2006 was characterised by very low abundance values in the euphotic layer, whereas the radiolarian populations were concentrated in the mesopelagic layer. Radiolarians were found in the deep-sea layer only during August 2005. The radiolarians were dominated by spumellarian and nassellarian species. During the third period, from May through June 2006, phaeodaria were absolutely predominant. During 2007, the percentages of phaeodaria decreased, increasing again during 2008 and 2009.

In the euphotic zone, radiolarians were rare at depths from 0 to 50 m. The number of radiolarians was almost always greater in the sub-surface layer from 50 to 100 m, whereas high numbers were recorded only during October 2001 (169 ind. m^{-3}) and during August 2002 (101 ind. m^{-3}) (Fig. 6a). The juvenile form of the species *Eucyrtidium acuminatum* represented 98% of the total number of radiolarians in the

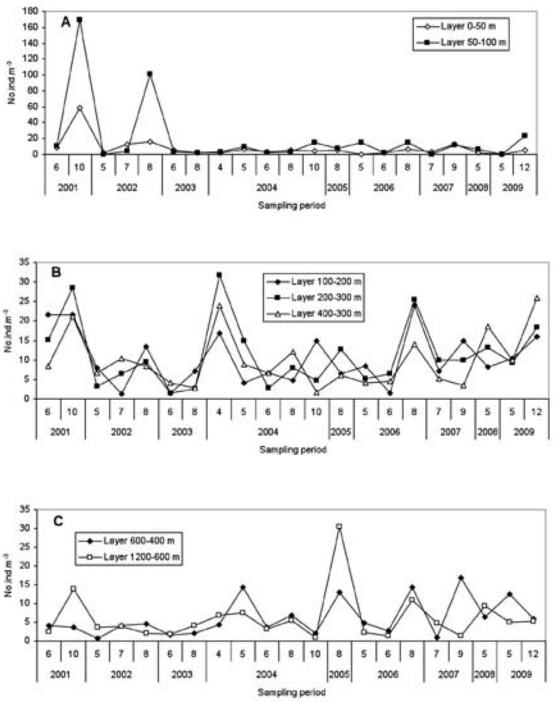

Fig. 6. Variations in total radiolarian abundance at station S1000/1200 from 2001 to 2009. (a. 0-100 m layers; a. 100-300 m layers; c. 400-1200 m layers)

surface layers, whereas the juvenile form of *Theocorythium trachelium* represented 79% of the total number of radiolarians in the subsurface layers.

The abundance of radiolarians between the depths of 100 to 400 m in the mesopelagic zone varied only slightly, and the correlation between layers was significant (between the first and second layers, Rs=0.70, p<0.05, n=21; between the second and third layers, Rs=0.79, p<0.05; n=21). The abundance values low with peaks from 25 – 30 ind. m^{-3} (Fig. 6b) were recorded. The maximum values were found in the layers between the depths of 200 – 300 m. During October 2001, the dominant species were *Challengeria xiphodon* at 42 % and *Stylodictya multispina* at 14 % of the total number of radiolarians. During April 2004, *Challengeria xiphodon* and *Euphysetta lucani* had a total relative abundance of 46 %; during August 2006, *Hexacontium pachydermum*, *Stylodictya multispina*, *Botryostrobus auritus/ australis* and *Challengeranium diodon* had a total relative abundance of 51 %; and during December 2009, *Lirella bullata*, *Challengeria xiphodon, Botryostrobus auritus/ australis* and *Cornutella profunda* had a total relative abundance of 47 %.

The variability of both layers in the deep-sea zone was almost identical between the depths of 1,200-400 m, and the correlation between the layers was high and significant (Rs=0.4, p<0.05; n=21). Generally, the abundance values were very low, except in August 2005, when a value of 131 ind. m^{-3} (Fig. 6c) was observed for the deepest layer. The dominant species were *Challengeranium diodon* and *Challengeria xiphodon*, at 72% of the total number of radiolarians.

DISCUSSION

A standard and universal methodology for qualitative, quantitative, spatial and temporal research on recent radiolarians has not yet been defined. The lack of a uniform methodology is particularly apparent for deep-sea research. The most frequently used methods involve the sampling of the sediment surface, sediment traps and plankton nets of various sizes. A very detailed review covering the inadequacies and positive aspects of sampling methodology has been published by Boltovskoy (BOLTOVSKOY, 1999). During the many years of our research performed in the deep southern Adriatic, we used a Nansen net 53-µm mesh equipped with a closing system to sample a smaller-sized fraction of the zooplankton (KRŠINIĆ, 1998; KRŠINIĆ & GRBEC, 2002). The same net was used during recent research. The use of the same net allows a comparison to be made between radiolarians and other zooplankton groups. However, we also discussed the problems involved in conducting research on the abundance of living radiolarians with large spines. One of the most common and most frequent species in the euphotic zone was the phaeodarian species *Aulatractus fusiformis,* with specimens that may attain a size of 8 mm. Due to the long-bladed spines that characterise their shell structure, many specimens become entangled with gelatinous macrozooplanktonic organisms in the plankton samples. Therefore, the method used proved inadequate for the accurate assessment of total population abundances for radiolarians. Moreover, certain colonial radiolarians were not included in quantitative consideration of this research. These colonial forms appeared occasionally in great numbers (ENRIQUES, 1919).

The radiolarian fauna is rich, with a total of 95 taxa. With the copepod (HURE & KRŠINIĆ, 1998) and tintinnid fauna (KRŠINIĆ, 2010), the radiolarians can be considered one of the most diversity plankton groups in the Adriatic Sea. The copepod and tintinnid fauna includes many estuarine and neritic species, whereas radiolarians are exclusively in open sea. Therefore, their diversity knowledge is of importance for partially closed seas, such as the Adriatic. Earlier research (KRŠINIĆ, 1998) cited 53 species of radiolarians in the southern Adriatic. Accordingly, based on many years of study and the most recent research, the radiolarian faunal list for the Adriatic Sea has been enriched by 49 taxa. The importance of long-term research for understanding radiolarian diversity must be stressed. This point is also valid for other groups of zooplankton. A study of radiolarians in the eastern part of the Mediterranean by ABBOUD-ABI SAAB (1988) cites 56 species. KLING & BOLTOVSKOY (1999) report a total of 325 radiolarian taxa in the South Atlantic. ISHITANI & TAKAHASHI (2007) report a total of 167 radiolarian taxa from the waters surrounding Japan. ZHANG *et al.* (2009) report 241 polycystine-radiolarian species from the northern South China Sea. Due to geomorphology, bathymetry and cyclonic current regimes, radiolarians primarily inhabit the deep South Adriatic. This distribution has also been revealed by earlier data collected during 10 periodic cruises in the open waters of the southern Adriatic from the Strait of Otranto to the Palagruža Sill (October 1985-May 1990) aboard the vessel «Andrija Mohorovičić» (KRŠINIĆ, 1988; 1998; KRŠINIĆ & GRBEC, 2002). During cruises in October 1985, 12 radiolarian species were recorded in the subsurface layer at stations along the Palagruža Sill, whereas a rich fauna was found in the region south of the Otrant (KRŠINIĆ, unpublished data). The analysis of the vertical distribution of the samples showed that at most 40 species occurred in the layers from depths of 100-400 m, with the lowest numbers in the sub-surface layers. The present study found few radiolarians in the subsurface layers from depths of 0-50 m at the coastal station S-100. According to the results of HOLLANDE & ENJUMET (1960) for the Bay of Algiers, the richest radiolarian fauna occurs in the zone between depths of 100 and 300 m and becomes scarce during the summer months between depths of 0 and 300 m. From 2001 through 2009, the most frequent were the phaeodarian *Challengeria xiphodon*, *C. willemoesii* and *Phaeodina loricata* were occasionally present in the deepest layers of the Jabuka Pit. *Aulacantha scolymantha* was occasionally present in the sub-surface layer. The immigration of species from the southern waters of the Adriatic to the central Adriatic waters occurs during the winter months, when the ingoing eastern Adriatic currents were most intense (ZORE-ARMANDA, 1968). We did not record radiolarians further north, and older research cites only a few species (ISSEL, 1922).

A relatively small number of radiolarian species were permanently present in the southern Adriatic. The populations of most of the species were renewed by the incoming eastern Adriatic current from the Ionian Sea, which was more intense during the winter period, and by the ingression of Levantine intermediate waters. The intensity with which LIW enter differs according to the season and particularly from year to year. Periods with a strong intrusion of LIW into the Adriatic are ingression years (BULJAN & ZORE-ARMANDA, 1976, VILIBIĆ & ORLIĆ, 2001). Although the high salinity values at depths of 100 to 150 m indicate the strong intrusion of LIW during the spring-summer period in 2004, as confirmed by research in the Palagruža Sill region (ŠOLIĆ *et al.*, 2008), no increase in radiolarians was recorded during this period. Subsequent to August 2006, however, the data showed that the numbers of the species grouped under polycystina increased significantly. According to the known geographic distributions in the Atlantic (BOLTOVSKOY, 1999), many of the recorded species belong to the warm waters of the Equatorial or Subtropical provinces. Therefore, our results can be tied to a bi-modal circulation in the Ionian Sea. Between 2003 and 2006, there was a cyclonic upper layer circulation in the Ionian Sea (GAČIĆ *et al.,* 2010), whereas an anti-cyclonic circulation started in 2006. It is possible that this anti-cyclonic pattern enabled the entry of West Mediterranean species into the Adriatic (CIVITARESE *et al.,* 2010). Therefore, radiolarians can be a good indicator of the intrusion of different water masses from the Ionian Sea into the southern Adriatic.

Because of the great differences among sampling methods and the different net mesh sizes used, it is very difficult to compare the quantitative data from different sources. Much of the research on solitary-living radiolarians is based on the sampling of the oceanic surface layers. According to CIFELLI & SACHS (1966), the radiolarian maximum in the Caribbean Sea was 27 ind. m^{-3}. SWANBERG & BJØRKLUND (1986) found an abundance of 2000 ind. m^{-3} during the summer in Sognefjord, whereas the abundance of radiolaria approached 10,000 ind. m^{-3} in glacial river input and in highly stratified land-locked pools. TAKAHASHI (1983/84) found abundances of 1 x 10^3 to 43 x 10^3 ind.m^{-3}. The abundance of polycystine-radiolarian species in the northern South China Sea was from 1,167 to 3,366 ind.m^{-3} (ZHANG *et al.,* 2009). For the coastal region of Lebanon, ABBOUD-ABI SAAB (1988) found that the abundance of polycystines was 5000 ind. m^{-3} in February 1979. Earlier research on radiolarians in the Adriatic Sea (KRŠINIĆ, 1988; 1998; KRŠINIĆ & GRBEC, 2002) found a relatively low abundance. Relatively higher values were noted in October 1985 and March 1990, but the average values did not exceed 100 ind. m^{-3}. During new research along the transect in the southern Adriatic and during many years of research in the central part of the South Adriatic Pit, the abundance of radiolarians proved to be low, not exceeding 180 ind. m^{-3}. Such low abundance values for radiolarians were in contrast to the abundance of phytoplankton (VILIČIĆ, 1998), tintinnids (KRŠINIĆ, 2010), nauplii and postnaupliar copepods (KRŠINIĆ & GRBEC, 2012). The radiolarian populations in the central part of the South Adriatic are characteristically few in number in the 0 to 100 m layers, except juvenile specimens a few times. However, tintinnids, nauplii and postnauplii copepods were always very numerous in this layer. Compared with the abundance of radiolarians in many other regions, the radiolarian populations were also low, with small variations in abundance. On a scale of many years, however, they are occasionally most abundant at depths of 100 and 400 m. This increase in abundance occurs simultaneously with the increase in the percentage of phaeodarians relative to the total number of radiolarians in the mesopelagic and deep-sea layers. The increase in abundance on the Dubrovnik transect is also due to the increase of phaeodaria, and similar results were noted in earlier research (KRŠINIĆ, 1988, 1998). It can therefore be concluded that phaeodarians are quantitatively the most important radiolarians in the Adriatic Sea. Most of the species are consistently present in the subsurface to deepest layers. Only certain species, e.g., *Entocannula circularis*, *Conchophacus diatomeus* and *Porospathis holostoma*, appear occasionally as indicators of the ingression of water masses into the Adriatic from the Ionian Sea. According to GOWING & BENTHAM (1994), phaeodarians consume a great variety of food items ranging from organic detritus, bacteria, nanoplankton, algae, and coccoliths to tintinnids. We can therefore assume that the intrusion of warm, highly saline Mediterranean waters into the intermediate layers (LIW) of the southern Adriatic Pit is enriched by phytoplankton from the Albanian boundary zone in late spring (ŠILOVIĆ *et al.,* 2011). The highest abundance of radiolarians was recorded in the open waters of the subsurface layers at station S-300 on the Dubrovnik transect in April 1993. It is probable that picoplankton and organic detritus have a great influence on phaeodarian populations in the mesopelagic layer during the spring. However, we can assume that during the summer and at the beginning of the fall the dense waters that arrive from the northern and central Adriatic in the deeper layers of the southern Adriatic (VILIBIĆ & ORLIĆ, 2002; VILIBIĆ, 2003) also carry picoplankton and detritus that affect phaeodarian population growth.

Dead phaeodarian cells were very rare in the plankton. According to previous research, their skeletons are rarely found in sediments.

It is probable that the rarity of phaeodarians is a result of their rapid dissolution (TAKAHASHI *et al.,* 1983). However, it can be assumed that phaeodarian cells with skeletons, whose content is primarily organic, can be food for carnivorous copepods. Because the oncaeid copepods were a dominant group of copepods in the mesopelagic layers of the southern Adriatic, where they represent 80% of the copepod population (KRŠINIĆ, 1998) we can assume that oncaeids can be predators of phaeodarians in this layer. SWANBERG (1979) mentions amphipods of the family Hyperiidae as possible grazers of radiolarian central capsules. According to VINOGRADOV (1972), the intestinal contents of a number of deep-sea gammarids and copepods contained traces of radiolarian phaeodia, indicating that these organisms formed a major component of their diet. ANDERSON *et al.* (1984) stated that crustacean prey by a spongiose skeletal radiolarian. We did not investigate the diets of copepods in this paper. The study addressed the presence of oncaeid copepods in the southern Adriatic. The results of the study showed that the vertical distributions of oncaeid copepods and radiolarians were similar. They also indicated the variability found during many years of research. These results suggest the possibility of further research to demonstrate the connection between radiolarian and oncaeid copepod populations. Moreover, it is necessary to compare the distribution of radiolarians in the plankton and in the surface sediment within the area between the deep South Adriatic and the central Adriatic shelf and coast.

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Radiolariji u planktonu Jadranskog mora (Istočni dio Sredozemnog mora)

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SAŽETAK

Za istraživanje radiolarija u južnom Jadranu uzorci su sakupljeni za vrijeme pet krstarenja na tri postaje uzduž dubrovačkog transekta (postaje S-100 do S-1000) od travnja 1993. do veljače 1995. Također su uzorci sakupljeni za vrijeme 21 krstarenja na dubokoj postaji, S-1000/1200, od lipnja 2001. do prosinca 2009. Uzorci su sakupljeni u 2 do 8 slojeva sa Nansenovom mrežom 53 μm opskrbljena sa mehanizmom za zatvaranje. U središnjem dijelu južnojadranske kotline zabilježili smo ukupno 95 radiolarijskih taksona: 32 spumelarije, 46 naselarija i 17 feodarija. Ovim istraživanjima smo obogatili s 49 taksona faunu radiolarija Jadranskog mora. Najčešće vrste su feodarij *Challengeron xiphodon*, spumelarij *Stylodictya multispina* i naselarij *Cornutella profunda*, koje su prisutne u 99% uzorkovanja. Radiolarije su rijetko prisutne u obalnim vodama i u srednjem Jadranu, dok je njihova najveća abundancija u najdobljem dijelu južnojadranske kotline. Feodariji sudjeluju od 20 do 86 % u ukupnoj prosječnoj abundanciji. Redovito vrlo mala brojnost je u eufotičkom sloju osim u listopadu 2001, kada je zabilježen maksimum od 169 ind. m^{-3}. Juvenilne jedinke vrste *Eucyrtidium acuminatum* činile su 98 % od ukupnog broja u uzorku. U najvećem broju slučajeva maksimalna abundancija je bila u sloju od 200-300 m. Populacija radiolarija se obnavlja posredstvom ulazne istočno jadranske struje iz Jonskog mora. Navedena struja je intenzivnija zimi s uplivom Levantinske intermedialne vodene mase (LIW). Prepostavljamo da su karnivorni kopepodi potencijalni grabežljivci feodarija u dubokim slojevima u južnom Jadranu.

Ključne riječi: Radiolariji, raznolikost, vertikalna raspodjela, indikatorske vrste, vodene mase, Jadransko more