

Radiolarian distribution in East equatorial Pacific plankton

Tropical Pacific
Zooplankton distribution
Living radiolaria distribution
Radiolaria
Pacifique tropical
Distribution du zooplancton
Distribution des radiolaires vivants
Radiolaria

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ABSTRACT

On the basis of radiolarian data, four major areas can be recognized in the Eastern equatorial Pacific Ocean (transected from approximately 9°N, 80°W to 2°N, 140°W to 17°N, 155°W): 1) Between 5°N, 80°W and 2°N, 95°W, with high overall productivity and low radiolarian abundance and diversity; *Spongodiscus* sp. A, and to a lesser extent *D. tetrathalamus*, are the dominating taxa in this assemblage. 2) Along the equator, between approximately 95°W and 140°W. The productivity and planktonic standing stock of this area decrease to the west, while its radiolarian diversity and abundance increase, as well as the diversity of some other zooplankters. This area can be further subdivided into two sections at 124°W, the western one being conspicuously richer both quanti- and qualitatively than the eastern section. *O. stenozona* + *T. octacantha* are characteristic of this area. 3) From approximately 6°N, 138°W to 10°N, 142°W; radiolarian abundance and diversity drop sharply, as well as overall planktonic productivity and standing stock. 4) From approximately 10°N, 142°W to 17°N, 153°W; there is a further decrease in radiolarian abundance and diversity.

Radiolarian distribution shows good agreement with surface water-masses (South Equatorial Current, Equatorial Counter Current, North Equatorial Current), and with previous biogeographic zonations produced on the basis of several zooplanktonic groups. Also there is adequate coincidence with the distribution of radiolarian shells on the sea-floor of the same area. The distribution of specimens and species seems to be coincident with adverse near-shore conditions and zooplanktonic grazing pressure in the easternmost section, and with planktonic productivity in the western part of the transect.

The uneven distribution of Nassellaria might be explained by their more oceanic (rather than neritic) preferences, and by the shallowness of the thermocline layer which supplies nassellarian specimens to surface waters.

The similarity between the specific inventory recorded and those of previous works which studied radiolarians from the same and/or analogous areas is extremely low, due mainly to systematic ambiguities, as well as to very high specific diversities of radiolarian assemblages.

Oceanol. Acta, 1985, 8, 1, 101-123.

RÉSUMÉ

Distribution des radiolaires dans le plancton du Pacifique est-équatorial.

D'après les données recueillies sur les radiolaires, il y a lieu de démarquer quatre secteurs principaux dans la zone équatoriale Est de l'Océan Pacifique (environ 9°N, 80°W à 2°N, 140°W à 17°N, 155°W): 1) Entre 5°N, 80°W et 2°N, 95°W, présentant une haute productivité générale, une faible abondance ainsi qu'une faible diversité en radiolaires *Spongodiscus* sp. A et, d'une façon plus restreinte, *Didymocyrtes tetrathalamus*, se trouvent les taxa dominants dans cet assemblage.

2) Au long de l'équateur, entre 95° et 140° environ: la productivité et les réserves planctoniques de ce secteur diminuent vers l'ouest alors que leur diversité et leur abondance augmentent, de même que la diversité de quelques autres zooplancteurs. Ce secteur peut être subdivisé en deux sous-secteurs, à 124°W, celui de l'ouest étant plus riche, aussi bien en qualité qu'en quantité, que celui de l'est. *Octopyle stenozona* et *Tetrapyle octacantha* sont caractéristiques de ce secteur. 3) A partir d'environ 6°N, 136°W à 10°N, 142°W; l'abondance en radiolaires et la diversité tombent brusquement, ainsi que la productivité planctonique et les réserves. 4) A partir d'environ 10°N, 142°W jusqu'à 17°N, 153°W; il se produit une diminution dans l'abondance en radiolaires et la diversité.

La distribution des radiolaires montre une relation étroite avec les masses d'eau de la surface (courant sud-équatorial, contre-courant équatorial et courant nord-équatorial) et avec les zones biogéographiques précédentes produites sur la base de plusieurs groupes zooplanctoniques. Il existe également une coïncidence avec la distribution des coquilles de radiolaires dans les fonds de mer du même secteur. La distribution des spécimens et des espèces semble répondre à des conditions inadéquates à proximité de la côte et à la pression des pâtures zooplanctoniques dans le secteur plus oriental, et à la productivité planctonique dans la partie occidentale du transect. La distribution irrégulière de *Nassellaria* pourrait être expliquée par ses préférences océaniques plutôt que néritiques et par la superficialité de la couche de la thermocline fournissant les spécimens nassellariens aux eaux superficielles.

La similarité entre les citations spécifiques indiquées et celles des travaux précédents portant sur les radiolaires des mêmes secteurs ou des secteurs analogues est extrêmement faible, principalement du fait des ambiguïtés systématiques, ainsi que de la très importante diversité spécifique des associations de radiolaires vivants.

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INTRODUCTION

Radiolarian studies, undertaken chiefly by geologists and paleontologists, have traditionally centered on taxonomic problems and applications to stratigraphy. During the last few years, however, good results have been achieved in the application of *Polycystina* for biogeographical purposes, defining currents and water masses (for recent reviews on the subject see Casey, 1977; Kling, 1978; Boltovskoy, 1981). In this respect, the Pacific Ocean is probably the area which yielded more investigations, both in number and in degree of detail and coverage (e.g., Nigrini, 1968; 1970; Petrushevskaya, 1969; 1971 a; Casey, 1971 a, b; Sachs, 1973; Renz, 1976; Molina-Cruz, 1978; Moore, 1978). However, most of these used sediment samples only and dealt with limited fractions of the total assemblages present. In addition, they centered their attention on north-south distributional patterns. As a consequence, overall density trends, east-west abundance and diversity patterns and close causal examination of radiolarian distribution with respect to planktonic productivity and composition have been largely neglected. Meanwhile, these variations can give much useful information on the characteristics of the environments studied, especially in the case of tropical highly diversified communities. They can also pose interesting questions both from a purely biogeographical point of view and in connection with problems related to ecological studies, such as the

dynamics of oceanic ecosystems, availability of niches in various environments, conditions for deployment of different taxocoenoses and their maintenance and dispersion.

MATERIAL AND METHODS

Materials for this study were collected in July-August 1976 during Leg III of the "Pleiades" expedition (R/V Melville, Scripps Institution of Oceanography, University of California, San Diego; Fig. 1A). All samples were collected while the ship was under way, from a depth of 4.6 ± 2.1 m, filtering water from a faucet connected to the sea-water system through a .044 mm metal sieve for approximately 60 to 80 min. The samples were frozen while on board, and subsequently fixed with non-neutralized formaldehyde. In the laboratory, radiolarians were selected manually by means of a micropipette, one by one, rinsed two or three times in distilled water in order to eliminate salt crystals from their siliceous surfaces, treated with diluted HCl, rinsed again and then mounted in Canada Balsam in the usual way (Boltovskoy *et al.*, 1983). All radiolarians were counted and over 85 % were identified to the species level (Tab. 1, Plates 1 through 5). Sample n°22 collected sedimentary biological remains washed off the box core which at the time was being hauled on board; therefore its yield is shown on Table 1, but is ignored in most subsequent discussions.

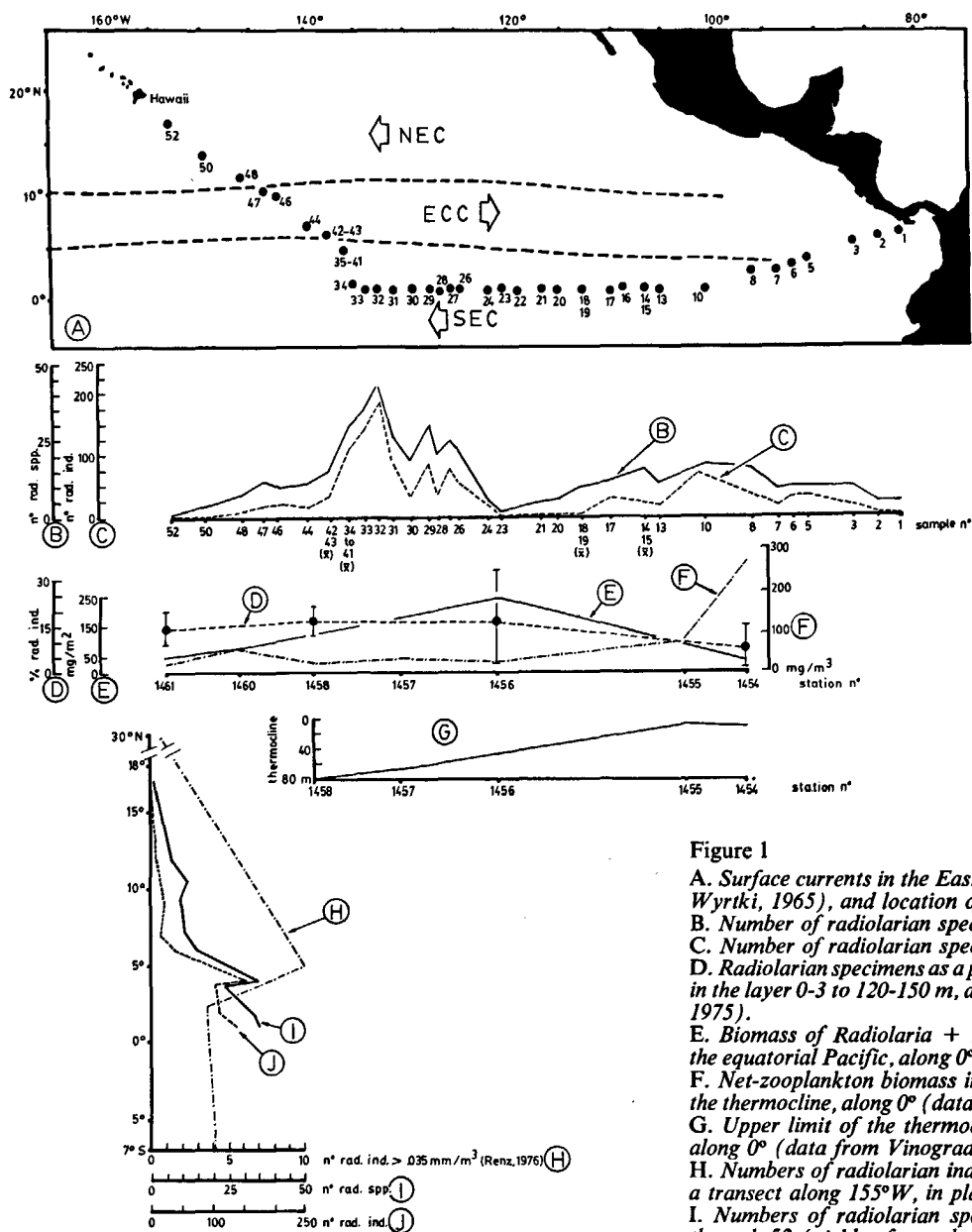


Figure 1

A. Surface currents in the Eastern Equatorial Pacific (chiefly from Wyrтки, 1965), and location of the samples studied.

B. Number of radiolarian species per sample.

C. Number of radiolarian specimens per sample.

D. Radiolarian specimens as a percentage of total microzooplankters in the layer 0-3 to 120-150 m, along 0° (from Tumantseva, Sorokin, 1975).

E. Biomass of Radiolaria + Foraminifera in the upper 150 m of the equatorial Pacific, along 0° (from Tumantseva, Sorokin, 1975).

F. Net-zooplankton biomass in the layer 0 m to the upper limit of the thermocline, along 0° (data from Vinogradov, Semenova, 1975).

G. Upper limit of the thermocline layer in the equatorial Pacific, along 0° (data from Vinogradov, Semenova, 1975).

H. Numbers of radiolarian individuals recorded by Renz (1976) in a transect along 155°W, in plankton samples.

I. Numbers of radiolarian species per sample in our samples 33 through 52 (yields of samples 35, 37, 40; 36, 38, 39, 41; and 42, 43 have been averaged).

J. Numbers of radiolarian specimens per sample (cf. 1).

In B through J, stations and curves are arranged following approximately the longitudes of map A. Station numbers 1454 through 1461 are those of the papers mentioned for the corresponding curves.

SURFACE HYDROLOGY OF THE AREA

The general pattern of the Pacific equatorial current system has been comprehensively described by Sverdrup *et al.* (1942), and much useful information has been subsequently reported by Cromwell (1953), Cromwell and Reid (1956), Wyrтки (1965), and others.

In brief, the area of this study is characterized by three currents: the North Equatorial Current (NEC), the Equatorial Counter Current (ECC), and the South Equatorial Current (SEC; Fig. 1A).

The NEC is fed from the California Current and by water from the eastern tropical Pacific. Its southern boundary, in August, lies between approximately

8°N (eastern portion) and 10 to 12°N (western portion).

The ECC flows between 4 and 10-12°N, but its width varies with the season, reaching highest values (about 5° in latitude) in August through October. East of 90°W the ECC splits off, its waters turning north and northwest and south and southwest to enter the NEC and the SEC respectively. The area east of 90°W is influenced by the Peru Current and hosts active upwellings and geostrophic divergence.

The SEC occupies a broad band, its northern boundary being located at approximately 4°N. One of its outstanding features is the presence of a divergence of sub-surface waters at or near 0°, and a convergence between the equator and the southern boundary of the ECC.

Sample n°	SAMPLES		SPECIES
	Latitude N	Longitude W	
1	64°54'	61°54'	<p>Polycystina s.l.</p> <p>Spumellaria s.l.</p> <p>COLLOSPHAERIDAE</p> <p><i>Acrosphaera murrayana</i></p> <p><i>Acrosphaera spinosa</i></p> <p><i>Buccinosphaera invaginata</i></p> <p><i>Collosphaera gtebulenta</i></p> <p><i>Collosphaera huxleyi</i></p> <p><i>Collosphaera macropora</i></p> <p><i>Collosphaera tuberosa</i></p> <p><i>Siphonosphaera polysiphonia</i></p> <p><i>Solenosphaera polymorpha</i></p> <p><i>Solenosphaera quadrata</i></p> <p><i>Solenosphaera zanguebarica</i></p> <p>ACTINOMMIDAE s.l.</p> <p><i>Acanthosphaera actinota</i></p> <p><i>Acanthosphaera pinchuda</i></p> <p><i>Actinomma arcadophorum</i></p> <p><i>Actinomma leptodermum</i></p> <p><i>Actinomma sol</i></p> <p><i>Astrosphaera hexagonalis</i></p> <p><i>Cenosphaera elysia</i></p> <p><i>Cenosphaera favosa</i></p> <p><i>Centrocebus octostylus</i></p> <p><i>Cladococcus cervicornis</i></p> <p><i>Cromyechinus antarctica</i></p> <p><i>Haliomma erinaceum</i></p> <p><i>Haliomma</i> sp.</p> <p><i>Helianter hexagonium</i></p> <p><i>Heliosphaera radiata</i></p> <p><i>Hexacoentium armatum</i></p> <p><i>Hexacoentium axotrias</i></p> <p><i>Hexacoentium entacanthum</i></p> <p><i>Hexalonche anaximandri</i></p> <p><i>Octodendron pinetum</i></p> <p><i>Plegmosphaera</i> sp.</p> <p><i>Pytiomma</i> sp.</p> <p><i>Spongodictyon spongiosum</i></p> <p><i>Spongoplegma rugosa</i></p> <p><i>Spongoplegma</i> sp. aff. <i>S. rugosa</i></p> <p><i>Spongosphaera streptacantha</i></p> <p><i>Stigmosphaera</i> sp.</p> <p><i>Stylosphaera melpomene</i></p> <p><i>Stylosphaera</i> sp. A</p> <p><i>Stylosphaera</i> sp. B</p> <p><i>Stylosphaera</i> sp. C</p> <p>? <i>Styptosphaera spumacea</i></p> <p><i>Thecosphaera</i> ? <i>diplococcus</i></p> <p><i>Thecosphaera inermis</i></p> <p><i>Thecosphaera phaenaxonia</i></p> <p><i>Thecosphaera</i> sp. aff. <i>Actinomma fenestratum</i></p> <p><i>Xiphactraetus pluto</i></p> <p><i>Xiphostylus trogon</i></p> <p>COCCODISCIDAE</p> <p><i>Didymocystis tetrathalamus</i></p>
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Sample n°	SAMPLES		SPECIES
	Latitude N	Longitude W	
1	64°54'	61°54'	<p>PHACODISCIDAE</p> <p><i>Heliodiscus asteriscus</i></p> <p><i>Sethodiscus macrococcus</i></p> <p>SPONGODISCIDAE s.l.</p> <p><i>Amphiropalum ypsilon</i></p> <p><i>Dictyoconyne profunda</i></p> <p><i>Dictyoconyne truncatum</i></p> <p><i>Euchitonia elegans</i></p> <p><i>Euchitonia furcata</i></p> <p><i>Euchitonia</i> spp.</p> <p><i>Hymeniasstrum koellikeri</i></p> <p><i>Hymeniasstrum</i> spp.</p> <p><i>Myelastrium</i> sp.</p> <p><i>Ponodiscus</i> sp. aff. <i>P. micromma</i></p> <p><i>Ponodiscus</i> sp.</p> <p>? <i>Spongaster pentas</i></p> <p><i>Spongaster tetras</i></p> <p><i>Spongocore cylindrica</i></p> <p><i>Spongodiscus resurgens</i></p> <p><i>Spongodiscus</i> sp. A</p> <p><i>Spongopyle setosa</i></p> <p><i>Spongotrochus glacialis</i></p> <p><i>Sponguus</i> sp.</p> <p><i>Stylochlamyidium asteriscus</i></p> <p><i>Stylochlamyidium multispina</i></p> <p>LITHELIDAE s.l.</p> <p><i>Larcopeyle buetschlii</i></p> <p><i>Larcopeyla quadrangula</i></p> <p><i>Lithelius alveolina</i></p> <p><i>Lithelius minor</i></p> <p><i>Lithelius</i> sp. aff. <i>L. spiralis</i></p> <p><i>Pylospira octopyle</i></p> <p>? <i>Streblacantha circumtexta</i></p> <p><i>Tholospyra cervicornis</i></p> <p>PYLONIIDAE s.l.</p> <p><i>Octopyle stenozona</i> + <i>Tetrapyle octacantha</i></p> <p>? <i>Phonticium clevei</i></p> <p><i>Pylolena armata</i></p> <p><i>Pylonium</i> sp.</p> <p><i>Nassellaria</i> s.l.</p> <p>SPYRIDAE s.l.</p> <p><i>Acanthodesmia viniculata</i></p> <p><i>Amphispyris reticulata</i></p> <p><i>Giraffospyris circumflexa</i></p> <p><i>Lophospyris pentagona</i></p> <p><i>Semantis</i> sp.</p> <p><i>Tholospyris anthophora</i></p> <p><i>Tholospyris</i> sp.</p>
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																																																				PLAGONIIDAE s.l.
																																																				<i>Callimitra carolotae</i>
																																																				<i>Clathrocanium coarctatum</i>
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<i>Spiroclytis scalaris</i>																																																				
CANNOBOTRYIDAE																																																				
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<i>Botryoclytis scutum</i>																																																				
<i>Centrobotrys thermophila</i>																																																				

Table 1

Location of the samples and radiolarian taxa recorded (as a percentage of total yields of each sample). Numbers of species and of specimens per sample ranged from 1 (samples n°40 and 52) to 79 and 514, respectively (sample n°22); averages: 18.3 (species) and 62.9 (specimens).

The picture thus outlined is valid for the period from May to December, and is most conspicuously developed between August and October.

RADIOLARIAN ABUNDANCE AND DIVERSITY PATTERNS

In total, 141 radiolarian taxa were recorded in the 44 plankton samples with Polycystina (Tab. 1, Fig. 1A). Twenty-nine of these occurred only once — in sample n°22 which was heavily contaminated with benthic material (see "Material and methods").

Only 28 species were present in 10 or more samples, and these comprised around 70% of all the radiolarian shells recorded, while the remaining 30% were distributed among the other 112 taxa. Excluding the species which only appeared in sample n°22, 40 were recorded only once or twice, being usually represented by one or two specimens in the entire collection.

Figures 1B and C show the overall distribution of the numbers of species and specimens in the samples

(a regression/correlation analysis of these log-transformed data yielded highly significant figures: $r = 0.975^{***}$; y (number of species) = $0.18 + 0.68 x$). Although no absolute quantitative data (as referred to surface or volume unit) are available, since all the samples were taken following the same procedure and filtering for similar periods of time, one can assume that the results are comparable within the collection.

East-west pattern

Figure 1A, B shows that radiolarians are scarce in the eastern part of the transect; between samples 5 and 24 their numbers are more or less stable and moderate, peaking between approximately 124°W and 135°W.

The eastern east Pacific is the most productive area occupied by our stations (King, Hida, 1957; Vinogradov, Voronina, 1963; Blackburn, 1966; Bogorov, 1967; Desrosières, 1969; Gueredrat, 1971; Sorokin *et al.*, 1975; Vinogradov, Semenova, 1975; see also Fig. 1F). This zone (our samples 1 through 5-7) has moderate to great neritic influence, and

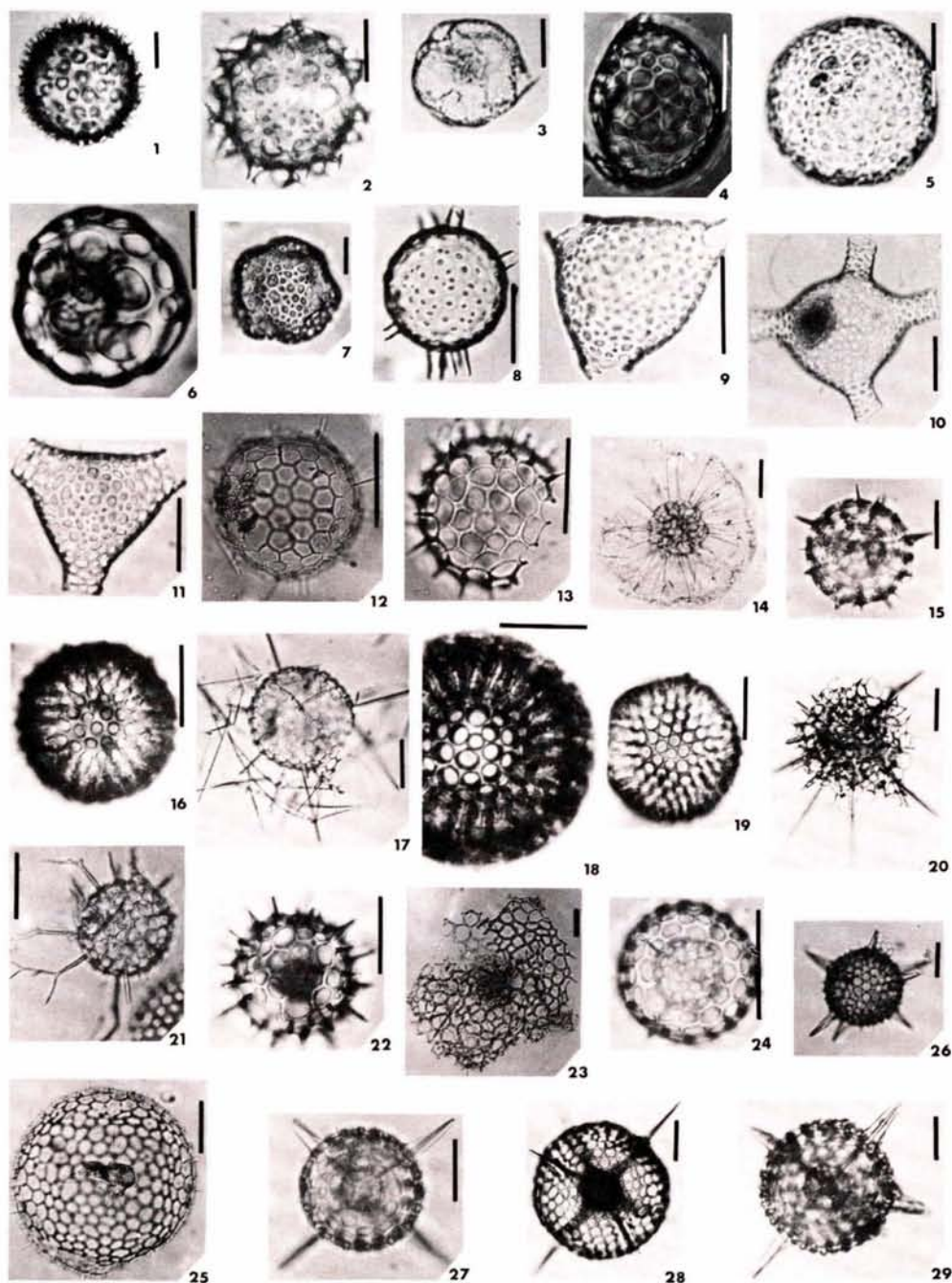


Plate 1

- | | |
|---|---|
| 1. <i>Acrosphaera murrayana</i> (22A, P45/4) | 16. <i>Actinomma sol</i> (22A, O40/2) |
| 2. <i>Acrosphaera spinosa</i> (41, J35) | 17. <i>Astrosphaera hexagonalis</i> (39B, Q55) |
| 3. <i>Buccinosphaera invaginata</i> (30, X45/1) | 18. <i>Cenosphaera elysia</i> (22A, J47/4) |
| 4. <i>Collosphaera glebulenta</i> , broken specimen (42, J43) | 19. <i>Cenosphaera favosa</i> (22A, R26/4) |
| 5. <i>Collosphaera huxleyi</i> (46, X42) | 20. <i>Centrocubus octostylus</i> (36, P46/4) |
| 6. <i>Collosphaera macropora</i> (32, U58) | 21. <i>Cladococcus cervicornis</i> (36, N45/4) |
| 7. <i>Collosphaera tuberosa</i> (22A, V32) | 22. <i>Cromyechinus antarctica</i> , external shell not yet formed (22A, E35/1) |
| 8. <i>Siphonosphaera polysiphonia</i> (30, V49/1) | 23. <i>Haliomma erinaceum</i> , broken specimen (39B, Z50/3) |
| 9. <i>Solenosphaera polymorpha</i> (22A, O24/1) | 24. <i>Haliomma</i> sp. (22A, H29) |
| 10. <i>Solenosphaera quadrata</i> (32, S43) | 25. <i>Heliaster hexagonium</i> (33, Q27/1) |
| 11. <i>Solenosphaera zanguebarica</i> (32, L35) | 26. <i>Heliosphaera radiata</i> (22A, O35) |
| 12. <i>Acanthosphaera actinota</i> (34, W36/3) | 27. <i>Hexacontium armatum</i> (22A, Y22) |
| 13. <i>Acanthosphaera pinchuda</i> (22A, M41/4) | 28. <i>Hexacontium axotrias</i> (36, O34/4) |
| 14. <i>Actinomma arcadophorum</i> (3, T26) | 29. <i>Hexacontium entacanthum</i> (16, N35) |
| 15. <i>Actinomma leptodermum</i> (22A, U30) | |

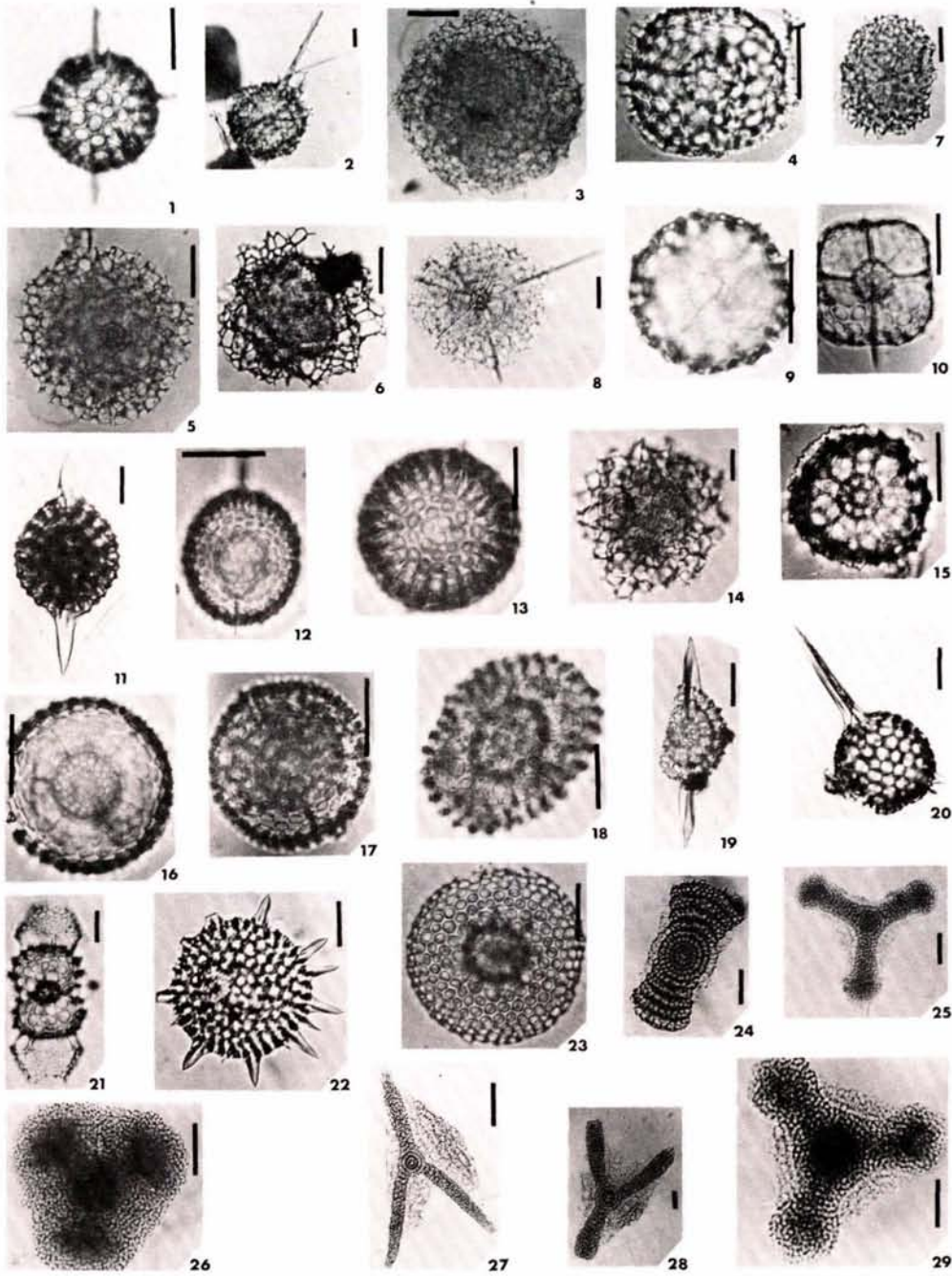


Plate 2

1. *Hexaloncne anaximandri* (22A, O30)
2. *Octodendron pinetum* (34, W30/1)
3. *Plegmosphaera* sp. (36, Q42)
4. *Pytiomma* sp. (38, T43/2)
5. *Spongodictyon spongiosum* (35, V38/3)
6. *Spongoplegma rugosa* (8, W43/3)
7. *Spongoplegma* sp. aff. *S. rugosa* (26, K30/4)
8. *Spongosphaera streptacantha* (6, O25/4)
9. *Stigmosphaera* sp. (22, E33)
10. *Stylosphaera melpomene* (10, M37)
11. *Stylosphaera* sp. A (22A, W28)
12. *Stylosphaera* sp. B (22A, K24)
13. *Stylosphaera* sp. C (22A, M28)
14. ? *Styptosphaera spumacea* (13, K42)
15. *Thecosphaera* ? *diplococcus* (37, O46)
16. *Thecosphaera inermis* (22A, K45/2)
17. *Thecosphaera phaenaxonia* (16, O37/3)
18. *Thecosphaera* sp. aff. *Actinomma fenestratum* (43, R36/3)
19. *Xiphatractus pluto* (22A, W23)
20. *Xiphostylus trogon* (22A, H35)
21. *Didymocyrtis tetrathalamus* (33, L34/4)
22. *Heliodiscus asteriscus* (32, L57/2)
23. *Sethodiscus macrococcus* (34, X33)
24. *Amphirhopalum ypsilon* (10, N31)
25. *Dictyocoryne profunda* (31, P36/1)
26. *Dictyocoryne truncatum* (36, Q41/1)
27. *Euchitonina elegans* (34, O35)
28. *Euchitonina furcata* (33, M25/4)
29. *Hymeniastrum koellikeri* (17, N24/8)

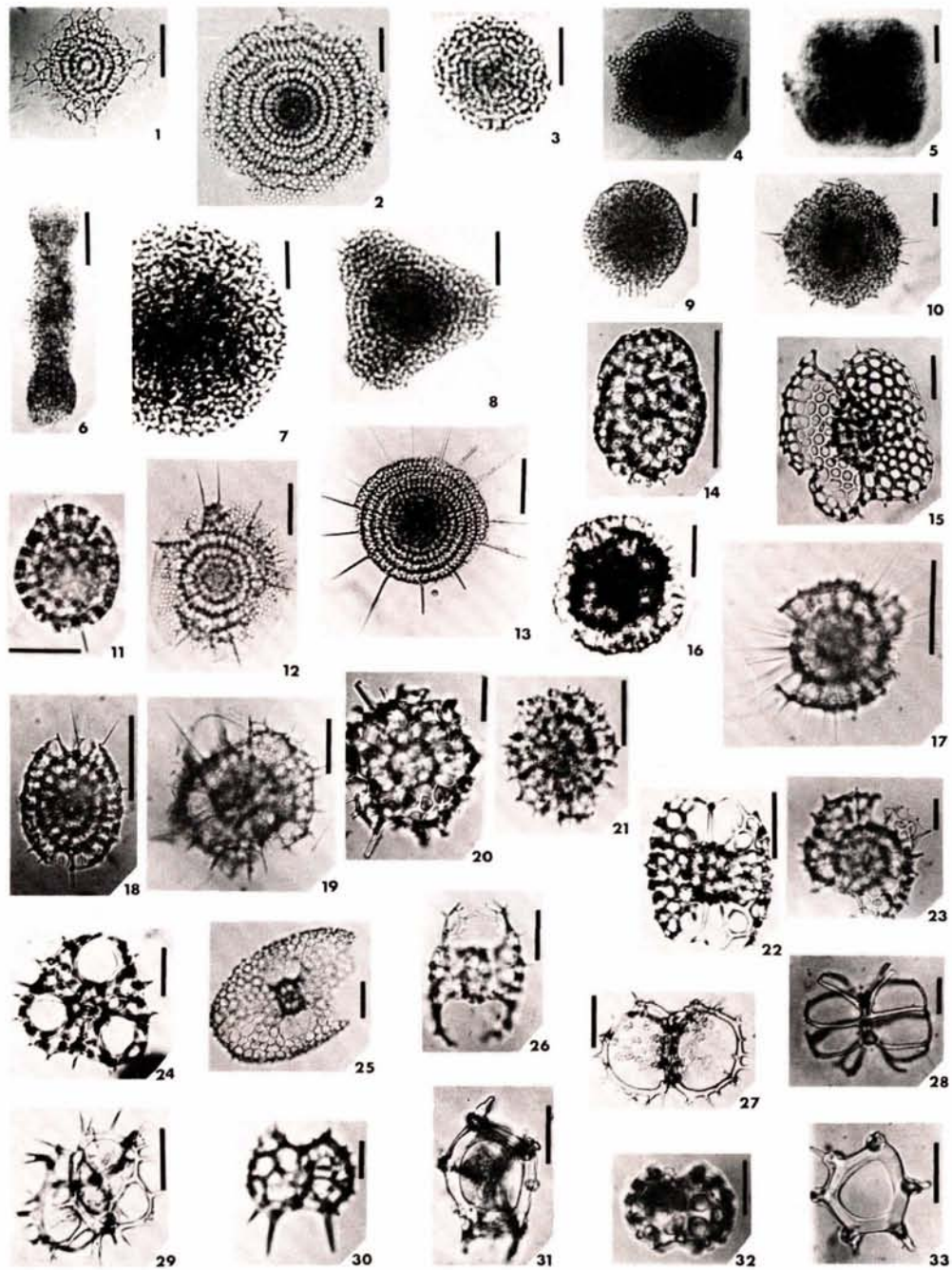


Plate 3

- | | |
|--|--|
| 1. <i>Mvelastrum</i> sp. (35, T34) | 18. <i>Lithelius</i> sp. aff. <i>L. spiralis</i> (28, W37/2) |
| 2. <i>Porodiscus</i> sp. aff. <i>P. micromma</i> (16, U54/4) | 19. <i>Rytospira octopyge</i> (33, Y26/2) |
| 3. <i>Porodiscus</i> sp. (41, N31/2) | 20. ? <i>Streblacantha circumtexta</i> (39A, M34/1) |
| 4. ? <i>Spongaster pentas</i> (29, O41) | 21. <i>Tholospira cervicornis</i> (22C, X36) |
| 5. <i>Spongaster tetras</i> (32, P37/3) | 22. <i>Octopyle stenozona</i> (39A, P27/4) |
| 6. <i>Spongocore cylindrica</i> (22B, S34) | 23. ? <i>Phorticium clevei</i> (22C, E33/4) |
| 7. <i>Spongodiscus resurgens</i> (22B, N28) | 24. <i>Pylolena armata</i> (16, Z34/4) |
| 8. <i>Spongodiscus</i> sp. A (34, V27) | 25. <i>Pylonium</i> sp. (16, O47) |
| 9. <i>Spongopyle setosa</i> (22B, J35) | 26. <i>Tetrapyle octacantha</i> (36, O37/3) |
| 10. <i>Spongotrochus glacialis</i> (30, V45) | 27. <i>Acanthodesmia vinculata</i> (36, N36/3) |
| 11. <i>Spongurus</i> sp. (22A, E35/1) | 28. <i>Amphispyris reticulata</i> (35, N38) |
| 12. <i>Stylochlamyidium asteriscus</i> (28, Y48/3) | 29. <i>Giraffospyris circumflexa</i> (36, O32/1) |
| 13. <i>Stylodyctia multispina</i> (36, S39/2) | 30. <i>Lophospyris pentagona</i> (34, X38/1) |
| 14. <i>Larcopyle buetschlii</i> (14, N30/3) | 31. <i>Semantis</i> sp. (36, N40/2) |
| 15. <i>Larcospira quadrangula</i> (32, K56) | 32. <i>Tholospyris anthophora</i> (42, M40/4) |
| 16. <i>Lithelius alveolina</i> (22A, G34) | 33. <i>Tholospyris</i> sp. (31, W43/2) |
| 17. <i>Lithelius minor</i> (28, C34) | |

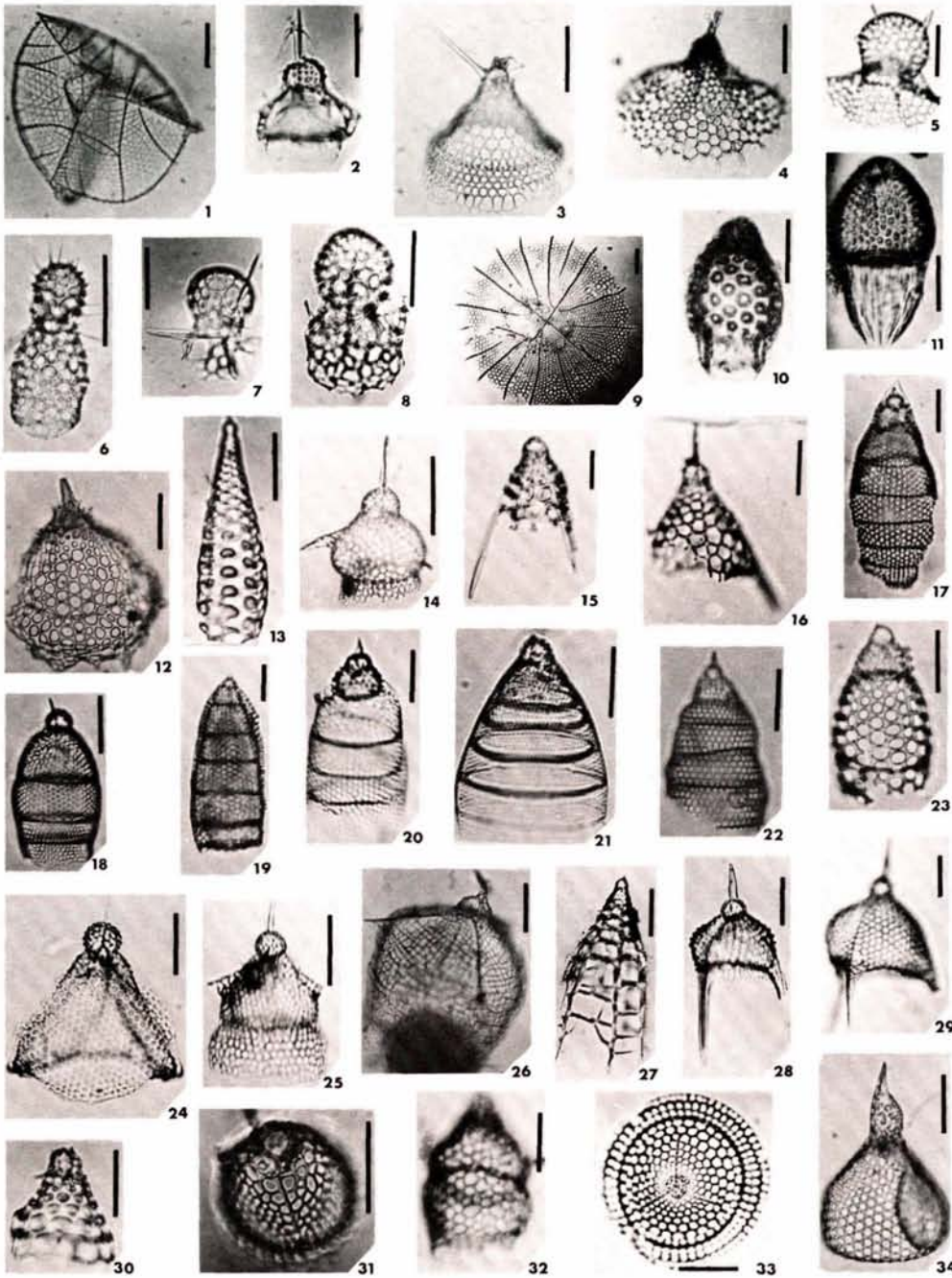


Plate 4

1. *Callimitra carolotae* (36, R48/3)
2. *Clathrocanium coarctatum* (35, S33)
3. *Corocalyptra cervus* (28, R36/2)
4. *Lampromitra sinuosa* (22D, N38)
5. *Lophophaena* sp. aff. *L. capito* (34, T25/3)
6. *Lophophaena hispida* (41, G20/1)
7. *Peridium spinipes* (21, Q37)
8. *Peromelissa phalacra* (22D, S32/1)
9. *Sethophormis aurelia* (27, O34)
10. *Carpocanarium papillosum* (22D, P43)
11. *Carpocanium* spp. (33, D35)
12. *Clathrocyclas cassiopeiae* (32, G55)
13. *Cornutella profunda* (22D, M36/2)
14. *Corocalyptra columba* (38, M35/4)
15. *Dictyophimus hirundo* (22D, Q33/2)
16. *Dictyophimus infabricatus* (22D, Q35)
17. *Eucyrtidium acuminatum* (22D, N37)
18. *Eucyrtidium anomalum* (36, R46)
19. *Eucyrtidium dictyopodium siphonostomum* (16, O47)
20. *Eucyrtidium hexagonatum* (32, F59)
21. *Eucyrtidium hexastichum* (36, O49)
22. *Eucyrtidium* sp. (22D, P29)
23. ? *Eucyrtidium teuscheri* (22D, N38)
24. *Lipmanella bombus* (27, F33/1)
25. *Lipmanella virchowii* (15, S45/4)
26. *Lithopilium reticulatum* (38, J46)
27. *Peripyramis circumtexta* (22D, R43)
28. *Pterocanium praetextum* (27, H39/1)
29. *Pterocanium trilobum* (36, T39/2)
30. *Theocalyptra davisiana* (22D, K37/3)
31. *Theocalyptra* sp., inverted specimen (38, F48)
32. ? *Theocorys veneris* (22D, D40/4)
33. *Theopilium tricostatum* (14, Q31)
34. *Antocyrtidium ophirensense* (28, J47)

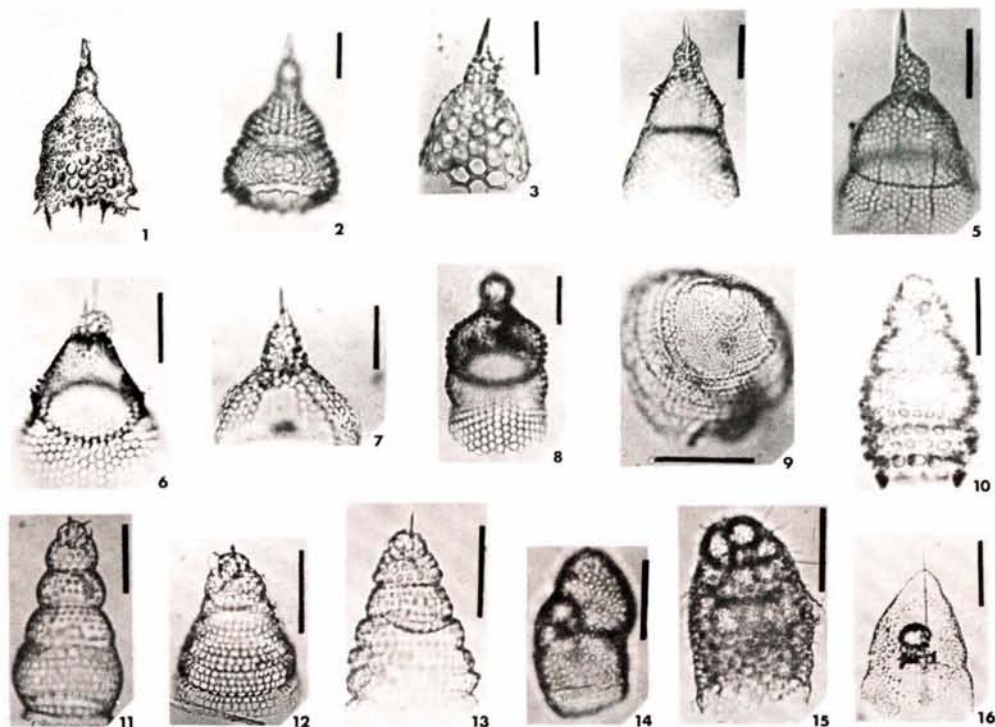


Plate 5

1. *Lamprocyclus maritatis maritatis*, line-drawing (13, P37)
2. *Lamprocyclus maritatis polypora* (16, P37/1)
3. *Lamprocyrtis nigrinae* (22D, O33/4)
4. *Pterocorys campanula* (29, U24)
5. *Pterocorys hertwigii* (33, X41)
6. *Pterocorys zancleus* (37, N30)
7. *Pterocorys* sp. (20, S36)
8. *Theocorythium trachelium* (33, H32)
9. ? *Udan undulata* (34, W38)
10. *Botryostrobos aquilonaris* (22D, O36/3)
11. *Botryostrobos auritus/australis* group (22D, P38)
12. *Spirocyrtis cornutella* (24, B35/3)
13. *Spirocyrtis scalaris* (27, Y38)
14. *Acrobotryssa cribosea* (22D, R34)
15. *Botryocyrts scutum* (31, W42/2)
16. *Centrobotrys thermophila* (39B, Y52/3)

active nutrient input is due to coastal upwelling and geostrophic divergence (McGowan, 1974). Furthermore, nutrient enrichment is enhanced by the influence of the Peru Current and by the fact that the thermocline is here close to the surface (about 10 m at 90°-100°W *cf.* Vinogradov, Semenova, 1975; *see also* Fig. 1G). Thus, low radiolarian abundance and specific diversity in our easternmost samples are opposed to the overall high productivity and phyto- and zooplanktonic standing stocks [note that the term "diversity" is used in this report as a more or less simple relationship between the numbers of species and of individuals. On the other hand, we calculated and plotted the diversity index of each sample according to the Shannon-Weaver (1949) formula; this curve was identical to Figures 1B, C (numbers of species and numbers of individuals) and hence supports our use of the expression in the strict sense as well].

The same phenomenon seems to hold true for other microzooplankters as well: Tumantseva and Sorokin (1975) found that both the percentage and the absolute abundance of microzooplankters in general (and of Radiolaria in particular) are considerably higher between 122° and 140°W, than at 97°W (Fig. 1D, E).

There are several reasons which might be responsible for this phenomenon. A major factor seems to be

the circumstance that radiolarians are usually scarce in neritic waters (Khabakov *et al.*, 1959; Kruglikova, 1969; 1981; Merinfeld, 1978; Boltovskoy, 1980). In addition, the area covered by our samples 1 through 5-7 is influenced by the relatively cold waters of the Peru Current (*see above*). For most — if not all — marine plankters cold and temperate-water assemblages are less diverse than tropical ones (*see, for example, Beklemishev, 1969*). The tropical, highly diversified radiolarian assemblage is, at this longitude, conspicuously shifted northwards (Nigrini, 1970; Kanaya, Koizumi, 1966), thus reflecting the limiting influence of the Peru Current. Finally, there is a third cause which might account, at least in part for the low diversity in this highly productive region. It is known that, in general terms, highly productive areas tend to host less diverse communities than poorer areas; the latter are more mature systems and therefore their assemblages are specifically richer (Margalef, 1963; 1967). Patrick (1970), Lubchenko (1978) noticed that diversity of algae might depend upon the grazing pressure: intense grazing lowers the population, thus eliminating marginal species. Furthermore, Merinfeld (1978) pointed out that radiolarians are usually scarce in environments of high biological productivity since their slow reproductive rhythm does not allow them to compete successfully with abundant carnivorous plankters.

The influence of zooplanktonic grazers on the abundance and diversity of radiolarian assemblages is indirectly supported by the following observation. Our samples taken between 07:00 hs and 20:00 hs averaged approx. 71 specimens per sample, while those taken during the night yielded approx. 47 specimens per sample. It is our feeling that if these day-night differences are not due to chance (the results of the *t*-test performed showed that these means differed significantly only at the 10 % level), they should be attributed to grazing pressure rather than to vertical migration phenomena. There are practically no data on diel vertical migrations in Radiolaria, although Casey (1966) suggested that these protozoans do not experience this kind of displacements. On the other hand, information from related plankters such as Foraminifera is contradictory (e.g., Parker, 1960; Smith, 1963; Bé, Hamlin, 1967; Holmes, 1982), but much evidence supports the conclusion that they do not migrate either (Boltovskoy, 1973). In tropical areas in general, and in the equatorial Pacific in particular, larger zooplankters have conspicuous direct daily vertical migrations (Vinogradov, 1968; Menshutkin, Rudjakov, 1975; Timonin, 1975); if their grazing pressure on microplankton is high, one should expect lower surface standing stocks at night, when most grazers are concentrated in the upper layers. This phenomenon was effectively reported by Bé (1960) for planktonic foraminifera, and by Koblenz-Mishke and Semenova (1975) for equatorial Pacific phytoplankton, and might also be valid for Radiolaria.

The increase of radiolarian diversity toward the west, peaking at our westernmost samples taken still within the SEC (Fig. 1B) is coincident with the data reported for some other zooplankters such as Copepoda (Gueredrat, 1971) and fish larvae (Gorbunova, 1975).

North-South pattern

Our samples 32-33 through 52 crossed three currents: SEC, ECC and NEC. Radiolarian abundance and diversity dropped dramatically at the SEC-ECC boundary, and further at the ECC-NEC limit (Fig. 1B, C, I, J).

Although, as already discussed, radiolarian abundance trends did not follow the general phyto- and zooplanktonic patterns along the equator between 80-90°W and 130°W, both show good agreement in the SE-NW part of the transect.

One of the most outstanding features of the Equatorial Pacific is the divergence of subsurface waters at the Equator (King, Hida, 1957). On the other hand, Cromwell (1953), Cromwell and Reid (1956) and later studies confirmed the presence of a sharp convergence between the equator and the southern boundary of the ECC. This convergence can concentrate buoyant organisms that tend to remain on or near the surface.

The fact that phytoplankton and zooplankton standing stocks are conspicuously higher at the equator than in the rest of the equatorial system has been confirmed by numerous investigations (e.g. King, Demond, 1953; King, Hida, 1957; Bogorov, 1967; Beers, Stewart, 1971; Venrick *et al.*, 1973; McGowan, 1974). Also radiolarian abundances were found to peak at or near to the equator, both in the plankton (Haeckel, 1887; King, Hida, 1957; Heinrich, 1968; Beers, Stewart, 1971; Petrushevskaya, 1971 *a*; Renz, 1976; Fig 1H) and in the sediments (Kruglikova, 1969; Petrushevskaya, 1971 *a*; Renz 1976). The increase in zooplankton abundance at the equator seems to be even more dramatic for Radiolaria than for most other zooplankters (Heinrich, 1968). Our results confirm these investigations, stressing the difference between strictly equatorial and subequatorial radiolarian assemblages (Fig. 1I, J; results of the correlation/regression analysis based on log-transformed ($x = \log x + 1$) data of samples 33 through 52: $r = 0.968^{***}$, y (number of species) = $0.69 + 0.068x$).

The above-mentioned unevenness in the distribution of Radiolaria along the transect is further stressed by the figures given in Table 2. According to the surface hydrology of the area in August, samples 1 through 5-7 have been taken in waters off the eastern boundary of the ECC; 5-7 through 41 in the SEC; 42 through 47 in the ECC; and 48 through 52 in the NEC (Fig. 1A). The numbers of species and individuals per sample are conspicuously higher in the SEC than in all other areas (Fig. 1B, C; Tab. 2). Lowest figures fall within the easternmost area and the NEC, southeast from Hawaii (according to Kruglikova, 1981, the sediments of this zone is also poor in Radiolaria). Our difference between eastern area and NEC samples is also in good agreement with Takahashi's (1981) results; in sediment traps placed at 15°21.1'N, 151°28.5'W (around our NEC samples) this author found a vertical flux and a standing stock of Radiolaria about 2.6 times lower than in traps placed in the Panama Basin (5°21'N, 81°53'W; around our eastern sector area). According to Table 2 a similar ratio for our samples yields 2.5.

Table 2

Average numbers and ranges of radiolarian specimens and species recorded within each of the four areas transected (sample n° 22 excluded)

	Specimens/sample (range)	Species/sample (range)
Eastern area (samples 1-7)	16.5 (5-29)	8.2 (5-10)
SEC (samples 5-41)	66.8 (1-264)	20.2 (1-44)
ECC (samples 42-47)	26.8 (21-49)	12.8 (10-19)
NEC (samples 48-52)	6.6 (1-11)	4 (1-7)

SPUMELLARIA-NASELLARIA PERCENTAGE RELATIONSHIPS

Judging from data based on investigations of whole assemblages (rather than on selected species) there seem to be conspicuous variations in the Nassellaria-Spumellaria ratios reported (*see*, for example, text-Fig. 8 in Boltovskoy, Riedel, 1980). These differences might be due, at least in part, to the fact that the taxonomy of Nassellaria has undergone several major revisions in recent years (*e.g.*, Goll, 1968; 1969; Petrushevskaya, 1965; 1981; Sanfilippo, Riedel, 1970; Foreman, 1973; Nigrini, 1977), and therefore their identifications at the specific level are more readily undertaken by specialists. At the same time, there might also be a tendency to lump together many poorly defined Sphaeroidea (*e.g.*, *Cenosphaera* spp., *cf.* Nigrini, Moore, 1979; several two-spined spherical and oval-shaped forms), some Spongodiscidae such as *Porodiscus* spp. (Nigrini, Moore, 1979), numerous litheliids and pyloniids of variable (?), irregular and complicated structure, *etc.* However, even taking this circumstance into account, the differences in the Nassellaria/Spumellaria ratios (specimens and/or species) are seemingly significant (Benson, 1966; Petrushevskaya, 1966; 1971 *b*; Kruglikova, 1969; McMillen, 1975; Takahashi, Honjo, 1981), although neither a general trend nor the biological implications of these variations have yet been clearly established.

Our data (Fig. 2) show that Nassellaria were far less abundant than Spumellaria; only one sample (n°21) yielded more nassellarian than spumellarian specimens, while most others had much less than 50% of the former. On average, nassellarian individuals accounted for only 23% of all radiolarians recorded,

and their taxa comprised 40% of the entire inventory. The percentage of nassellarian individuals drops to zero at both extremes of the transect, where overall radiolarian abundance is low (Fig. 2B); this might indicate that the group as a whole is less resistant to adverse and/or near-shore conditions (*see* "Radiolarian abundance and diversity patterns"), which is in agreement with Benson's (1966) interpretation of Gulf of California sedimentary assemblages.

Radiolarian abundance maxima did not overlap nassellarian percentage maxima, the latter being displaced to the east (Fig. 2A, B). There is some evidence supporting the assumption that Nassellaria tend to inhabit deeper layers than Spumellaria (Haecker, 1908; Kling, 1979; Takahashi, Honjo, 1981), and that discontinuities in the vertical distribution of these plankters are closely related to characteristics of the hydrological profile of the corresponding water-mass (Casey, 1977; Kling, 1979). In the area of our Nassellaria-richest samples (approximately 110°W to 125°W) the upper limit of the thermocline layer is at a depth of about 25 to 45 m, while farther west it drops down to approx. 80 m (Vinogradov, Semenova, 1975; Fig. 1G and 2C). Therefore, it is possible that the vicinity of the thermocline layer was responsible for higher nassellarian percentages in our eastern surface samples.

Most investigations based upon vertical plankton samplings down to considerable depths and/or upon sedimentary materials reported much higher percentages of nassellarian taxa than we do (*e.g.*, Benson, 1966; 59.5%; Nigrini, 1967: 55.5%; Renz, 1976: 78%; Kling, 1979: 75%; Takahashi, 1981: 50.9%; Takahashi, Honjo, 1981: 48.5%) and specimens (*e.g.*, Petrushevskaya, 1966; 1971 *b*: 70 to 83% in the tropical Pacific; Kruglikova, 1969: up to 75% in the

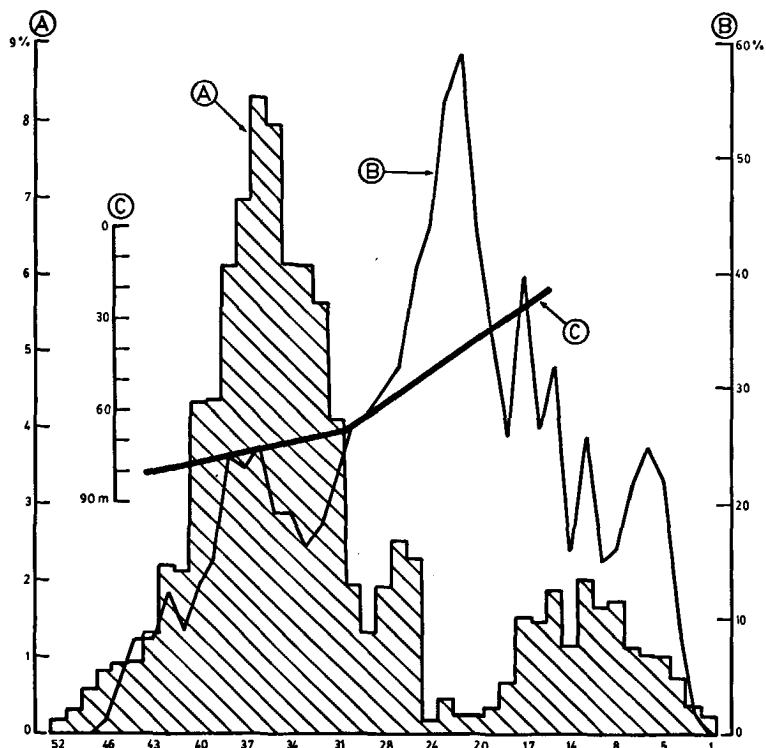


Figure 2

Distribution of total Radiolaria and of Nassellaria in the samples, and depth of the upper limit of the thermocline layer (according to data from Vinogradov, Semenova, 1975). A. Radiolarian shells per sample as a percentage of entire collection; B. Percentage of nassellarian shells per sample; C. Depth of the upper limit of the thermocline layer. Data in A and B are averages of three consecutive discreet values, except extremes; sample n° 22 eliminated.

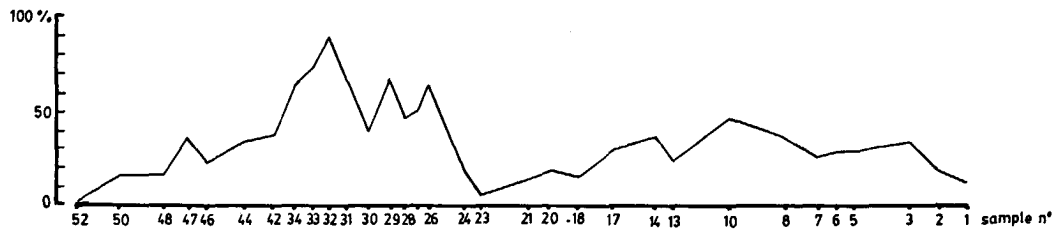


Figure 3

Percentages of species belonging to the 28 most common taxa (those present in 10 or more samples) per sample.

same area; Takahashi, 1981: 74.9% in two sediment trap stations in the tropical Pacific). If one takes into consideration that Nassellaria tend to show a poorer preservation than Spumellaria both in the water-column and in the sediments (Takahashi, 1981), our results furnish additional evidence to Haecker's (1908) observations that deep-dwelling Radiolaria have a higher percentage of bilaterally symmetrical forms than surface living ones.

DISTRIBUTION PATTERNS OF SOME SELECTED SPECIES

Of the 141 radiolarian taxa recorded, only 28 were present in more than 10 samples. Figure 3 represents the occurrence of these species in the collection; the conspicuous similarity between this curve and the one for all the species found (Fig. 1B, C) suggests that the distribution of the commonest taxa followed, in general terms, the same pattern valid for the entire inventory (Pearson's r for log-transformed ($x = \log x + 1$) data yielded highly significant values; data on Figure 1B vs. data on Figure 3: $r = 0.938^{***}$, and Figure 1C vs. Figure 3: $r = 0.914^{***}$). However, the relative abundance of individual species and specimens among samples was, in some cases, quite uneven, suggesting affinities with particular environments, or at least different tolerances. In order numerically to express this visual impression the percentages of individuals of each species per sample

were calculated and then averaged within each of the four areas covered by the transect (coastal, SEC, ECC, NEC). In order to compensate for probable shifts and changes in the limits considered (Fig. 1A), the averages were calculated overlapping slightly the extremes of each area (Tab. 3).

Octopyle stenozona + *Tetrapyle octacantha* were absent from samples 1 and 2, and their highest percentages were recorded in samples taken in the SEC. In the ECC, and especially in the NEC their abundances were conspicuously lower. Although some reports based on sediments samples consider these taxa as typical of subequatorial environments (e.g. Robertson, 1975; Molina-Cruz, 1978), Renz's (1976) results indicate that they conspicuously peak at the equator (Pyloniidae fam. group. cf. Renz, *op. cit.*). In addition, Moore (1978) found that his "Tropical Factor" was clearly dominated by a single species-group: *T. octacantha* + *O. stenozona*.

Although the abundance of *Didymocyrtis tetrathalamus* peaked at the western SEC stations, it showed higher percentages in the coastal area and the ECC-NEC. Moore (1978) grouped this species with six others, stating that in the eastern tropical Pacific all of them tend to concentrate in the regions of counterflow between the wind-driven equatorial currents. Several other researchers included *D. tetrathalamus* either in tropical or in subtropical assemblages, or in both (e.g., Nigrini, 1967; 1970; Robertson, 1975; Renz, 1976; Molina-Cruz, 1978; Johnson, Nigrini, 1980; 1982). Our results suggest that *D. tetrathalamus* is more tolerant of adverse conditions

Table 3

Average percentages of selected species in the four areas transected by the expedition.

Species	Areas	Coastal (samples 1-7)	SEC (samples 6-43)	ECC (samples 35-48)	NEC (samples 46-52)
<i>O. stenozona</i> + <i>T. octacantha</i>		9.5	16.7	10.3	5.4
<i>D. tetrathalamus</i>		13.2	6.3	10.1	9.6
<i>Spongodiscus</i> sp. A		14.5	3.0	2.5	2.8
<i>S. tetras</i>		4.0	1.7	4.3	10.0
<i>Spongurus</i> sp.		0.0	1.3	1.5	8.4

than most other species, and that its relative abundance might furnish information about the fitness of warm waters for the deployment of radiolarian assemblages.

Spongodiscus sp. A are most probably juvenile forms of some three-armed spongodiscid (*Euchitonina*, *Dicthyocoryne*, *Hymeniastrum*). The distribution of this taxon is interesting in that it is one of the very few that presents maximum percentages in the "coastal area", sharply decreasing offshore. Since *Polycystina* tend to avoid near-shore waters (see above "Radiolarian abundance and diversity patterns") these findings might represent the marginal, underdeveloped individuals that survive at the distributional boundary of the group.

Spongaster tetras and *Spongurus* sp. yielded higher percentages in the NEC than in all other areas. Nigrini (1968) found higher percentages of *S. tetras* in the SEC and in the ECC than in the NEC, which is contradictory to our findings. Also Renz (1976) reports this species to be more abundant at the equator than north or south from it. However, our data are in agreement with Moore's (1978) results, who found *S. tetras* to be closely associated with the western tropical gyres (our NEC samples are the westernmost in the collection). The taxonomic status of *Spongurus* sp. is not clear at the present time, therefore the analysis of its distribution is postponed for the time being.

Our results for the relative abundances of the former 4 species in coastal and NEC samples are also in agreement with Takahashi's (1981) counts of sediment trap samples placed in Panama Basin and in NEC waters; he found around 2.16 times more *O. stenozona* + *T. octacantha* shells in the Panama Basin area than in the NEC (our ratio was 1.7), 6.6 times more *D. tetrathalamus* (our ratio: 1.3), and 6.6 times more *Spongodiscus* sp. A (our ratio: 5.1).

The differences between the faunistic assemblages of the currents considered were also put in evidence by a comparison between samples by means of Sørensen's (1948) index ($2C/A + B$; where A and B are the numbers of species in samples A and B, and C is the number of species present in both samples compared). Only the 28 commonest taxa have been used for this analysis. The matrix in question (Fig. 4) shows two areas with conspicuously clumped higher values. One of these encompasses samples 26 through 39; and the second affects samples 5, 8, 13, 44, 46 and 47. Some high figures also relate samples 42, 43, 44, 46 and 47. The first group defines the western section of our SEC samples, and the second suggests affinities between the impoverished "neritic" and ECC-NEC environments. High radiolarian diversity and low abundance might be responsible for lack of stronger affinities between the ECC and the NEC samples.

BIOGEOGRAPHICAL CONSIDERATIONS

Several authors have proposed biogeographical schemes for the Pacific Ocean (for recent review of the subject, see Van der Spoel, Pierrot-Bults, 1979). The most thorough and detailed are the ones produced by Beklemishev (1969; 1971) and McGowan (1971; 1974) with respect to zooplankton in general; and by Moore (1978) for radiolaria in the sediments.

Figure 5 illustrates the different areas, which fall within the limits of our transect, proposed by Beklemishev (1969), McGowan (1974) and Moore (1978). All three schemes separate an easternmost near-shore area, which is either an "impoverished faunal area" (Beklemishev, 1969), or hosts lower values for the "tropical factor" (Moore, 1978), or is outside of the boundaries of the basic (100% "core" region) of the equatorial fauna (McGowan, 1974). However, according to these authors, the location of the limit between the oceanic and the neritic environments varies from approx. 85°W to 105°W; our data suggest that it is located somewhere around 90°W (Fig. 1B, C, Fig. 5, Tab. 2, 3).

Our samples 8 through approximately 41 lie within the SEC; radiolarian abundance and diversity are here conspicuously higher than in the other areas transected (cf. Tab. 2, 3), but the western portion of this section (samples 26 through 41) is especially rich (Fig. 1B, C). This observation is also confirmed by the between-sample comparison performed by means of Sørensen's (1948) index (Fig. 4). Neither Beklemishev (1969; 1971) nor McGowan (1974) detected important faunal changes along the equator at approximately 125°W. On the other hand, the mid-ocean part of Moore's (1978) boundary of the .8 value for the "Tropical Factor" encompasses with perfect coincidence our richest samples (Fig. 5). Also Kruglikova (1981) plotted higher radiolarian densities in equatorial sediments west of approximately 125°W than between approximately 90-95°W and 125°W.

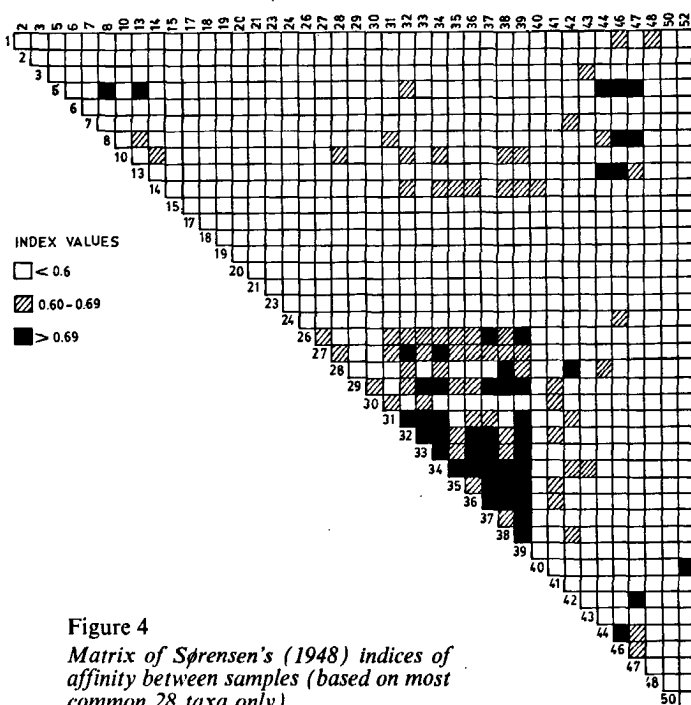


Figure 4
Matrix of Sørensen's (1948) indices of affinity between samples (based on most common 28 taxa only).

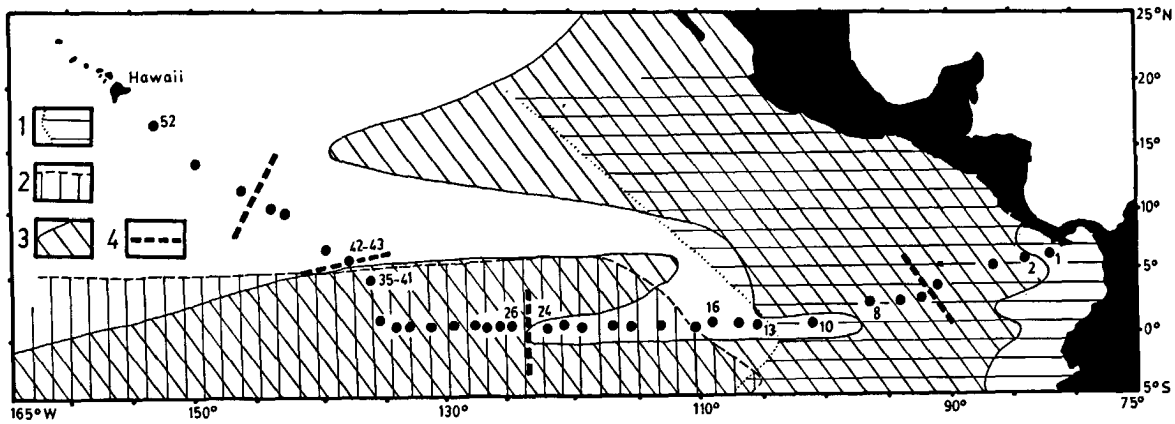


Figure 5

Biographical areas proposed for the eastern tropical Pacific. 1) impoverished faunal region (inhabited by < 50 % of equatorial species), cf. Beklemishev (1969; 1971); 2) basic equatorial biotic province (100 % of equatorial fauna present), cf. McGowan (1974); 3) 0.8 value contour for the "Tropical Factor" (based on Recent radiolarian sedimentary assemblages); cf. Moore (1978); 4) faunistic boundaries of the radiolarian assemblages studied.

The area north of 5°N (between 135 and 145°W) also lies outside of McGowan's (1974) "core" of the equatorial fauna, and marks Moore's (1978) limit of a lower value for the "Tropical Factor". In our collection, it was at this point where radiolarian diversity and abundance dropped sharply (Fig. 1B, C).

The ECC-NEC boundary shown by the samples under study is probably the same as Renz's (1976) limit between the Northern tropical and the equatorial domains, located by this author somewhere between 10°N and 15°N (both in plankton and in the sediments). Beklemishev (1969; 1971) does not show a faunistic limit in this area; whereas McGowan's (1974) northward extension of 60% of equatorial fauna representatives lies slightly south of Hawaii (also his ranges for the "Eastern Tropical Pacific" and north "Central" faunal assemblages overlap the area in question).

REPRODUCIBILITY OF QUALITATIVE RESULTS OF RADIOLARIAN COLLECTIONS

One of the basic assumptions of the scientific method that researchers apply throughout their investigations is the fact that the phenomena described can be reproduced by the same and/or other authors. But when limited biological collections from large areas are involved, the possibilities of exactly reproducing previous results are, obviously, seriously restricted. However, within the methodological limitations imposed, if one collects samples from a previously rather well covered area, one can expect that at least qualitative results will reasonably overlap those of preceding investigations.

However, our results of such a comparison show that the differences between our collection and those of several previous reports are much greater than expected. The exceptionally large number of polycystina species, and the obscure taxonomic status of most of them (due, at least in part, to their complex

architecture and a presumably high intraspecific variability) make such comparisons extremely difficult. Nevertheless these are possible, even if only on a tentative basis and yielding approximate results. We attempted a comparison with 9 previous works. Seven of these presumably reported all the taxa found in their respective samples, while the remaining two (Nigrini, 1968; Moore, 1978) only dealt with the dominant and, especially the latter, best defined taxa. Only illustrations and descriptions were compared, rather than original materials; therefore in many cases the correspondence between taxa remained under doubt. Since numerical values were used to assess the degree of similarity between our specific inventory and those of the authors considered, the compromise solution chosen was to register a positive correspondence for every two doubtful ones. Although the values thus obtained by no means intend to be exact and conclusive, they still reflect the differences in question (Tab. 4).

Renz (1976) thoroughly sampled an area which overlaps some of our sample sites; only 67 of her 191 and our 141 taxa were present in both collections. Benson (1966) performed a very detailed analysis of the radiolarians of the Gulf of California, the waters of which are nearly the same as those of the equatorial Pacific (and, hence, its radiolarian fauna is derived from that of the latter, cf. Benson, 1966, p. 35); still only 83 species were common to both Benson's and our collections, while the remaining 135 were lacking in one or other of the two. Takahashi (1981) studied a large collection from two sets of sediment traps placed in the NEC and in the Panama Basin (the corresponding locations were almost coincident with our samples n°50, 52 and n°1, 2, 3, respectively); only approximately 97 of our 141 and his ca. 240 (Takahashi, *op. cit.*, Tab. 2) taxa are present in both inventories. Similar situations are observed when comparing collections from the tropical and subtropical Atlantic (*e.g.*, McMillen, Casey, 1978; Boltovskoy, Riedel, 1980; Takahashi, Honjo, 1981).

Table 4
Comparison of the specific inventory of our collection with other authors' data.

			Sørensen's (1948) similarity index between our collection and other authors' data	Percentage of the most com- mon taxa of our collection recorded by other authors
Tropical and subtropical Pacific	Plankton	Renz (1976)	0.40	76.8
	Sediment traps	Takahashi* (1981)	0.51	87.5
		Benson (1966)	0.55	84.0
	Sediments	Moore (1978)	0.34	48.2
		Nigrini (1968)	0.13	17.8
Tropical, subtropical and temperate Atlantic	Plankton	Boltovskoy and Riedel (1980)	0.38	39.3
		McMillen and Casey (1978)	0.53	69.6
	Sediment traps	Takahashi and Honjo (1981)	0.47	80.3
World ocean	Plankton and sediments	Petrushev- skaya (1971 a)**	0.46	100.0

* Only taxa recorded in counting slides from stations P₁ and PB (Takahashi, *op. cit.*, Table 2) are considered.

**Nassellaria only.

Furthermore, not even all of our most common species (those recorded in 10 or more samples) were found by the reports considered (Tab. 4).

The discrepancies pointed out could be explained, at least in part, by our inability to compare adequately our identifications with the literature data reviewed, and by obscurities and inconsistencies in the systematics of several taxa. However, this cannot account for all the differences. Selective dissolution might have eliminated some delicate skeletons from Benson's (1966) materials, but Petrushevskaya (1971 a), Renz (1976), McMillen and Casey (1978), Boltovskoy and Riedel (1980), Takahashi (1981) and Takahashi and Honjo (1981) studied large planktonic collections or sediment trap samples from as high in the water column as 378 m.

Our collection is several orders of magnitude smaller than those of the authors considered, and still we recorded 73 species not found by Renz (1976), 57 by Benson (1966), 66 by Takahashi and Honjo (1981), 95 by Boltovskoy and Riedel (1980), 78 by McMillen and Casey (1978) and 44 by Takahashi (1981). Even Petrushevskaya (1971 a), in her extremely large collections of plankton and sediments from all areas of the World Ocean, failed to record 12 of our 57 Nassellaria. Although most radiolarian species are cosmopolitan (*i.e.*, inhabiting all oceans within the same ecological regions), one still could partly attribute to endemism the differences with Atlantic Ocean inventories (*i.e.*, McMillen, Casey,

1978; Boltovskoy, Riedel, 1980; Takahashi, Honjo, 1981). However, the similarity indexes with the latter are either closely comparable or higher than the ones with respect to tropical Pacific collections (Tab. 4). Nigrini (1970), Casey (1971 a, b) and Renz (1976) performed zoogeographical analyses of equatorial Pacific radiolarian assemblages. Nigrini (*op. cit.*), on the basis of surface sediment-samples, defined recurrent groups of species characterizing each of the six major biogeographical zones of the northern Pacific; the tropical group included 23 species. Casey (1971 b) established ten equatorial indicator species in Pacific sediments. When comparing these results with Renz's findings a very low degree of similarity becomes evident: the three sets of data have less than about 20% of the species in common.

What is, then, the reason for such a low degree of similarity between the qualitative yields of collections from the same and/or analogous areas? Recent polycystina are one of the most diversified groups of zooplankters; according to extreme estimates the number of living species could exceed 4,500 (Levine, 1963). On the other hand, precise and widely accepted limits for the definition of most radiolarian species are lacking. Therefore, often specimens belonging to opposite extremes of the variability spectrum of the same species are illustrated with different figures and are given different names. In other words, synonymy problems could be responsible for a great part of the discrepancies. This appreciation is supported

by the fact that the average percentage of our nassellarian taxa recorded by Benson (1966), Renz (1966), McMillen and Casey (1978), Takahashi (1981) and Takahashi and Honjo (1981) (67.2) was considerably higher than that of our spumellarian representatives (46.3); as stated above (see "Spumellaria-Nassellaria percentage relationships") nassellarian systematics is in better shape than the spumellarian one. Boltovskoy (1965) presented a thorough analysis of this type of situation with regard to Foraminifera, warning that "...the near future of this science is rather bleak if we do not undertake drastic and prompt measures for its salvation." (p. 388). Boltovskoy *et al.* (1983) stressed the urgent need for thorough radiolarian descriptions and illustrations in order to make identifications useful for subsequent workers. The conclusions reached in this investigation seem to furnish ample support to the dangers outlined.

The above-described is an artifact that can substantially lower similarities between different specific inventories. On the other hand, there also are "natural" characteristics which can help to further depress these similarities. Aside from taxonomic problems, Polycystina comprise a very large number of "good species", and their taxocoenoses are among the most diverse ever reported (Takahashi, Honjo, 1981). High specific diversities mean that the percentages that individual species contribute to the overall assemblage are very low and therefore the probabilities of recording them in successive samples are also small (*e.g.*, Shannon, Weaver, 1949).

Finally, seasonal and multi-annual variations and plankton patchiness are also factors that can introduce much variation in plankton samples in general, and in the yields of the plankton samples compared in particular.

This phenomenon has important implications: it precludes the possibility of close comparisons between investigations. As a result, subsequent studies cannot adequately incorporate previous data, and therefore must largely rely upon limited and fractionary information (*i.e.*, their own). In effect, as far as our knowledge goes, Moore's (1978) work

is the first and only attempt to directly incorporate other researchers data in a wide distributional analysis of Polycystina.

The fact that only 6 of the 28 most common taxa of our collection were also found by all 6 of the studies considered (excluded are Nigrini, 1968; Petrushevskaya, 1971 *a*; and Moore, 1978); and that at least 8 were not registered in the same or closely related water mass by Benson (1966) and/or Renz (1976), also calls into question the usefulness of many radiolarian species as indicators of marine water-masses. In effect, some of the prerequisites for a good indicator are abundance (including consistent presence) and easy identification (*cf.* E. Boltovskoy, 1978). Obviously either of these two conditions — or both — are not fulfilled by many of the species under consideration.

CONCLUSIONS

Radiolarian distribution in surface waters of the Eastern equatorial Pacific is determined by several factors: neritic influence, grazing pressure, overall planktonic abundance and depth of the thermocline layer. Limiting factors are different at different locations. Optimal conditions seem to occur in purely oceanic waters of high productivity, but where grazers are not as numerous as in the easternmost section.

Analyses of the distribution of whole assemblages, including changes in their abundance and diversity, rather than analyses of the distribution of selected species or species-groups, yield useful results in so far as they are in good agreement with detailed zoogeographical schemes based on planktonic organisms and on radiolarian patterns in bottom sediments.

Direct utilization of previous reports and their respective species-lists for biogeographical purposes is seriously restricted by taxonomic ambiguities and, probably, by high radiolarian diversities, as well as some other factors.

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APPENDIX Systematic reference list

- Acrosphaera murrayana* (Haeckel, 1887): Strelkov and Reshetnjak, 1971, p. 347, Fig. 25. *Choenicosphaera murrayana* Haeckel, Benson, 1966, p. 120, Pl. 2, Fig. 3. *Polysolenia murrayana* (Haeckel), Nigrini and Moore, 1979, p. S17, Pl. 2, Fig. 4 a, b. Remarks: see Bjørklund and Goll (1979) for detailed discussion concerning this generic name.
- Acrosphaera spinosa* (Haeckel, 1860): Strelkov and Reshetnjak, 1971, p. 340, Pl. 5, Fig. 33-38, Pl. 6, Fig. 39-41, 43, Pl. 8, Fig. 59; Boltovskoy and Riedel, 1980, p. 102, Pl. 1, Fig. 1-3; Takahashi and Honjo, 1981, p. 144, Pl. 1, Fig. 6. *Polysolenia* spp., Renz, 1976, p. 88, Pl. 1, Fig. 3.
- Buccinosphaera invaginata* Haeckel, 1887: Strelkov and Reshetnjak, 1971, p. 365, Pl. 4, Fig. 32; Nigrini, 1971, p. 445, Pl. 34.1, Fig. 2. *Collosphaera invaginata* Haeckel, Bjørklund and Goll, 1979, p. 1317, Pl. 3, Fig. 1-9. Remarks: it is our feeling that Bjørklund and Goll's (1979) amendment of the diagnosis of *Collosphaera* for encompassing collosphaerids with internal spines or tubules (e.g., *Buccinosphaera*) is not adequately justified. Hence, we prefer to use the original name, which in addition is unanimously accepted in the literature.
- Collosphaera glebulenta* Bjørklund and Goll, 1979, p. 1316, Pl. 2, Fig. 10, 11 (only).
- Collosphaera huxleyi* Müller, 1855: Strelkov and Reshetnjak, 1971, p. 332, Pl. 6, Fig. 21, 23, text-Fig. 19-21; Boltovskoy and Riedel, 1980, p. 103, Pl. 1, Fig. 5.
- Collosphaera macropora* Popofsky, 1917: Strelkov and Reshetnjak, 1971, p. 337, Pl. 4, Fig. 30, 31; Boltovskoy and Riedel, 1980, p. 103, Pl. 1, Fig. 6. ? *Collosphaera polygona* Haeckel, 1887, Strelkov and Reshetnjak, 1971, p. 338, Pl. 4, Fig. 26, 27; Renz, 1976, p. 86, Pl. 1, Fig. 10.
- Collosphaera tuberosa* Haeckel, 1887: Strelkov and Reshetnjak, 1971, p. 336, Pl. 4, Fig. 24, 25, text-Fig. 22; Boltovskoy and Riedel, 1980, p. 104, Pl. 1, Fig. 7.
- Siphonosphaera polysiphonia* Haeckel, 1887: Benson, 1966, p. 121, Pl. 2, Fig. 4; Takahashi and Honjo, 1981, p. 145, Pl. 1, Fig. 8. *S. polysiphonia* and *S. sp. cf. S. polysiphonia* Haeckel, Boltovskoy and Riedel, 1980, p. 104, 105, Pl. 1, Fig. 9, 10.
- Solenosphaera polymorpha* (Haeckel, 1887): Takahashi and Honjo, 1981, p. 146, Pl. 1, Fig. 12. *Otosphaera polymorpha* Haeckel, Nigrini, 1967, p. 23, Pl. 1, Fig. 8.
- Solenosphaera quadrata* (Ehrenberg, 1872): *Disolenia cf. variabilis* (Haeckel), Benson, 1966, p. 123, Pl. 2, Fig. 5. *Disolenia quadrata* (Ehrenberg), Nigrini, 1967, p. 19, Pl. 1, Fig. 5. *Solenosphaera pandora* Haeckel, Strelkov and Reshetnjak, 1971, p. 362, Pl. 10, Fig. 77, 78.
- Solenosphaera zanguebarica* (Ehrenberg, 1872): Strelkov and Reshetnjak, 1971, p. 360, Pl. 10, Fig. 74-76. *Disolenia zanguebarica* (Ehrenberg), Nigrini, 1967, p. 20, Pl. 1, Fig. 6; Renz, 1976, p. 87, Pl. 1, Fig. 2; Boltovskoy and Riedel, 1980, p. 105, Pl. 1, Fig. 11; Takahashi and Honjo, 1981, p. 145, Pl. 1, Fig. 11.
- Acanthosphaera actinota* (Haeckel, 1860): Boltovskoy and Riedel, 1980, p. 107, Pl. 1, Fig. 19. *Acanthosphaera tenuissima* (Haeckel), Renz, 1976, p. 99, Pl. 2, Fig. 1.
- Acanthosphaera pinchuda* Boltovskoy and Riedel, 1980, p. 108, Pl. 2, Fig. 1, text-Fig. 3.
- Actinomma arcadophorum* Haeckel, 1887: Nigrini, 1967, p. 29, Pl. 2, Fig. 3; Renz, 1976, p. 100, Pl. 2, Fig. 3.
- Actinomma leptodermum* (Joergensen, 1900): Nigrini and Moore, 1979, p. S35, Pl. 3, Fig. 7. *Echinomma leptodermum* Joergensen, Boltovskoy and Riedel, 1980, p. 111, Pl. 2, Fig. 9. Remarks: Bjørklund (1976a) synonymized *Echinomma* and *Actinomma*.
- Actinomma sol* Cleve, 1900: Boltovskoy and Riedel, 1980, p. 109, Pl. 2, Fig. 3. *Thecosphaera radians* Hollande and Enjumet, 1960, p. 111, Pl. 53, Fig. 4.
- Astrosphaera hexagonalis* Haeckel, 1887: Renz, 1976, p. 100, Pl. 2, Fig. 12; Takahashi and Honjo, 1981, p. 147, Pl. 2, Fig. 12.
- Cenosphaera elysia* Haeckel, 1887: Boltovskoy and Riedel, 1980, p. 106, Pl. 1, Fig. 14. *Cenosphaera riedeli* Blueford, 1982, p. 193, Pl. 1, Fig. 9 (only). Remarks: equatorial Pacific specimens have slightly fewer pores per quadrant than those described by Haeckel (1887) and by Boltovskoy and Riedel (1980).
- Cenosphaera favosa* Haeckel, 1887, p. 62, Pl. 12, Fig. 10 (non *C. favosa* Haeckel, in Blueford, 1982, p. 193, Pl. 1, Fig. 3, 4).
- Centrocubus octostylus* Haeckel, 1887, p. 278.
- Cladococcus cervicornis* Haeckel, 1860: Boltovskoy and Riedel, 1980, p. 110, Pl. 2, Fig. 5.
- Cromyechinus antarctica* (Dreyer, 1889): Petrushevskaya, 1967, p. 25, Fig. 13: 1-6, 14: 1-7; Boltovskoy, 1981, Fig. 155 a, a', 160: 30 a-c.
- Haliomma erinaceum* Haeckel, 1860: Renz, 1976, p. 101, Pl. 2, Fig. 4 a, b.
- ? *Acanthosphaera* sp. A, Takahashi and Honjo, 1981, p. 146, Pl. 1, Fig. 20.
- Haliomma* sp.
- Heliaster hexagonium* Hollande and Enjumet, 1960, p. 92, Pl. 41, Fig. 1, 2.

- Heliosphaera radiata* Popofsky, 1913: Benson, 1966, p. 160, Pl. 5, Fig. 1, 2.
- Hexacantium armatum* Cleve, 1900: Boltovskoy and Riedel, 1980, p. 112, Pl. 2, Fig. 10 A, B.
- Hexacantium axotrius* Haeckel, 1887: Boltovskoy and Riedel, 1980, p. 112, Pl. 2, Fig. 11; Takahashi and Honjo, 1981, p. 148, Pl. 3, Fig. 14. *Hexacantium laevigatum* Haeckel, Benson, 1966, p. 153, Pl. 4, Fig. 4 (only).
- Hexacantium entacanthum* Joergensen, 1900: Benson, 1966, p. 149, Pl. 3, Fig. 13, 14, Pl. 4, Fig. 1-3; Boltovskoy and Riedel, 1980, p. 112, Pl. 2, Fig. 12 A, B.
- Hexalonche anaximandri* Haeckel, 1887: Renz, 1976, p. 103, Pl. 2, Fig. 8; McMillen and Casey, 1978, Pl. 1, Fig. 8.
- Octodendron pinetum* Haeckel, 1887: ? [*Octodendron pinetum* Haeckel], Boltovskoy and Riedel, 1980, p. 113, Pl. 3, Fig. 2A, B.
- Plegmosphaera* sp. ? *Styptosphaera* sp., Takahashi and Honjo, 1981, p. 146, Pl. 1, Fig. 13.
- Pytiomma* sp.
- Spongodictyon spongiosum* (Mueller, 1858): Haeckel, 1887, p. 90. *Dictyosoma spongiosum* Mueller, 1858, p. 31, Pl. 2, Fig. 9-11. *Tetrasphaera spongiosa* Popofsky, 1913, p. 112, text-Fig. 23.
- Spongoplegma rugosa* Hollande and Enjumet, 1960, p. 104, Pl. 46, Fig. 3, Pl. 48, Fig. 6.
- Spongoplegma* sp. aff. *S. rugosa* Hollande and Enjumet, 1960.
- Spongosphaera streptacantha* Haeckel, 1862: Hollande and Enjumet, 1960, p. 97, Pl. 20, Fig. 5-7, Pl. 45, Fig. 4; Renz, 1976, p. 105, Pl. 2, Fig. 13.
- Stigmosphaera* sp.
- Stylosphaera melpomene* Haeckel, 1887, p. 135, Pl. 16, Fig. 1; Takahashi and Honjo, 1981, p. 147, Pl. 2, Fig. 14. *Styloactinarium bispiculum* Popofsky, 1913, p. 91, Pl. 2, Fig. 2; Benson, 1966, p. 141, Pl. 3, Fig. 8-11.
- Stylosphaera* sp. A. ? *Stylatractus* spp., Nigrini and Moore, 1979, p. S55, Pl. 7, Fig. 1 a, b.
- Stylosphaera* sp. B.
- Stylosphaera* sp. C.
- ? *Styptosphaera spumacea* Haeckel, 1887, p. 87. ? *Styptosphaera* ? *spumacea* Haeckel - Nigrini, 1970, p. 167, Pl. 1, Fig. 7, 8.
- Thecosphaera* ? *diplococcus* Haeckel, 1887, p. 81. ? *Thecosphaera* sp., Benson, 1966, p. 132, Pl. 2, Fig. 12 (only).
- Thecosphaera inermis* (Haeckel, 1860): Haeckel, 1887, p. 80.
- Actinomma inerme* Haeckel, 1862, p. 440, Pl. 24, Fig. 5.
- Thecosphaera phaenaxonia* Haeckel, 1887: ? *Thecosphaera entactinata* Haeckel, McMillen and Casey, 1978, p. 138, Pl. 1, Fig. 16.
- Thecosphaera* sp. aff. *Actinomma fenestratum* Stoehr, 1880, p. 94, Pl. 3, Fig. 2.
- Xiphatractus pluto* (Haeckel, 1887): Benson, 1966, p. 184, Pl. 7, Fig. 14-17; ? Takahashi and Honjo, 1981, Pl. 3, Fig. 4.
- Xiphostylus trogon* (Haeckel, 1887): *Lithomespilus trogon* Haeckel, 1887, p. 129, Pl. 14, Fig. 12.
- Didymocorytis tetrathalamus* (Haeckel, 1887): Sanfilippo and Riedel, 1980, p. 1010, text-Fig. 1 g. *Ommatartus tetrathalamus* (Haeckel), Renz, 1976, p. 107, Pl. 1, Fig. 6; Boltovskoy and Riedel, 1980, p. 114, Pl. 3, Fig. 3.
- Heliodiscus asteriscus* Haeckel, 1887: Nigrini, 1970, p. 168, Pl. 2, Fig. 1; Renz, 1976, p. 92, Pl. 2, Fig. 1; Boltovskoy and Riedel, 1980, p. 115, Pl. 3, Fig. 8.
- Sethodiscus macrococcus* Haeckel, 1887, p. 423, Pl. 33, Fig. 3; Boltovskoy and Riedel, 1980, p. 115, Pl. 3, Fig. 9 A, B. Remarks: some of these specimens merge with *H. asteriscus*.
- Amphirhopalum ypsilon* Haeckel, 1887: McMillen and Casey, 1978, p. 138, Pl. 3, Fig. 6; Boltovskoy and Riedel, 1980, p. 117, Pl. 3, Fig. 16; Takahashi and Honjo, 1981, p. 149, Pl. 5, Fig. 1.
- Dictyocoryne profunda* Ehrenberg, 1860: Renz, 1976, p. 92, Pl. 3, Fig. 1; Boltovskoy and Riedel, 1980, p. 115, Pl. 3, Fig. 10.
- Hymeniastrum euclidis* Haeckel, Nigrini, 1970, p. 168, Pl. 2, Fig. 4.
- Dictyocoryne truncatum* (Ehrenberg, 1861): Nigrini and Moore, 1979, p. S89, Pl. 12, Fig. 2 a, b. *Dictyocoryne* cf. *truncatum* (Ehrenberg), Benson, 1966, p. 235, Pl. 15, Fig. 1.
- Euchitonina elegans* (Ehrenberg, 1872): Nigrini and Moore, 1979, p. S83, Pl. 11, Fig. 1 a, b.
- Euchitonina furcata* Ehrenberg, 1872: Nigrini and Moore, 1979, p. S85, Pl. 11, Fig. 2 a, b.
- Hymeniastrum koellikeri* (Haeckel, 1862): Benson, 1966, p. 225, Pl. 12, Fig. 4-6. Remarks: this species is probably conspecific with *D. profunda*.
- Myelastrum* sp.: Myelastrinae subfamily group, Renz, 1976, p. 98, Pl. 3, Fig. 6.
- Porodiscus* sp. aff. *P. micromma* (Harting, 1863): Boltovskoy and Riedel, 1980, p. 117, Pl. 4, Fig. 1. *Porodiscus* (?) sp. B, Nigrini and Moore, 1979, p. S109, Pl. 14, Fig. 3, 4.
- Porodiscus* sp.: *Porodiscus* sp. A, Nigrini and Moore, 1979, p. S107, Pl. 14, Fig. 1, 2 a, b.
- ? *Spongaster pentas* Riedel and Sanfilippo, 1970, p. 523, Pl. 15, Fig. 3; McMillen and Casey, 1978, p. 138, Pl. 3, Fig. 14. *Spongaster* cf. *pentas* Riedel and Sanfilippo, Takahashi and Honjo, 1981, p. 149, Pl. 4, Fig. 10.
- Spongaster tetras* Ehrenberg, 1860: Boltovskoy and Riedel, 1980, p. 116, Pl. 3, Fig. 11. *Spongaster tetras tetras* Ehrenberg, McMillen and Casey, 1978, p. 138, Pl. 3, Fig. 12; Nigrini and Moore, 1979, p. S93, Pl. 13, Fig. 1; Takahashi and Honjo, 1981, p. 148, Pl. 4, Fig. 9.
- Spongocore cylindrica* (Haeckel, 1860): Boltovskoy and Riedel, 1980, p. 116, Pl. 3, Fig. 12. *Spongocore puella* Haeckel, McMillen and Casey, 1978, p. 138, Pl. 3, Fig. 9; Takahashi and Honjo, 1981, p. 149, Pl. 4, Fig. 20. *Spongocore diplocylindrica* Haeckel, Renz, 1976, p. 95, Pl. 3, Fig. 8.
- Spongodiscus resurgens* Ehrenberg, 1854: Petrushevskaya and Kozlova, 1972, p. 528, Pl. 21, Fig. 5; Boltovskoy and Riedel, 1980, p. 116, Pl. 3, Fig. 13; Takahashi and Honjo, 1981, p. 149, Pl. 4, Fig. 11.
- Spongodiscus* sp. A: Takahashi and Honjo, 1981, p. 149, Pl. 4, Fig. 13. *Spongodiscus* sp. aff. *S. resurgens* Ehrenberg, Renz, 1976, p. 96, Pl. 3, Fig. 10.
- Spongopyle setosa* Dreyer, 1889, p. 119, Pl. 11, Fig. 97, 98; Boltovskoy and Riedel, 1980, p. 116, Pl. 3, Fig. 14.
- Spongotrochus glacialis* Popofsky, 1908: Petrushevskaya, 1967, p. 43, Pl. 21, Fig. 21: I-VII, 22: I-VII, 26: I; Boltovskoy and Riedel, 1980, p. 117, Pl. 3, Fig. 15; Takahashi and Honjo, 1981, p. 149, Pl. 4, Fig. 17. *Spongotrochus multispinus* Haeckel, Renz, 1976, p. 97, Pl. 3, Fig. 9.
- Spongurus* sp. *Spongurus* (?) sp., Petrushevskaya, 1967, p. 33, Fig. 16: III, 26: I; Kling, 1977, p. 217, Pl. 2, Fig. 3.
- Stylochlamydidium asteriscus* Haeckel, 1887, p. 514, Pl. 41, Fig. 10; Boltovskoy and Riedel, 1980, p. 118, Pl. 4, Fig. 2. *Stylochlamydidium venustum* (Bailey), Kling, 1977, p. 217, Pl. 1, Fig. 5.
- Stylodyctia multispinata* Haeckel, 1860: Renz, 1976, p. 111, Pl. 3, Fig. 13; Boltovskoy and Riedel, 1980, p. 118, Pl. 4, Fig. 4A, B. *Stylodyctia validispina* Joergensen, Benson, 1966, p. 203, Pl. 9, Fig. 5, ?; Kling, 1977, p. 217, Pl. 2, Fig. 1; Nigrini and Moore, 1979, p. S103, Pl. 13, Fig. 5 a, b.
- Larcopyle buetschlii* Dreyer, 1889, p. 124, Pl. 10, Fig. 70; Benson, 1966, p. 280, Pl. 19, Fig. 3-5; Boltovskoy, 1981, p. 288, Fig. 155 b, b'.
- Larcospira quadrangula* Haeckel, 1887, p. 696, Pl. 49, Fig. 3; Benson, 1966, p. 266, Pl. 18, Fig. 7, 8; Renz, 1976, p. 90, Pl. 1, Fig. 12; Takahashi and Honjo, 1981, p. 150, Pl. 6, Fig. 2.
- Lithelius alveolina* Haeckel, 1887: Renz, 1976, p. 90, Pl. 1, Fig. 16.
- Lithelius minor* Joergensen, 1899: Benson, 1966, p. 262, Pl. 17, Fig. 9, 10; Kling, 1977, p. 217, Pl. 1, Fig. 16; Nigrini and Moore, 1979, p. S135, Pl. 17, Fig. 3, 4a, b.
- Lithelius* sp. aff. *L. spiralis* Haeckel, 1887: Boltovskoy and Riedel, 1980, p. 118, Pl. 4, Fig. 6.
- Pylospira octopyle* Haeckel, 1887, p. 698, Pl. 49, Fig. 4. *P. octopyle* Haeckel ?, Nigrini and Moore, 1979, p. S139, Pl. 17, Fig. 6 a, c. ? [*Pylospira octopyle* Haeckel], Boltovskoy and Riedel, 1980, p. 119, Pl. 4, Fig. 7. *Phorticium pylonium* (Haeckel), Benson, 1966, p. 252, Pl. 16, Fig. 8, 9 (only).
- Streblacantha circumtexta* (Joergensen, 1900): Bjørklund, 1976 b, Pl. 5, Fig. 9-12.
- Tholospira cervicornis* Haeckel group: Takahashi and Honjo, 1981, p. 150, pl. 5, Fig. 16-18.
- Octopyle stenozona* Haeckel, 1887, p. 652, Pl. 9, Fig. 11; Benson, 1966, p. 251, Pl. 16, Fig. 3, 4; Takahashi and Honjo, 1981, p. 150, Pl. 6, Fig. 7.
- ? *Phorticium clevei* (Joergensen, 1900): Petrushevskaya, 1967, p. 58, Fig. 32: I-II, 33: I-III, 34: I-V; Boltovskoy and Riedel, 1980, p. 119, Pl. 4, Fig. 10.
- Pylolela armata* Haeckel, 1887, p. 568, Pl. 48, Fig. 15. *Pylolela armata* Haeckel group, Takahashi and Honjo, 1981, p. 150, Pl. 6, Fig. 4. *Hexapyle dodecantha* Haeckel, 1887, p. 569, Pl. 48, Fig. 16; Benson, 1966, p. 275, text-Fig. 20, Pl. 18, Fig. 14-16; Renz, 1976, p. 113, Pl. 1, Fig. 11; McMillen and Casey, 1978, p. 138, Pl. 2, Fig. 22; Takahashi and Honjo, 1981, p. 150, Pl. 6, Fig. 3.

- Pylonium* sp. Benson, 1966, p. 250, Pl. 16, Fig. 2.
- Tetrapyle octacantha* Mueller, 1858: Benson, 1966, p. 245, Pl. 15, Fig. 3-10, Pl. 16, Fig. 1, text-Fig. 18; Boltovskoy and Riedel, 1980, p. 120, Pl. 4, Fig. 11.
- Acanthodesmia vinculata* (Mueller, 1857): Petrushevskaya, 1971 a, p. 278, Fig. 143: I-VIII, 144: I-VI; Boltovskoy and Riedel, 1980, p. 120, Pl. 4, Fig. 12; Takahashi and Honjo, 1981, p. 151, Pl. 7, Fig. 18, 19. *Eucoronis nephrosphyris* Haeckel, Benson, 1966, p. 304, Pl. 21, Fig. 6-8. *Giraffosphyris angulata* (Haeckel), Goll, 1969, p. 331, Pl. 59, Fig. 4, 6, 7, 9, text-Fig. 2; Renz, 1976, p. 167, Pl. 8, Fig. 5.
- Amphisphyris reticulata* (Ehrenberg, 1872): Goll, 1980, Pl. 6, Fig. 2-5. *Amphisphyris costata* Haeckel, Nigrini, 1967, p. 45, Pl. 5, Fig. 4; Takahashi and Honjo, 1981, p. 152, Pl. 8, Fig. 1, 2. *Liriosphyris reticula* (Ehrenberg), Goll, 1968, p. 1429, Pl. 176, Fig. 9, 11, 13. *Giraffosphyris circumflexa* Goll, 1969, p. 332, Pl. 60, Fig. 1-4, text-Fig. 2.
- Lophosphyris pentagona* (Ehrenberg, 1847).
Remarks: under this name specimens belonging to the subspecies *L. p. pentagona*, *L. p. hyperborea* and *L. p. quadriforis* (see Goll, 1976) have been lumped.
- Semantis* sp.
Tholosphyris anthophora (Haeckel, 1887): Goll, 1969, p. 324, Pl. 55, Fig. 1-4, text-Fig. 1; Goll, 1972, p. 967, Pl. 73, Fig. 1, 2, Pl. 74, Fig. 1-3.
- Tholosphyris* sp. ? *Tholosphyris* sp., Takahashi and Honjo, 1981, p. 152, Pl. 7, Fig. 16. *Lithocircus primordialialis* (Haeckel), Petrushevskaya, 1971 a, Fig. 137: VIII.
- Callimitra carolotae* Haeckel, 1887: Goll, 1979, p. 392, text-Fig. 1 (synon.); Robinson and Goll, 1978, p. 434, Pl. 1, Fig. 1-6, Pl. 2, Fig. 4-7, Pl. 3, Fig. 1-3. *Callimitra elisabethae* Haeckel, Takahashi and Honjo, 1981, p. 151, Pl. 7, Fig. 9, 10. *Callimitra emmae* Haeckel, Benson, 1966, p. 390, Pl. 25, Fig. 12. *Callimitra* sp., Renz, 1976, p. 162, Pl. 7, Fig. 1.
- Clathrocanium coarctatum* Ehrenberg, 1860: *Clathrocanium diadema* Haeckel, Takahashi and Honjo, 1981, p. 151, Pl. 7, Fig. 8. *Clathrocanium* cf. *coronatum* Popofsky, Benson, 1966, p. 394, Pl. 26, Fig. 1, 2. *Clathrocanium* spp., Renz, 1976, p. 163, Pl. 7, Fig. 5.
- Corocalyptra cervus* (Ehrenberg, 1873): Benson, 1966, p. 447, Pl. 30, Fig. 3-5; Renz, 1976, p. 129, Pl. 5, Fig. 2.
- Lampromitra sinuosa* Popofsky, 1913, p. 347, Pl. 31, Fig. 1, 2. *Ceratocyrtis sinuosa* (Popofsky), Petrushevskaya, 1971 a, p. 101, Fig. 53: II-VI. *Dictyophimus butschlii* Haeckel, Takahashi and Honjo, 1981, p. 152, Pl. 8, Fig. 14.
- Lophophaena* sp. aff. *L. capito* Ehrenberg, 1873: *Lophophaena* cf. *capito* Ehrenberg, Benson, 1966, p. 378, Pl. 24, Fig. 22, 23, Pl. 25, Fig. 1; Takahashi and Honjo, 1981, p. 151, Pl. 6, Fig. 22. *Lophophaenoma witjazii* Petrushevskaya, 1971 a, p. 118, Fig. 62: II-VII. *Lophophaenoma* sp. aff. *L. witjazii* Petrushevskaya, Renz, 1976, p. 159, Pl. 6, Fig. 14.
- Lophophaena hispida* (Ehrenberg, 1872): Petrushevskaya, 1971 a, p. 115, Fig. 61: I-III. *Lophophaena cylindrica* (Cleve), Renz, 1976, p. 159, Pl. 6, Fig. 21; Takahashi and Honjo, 1981, p. 151, Pl. 7, Fig. 2. *Acanthocorys variabilis* Popofsky, Benson, 1966, p. 373, Pl. 24, Fig. 19.
- Peridium spinipes* Haeckel, 1887, p. 1154, Pl. 53, Fig. 9; Takahashi and Honjo, 1981, p. 151, Pl. 6, Fig. 20. *Peridium* sp. aff. *P. spinipes* Haeckel, Boltovskoy and Riedel, 1980, p. 122, Pl. 5, Fig. 2. *Peridium* sp., Benson, 1966, p. 362, Pl. 24, Fig. 4, 5. *Psilomelissa calvata* Haeckel, Renz, 1976, p. 160, Pl. 6, Fig. 15.
- Peromelissa phalacra* Haeckel, 1887, p. 1236, Pl. 57, Fig. 11; Boltovskoy and Riedel, 1980, p. 122, Pl. 5, Fig. 3; Takahashi and Honjo, 1981, p. 151, Pl. 7, Fig. 3-5. *Lithomelissa monoceras* Popofsky, Renz, 1976, p. 158, Pl. 6, Fig. 12.
- Sethophormis aurelia* Haeckel, 1887, p. 1248, Pl. 55, Fig. 3; Petrushevskaya, 1971 a, p. 66, Fig. 29: II, 30; Renz, 1976, p. 165, Pl. 7, Fig. 16.
- Carpocanarium papillosum* (Ehrenberg, 1872): Nigrini and Moore, 1979, p. N27, Pl. 21, Fig. 3; Takahashi and Honjo, 1981, p. 155, Pl. 10, Fig. 17. *Dictyocephalus mediterraneus* Haeckel, Benson, 1966, p. 439, Pl. 29, Fig. 13.
Remarks: the generic assignment of this species follows Riedel and Sanfilippo's (1971) emended diagnosis of *Carpocanarium*.
- Carpocanidium* spp. *Carpocanidium petalosphyris* Haeckel, Benson, 1966, p. 434, Pl. 29, Fig. 9, 10, text-Fig. 25. *Carpocanidium* sp., Benson, 1966, p. 438, Pl. 29, Fig. 11, 12. *Carpocanidium obliqua* (Haeckel), Petrushevskaya, 1971 a, p. 240, Fig. 85: I-IV. *Carpocanistrum* spp., Renz, 1976, p. 151, Pl. 6, Fig. 4.
- Clathrocyclus cassiopeiae* Haeckel, 1887, p. 1390, Pl. 59, Fig. 5. *Clathrocyclus* ? sp., Benson, 1966, p. 457, Pl. 31, Fig. 2, 3.
- Cornutella profunda* Ehrenberg, 1854: Benson, 1966, p. 430, Pl. 29, Fig. 7, 8; Renz, 1976, p. 149, Pl. 7, Fig. 11; Boltovskoy and Riedel, 1980, p. 123, Pl. 5, Fig. 6 (synonymy); Takahashi and Honjo, 1981, p. 152, Pl. 8, Fig. 9.
- Corocalyptra columba* (Haeckel, 1887): Takahashi and Honjo, 1981, p. 153, Pl. 9, Fig. 16. *Corocalyptra killmari* Renz, 1976, p. 118, Pl. 4, Fig. 11.
- Dictyophimus hirundo* (Haeckel, 1887): Boltovskoy and Riedel, 1980, p. 124, Pl. 5, Fig. 20 (synonymy). *Pterocorys hirundo* Haeckel, Takahashi and Honjo, 1981, p. 154, Pl. 10, Fig. 6.
- Dictyophimus infabricatus* Nigrini, 1968, p. 56, Pl. 1, Fig. 6.
- Eucyrtidium acuminatum* (Ehrenberg, 1844): Nigrini, 1967, p. 81, Pl. 8, Fig. 3 a, b; Petrushevskaya, 1971 a, p. 217, Fig. 94, 95: I-III; Renz, 1976, p. 130, Pl. 5, Fig. 5.
- Eucyrtidium anomalum* (Haeckel, 1860): Benson, 1966, p. 496, Pl. 34, Fig. 4, 5; Petrushevskaya, 1971 a, p. 219, Fig. 98: I-IV; Renz, 1976, p. 131, Pl. 5, Fig. 8.
- Eucyrtidium dictyopodium siphonostomum* (Haeckel, 1887): Petrushevskaya, 1971 a, p. 218, Fig. 97: V (only).
Remarks: this species is probably conspecific with *Eucyrtidium hexastichum*.
- Eucyrtidium hexagonatum* Haeckel, 1887, p. 1489, Pl. 80, Fig. 11; Renz, 1976, p. 132, Pl. 5, Fig. 6. *Eusyringium siphonostoma* Haeckel, Benson, 1966, p. 498, Pl. 34, Fig. 6-9.
- Eucyrtidium hexastichum* (Haeckel, 1887): Petrushevskaya, 1971 a, p. 220; Renz, 1976, p. 132, Pl. 5, Fig. 9; Boltovskoy and Riedel, 1980, p. 124, Pl. 5, Fig. 10; Takahashi and Honjo, 1981, p. 153, Pl. 9, Fig. 12. *Lithostrobilus hexastichus* Haeckel, Benson, 1966, p. 506, Pl. 34, Fig. 13-16.
- Eucyrtidium* sp.
? *Eucyrtidium teuscheri* (Haeckel, 1887): Lithocampe (= *Eucyrtidium*) *teuscheri* (Haeckel), Petrushevskaya, 1971 a, Fig. 91: IV-VI.
- Lipmanella bombus* (Haeckel, 1887): Petrushevskaya, 1971 a, Fig. 101: I-VII. ? *Theopilium pyramidale* Popofsky, Renz, 1976, p. 126, Pl. 4, Fig. 13. ? *Dictyoceras pyramidale* (Popofsky), Takahashi and Honjo, 1981, p. 153, Pl. 9, Fig. 9.
Remarks: the generic name *Dictyoceras* (Haeckel, 1862) is a junior homonym of *Dictyoceras* Eichwald, 1860 (Mollusca) (cf. Petrushevskaya, 1981).
- Lipmanella virchowii* (Haeckel, 1860): *Dictyoceras acanthicum* Jørgensen, Benson, 1966, p. 417, Pl. 28, Fig. 8-10. *Lipmanella dictyoceras* (Haeckel), Kling, 1973, p. 636, Pl. 4, Fig. 24-26; Boltovskoy and Riedel, 1980, p. 125, Pl. 5, Fig. 12, (synonymy) *Dictyoceras neglectum* Cleve, Renz, 1976, p. 121, Pl. 4, Fig. 10. *Dictyoceras virchowii* Haeckel, Takahashi and Honjo, 1981, p. 153, Pl. 9, Fig. 7, 8.
- Lithopilium reticulatum* Popofsky, 1913, p. 379, Pl. 35, Fig. 4, 5; Renz, 1976, p. 164, Pl. 7, Fig. 2.
- Peripyramis circumtexta* Haeckel, 1887, p. 1162, Pl. 54, Fig. 5; Riedel, 1958, p. 231, Pl. 2, Fig. 8, 9; Boltovskoy, 1981, p. 291, 305, Fig. 160: 133; Takahashi and Honjo, 1981, p. 152, Pl. 8, Fig. 10, 11. *Cinclopyramis infundibulum* Haeckel, Renz, 1976, p. 149, Pl. 7, Fig. 12.
- Pterocanium praetextum* (Ehrenberg): Renz, 1976, p. 135, Pl. 5, Fig. 16 a, b; Takahashi and Honjo, 1981, p. 153, Pl. 9, Fig. 5, 6.
Remarks: although some of the specimens observed were undoubtedly assignable to either *P. p. praetextum* (Ehrenberg) or to *P. p. eucolpum* Haeckel (*sensu* Nigrini, 1967), most shells observed showed intermediate characteristics between both subspecies.
- Pterocanium trilobum* (Haeckel, 1860): Renz, 1976, p. 135, Pl. 5, Fig. 17. *Pterocanium proserpinae* Ehrenberg, Benson, 1966, p. 405, Pl. 27, Fig. 4 (? 3, 5).
- Theocalyptra davisiana* (Ehrenberg, 1861): Riedel, 1958, p. 239, Pl. 4, Fig. 2, 3, text-Fig. 10; Benson, 1966, p. 441, Pl. 29, Fig. 14-16.
- Theocalyptra* sp.
? *Theocorys veneris* Haeckel, 1887, p. 1415, Pl. 69, Fig. 5; Benson, 1966, p. 492, Pl. 33, Fig. 12, 13; Renz, 1976, p. 137, Pl. 5, Fig. 11, Takahashi and Honjo, 1981, p. 153, Pl. 9, Fig. 17. *Theocyrtis turris* Cleve, Boltovskoy and Riedel, 1980, p. 128, Pl. 5, Fig. 23.
- Theopilium tricostatum* Haeckel, 1887, p. 1322, Pl. 70, Fig. 6; Benson, 1966, p. 444, Pl. 30, Fig. 1, 2; Takahashi and Honjo, 1981, p. 152, Pl. 8, Fig. 12. *Theocalyptra* sp. Renz, 1976, p. 137, Pl. 5, Fig. 13.
- Anthocyrtidium ophirensense* (Ehrenberg, 1872): Renz, 1976, p. 143, Pl. 6, Fig. 25; Takahashi and Honjo, 1981, p. 154, Pl. 9, Fig. 22. *Anthocyrtidium cineraria* Haeckel, Benson, 1966, p. 472, Pl. 32, Fig. 6-9.

Lamprocyclus maritatis maritatis Haeckel, 1887: Nigrini, 1967, p. 74, Pl. 7, Fig. 5; Takahashi and Honjo, 1981, p. 154, Pl. 9, Fig. 26. *Lamprocyclus maritatis* Haeckel, Benson, 1966, p. 475, Pl. 32, Fig. 10-12; Renz, 1976, p. 145, Pl. 6, Fig. 26.

Lamprocyclus maritatis Haeckel, 1887, *polypora* Nigrini, 1967, Nigrini, 1967, p. 76, Pl. 7, Fig. 6; Takahashi and Honjo, 1981, p. 154, Pl. 9, Fig. 23, 24.

Lamprocyrtis nigrinae (Caulet, 1971): Nigrini and Moore, 1979, p. N81, Pl. 25, Fig. 7, *Conarachnium nigrinae* Caulet, 1971, p. 3, Pl. 3, Fig. 1-4, Pl. 4, Fig. 1-4. *Conarachnium* sp., Benson, 1966, p. 479, Pl. 33, Fig. 2, 3.

Pterocorys campanula Haeckel, 1887, p. 1316, Pl. 71, Fig. 3; Takahashi and Honjo, 1981, p. 154, Pl. 10, Fig. 4, 5. Remarks: this species is probably conspecific with *P. zancleus*.

Pterocorys hertwigii (Haeckel, 1887): *Eucyrtidium hertwigii* Haeckel, 1887, p. 1491, Pl. 80, Fig. 12. *Phormocyrtis fastuosa* (Ehrenberg), Benson, 1966, p. 485, Pl. 33, Fig. 6, 7. *Theoconus hertwigii* (Haeckel), Renz, 1976, p. 146, Pl. 6, Fig. 22.

Pterocorys zancleus (Mueller, 1858): Takahashi and Honjo, 1981, p. 154, Pl. 10, Fig. 1-3. *Theoconus zancleus* (Müller), Benson, 1966, p. 482, Pl. 33, Fig. 4, 5.

Pterocorys sp.

Theocorythium trachelium (Ehrenberg, 1872): Boltovskoy and Riedel, 1980, p. 127, Pl. 5, Fig. 22 (synonymy).

? *Udan undulata* Renz, 1976, p. 128, Pl. 4, Fig. 2 a, b.

Botryostrobus aquilonaris (Bailey, 1856): Nigrini, 1977, p. 246, Pl. 1, Fig. 1. *Siphocampium erucosum* (Haeckel), Benson, 1966, p. 527, Pl. 35, Fig. 18-20.

Botryostrobus auritus/australis (Ehrenberg, 1844) group: Nigrini, 1977, p. 246, Pl. 1, Fig. 2-5.

Spirocyrtis cornutella Haeckel, 1887, p. 1509, Pl. 76, Fig. 13; Petrushevskaya, 1971 a, Fig. 126: V-VIII; Boltovskoy and Riedel, 1980, p. 128, Pl. 5, Fig. 24.

Spirocyrtis scalaris Haeckel, 1887, p. 1509, Pl. 76, Fig. 14; Nigrini, 1977, p. 259, Pl. 2, Fig. 12, 13; Renz, 1976, p. 142, Pl. 6, Fig. 1.

Acrobotryssa cribosa Popofsky, 1913, p. 322, text-Fig. 29; Benson, 1966, p. 342, Pl. 23, Fig. 15, text-Fig. 22.

Botryocyrtis scutum (Harting, 1863): Nigrini and Moore, 1979, p. N105, Pl. 28, Fig. 1 a, b. *Haliomma scutum* Harting, 1863, p. 11, Pl. 1, Fig. 18. *Botryocyrtis* sp., Renz, 1976, p. 153, Pl. 7, Fig. 13.

Centrobotrys thermophila Petrushevskaya, 1965, p. 115, Fig. 20; Nigrini, 1967, p. 49, Pl. 5, Fig. 7, text-Fig. 26.