

Holocene Radiolaria from Sediments of the Gulf of California

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The following text is excerpted and revised from my 1966 Ph.D. thesis from the University of Minnesota, Minneapolis, Minnesota, USA, "Recent Radiolaria from the Gulf of California." It reflects the information about the Gulf of California (with a few more recent updates) and the state of radiolarian taxonomy available at that time. I am indebted to William R. Riedel of the Scripps Institution of Oceanography who introduced me to and first mentored me on the study of these beautiful siliceous protist skeletons.

In 2003, I spent two months in Oslo, Norway, with Kjell Bjørklund and Jane Dolven to revise and update the taxonomy of the radiolarian taxa I defined and described in 1966 and which now appear in www.radiolaria.org under Radiolarian species info: Holocene (Recent)--Gulf of California. The Appendix lists the revised names followed by Benson's (1966) names and cited illustrations that conform to our 2003 concept of each taxon.

I have included summaries of later studies of radiolarian distributions in the Gulf by Molina-Cruz (1986), Pisiás (1986), and Molina-Cruz et al. (1999). I have renamed taxa listed in those studies to reflect the updated taxonomy found in radiolaria.org. See the synonymies in radiolaria.org for each taxon for names used by the above authors in their studies.

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Gulf of California Radiolarian Sampling Sites and Procedures

Samples (prefix VS-R) of sediment from the uppermost part of 28 of the cores collected from the Gulf of California by the *Vermilion Sea Expedition* of 1959 were used in the study. The stations sampled are distributed throughout the Gulf from south of its entrance to the vicinity of the Colorado Delta in the north (Fig. 1, Table 1). The sample coverage is adequate for study of the regional distribution of radiolarians in the Gulf sediments but is inadequate for the determination of detailed biofacies. Also, Figure 1 shows the locations of DSDP Leg 65 coring sites (Benson, 1983).

The uppermost centimeter of each core collected by the *Vermilion Sea Expedition* was removed for study of live foraminifers (Phleger, 1964). The portions sampled for the present study represent the 1-3 cm or 3-5 cm depth intervals of these cores. Approximately 5-10 cm³ of sediment was sampled. Information on the sediments of the upper 10 cm of each core of the stations is given by van Andel (1964, "R" stations, Appendix B). On the basis of sedimentation rates determined by van Andel (1964, Table XVII), all samples are of Holocene age.

The HCl-insoluble, clay-free (>62 μm fraction) residues obtained from the sediments were mounted on permanent microscope slides for taxonomic study and making counts. The residues from nearly all stations contain predominantly radiolarians or diatoms.

During the course of taxonomic study it was necessary to observe tests in orientations other than those in the permanent slides. For this purpose wet slides were prepared from a portion of the sample residues. The residues were placed on a glass slide, a few drops of xylene were added, and Canada balsam was added. The residue was mixed with a dissecting needle. In order to prop up the cover glass a few grains of sand were added. By manipulation of the cover glass with a dissecting needle, specimens could be rolled to the orientation required for study.

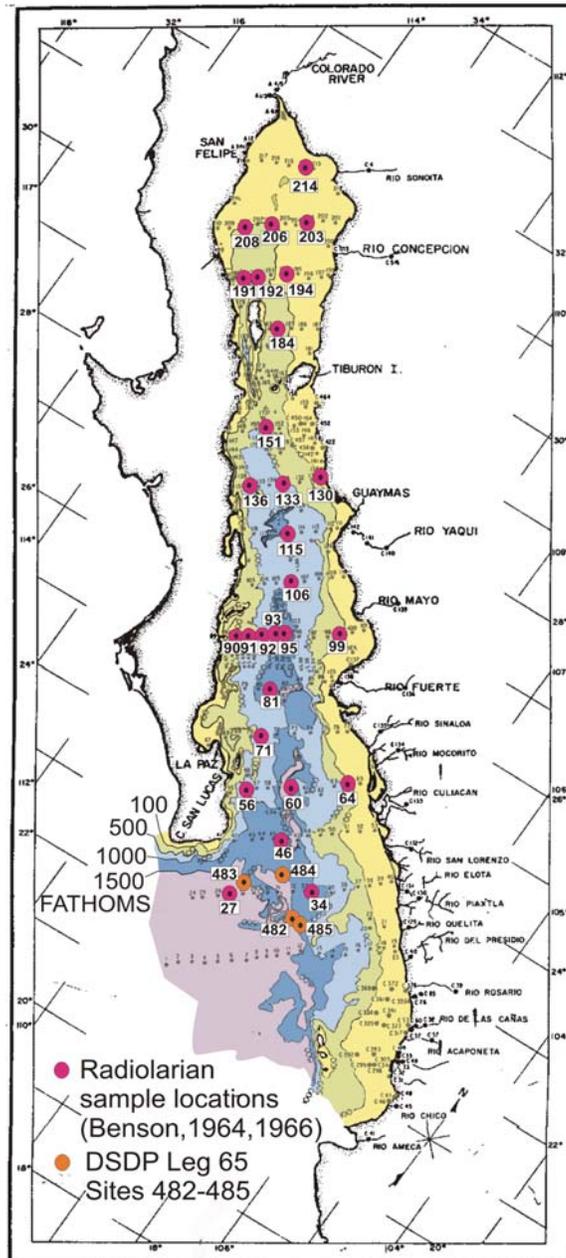


Figure 1. Map of the Gulf of California showing sample locations of Benson (1964, 1966, and 1983).

Table 1. Sample Station Locations and Water Depths

Station VS-R-	Latitude Degrees N	Longitude Degrees W	Water Depth Meters
27	22.64	108.87	2891
34	23.27	107.89	2370
46	23.65	108.63	2452
56	23.96	109.52	1738
60	24.34	108.97	2708
64	24.76	108.39	714
71	24.71	109.81	1263
81	25.32	110.11	2470
90	25.66	110.97	421
91	25.76	110.82	293
92	25.86	110.67	1107
93	25.97	110.48	1318
95	26.03	110.39	1696
99	26.43	109.75	348
106	26.66	110.77	1519
115	27.21	111.23	1781
130	28.01	111.30	113
133	27.74	111.64	1116
136	27.45	112.73	849
151	28.21	112.33	842
184	29.37	113.08	357
191	29.71	113.87	805
192	29.81	113.71	479
194	30.05	113.42	137
203	30.76	113.57	75
206	30.48	114.00	179
208	30.27	114.28	128
214	31.32	114.28	31

Gulf of California Submarine Topography

The Gulf of California is a young rifted ocean basin 600 miles long and averaging less than 100 miles in width. It trends NW-SE between the westward-dipping fault blocks of Baja California on the west and the westward-dipping fault blocks of the Mexican mainland on the east. It began to form between three and four million years ago when Baja California split away from the Mexican mainland.

The floor of the Gulf is characterized by a series of fault-controlled basins deepening to the south (Fig. 2), ranging from continental shelf depths (100 fathoms or less) in the north to near oceanic (1600-2000 fathoms) in the south. (van Andel, 1964). On both sides the Gulf is bounded by steep escarpments and ridges with slopes up to 38° but generally less than 15° . Steep slopes mostly of fault origin are most common on the western side. Well-developed shelves or terraces are confined to the eastern margin of the central and southern Gulf. The western margin has practically no shelf development, although there is a sharp shelf break along much of the coastline and around major islands at a depth of about 55 fathoms. The eastern shelf is wider and more continuous, ranging in width from a few to as much as 30 miles. Several canyons originate at the shelf break and terminate in small fans at the base of the slopes. Most of the canyons occur off the tip of the Baja California Peninsula. A large deep-sea fan occurs off the Rio Fuerte delta.

The northern part of the Gulf between Tiburon and Angel de la Guarda Islands and the mouth of the Colorado River is filled by thick alluvial deposits of the Colorado River. The floor of the Gulf here is smooth, bowl-shaped, and relatively shallow with depths not exceeding 200 fathoms. Sal si Puedes Basin is an elongate deep basin between Baja California and the chain of islands extending southeastward from Isla Angel de la Guarda. Sal si Puedes and Tiburon basins lack significant recent sediment cover, a fact which may be the result of non-deposition or scour by tidal currents in this constricted region of the Gulf.

In the central and southern Gulf four major elongated basins trend subparallel to the Gulf axis. From north to south these basins are Guaymas, Carmen, Farallon, and Pescadero. Mazatlan Basin is a smaller depression lying in the deep sea floor off the mouth of the Gulf and is separated from the Pescadero Basin to the north by a topographic rise. Rusnak, et al. (1964) state that the general rectangular shape and the zig-zag patterns of these basins appear to result from two intersecting sets of faults, and together the basins form a system of grabens *en echelon*. Major faults defining the basins trend about 30° west of the northwest-trending Gulf axis and are right-lateral strike-slip faults *en echelon*. Complementary orthogonal tension faults trend north, north-northeast, and northeast and are represented by central deeps that are orthogonal to the right-lateral slip traces of the major axial basins. The total displacement along the strike-slip faults has been estimated at between 160 and 240 nautical miles.

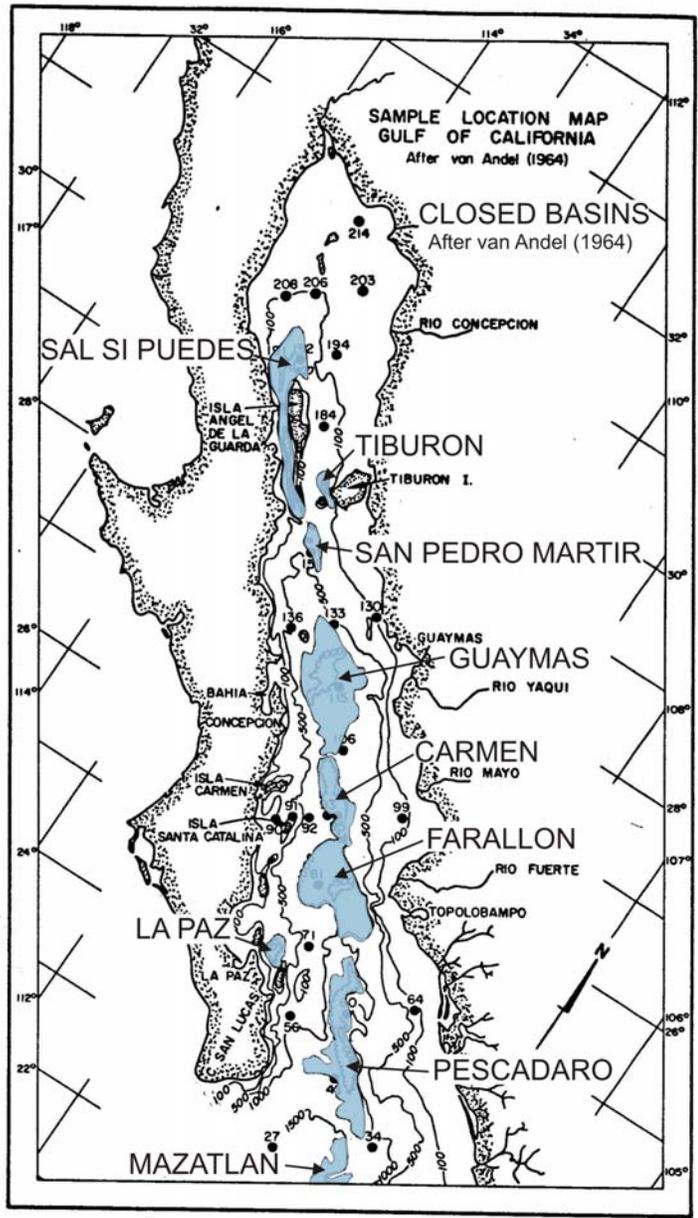


Figure 2. Closed basins of the Gulf of California.

Figure 3 shows the tectonic features of the Gulf of California. As described by Lewis, Robinson, et al. (1983, p. 5):

The crest of the East Pacific Rise extends northward...to the Tamayo Fracture Zone at the mouth of the Gulf. North of the Tamayo Fracture Zone, the rise is broken into a series of small spreading centers offset by...transform faults oriented obliquely to the axis of the Gulf...The spreading centers are expressed bathymetrically as deep basins which are partially filled with variable thicknesses of sediment derived from the adjacent land masses. New ocean crust is currently being formed along the crest of the East Pacific Rise and along short spreading segments within the Gulf itself. Thus, the Gulf of California represents a transition zone between a predominantly spreading environment on the south to a predominantly transform environment on the north [where it becomes the San Andreas transform fault]. Axial spreading in the Gulf occurs at a rate of about 6cm/yr.

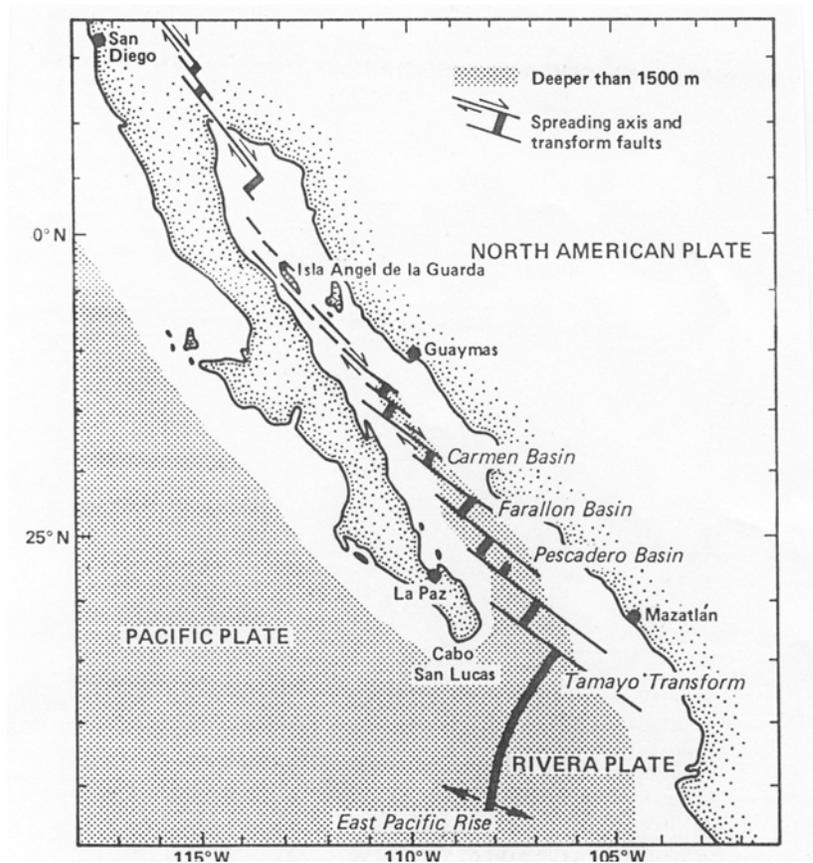


Figure 3. Tectonic features of the Gulf of California (Lewis, Robinson, et al., 1983).

Gulf of California Sediments

Surface sediments of the Gulf of California are described by Byrne and Emery (1960) and van Andel (1964). Heavy and light mineral studies by van Andel (1964) show that the highly immature sediments of the Gulf are derived primarily from local and rather unstable sediment sources. The northern Gulf is covered with Colorado River sediments probably deposited for the most part during the post-Pleistocene sea level rise with little or no modern deposition. On the whole, transportation appears to be mainly longitudinal in this region. The central and southern Gulf, however, are filled entirely from the sides, and there is little if any longitudinal transportation. The eastern margin with its higher precipitation and with many permanent streams is a much more prolific supplier of sediment than the arid Baja California Peninsula. The zone of marine sediments derived from the Peninsula is relatively narrow and terminates approximately at the foot of the western slope. The eastern sources supply not only all the sediments forming the wide coastal plain and covering the continental shelf and slope, but also extend into most of the Gulf basins.

Van Andel (1964) describes the lithofacies of the Gulf as follows. In general, fine-grained sediments predominate, particularly in the southern and central Gulf. More than half of these deposits are diatomaceous. Diatomites begin as slope deposits north of the Fuerte River but cover the entire central Gulf below the edge of the continental shelf. They continue well into the northern Gulf, particularly around Isla Angel de La Guarda. Silty clays predominate both on the slopes and in the basins of the southern Gulf where biogenous silica production is much lower with respect to terrigenous sediment supply. On the rugged western slope north of La Paz, coarse, locally highly glauconitic, foraminiferal calcarenites extend from the shelf edge to approximately 300 fathoms. They show ample evidence of down-slope displacement. Highly volcanic coarse sands and gravels are found north and south of the sills separating the Sal si Puedes Basin from the central Gulf. Finer and more uniform sands occur southeast of Tiburon Island. Silty clays fringe the deep-water portion of the Sal si Puedes Basin and occur in some of the deepest parts east of Isla Angel de la Guarda. Around isolated banks and hills sandy foraminiferal and radiolarian sediments are found. Sediments of the narrow western shelf are coarse, very calcareous sands and calcarenites and reflect low terrigenous sediment supply. Such sediments are generally absent from the eastern shelf whose sediments are less coarse and not very calcareous. On the outer shelf and upper slope a transitional zone of clayey silt is well-developed. Similar clayey silts occur off the Colorado and Concepcion River deltas. These clayey silts are separated almost everywhere from the coast and the rivers that supplied them by a wide belt of glauconitic and foraminiferal sand, commonly mottled in structure. Similar sands occupy a very large, shallow area in the northern Gulf. Sands southeast of Tiburon Island differ from all other shelf sands in the general absence of glauconite and calcareous components.

Biogenous Components. Van Andel (1964) discusses the importance of the biogenous deposits of the Gulf of California. The distribution of radiolarians (Fig. 4) shows that percentages of the 60-250 μm fractions are high outside the Gulf and decrease from the Pacific toward the upper Gulf. Radiolaria are concentrated on the slopes rather than on the basin floors, particularly in the central Gulf. Percentages are reduced in areas of rapid deposition, e.g., around Cape San Lucas and off the Fuerte and Yaqui River deltas. In general, the radiolarians form less than one per cent by weight of the Gulf sediments. In deep-water deposits outside the Gulf and in slope sediments of the southern Gulf, up to 50 per cent of the coarse fraction may consist of radiolarians, except where dilution with terrigenous

material is high. In the central Gulf they are important only in slope deposits, and their percentage is much reduced because of the high frequency of diatoms. In the north-central and northern basins radiolarians are restricted to the fine-grained sediments of the deepest parts and normally are absent in the coarser sediment of the zone above 200-300 fathoms because of dilution with terrigenous sand.

Diatoms are quantitatively much more important and may constitute up to 50 per cent of the sediments of the central Gulf (Fig. 5). South of latitude 26° N., however, biogenous silica is almost exclusively radiolarian. Diatoms are concentrated on the slopes in the southern and central Gulf, but percentages are higher on the western slopes because of less dilution with terrigenous sand. In the north-central and northern Gulf, the fine-grained deposits of the basins contain large numbers of diatoms, whereas the sandy slopes are barren, a situation parallel to that of the radiolarian distribution. The coarse fractions of shelf and nearshore areas only locally contain significant percentages of diatoms.

Foraminifers occur principally in the coarse fraction. Planktonic foraminifers are widespread in the Gulf except near Cape San Lucas, on the sandy slopes of the north-central Gulf, and in shelf areas. Benthic foraminifers are most abundant on slope areas and have a more uniform distribution along the western slope in contrast to the eastern slope. They are almost absent in the basins of the central and southern Gulf.

The average organic carbon content of the Gulf sediments is strikingly high, ranging from 0.8-7.4% on the slopes and 0.4-4.0% in the basins (van Andel, 1964). The organic carbon distribution appears to possess the same concentration on slopes as does the biogenous components mentioned above. Primary factors in this distribution are the rates of organic productivity, deposition, and decomposition.

In summary, van Andel (1964) states that biogenous silica and organic matter are concentrated on the slopes rather than in the basins. The amounts of terrigenous sand in the slope sediments are not greater than those in the basin sediments. The coarse fraction of slope samples is significantly richer in radiolarians, diatoms, and benthic foraminifers than is the coarse fraction of the basin sediments. This is not true with the planktonic foraminifers. Slope sediments in the central Gulf do not appear to contain more biogenous opal in all fractions combined than do the basin sediments. If approximately 1 to 3 per cent of coarse biogenous components and organic carbon were removed from slope samples, they would be indistinguishable from basin deposits. Van Andel (1964) concludes that the concentration of biogenous material on the slopes is a result of (1) the higher relative rate of biogenous deposition near the sources of high productivity along the Gulf margins, e.g., areas of upwelling, (2) the preservation of the more perishable products on the slope regions which coincide with the oxygen minimum zone in the Gulf (less than 0.5 ml/l between 100 and 700 fathoms), and (3) the suggestion of sorting processes which concentrate coarse biogenous material on the slopes, allowing fine particles, including organic matter, to be uniformly distributed.

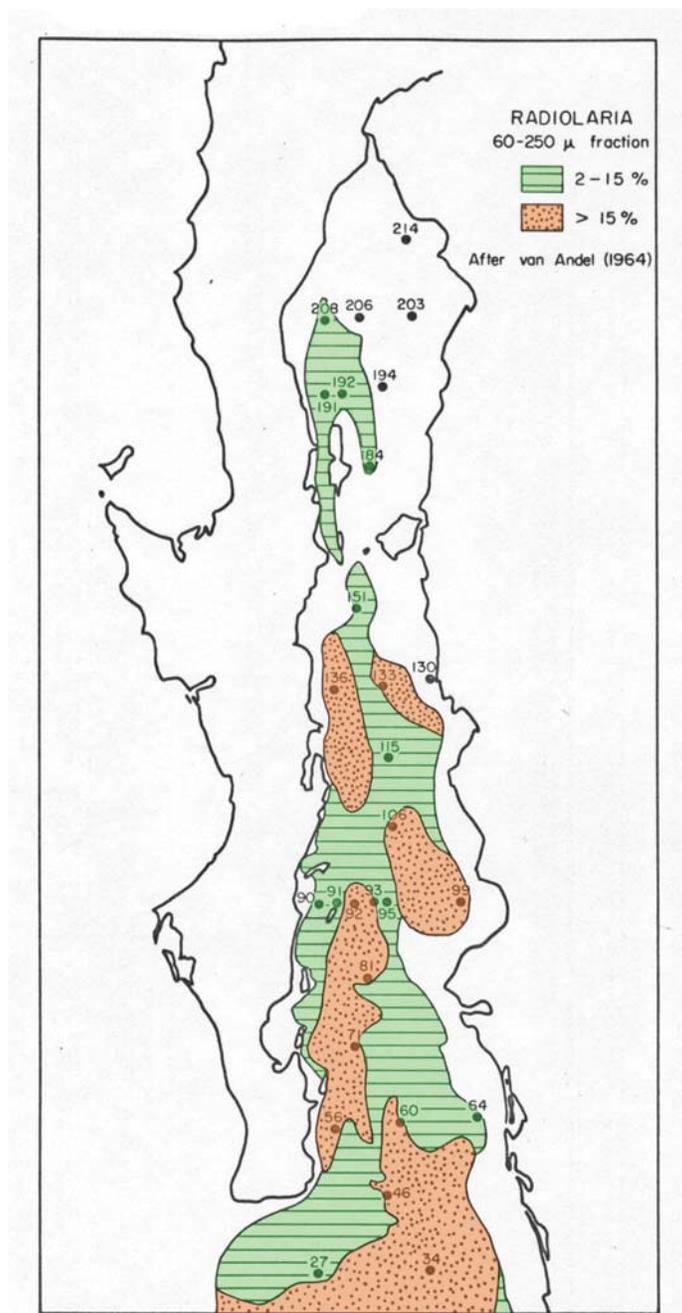


Figure 4. Percent radiolarians in 60-250 μm fraction of surface sediments.

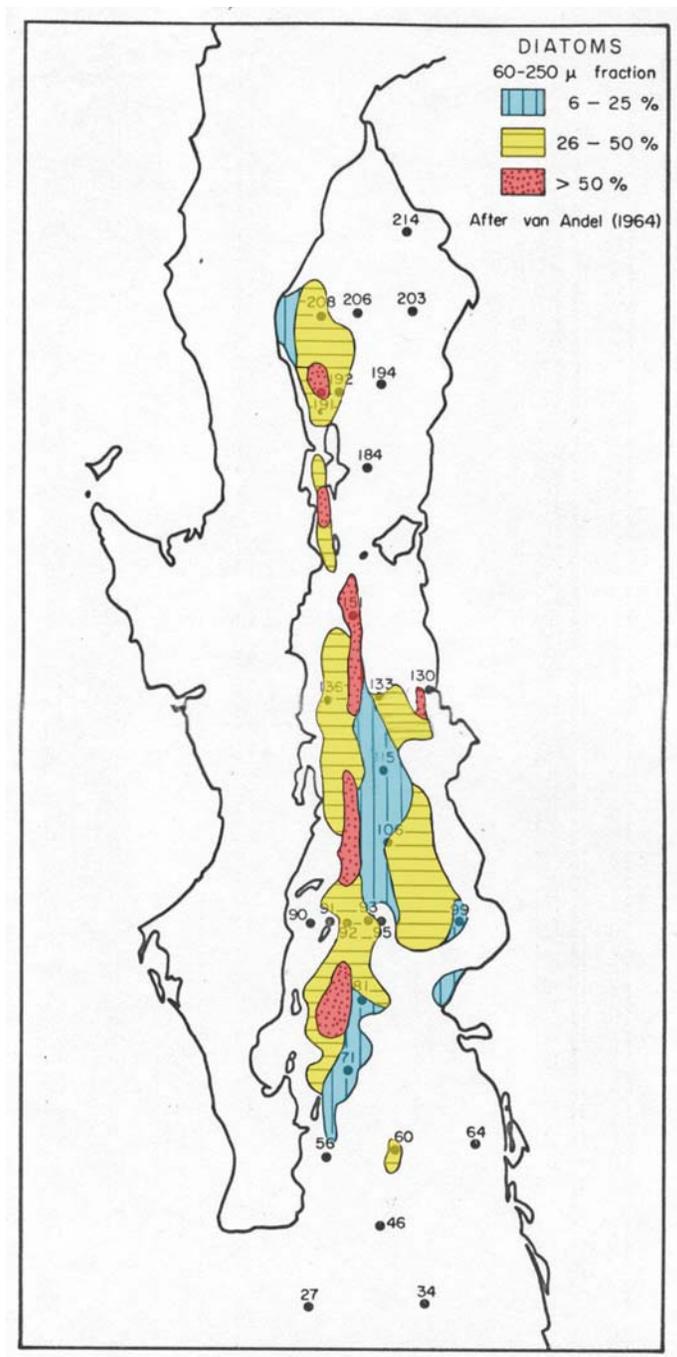


Figure 5. Percent diatoms in 60-250 μ m fraction of surface sediments.

Gulf of California Climate and Oceanography

The following summarizes the state of knowledge in 1966 of Gulf of California climate and oceanography. More recent information may be found in Molina-Cruz (1988) and Molina-Cruz et al. (1999).

Climate. The climate ranges from dry, desert-like in the north with mean annual rainfall less than 10 cm, through dry steppe and mild in the middle (mean annual rainfall 10-25 cm), to tropical savanna at both sides of the mouth (mean annual rainfall 50-75 cm or more). In general, the west coast of the Gulf receives only half as much rain as the east coast (Roden, 1958). The range in mean annual air temperature increases from about 6°C (January mean 22°C, July mean 28°C) at Cabo Corrientes, on the mainland of Mexico between latitudes 20° and 21°N., to 18°-20°C near the mouth of the Colorado River (January mean 14°C, July mean 34°C). Winds in the Gulf are extremely variable. Near the coast the land and sea breeze system prevails. In the offshore regions northwesterly winds prevail throughout the entire Gulf during winter and are responsible for upwelling along the east coast. During the summer southeasterly winds prevail in the southern half of the Gulf but blow for only one or two months in the northern half. They are responsible for upwelling along the west coast. Violent storms known as chubascos occur during the rainy season from June to October in the southern Gulf. Hurricanes are most common in September and October. Those which enter the Gulf are dissipated before they reach the islands of Tiburon and Angel de la Guarda.

Horizontal Distribution of Properties. Evaporation from the sea surface is responsible for the high salinity of the surface waters of the Gulf (34.8-36.0‰). Over the entire surface of the Gulf Roden (1958) estimated the rate of evaporation as 5.25×10^{11} m³/year or 1.7×10^4 m³/sec. Evaporation exceeds precipitation during all months of the year. The salinities at a depth of 10 m range mostly between 35.0 and 35.8‰ in the northern two-thirds of the Gulf and are 1‰ to 2‰ higher than those at comparable latitudes outside the Gulf. In the southern third of the Gulf, between Cabo San Lucas, Cabo Corrientes, and the Mexican mainland, offshore salinities range mostly between 34.6‰ and 35.0‰ (Roden, 1964). The lowest salinities are found off river mouths in the southeastern part of the Gulf during the rainy season whereas the highest salinities occur in shallow protected bays where evaporation is strong. The average salinity of the upper 200 m shows almost no seasonal variation (Roden and Groves, 1959). The dilution effect of the Colorado River and other rivers entering the Gulf is apparently negligible. Byrne and Emery (1960) state that Roden's estimate of the rate of inflow of water into the Gulf is about 1200 times the average annual addition of water to the Gulf by runoff of streams.

The water temperatures at a depth of 10 m are warmer from April to September and about equal during the remaining months of the year as compared to those in the neighboring Pacific. The annual range in offshore as well as coastal areas is large and increases from about 9°C (21°C-30°C) near Cabo Corrientes to about 15°C (16°C-30°C) near the mouth of the Colorado River (Roden, 1964). Throughout the year lower temperatures prevail around Isla Angel de la Guarda which is an area characterized by strong tidal mixing. In winter low temperatures along the east coast and in lee of Isla Tiburon are related to upwelling caused by northwesterly winds. Upwelling caused by southeasterly winds in summer leads to lower temperatures along the west coast (Roden and Groves, 1959).

Dissolved oxygen content in the surface waters ranges between 4 and 6 ml/l and in

some places reaches concentrations of 9 ml/l. The highest concentrations occur in spring, thus indicating high biological activity. The surface waters are generally saturated with respect to oxygen, and deviations of more than 15% from the saturation value occur only rarely (Roden and Groves, 1959). Undersaturation frequently occurs in the vicinity of Isla Tiburon and Isla Angel de la Guarda.

Vertical Distribution of Properties. The bulk of water in and near the central and southern Gulf of California below the thermocline is nearly the same as in the equatorial Pacific (Roden, 1958). At the surface this water is slightly modified by extensive evaporation and, seaward from Cape San Lucas, by admixture with water brought south by the California Current. At depth the salinity minimum of the Gulf waters lies between 34.5‰ and 34.6‰ and has a corresponding temperature of between 5°C and 7°C.

Roden (1958) divides the Gulf waters into (1) a shallow upper layer 20-40 m deep where the distribution of properties is rather uniform due to wind stirring, (2) a layer between approximately 50 and 150 m that varies with the season and where the temperature, salinity, and oxygen content decrease rapidly, and (3) a deep layer between the thermocline and the bottom where the concentrations remain fairly constant from one season to another. Salinity shows a minimum (34.48-34.54‰) between 600 and 800 m and increases slightly toward the bottom. There is no oxygen minimum in the northern Gulf between the Colorado River and Tiburon Island, but a pronounced minimum (less than 0.5 ml/l) is present south of this region between approximately 100-200 and 1,200 m. Below 1,200 m the values rise again to 1 ml/l in the southern basins and even higher at the Gulf entrance (Parker, 1964). The zone of minimum oxygen values intersects the slopes of the Gulf. Waters overlying the slopes are the sites of maximum upwelling and abundant plankton blooms. Calvert (1964) correlates the presence of laminated diatomites on the slopes with the oxygen minimum zone. Laminations in these regions are preserved due to the lack of burrowing organisms.

The upper 200 m of water in different regions of the Gulf are characterized in Table 2. Each region is characterized by Roden (1964) as follows.

The northern Gulf represents the region between the Colorado River and Isla Tiburon. It is characterized by large seasonal and year-to-year changes of temperature and salinity in the upper 150 m. In spring the salinities tend to be higher along the Baja California coast than along the Sonoran coast. In summer the highest salinities occur in the more central parts of the Gulf. Convective overturn due to winter cooling is possible but has not been documented. It can be expected to reach to roughly 100 m but only near the coast. Roden (1958) cites Sverdrup et al. (1941) who states that cooling of high saline water in winter leads to the formation of a bottom water mass (temperature above 10°C, salinity above 34.9‰ and with a relatively high oxygen content). This water fills the basins of the northern shelf and moves southward along the coast of Baja California.

The Ballenas Channel is coincident with the Sal si Puedes Basin between the coast of Baja California and Isla Angel de la Guarda and the chain of islands extending southeastward from it. The sill depth of this channel is 250 m. Below this, high temperatures, salinities, and oxygen concentrations prevail and the water at great depths has the same properties as those at sill depth. Apparently this is the result of tidal mixing. Strong tidal currents have been observed in the channel. Above 250 m the exchange of water between the northern and southern parts of the Gulf is unrestricted.

Table 2. Range of Temperature, Salinity, and Oxygen in the Upper 200 Meters of Gulf of California Waters

After Roden (1964) and Roden and Groves (1959)

	Water Depth(m)	Temperature (°C)	Salinity (‰)	Oxygen (ml/l)
Northern Gulf	10	14-30	35.0-35.8	4.5-5.5
	150	14-17	35.2	2.0-3.0
Ballenas Channel	10	15-29	35.2-35.4	3.4-.0
	200	13-15	35.1-35.2	2.0-3.0
Central Gulf	10	16-30	34.8-35.4	3.6-6.0
	200	12-14	34.9-35.0	0.5-3.0
Southern Gulf	10	20-30	34.6-35.2	4.4-6.0
	200	12-13	34.8-34.9	0.1-0.5

The central part of the Gulf represents the region between Isla Tiburon and Topolobampo. The water is in open communication with the Pacific Ocean. Below the thermocline, which is well developed between April and October, the water is essentially the same as in the equatorial Pacific. Roden and Groves (1959) refer to the water above the thermocline as “Gulf water” which is equatorial water that has been transformed at the surface by evaporation. The distribution of temperature, salinity, and oxygen concentration in this water is complicated by upwelling along the east coast in winter and along the west coast in summer. In late summer there is a salinity minimum between 25 m and 75 m in the eastern half of the Gulf and a maximum off the Baja California coast. The former probably represents a summer surface current that flows northward along the coast of Mexico and enters the Gulf of California. The latter may represent either a southward movement of high-salinity water from the northern regions of the Gulf or may indicate the influence of Bahia Concepcion, the salinity of which is very high (36.3‰) (Roden, 1964).

The southern Gulf between Topolobampo and Cabo Corrientes has a well developed thermocline throughout the year. The distribution of temperature, salinity, and oxygen concentration in the upper 200 m during winter and spring is complicated by upwelling, by northward flow of low salinity water (less than 34.7‰) at about 100 m in the axial portion, and by southward flow of high salinity water at a depth of about 50 m along the west coast. During June and August the upper salinity minimum extends across the Gulf at a depth of 50-100 m with minimum values between 34.5‰ and 34.7‰. Below 200 m the distribution of temperature, salinity, and oxygen is similar to that in the central Gulf.

General Circulation. Direct measurements of surface currents in the interior regions of the Gulf have not been made. Ship drift indicates a predominant southeasterly flow in winter and spring and a northwesterly flow in summer and fall (Roden, 1964).

Exchange of water between the Gulf and the Pacific Ocean must compensate each other closely. Across latitude 23°N, Roden (1958) estimated the exchange of water and salt assuming conservation of these properties. He observed that inflow nearly balances outflow. During winter if it is assumed that outflowing water extends over a depth range of 50 m and inflowing water over 1500 m, the velocity of the former is 7 cm/sec and of the latter is 0.3

cm/sec. Later, Roden (1964) estimated that the net surface current across the Gulf entrance is 10 cm/sec in February and represents outflow, and in August it is 21 cm/sec and represents inflow. These are in reasonable agreement with the observed ship drifts.

Roden (1964) states that the available data are insufficient to decide whether compensation takes place by opposite flow at different levels, or by opposite flow along the shores of the Gulf, or both. Earlier studies indicate opposite flow along the shores. At subsurface depths of 200 m and 400 m Roden (1958) reports a tongue of warm, high saline and oxygen-rich water moving out of the Gulf along the coast of Baja California and a tongue of low saline, cool, and oxygen-poor water entering the Gulf from the south. The former possibly originates in the northern Gulf as the bottom water mass mentioned previously, and the latter shows the same characteristics as the equatorial Pacific water. The data for these conclusions were obtained during February and March, 1939. Byrne and Emery (1960) state that data collected during the winter of 1957 verify Roden's earlier conclusions. Roden and Groves (1959) state that outflow of Gulf water seems to occur along the western coast, often at depths around 50 m, and that inflow occurs mostly along the east coast and is concentrated around 100 m. Indirect evidence that currents on both sides of the Gulf flow in opposite directions is given by Parker (1964). The northward flowing current along the eastern margin apparently accounts for the presence of Panamic species of macro-invertebrates with planktonic larvae in the Gulf. Many mollusk and crustacean species that occur on the eastern side of the Gulf are absent on the western side and vice versa. Swain (1966) states that about twice as many species of Ostracoda are restricted to the western side as to the eastern side. This may be the result of currents on both sides that flow in opposite directions.

Cool, low saline water of the California Current does not enter the Gulf. Roden (1958) describes a front seaward from Cape San Lucas as well as one in the vicinity of Cabo Corrientes. Outflowing Gulf water pushes aside the water of the California Current in the vicinity of Cabo San Lucas; consequently, the latter cannot enter the Gulf. Phleger (1964) states that oceanic water entering the Gulf is entirely from the tropical Pacific. Living planktonic foraminifers in the Gulf are exclusively of the West Central Pacific planktonic foraminiferal fauna. The benthic fauna (mainly mollusks) belongs to the Panamic-Pacific zoogeographic province. The presence in the Gulf of three benthic foraminiferal species previously reported only from off Central America indicates an affinity of the Gulf fauna with that of the Panamic zoogeographic province. Most of the other species, however, live in the California areas as well. Swain (1966) states that among the 91 species of Ostracoda in the Gulf, more than half are indigenous, whereas about 20% are derived from Pacific coastal regions from Central America to southern California and another 20% from the Caribbean-Gulf of Mexico region. Because the complete world-wide distribution pattern of living radiolarian species is unknown, the immediate source of the Gulf assemblage is unknown. Because the waters of the Gulf are derived from the eastern Equatorial Pacific, the radiolarian assemblage in the Gulf is regarded as tropical Pacific.

Upwelling and Biological Productivity. The distribution of areas of known upwelling in the Gulf is shown in Figure 6. Roden and Groves (1959) state that with northwesterly winds during winter, upwelling occurs along the east coast. Predominantly southeasterly winds during summer are responsible for upwelling along the west coast. The areas of upwelling are found mostly in wind lee of capes, points, and islands. The upwelled water is of low temperature and is usually of low salinity except along the west coast, where an intermediate salinity maximum is present at a depth of 50 m.

The areas of upwelling correspond fairly closely to known occurrences of plankton

blooms in the Gulf (Fig. 7). An extensive area of blooms also corresponds to the region of strong tidal mixing in the Ballenas Channel.

Roden (1958) states that upwelling is important in the Gulf as a means of replenishing the depleted surface layers with plant nutrients from below. Unfortunately, no data on the concentration of plant nutrients in regions of upwelling are available. Roden further states that increased wind mixing and winter convective overturn may be of equal importance in fertilizing the surface waters. The latter is important in the northernmost part of the Gulf. Apparently strong tidal mixing is likewise important in this respect.

Van Andel (1964) states that, based on the available data, plankton blooms, and, therefore, organic productivity, occur primarily along the Gulf margins and in part over shelf areas. Although data on water chemistry are not published, Revelle (1950) states that silica and phosphate were present in very low concentrations in the surface waters of the Gulf prior to the development of northwesterly winds of gale force, beginning in November. With the development of these winds warm surface waters were blown southward. Upwelled water from moderate depths was cooler and lower in oxygen concentration. Measurements of dissolved silica and phosphate showed a marked increase in the surface layers. As these nutrients were utilized by growing diatoms and other phytoplankton, they underwent a marked decrease. Measurements of the amount of oxygen liberated in one day *in situ* between the surface and 40 m revealed approximately 2 mg/cm²/day of dry organic matter production, or about 100 pounds of diatoms per acre per day. At the same time quantitative phytoplankton samples showed a marked increase. During and immediately after the blooms, the number of diatoms falling to the bottom is great (Byrne and Emery, 1960).

Byrne and Emery (1960) summarize studies of the diatoms in the Gulf. More than 31 genera and 67 species have been reported, but most of the frustules remaining in the sediments are of *Thalassiothrix longissima*, *Coscinodiscus* sp., and *Pseudoeunotia doliolus*. Dissolution of silica destroys many of the frustules. Revelle (1950) states that in contrast to open sea areas where frustules are dispersed and dissolved, the deep waters of the Gulf contain an abundance of frustules, and determinations of dissolved silica indicate that the deep waters have about 30 per cent more silica in solution than do those of the open sea. The amount of silica in the deep water increases from the mouth of the Gulf to the central Gulf west of Guaymas. Revelle (1950) suggests that diatoms settle in the latter region without dissolving because the deep waters are nearer to saturation with respect to silica. No specimens of radiolarians from the Gulf sediments show significant signs of dissolution, regardless of their size.

Revelle (1950), Byrne and Emery (1960), and van Andel (1964) conclude that the Gulf of California acts as a sink for Pacific silica. Silica-rich Pacific water enters the Gulf at moderate depths and is brought to the surface by means of upwelling. Diatom blooms lead to a continuous accumulation of silica on the Gulf floor. Van Andel (1964) states that the annual supply of silica by means of water exchange between the Gulf and the Pacific Ocean is more than enough to account for all the biogenous opal formed. Byrne and Emery (1960) state that although the concentration of dissolved silica in the Gulf waters even at depth is less than that of the Colorado River (10 versus 14 ppm SiO₂), the much greater volume of incoming sea water than of river flow— 3.75×10^{13} m³/year versus 37,469 m³/year for all river flow into the Gulf (Roden, 1958; van Andel, 1964)—means that upwelled sea water can supply many hundred times more silica to diatoms than can the rivers.

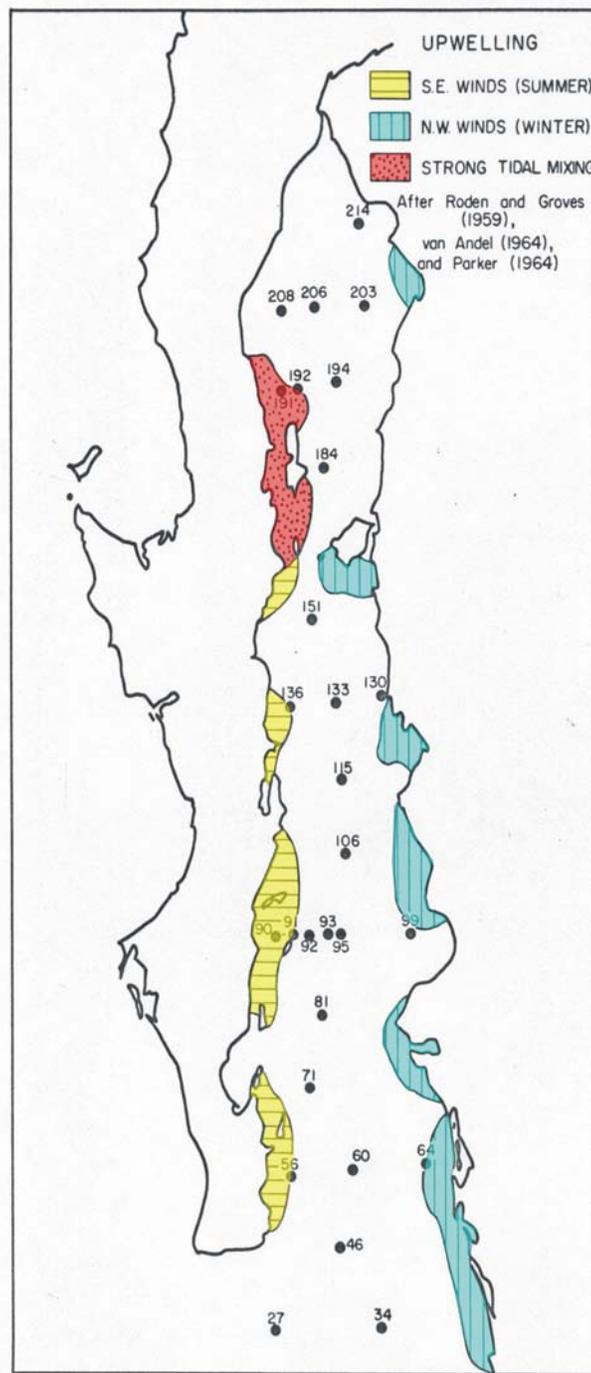


Figure 6. Areas of upwelling in the Gulf of California.

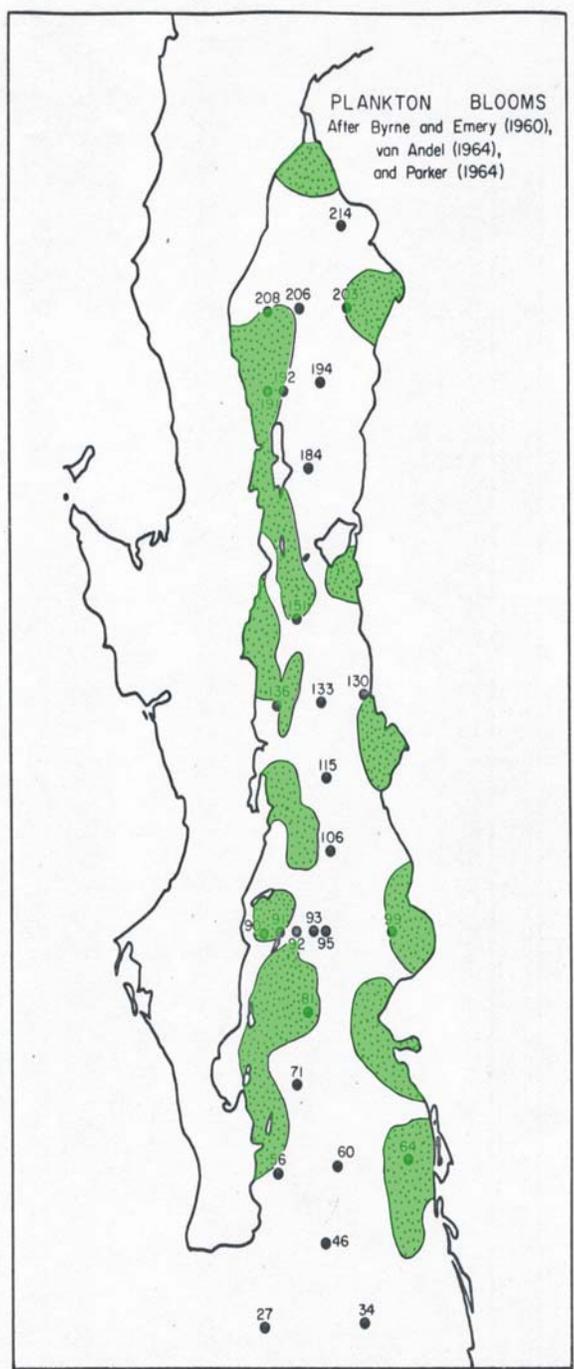


Figure 7. Areas of observed plankton blooms in the Gulf of California.

Distribution of Radiolarians in Surface Sediments of the Gulf of California (Benson, 1966)

All permanent slides prepared from the HCl-insoluble, clay-free residues of sediments from the 28 sampling station in the Gulf were scanned to determine presence or absence of individual taxa. Except for stations with few radiolarians, a total of 500 tests were counted for each station in a diagonal traverse across the 22 mm x 40 mm area under the cover glass. Table 3 summarizes the tabulations at each station.

Table 3. Summary Of Radiolarian Tabulations At Each Station

Station VS-R-	Number of Spumellarian Tests	Number of Nassellarian Tests	Total Counted	Test Ratio S/N	Number of Identified Spumellarian Taxa	Number of Identified Nassellarian Taxa	Total Number of Taxa	Ratio of Taxa S/N
27	382	118	500	3.24	57	61	118	0.93
34	323	177	500	1.82	61	86	147	0.71
46	326	174	500	1.87	62	82	144	0.76
56	319	181	500	1.76	59	80	139	0.74
60	301	199	500	1.51	58	86	144	0.67
64	336	164	500	2.05	39	56	95	0.70
71	403	97	500	4.15	55	67	122	0.82
81	251	249	500	1.01	55	77	132	0.71
90	326	87	413	3.75	35	21	56	1.67
91	335	165	500	2.03	52	67	119	0.78
92	339	161	500	2.11	53	79	132	0.67
93	251	249	500	1.01	53	86	139	0.62
95	344	156	500	2.21	46	50	96	0.92
99	377	123	500	3.07	46	36	82	1.28
106	233	267	500	0.87	54	81	135	0.67
115	176	324	500	0.54	43	75	118	0.57
130	98	7	105	14.0	27	7	34	3.85
133	168	332	500	0.51	46	74	120	0.62
136	220	280	500	0.79	42	71	113	0.59
151	189	311	500	0.61	38	64	102	0.59
184	357	143	500	2.50	46	50	96	0.92
191	105	395	500	0.27	34	45	79	0.76
192	150	316	466	0.47	38	51	89	0.75
194	370	32	402	11.56	29	9	38	3.22
203	1	-	1	-	1	-	1	-
206	155	46	201	3.37	24	12	36	2.00
208	200	231	431	0.87	28	22	50	1.27
214	0	2	2	-	0	2	2	-

Total Number of Taxa. The total number of taxa (counting groups, some of which may represent more than one species) at a station decreases from a maximum of 147 at station 34 to 1 at station 203. The axial stations of the gulf have higher numbers of taxa than those located along the margins. Of the axial stations there is a distinct break between stations 106 (135 taxa) and 115 (118 taxa). North of 106 the total number of taxa decreases and does not exceed 120. The northward decrease may reflect increased dilution of radiolarian tests by terrigenous sediments with concomitant decrease in observed taxonomic diversity. Ecological factors responsible for the northward decrease may be the higher than average temperature and salinity and greater range in these properties as one goes northward (Table 2), i.e., less open oceanic conditions toward the northern Gulf. Decreased concentrations of radiolarian tests and taxa in samples from stations along the Gulf margins may be explained by dilution effects of increased amounts of terrigenous or calcareous sediment and, in areas of upwelling, by high numbers of diatom frustules.

Spumellarian/Nassellarian (S/N) Test Ratio. At all stations in the southern part of the Gulf south of station 106, the numbers of spumellarian tests are greater than those of nassellarians (S/N 1.01–4.15). In the northern Gulf, spumellarian tests exceed nassellarian tests at stations 184, 194, and 206, which may be due to the increased frequency of a few spumellarian taxa that respond to coastal upwelling, or to the fact that a few spumellarian species are the dominant members of the total Gulf assemblage and may have a greater tolerance for the less than open oceanic conditions here and at the Gulf margins. The S/N test ratio is <1 at stations 191, 192, and 208 which are in regions of upwelling and diatom-rich sediments. In general, S/N test ratios are <1 only in the latter areas which may reflect the increased frequency of certain nassellarian taxa that respond to upwelling resulting in high diatom production.

Spumellarian/Nassellarian (S/N) Taxon Ratio. The ratio of numbers of spumellarian to nassellarian taxa is generally <1 (average 0.84) for stations in the southern half of the Gulf (south of 115). The average ratio for stations in the northern half is 1.38 and is >1 at the Gulf margin stations 90, 99, and 130 and at the northernmost Gulf stations 194, 206, and 208. Whether or not these are significant differences, the ratios may indicate that higher numbers of nassellarian taxa occur in sediments underlying the more nearly oceanic waters of the southern Gulf and in the deeper axial regions of the northern Gulf.

Radiolarian Assemblages. The major effort of my study (Benson, 1966) of the radiolarians from surface sediments of the Gulf of California was of their systematics and taxonomy. The sample coverage in the Gulf (Fig. 1) was not designed to establish strictly defined assemblages of radiolarian taxa; therefore only broad distributional patterns were determined. My results indicated that most taxa conform to one of the following: (1) a cosmopolitan assemblage whose members do not undergo significant changes in frequency throughout the Gulf except for local responses to upwelling; (2) a more nearly oceanic assemblage whose members are either confined to the southern half of the Gulf or undergo a northward decrease in frequency; and (3) an assemblage whose members increase in relative frequency northward either as a result of (a) upwelling that also accounts for high diatom production, or (b) the decrease or absence of other species that are less tolerant of the higher salinity and temperature and greater annual range in these properties in the surface waters of the northern Gulf.

Predominant Taxa in Holocene Sediments of the Gulf of California.

Benson (1966) devised a simple ranking method that identifies the predominant members of the entire Gulf of California radiolarian assemblage recovered from the upper 1-3 or 3-5 cm of each core. The fifteen most abundant taxa (counting groups) were determined as follows. The ten most abundant taxa at each station, except stations 203 and 214, were scored according to their rank at the station, with a score of 10 for the most abundant to a score of 1 for the tenth most abundant. Scores were totaled for each taxon, and the fifteen taxa with the highest scores were ranked accordingly. Results are shown in Table 4. Names of taxa are those now applied in radiolaria.org (2003-4) to those of Benson (1966).

Table 4. Predominant Taxa in Holocene Sediments of the Gulf of California

Taxon	Ranking Score
<i>Phortidium pylonium</i> group	184
<i>Tetrapyle octacantha</i> group	178
<i>Drupptractus variabilis</i>	127
<i>Hexacantium</i> sp. cf. <i>H. giganteum</i>	124
<i>Eucyrtidium hexagonatum</i>	118
<i>Stylodictya tenuispina</i> , <i>Stylochlamyidium asteriscus</i> , <i>S. venustum</i> group	114
<i>Spirocyrtis scalaris</i> plus <i>Stichocorys seriata</i>	67
<i>Lithomelissa pentacantha</i>	65
<i>Larcospira minor</i>	45
<i>Pterocorys clausus</i> plus <i>P. minythorax</i>	36
<i>Hexapyle dodecantha</i> group	29
<i>Ceratocyrtis histricosus</i> s.l.	29
<i>Drupptractus irregularis</i>	28
<i>Cycladophora davisiana</i>	27
<i>Pseudocubus obeliscus</i>	23

The assemblage at station 106 is considered transitional between the southern and northern assemblages but is included within the latter. Table 5 lists the ranks and scores of the predominant taxa in the southern Gulf (stations south of 106). Table 6 lists ranks and scores for the northern group of stations.

Table 5. Predominant Taxa of the Southern Gulf of California Stations

Taxon	Ranking Score
<i>Tetrapyle octacantha</i> group	127
<i>Phortidium pylonium</i> group	109
<i>Drupptractus variabilis</i>	106
<i>Stylodictya tenuispina</i> , <i>Stylochlamydium asteriscus</i> , <i>S. venustum</i> group	96
<i>Hexacontium</i> sp. cf. <i>H. giganteum</i>	50
<i>Eucyrtidium hexagonatum</i>	38
<i>Pterocorys clausus</i> plus <i>P. minythorax</i>	36
<i>Larcospira minor</i>	35
<i>Hexapyle dodecantha</i> group	29
<i>Drupptractus irregularis</i>	27
<i>Cycladophora davisiana</i>	27

Table 6. Predominant Taxa of the Northern Gulf of California Stations

Taxon	Ranking Score
<i>Eucyrtidium hexagonatum</i>	80
<i>Phortidium pylonium</i> group	75
<i>Hexacontium</i> sp. cf. <i>H. giganteum</i>	74
<i>Spirocyrtes scalaris</i> plus <i>Stichocorys seriata</i>	66
<i>Lithomelissa pentacantha</i>	62
<i>Tetrapyle octacantha</i> group	51
<i>Stylodictya tenuispina</i> , <i>Stylochlamydium asteriscus</i> , <i>S. venustum</i> group	28
<i>Pseudocubus obeliscus</i>	23
<i>Ceratocyrtes histricosus</i> s.l.	23
<i>Drupptractus variabilis</i>	21

Upwelling/diatomite assemblage. Certain species have increased abundances at one or more stations within areas of upwelling (Fig. 6) and/or in areas with high diatom percentages in the sediments (Fig. 7):

Phortidium pylonium group
Actinosphaera acanthophora
Didymocyrtis tetrathalamus
Eucyrtidium erythromystax
Ceratocyrtes histricosus s.l.
Lithomelissa pentacantha
Lithomelissa thoracites
Pseudocubus obeliscus
Spirocyrtes scalaris plus *Stichocorys seriata*
Drupptractus variabilis

Stations 191, 192, and 208 are in an area of strong tidal mixing in and near the Ballenas Channel and an area of plankton blooms. Dominant taxa at these stations are *Tetrapyle octacantha* group, *Hexacantium* sp. cf. *H. giganteum*, *Lithomelissa pentacantha*, and *Lithomelissa thoracites*

Relative Abundances of Dominant Taxa. Benson (1983) listed dominant Gulf of California radiolarian species by relative abundances on the basis of data from Benson (1966). Table 7 lists these with taxon names updated to correspond to those in Radiolaria.org.

Table 7. Relative Abundances of Dominant Holocene Radiolarians in Gulf of California Sediments (after Benson, 1966, 1983)

Taxon	Ave. % Per Station	No. of Stations Where Present
<i>Tetrapyle octacantha</i> group	6.8	26
<i>Phorticium pylonium</i> group	6.1	26
<i>Drupptractus variabilis</i>	4.6	25
<i>Hexacontium</i> sp. cf. <i>H. giganteum</i>	3.9	25
<i>Eucyrtidium hexagonatum</i>	3.8	26
<i>Stylodictya tenuispina</i> , <i>Stylochlamydidium asteriscus</i> , <i>S. venustum</i> group	3.8	26
<i>Lithomelissa pentacantha</i>	2.7	23
<i>Spirocyrtis scalaris</i> plus <i>Stichocorys seriata</i>	2.4	25
<i>Larcopyle buetschlii</i> group	2.3	24
<i>Larcospira minor</i>	2.1	25
<i>Hexapyle dodecantha</i> group	1.8	26
<i>Didymocyrtis tetrathalamus</i>	1.7	26
<i>Pterocorys clausus</i> plus <i>P. minythora</i>	1.7	21
<i>Euchitonia</i> sp. cf. <i>E. furcata</i>	1.6	26
<i>Peromelissa phalacra</i>	1.5	25
<i>Drupptractus irregularis</i>	1.5	23
<i>Lithomelissa pentacantha</i> juveniles (formerly <i>Plectacantha oikiskos</i>)	1.4	16
<i>Ceratocyrtis histricosus</i> s.l.	1.4	22
<i>Pseudocubus obeliscus</i>	1.4	23
<i>Actinosphaera acanthophora</i>	1.2	25
<i>Pterocanium auritum</i>	1.2	23
<i>Cycladophora davisiana</i> s.l.	1.0	18
<i>Spongodiscus biconcavus</i>	1.0	26
<i>Theopilium tricostatum</i>	1.0	23
<i>Actinomma antarcticum</i> plus <i>A. medianum</i>	0.9	19
<i>Hexacontium laevigatum</i>	0.8	23
<i>Plectacantha</i> sp.	0.8	17
<i>Anomalacantha dentata</i>	0.7	20

Later Studies of Radiolarian Distributions in the Gulf of California

Later studies of Gulf of California radiolarians determined the distribution of the taxa based on more sophisticated statistical analyses.

Molina-Cruz (1986) used Q-mode factor analysis to define and map six factors that explain the distribution of radiolarians from 108 surface sediment samples from the Gulf. Table 8 lists the predominant taxa (names follow radiolaria.org designations) for each factor and the VS-R stations of Benson (1966) that fall within the map boundaries for each factor.

Table 8. Distribution of Radiolarians in Surface Sediments of the Gulf of California According to Q-Mode Factor Analysis (Molina-Cruz, 1986)

	Guaymas Factor	Subtropical Factor	Upwelling Factor	Transitional Factor	Ballenas Channel Factor	California Current Factor
VS-R Stations	99, 133, 136, 151, 191, 192, 206, 208	27, 34, 46, 56, 60, 64, 71, 81	56, 64, 90, 91, 99, 130, 151	81, 92, 93, 95, 106	191, 192, 208, 206	27
Dominant Taxa	<i>Lithomelissa pentacantha</i> , <i>Lithomelissa thoracites</i>	<i>Tetrapyle octacantha</i> group, <i>Pterocorys clausus</i> , <i>Drupptractus variabilis</i>	<i>Phorticium pylonium</i> group	<i>Eucyrtidium hexagonatum</i> , <i>Drupptractus variabilis</i> , <i>Lithomelissa pentacantha</i> , <i>Pseudocubus obeliscus</i>	<i>Hexacantium</i> sp. cf. <i>H. giganteum</i>	<i>Cycladophora davisiana</i> , <i>Drupptractus irregularis</i> , <i>Botryostrobos aquilonaris</i> , <i>Botryostrobos auritus-australis</i> group

Regarding the California Current Factor, Benson (1983, Fig. 3) shows a strong correlation between water depth and relative percentage of *Cycladophora davisiana* s.l. in each Holocene sample of Benson (1966) from the Gulf. This taxon is probably representative of faunas living in submerged colder water masses that contribute to the overall assemblage in the Gulf sediments. *Cycladophora davisiana* s.l. is also a quantitatively important member of the Quaternary assemblage at DSDP Leg 65 sites. See Molina-Cruz (1988) for further discussion of the late Quaternary distributions of *Cycladophora davisiana*, *Drupptractus variabilis*, and *Tetrapyle octacantha* group as they relate to the oceanography of the Gulf of California.

In a later study, **Molina-Cruz et al. (1999)** analyzed the distribution of radiolarians in the water column from 24 vertically stratified plankton samples from the surface to 600 m in the Carmen and Guaymas basins and from surface to 1000 m in the Pescadero Basin (at the mouth of the Gulf). Table 9 summarizes their results. Their purpose was to determine the affinity of predominant species for specific water masses and to investigate how circulation and mixing processes in the Gulf influence the formation of the radiolarian thanatocoenose.

Table 9. Distribution of Radiolarians in the Water Column in the Carmen, Guaymas, and Pescadero Basins of the Gulf of California (Molina-Cruz et al., 1999)

	Factor 1 Upwelling Water	Factor 2 Intermediate Water	Factor 3 Subtropical Water	Factor 4 Gulf of California Water	Factor 5 Guaymas Water
Dominant Taxa	<i>Plectacantha</i> a sp.	<i>Drupptractus</i> <i>variabilis</i> , <i>Stylochlamydidium</i> <i>venustum</i>	<i>Tetrapyle</i> <i>octacantha</i> [they may include <i>Octopyle stenozoa</i> as show in their Pl. 1, Fig. 1], <i>Botryocirtis</i> <i>scutum</i> , <i>Arachnocorallium</i> <i>calvata</i> is probably a non-indicator as it is cosmopolitan	<i>Phorticium</i> <i>pylonium</i> group, <i>Anomalacantha</i> <i>a dentata</i> , <i>Spongopyle</i> <i>osculosa</i>	<i>Lithomelissa</i> <i>thoracites</i> plus <i>Lithomelissa</i> <i>pentacantha</i> , <i>Peridium</i> <i>longispinum</i> , <i>Arachnocorallium</i> <i>calvata</i>

Molina-Cruz et al. (1999) characterize the radiolarian assemblages and water masses as follows. The Subtropical Water assemblage accounts for 12.7 % of the plankton variability. The subtropical water mass is an incursion into the Gulf from the Pacific Ocean. The radiolarian assemblage occurs in both surface and subsurface subtropical water which is differentiated by temperature and salinity at about 70 m. The water mass reached the northern part of the Farallon Basin in the Gulf.

The assemblage of the Upwelling Factor was found in the northwestern part of the Carmen Basin near Carmen Island and accounts for the largest amount of planktonic radiolarian variability of 37.78%. Common strong upwelling has been documented between the Carmen and Guaymas basins. Plankton samples contained numerous diatom frustules, and the authors infer that the radiolarian assemblage is influenced by coastal upwelling processes. Although *Plectacantha* sp. [identified by Molina-Cruz et al. (1999) as *Plagiacantha panarium*] is the dominant species, Benson (1966) found it rare in the Gulf, and he did suggest that its greater frequency in the northern Gulf corresponds to stations located within or near areas of diatomite-rich sediments.

Guaymas Water has species common to both the surface mixed-layer of the Guaymas Basin and the subsurface waters of the northwestern Carmen Basin. The factor accounts for 6.0% of the variability of the plankton data. Molina-Cruz et al. (1999) interpret the origin of

the assemblage to be from the subduction of denser evaporated surface water from the Guaymas Basin toward the south. The assemblage appears to be related to mixing and circulation processes (including coastal upwelling) associated with the northeast to southwest movement of water in the Gulf.

Intermediate Water represents the incursion of the Pacific intermediate water mass into the Gulf. The factor accounts for 18.34% of the plankton variability and is most important below 350 m water depth at the Pescadero Basin sampling station. The assemblage occurs as far north as the Guaymas Basin.

The Gulf of California Water Factor accounts for 9.7% of the plankton variability with highest factor-loadings at the Guaymas Basin station between 200 and 400 m water depth. The water mass sinks and subducts toward the south, as does Guaymas Water, but forms farther north than does the latter.

Pisias (1986) applied Q-mode factor analysis to radiolarian populations from 54 surface sediment samples from intermediate water depths in the Gulf of California. The study was part of one to study the varved sediments of the Gulf that are found where the continental shelf intersects the oxygen minimum zone of the eastern Pacific, limited to water depths of 1000 m or less, i.e., limited to the shelf regions of the Gulf. Table 10 lists the important components of the three radiolarian assemblages he identified (names follow Radiolaria.org designations).

Table 10. Radiolarian Assemblages in Varved Surface Sediments in the Gulf of California (Pisias, 1986)

	Gulf Assemblage	Subtropical Assemblage	California Assemblage
Dominant Taxa	<i>Lithomelissa pentacantha</i> , <i>Eucecryphalus clinatus</i> , <i>Spirocyrtis scalaris</i> plus <i>Stichocorys seriata</i> , <i>Arachnocorallium calvata</i> plus <i>Peridium</i> sp. cf. <i>P. longispinum</i> , <i>Pseudodictyophimus gracilipes</i> plus <i>P. platycephalus</i> , <i>Lithomelissa thoracites</i>	<i>Tetrapyle octacantha</i> group plus <i>Octopyle stenozona</i>	<i>Hexacantium</i> sp. cf. <i>H. giganteum</i> , <i>Eucyrtidium hexagonatum</i> , <i>Actinosphaera acanthophora</i> , <i>Actinomma delicatulum</i>

Pisias (1986) characterizes the assemblages as follows. The important species of the Gulf Assemblage live in the near surface zone, with maximum values in samples from between 600 and 800 m water depth. The assemblage is most important in the north-central part of the Gulf with highest values at 28° N; the maximum in the assemblage coincides with the depth of strong southerly flow of warmer higher salinity water out of the Gulf.

The Subtropical Assemblage is dominant at the mouth of the Gulf and decreases in importance northward. The assemblage shows an apparent increased penetration along the

eastern margin of the Gulf consistent with the observed surface water flow patterns. It has high values in samples from shallow sites and those from >800 m, and a distinct minimum at intermediate depths.

The California Assemblage is abundant in two regions—in the central Gulf off Guaymas and along the southwestern side of the Gulf. Both areas are centers of upwelling and high surface productivity. The species of this assemblage prefer the cold eastern boundary currents of the open Pacific; however, Pisas (1986) states that it is not yet possible to determine if the assemblage is associated with advection of California Current waters into the Gulf of California.

Radiolarian Systematics

Benson (1966) defined the species of Radiolaria from the Gulf of California as morphological, not typological, species. Following the advice of William R. Riedel during his consultations with him at the Scripps Institution of Oceanography, species definition involved selection of certain morphological characters of the test which are constant within a particular group of individuals. If no gradational forms were observed between this natural group and another closely related group, the groups were given the status of species. Thousands of individual tests were studied in order to distinguish constant characters from those subject to intraspecific variation. Unless a species was rare in occurrence throughout the Gulf, measurements of thirty individual tests from each species were made. The numerical data were used for characterizing the species, although some of the measurements were useful in defining them.

In most cases the species had been described by earlier workers, many of whom, however, based their definitions of a species on a single type specimen. Benson (1966), therefore, placed more emphasis on accurate definition, description, and illustration of each species than on which name should be applied to them. Since that time radiolarian taxonomy advanced to a point where revision of Benson's taxonomy became necessary. Benson and Bjørklund in 2003 made these revisions, and the results are now available in www.radiolaria.org under Holocene-Gulf of California. A list of the revised names applied to Benson's (1966) names of taxa appears in the Appendix.

Age of the Gulf assemblage. The tests represent accumulations of perhaps hundreds of generations, but no evolutionary changes in their morphology were observed. Since the material sampled comes from within the upper six centimeters of sediment from the cores, the total time elapsed for this interval to have accumulated represents, at most, only a few hundred years. This conclusion is based on the few radiocarbon dates and corrected sedimentation rates calculated from them by van Andel (1964, Table 7). The lowest rate from station R-16 off the eastern slope of Mazatlan is 12 cm/1000 years; the highest rate from station R-190 in the Sal si Puedes Basin is 316 cm/1000 years; station R-47 in the Pescadero Basin in the axial portion of the Gulf at its mouth has a rate of 46 cm/1000 years. For all practical purposes a very recent fauna was investigated and should be considered as post-Pleistocene.

Ontogeny of the test. One problem encountered for most species was the recognition of various stages in the ontogenetic development of the individual test. Growth of tests is accomplished by addition of new structures, not by expansion or molting. For example, amongst the Spumellaria the number of concentric shells may be variable within a species. Thus, if a species or genus is characterized by three concentric shells, incomplete forms with one or two shells cannot be placed in a separate taxon. In certain nassellarian species the number of post-cephalic joints is subject to variation and cannot be used as a specific character. In other species the number of joints is constant; however, incomplete forms recognizable as belonging to such species, but lacking one or more of the joints, had been placed in separate taxa, in most instances in separate genera. Several of these "ontogenetic species" were observed from the Gulf and were placed in synonymy if they showed a series of gradational changes to the complete or fully developed form. In several species the fully developed individual was not previously described. Benson (1966) named the Gulf species he defined for the most fully developed morphological form described in the literature available at that time. An example of this is *Zygocampe chrysalidium* (Haeckel) which Benson (1966)

named for *Didymocyrtilis tetrathalamus* (Haeckel). Haeckel's (1887, pl. 40, fig. 13) illustration of *Z. chrysalidium* shows 8 polar caps at one pole of the figure-8 shell with the eighth cap surmounted by a fenestrated three-bladed spine or tube; at the other pole there are only 7 caps, the seventh cap being without a fenestrated spine or tube but, instead, with spines which appear to represent a rudimentary eighth cap. Benson (1966) considered this form the most fully developed and named the species on this basis.

Availability of silica. Whether or not individuals of a species are fully developed is hypothesized, at least in part, to be a function of the availability of dissolved (colloidal?) silica to the individual radiolarian animal. Also, such features as the thickness of shell walls, the state of development of polygonal frames surrounding pores, the length and breadth of main spines, the number and length of secondary spines are subject to intraspecific variation and are regarded as a function of the availability of dissolved silica. In some spumellarian species the number of concentric shells or rings and in some nassellarian species the number of joints appear to be dependent on this factor as well, but in other species these features are constant. Secondary structures such as an outer shell or mantle, although probably genetically controlled, seem to be dependent on the availability of dissolved silica. Indirect evidence of the importance of dissolved silica as a factor accounting for much of the intraspecific variation observed was gained from study of assemblages from regions of highly diatomaceous sediment in the central and northern Gulf (stations 106, 115, 136, 133, 151, 191, 192). Many species present in this region are represented both by individuals with thin-walled tests and few or short spines and by others with thick-walled, spinose tests having additional secondary structures. The former are hypothesized to have been built by radiolarians after the depletion of silica in the surface waters following diatom blooms, and the latter were built during periods of upwelling when the surface waters became enriched in dissolved silica.

Morphology of spumellarian tests. The Spumellaria are characterized by latticed or spongy tests whose growth is outward from a common center. Growth more or less equal in all directions produces spherical or subspherical tests. Unequal growth in three dimensions results in tests that are biaxially ellipsoidal, triaxially ellipsoidal, and discoidal.

Many genera are characterized by concentric shells that are supported by radial beams arising from the surface of the innermost shell. If the beams continue beyond the outside of the outer shell as spines, the spines are termed main spines. All other spines are termed by-spines or secondary or accessory spines. The individual shells of a concentric system of shells are referred to as first, second, third, etc., the innermost shell being the first. Occasionally, reference is made to cortical and medullary shells. If the inner shell or shells are widely separated from the outer one or ones, they are designated medullary, the outer being cortical.

The nature of the lattice of each shell is described by the shape, size and arrangement of the pores as well as the number of pores counted along half the shell circumference. The bars separating pores are referred to as intervening bars. In many species they are surmounted by raised edges that intersect around each pore to form a polygonal (generally hexagonal) frame. The by-spines in the majority of species originate from the nodes (points of intersection) of the intervening bars.

In many species secondary structures are present in a few individuals. They include such features as an additional outer shell (or shells) or a thin-walled, small-pored mantle or veil surrounding all or a portion of the test.

Morphology of nassellarian tests. The basic structure observed in all nassellarian

tests studied from the Gulf of California is diagrammatically illustrated in Figure 8A. For purposes of orientation the median bar (MB) is horizontal and lies in the sagittal (vertical) plane of the test. According to Haeckel (1887) the central capsule lies above the median bar with its basal pole resting directly upon it. The central capsule of the Nassellaria is commonly lobulated with the lobes hanging downward from its main portion, each lobe separated by one of the basic spines or bars arising from the median bar. From the ventral end of the median bar arise a pair of divergent spines, their angle of separation bisected by the sagittal plane. These spines are termed the primary lateral spines, a left (L_1) and a right (L_r). In most species from the Gulf the proximal portions of the spines are nearly horizontal or extend slightly downwards; in a few they extend slightly upwards. In all species they point in a ventral direction, the angle each makes with the sagittal plane being acute but variable, in a few species approaching 90° . From the dorsal end of the median bar arises the dorsal spine (D) which in all species lies in the sagittal plane and extends downward in a dorsal direction, making an acute angle with the dorsal projection of the median bar. If the basic structure shown in Figure 8A is viewed from above it gives the appearance of three spines diverging from a common point, especially in tests having a very short median bar.

The basic structure shown in figure 8A is recognizable in all nassellarian species from the Gulf, but with the exception of only a few species, other structures occur as well, most commonly the apical and vertical spines or bars shown in figure 8B. The apical and vertical spines both lie in the sagittal plane, thus in the same plane as the median bar and dorsal spine. The term spine is used for that portion of the basic element that extends freely, terminating before joining any other part of the test. The term bar is used for that portion of the element that does not extend freely but, instead, joins with some other structure of the test. The apical spine (or bar) arises from the dorsal end of the median bar and extends upward but generally in a dorsal direction, although in several species it is nearly vertical. The angle it makes with the dorsal projection of the median bar is variable but generally greater than 45° . The vertical spine arises from the ventral end of the median bar and extends generally upward in a ventral direction. In all species the angle it makes with the ventral projection of the median bar is less than the corresponding angle between the apical spine and dorsal projection of the median bar, i.e., the apical spine is steeper than the vertical spine. In a few species the vertical spine is nearly horizontal in its proximal portion but was never observed to project downwards, although its distal portion may have a slight downward curvature in a few species.

If the apical and vertical bars are joined by the superior bar (SB), the sagittal ring is formed, the character that is well-developed in the Family Spyridae. In most species the ring is three-bladed in cross-section except for the median bar and the proximal portions of the apical and vertical bars which are circular to elliptical in section. In general, one of the blades lies in the sagittal plane and extends inward; the other two blades extend laterally outward, each at approximately a 120° angle from the sagittal blade. Lateral spines or bars arise, generally in pairs, from the edges of the lateral blades to form the groundwork of the latticed cephalis. The apical and vertical spines are generally collinear with the apical and vertical bars of the ring, respectively. The shape of the ring is either approximately that shown in figure 8B or approaches a D-shape as shown in figure 8C.

The axial spine (Ax) arises from the ventral end of the median bar, from its lower surface, and projects vertically downward in the sagittal plane. Nearly every nassellarian test observed from the Gulf has some indication of the presence of this spine which is always thinner than the primary spines. It varies from a rudimentary stub of a thorn, to a thin unbranched spine, to a very long spine, in some species with distal arborescent branches.

Jørgensen (1905) recognized a pair of divergent spines directed latero-dorsally and downward, arising from the base of the apical spine. These he termed the secondary lateral spines (l) because they are not universally present in the Nassellaria. In specimens from the Gulf these spines, when present, generally lie in the horizontal plane, arise at or near the dorsal end of the median bar and extend dorso-laterally.

In most Nassellaria, the dorsal, primary lateral, vertical, and secondary lateral. (if present) spines are united by a ring-like structure which Haeckel (1887) refers to as the cortinar or basal ring. Figure 8C diagrammatically shows the nature of this ring and the pores that are bounded by it and the basic structural elements. Haeckel states that the ring is horizontal and lies in one plane. In *Acanthodesmia vinculata* the basal ring is large and nearly coplanar and horizontal, but for the majority of the Nassellaria either only part of the ring or none of it is in a horizontal plane. It is commonly referred to as the collar ring because the median bar, which bisects the ring, is commonly located at the level of the constriction or “neck(or collar) region” between the latticed cephalis and thorax (next joint below cephalis) or within the upper part of the thoracic cavity.

In many nassellarian species the collar ring as a definite structure is not always recognizable. It represents the base of the latticed cephalis or at least the base of its lateral and ventral sides, and, consequently it appears as a ring in many tests only because the lowest pores of the latticed cephalis are lined up along its periphery as shown in Figure 9. In many species, however, the structures comprising the ring are actually visible as continuous ribs in the cephalic wall. In still other species, the ring is not present in the wall of the cephalis or thorax; the basic spines arising from the median bar penetrate the walls of the cephalis and/or thorax, but no ribs defining a collar ring are present between these latticed joints.

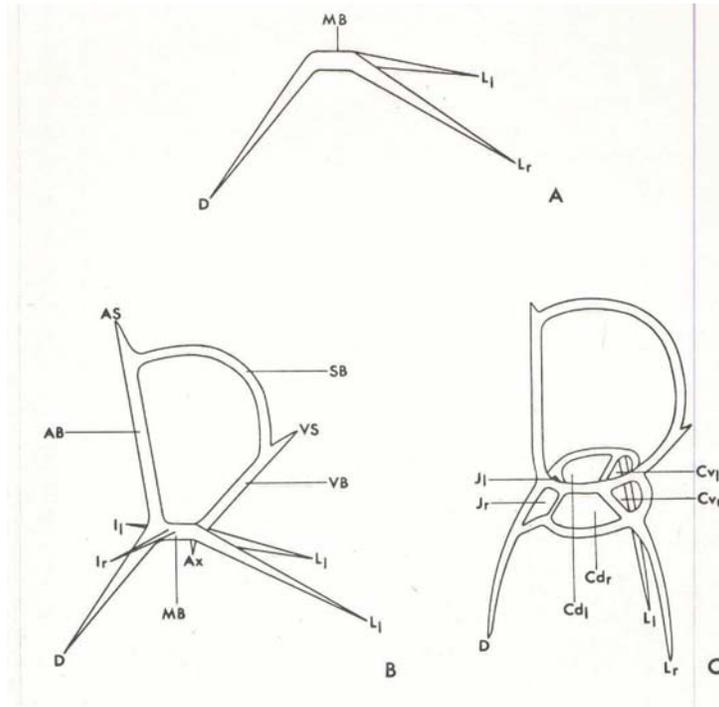


Figure 8. Basic structures of nassellarian tests.

- A.** Structure common to all Nassellaria from the Gulf; MB, median bar; D, dorsal spine; L_l and L_r , left and right primary lateral spines, respectively.
- B.** Remaining basic structures except collar ring; l_l and l_r , left and right secondary lateral spines, respectively; Ax, axial spine; AB, apical bar; AS, apical spine; VB, vertical bar; VS, vertical spine; SB, superior bar of sagittal ring (absent in species with incomplete sagittal ring).
- C.** Diagram showing collar ring and **type A collar pores** (after Riedel, 1958); J_l and J_r left and right jugular pores, respectively; Cd_l and Cd_r , left and right cardinal pores, respectively; Cv_l and Cv_r , left and right cervical pores, respectively.

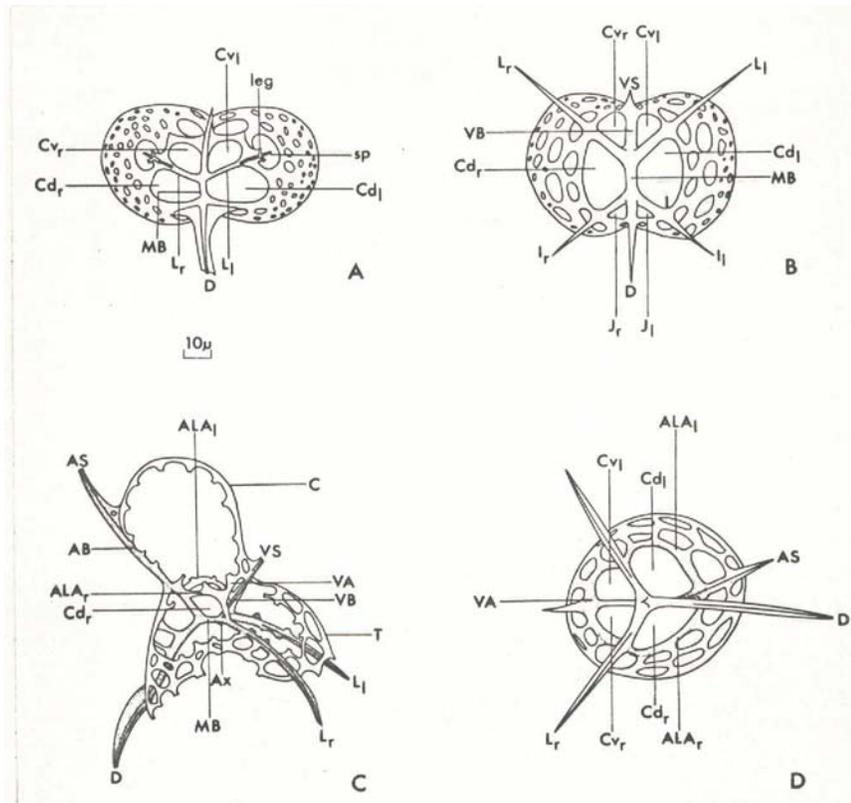


Figure 9. Basic nassellarian structures shown in actual specimens.

- A.** Basal view of *Phormospyris stabilis scaphipes* (= *Tristylospyris scaphipes*) showing the four collar pores (slide VS-R-191b, 1-3 cm); sp, short thin spine extending from and collinear with the left primary lateral bar (a similar spine extends from the right primary lateral bar); leg (terminology of Benson, 1966; =foot), prominent three-bladed apophysis descending from the junction of the left primary lateral bar with the collar ring (a similar leg [=foot] associated with the right primary lateral bar, and a third corresponds to the dorsal spine); remaining symbols as in fig. 8.
- B.** Basal view of a specimen with six collar pores (after Popofsky, 1913, p. 242, fig. 6e).
- C.** Right lateral cut-away view of *Dictyophimus* sp. cf. *D. tripus* showing relationship of basic structures to latticed test and illustrating **type B cardinal pores** (slide VS-.R-106b, 1-3 cm); C, cephalis; T, thorax; ALA₁ and ALA_r, left and right apical-lateral arches, respectively; VA, ventral arch of collar ring.
- D.** Diagram of basal view of a generalized specimen to illustrate the **type B cardinal pores**.

Because of the difficulty in recognition of a collar ring in all nasellarian species, it is more convenient to refer to the pores (herein referred to as collar pores) which are divided by the basic spines or bars arising from the median bar. Popofsky (1913) named these pores, and his terminology is used. In order to observe these pores it is necessary to orient specimens so that one is looking down on them through the top of the cephalis (apical view) or looking through the thoracic cavity from below (basal view). Figure 8C is a perspective, diagrammatic view of these pores from the right side of the test showing the full development of six collar pores. The median and vertical bars bisect the collar ring; therefore, the six basal pores are represented by three pairs of pores, each member of a pair being of equal size and similar shape. The cardinal pores (Cd_r and Cd_l , right and left cardinal pores, respectively) are defined by the median bar, the primary and secondary lateral bars, and the lateral periphery of the collar ring (or wall of the cephalo-thorax if the collar ring is not a distinct rib). The cervical pores (Cv_r and Cv_l) are defined by the primary lateral and vertical bars and by the ventro-lateral portion of the collar ring, herein referred to as the ventral arch (VA). The jugular pores (J_r and J_l) are defined by the dorsal and secondary lateral bars and the dorso-lateral portion of the collar ring. Because the secondary laterals are not universally present, the jugular pores are secondary.

Benson (1966) recognizes two types of cardinal pores; **type A** illustrated in figures 8C and 9A and B, and **type B** illustrated in figures 9C and 9D. He refers to these two types in his species descriptions.

The cardinal pores of **type A** generally lie in a horizontal plane (or at least a plane containing the median bar and perpendicular to the sagittal plane and defined by the primary and secondary lateral bars. The cervical pores lie in the approximate plane of the vertical bar, thus a plane defined by the ventrally ascending ventral arch and vertical bar. Each cervical pore of the pair, however, lies in a plane that descends slightly to each side from the vertical bar; therefore, the pair of cervical pores is not strictly coplanar. To illustrate this, figures 9A and 9B show basal views of two species belonging to the Family Spyridae. There are four collar pores present in figure 9A, the cardinals and cervicals. The secondary lateral bars are actually present but no jugular pores are present between them and the dorsal foot; the bars are represented by raised ribs extending laterally at the base of the two lateral blades of the three-bladed dorsal foot. Six collar pores are diagrammatically illustrated in figure 9B in which a pair of jugular pores are present between the secondary lateral and dorsal bars. Because the secondary lateral bars are nearly horizontal but the dorsal bar descends rather steeply, each of the pair of jugular pores generally lies in a plane slanting inward and dorsally toward the dorsal bar. The cardinal pores are generally of a trapezoidal shape and are larger than the subtriangular cervical and jugular pores, the latter being smaller than the former.

Cardinal pores of **type B** are illustrated in figures 9C and 9D. The secondary lateral spines (bars) are absent, and the collar ring is represented by the ventrally ascending ventral arch and a pair of arches extending latero-ventrally from the apical bar and joining the ventral arch at the distal end of the primary lateral bars. Benson (1966) named these arches the left and right apical-lateral arches (ALA_l and ALA_r , respectively). Both arise at a common point from the apical bar a short distance above its junction with the median bar, extend laterally a short distance perpendicular to the apical bar in a plane perpendicular to the sagittal plane and containing the apical bar, and curve ventrally and downward to the junction with the ventral arch and primary lateral bars. In basal (Fig. 9D) or apical views the apical-lateral and ventral arches give the appearance of a collar ring. In dorsal view the type B cardinal pores appear as a pair of large pores on either side of the apical bar at the base of the dorsal face of the latticed

cephalis. The ventral and apical-lateral arches represent the base of the latticed cephalic wall. In species of the Family Pterocorythidae, the apical-lateral arches are represented by ribs coincident with dorso-lateral furrows separating a pair of dorso-lateral lobes at the base of the latticed cephalis.

Most of the basic structures as discussed above are of generic or suprageneric importance. The distinction between species is based upon characteristics of the latticed portions of the test—cephalis, thorax, and abdomen—as well as on minor variations in some of the basic structures.

The cephalis is generally ovoid, ellipsoidal, or subspherical and envelops the lobate central capsule of the radiolarian animal. It is convenient to refer to its dorsal, lateral, ventral, and upper surfaces or faces. In the majority of species the dorsal face contains the apical bar as a rib in the sagittal plane, often coincident with a furrow or dorsal sagittal stricture. In the Family Spyridae, the D-shaped sagittal ring is free or is embedded into the latticed cephalis where it occupies a sagittal constriction on the dorsal, upper, and ventral faces of the cephalis, separating the cephalis into a left and right lobe. In other groups the sagittal ring is incomplete and consists of the apical and vertical bars only. The apical bar is free within the cephalis of some species in which case it is referred to as a columella, either located within the dorsal half of the cephalic cavity or nearly centrally. In most species the continuation of the apical bar outside the cephalic wall is represented by a spine, short thorn, or robust spine called a horn. These structures are, in general, collinear with the apical bar. The apical spine or horn arises from various positions on the cephalic wall. In most species it arises from the top of the dorsal face of the cephalis and extends nearly vertically. In some species, especially those with an apical bar present as either an internal columella or as a rib that curves ventrally in the dorsal and upper faces, the apical spine or horn arises from the upper face of the cephalis, either from the center of this face or dorsally from the center (eccentric). In a few species the apical spine arises from the dorsal cephalic face near its base and ascends dorsally at a low angle. The vertical spine is in nearly all species collinear with the vertical bar and arises from the neck region—the constriction between cephalis and thorax. It varies from a short thorn or thin conical spine to a heavy horn. In a few species the vertical spine or horn arises from the ventral face of the cephalis at or near its top and is collinear with a vertical bar that is free within the cephalic cavity. In several species the vertical spine is absent. The vertical bar is nearly universally present, but in some species it is of variable development, either present, rudimentary, or absent. In a few species with the vertical bar absent or only rudimentary, a vertical spine, however, is present and arises from the ventral arch of the collar ring. If the vertical bar is absent, the cervical pores are represented by one large pore bounded by the primary lateral bars and the ventral arch of the collar ring.

The cephalis is separated from the thorax by either a definite constriction between the two or by a distinct change in contour. In a few species the distinction between cephalis and thorax is not clear-cut—the cephalis is depressed within the thorax with the wall of the thorax merging with that of the cephalis. The shape of the thorax is either bell-shaped (campanulate), pyramidal (three-sided), conical, or cylindrical. In many species the primary lateral and dorsal bars of the collar ring are intimately associated with the thorax as either ribs in the thoracic wall or as spines piercing the thoracic wall. The ribs either occupy furrows separating three convex outward lobes of the thorax, have no influence on the cross-sectional shape of the thorax, or are represented by raised ribs or “wing-like” apophyses terminating as spines. The ribs generally terminate as free spines of variable shape and size that arise from the thoracic wall either above the base of the thorax or at its base or mouth. Certain species

are characterized by the extension of thoracic ribs as heavy, prominent spines projecting downward below the thorax. These are termed feet. Whether these structures should be termed feet or spines is somewhat subjective—a decision similar to that involving a choice between apical spine and horn. Feet also are present in species without a thorax, especially in members of the Family Spyridae in which they arise directly from the collar ring (Fig. 9A).

The next joint developed below the thorax is termed the abdomen. If successive joints are present below this, they are termed post-abdominal joints. Their cross-sectional shape is generally circular. The joints are separated from one another by either a definite horizontal ring which is a continuous ring raised on the inner surface of the test cavity (inner septal ring), a definite annular constriction of the test outline, or both. Species with three prominent feet that arise either from the cephalis or thorax commonly have a latticed network developed between the feet forming either a thorax or abdomen as the case might be, but this character is subject to intraspecific variation. In several species the thoracic ribs discussed above continue in the wall of the abdomen or even post-abdominal joints, but this is also subject to intraspecific variation.

The basal opening of the nassellarian test is termed the mouth. It is generally constricted in fully-developed forms of species, and in a few species it is completely closed by a lattice. Haeckel (1887) subdivided most of his families into subfamilies depending upon whether the mouth was open or closed. In some species from the Gulf a few individuals have their basal mouths closed.

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APPENDIX

Suprageneric Classification and List of Gulf of California Holocene Radiolaria

At the suprageneric level, Benson (1966) organized broad groupings of tests based on their geometry and structure. Although these correspond to several of Haeckel's orders, he was of the opinion that the groupings should have only superfamily status, at most. For this reason he followed the suprageneric classification of Campbell (1954) in the *Treatise on Invertebrate Paleontology* which is based almost completely on Haeckel's system (1887). Loeblich and Tappan (1961) revised several of the names of Campbell's families and superfamilies in accordance with the *International Code of Zoological Nomenclature*, and Benson (1966) used these names where Campbell's (1954) names were found to be in error.

For the present text (2005), I list below the Gulf of California Holocene radiolarian taxa of Benson (1966) according to the classification scheme and synopses used by Boltovskoy (1998) which are based chiefly on the scheme proposed by Riedel (1967, 1971) for extant families only. Names of radiolarian taxa or taxon groups that are listed first are the revisions by Benson and Bjørklund in 2003 of Benson's (1966) taxa and that now appear in www.radiolaria.org under Radiolarian species info menu: Holocene (Recent)---Gulf of California. Following each name and in brackets is the name Benson (1966) used for the taxon plus his figure(s) that correspond to the 2003 concept of the taxon. In addition, in 2003 Benson and Bjørklund identified species from the Gulf that were not recorded by Benson (1966). These are noted in brackets following the listed species. See radiolaria.org for references given for each taxon.

Kingdom **PROTISTA**

Phylum **SARCODINA**

Class **ACTINOPODA**

Subclass **RADIOLARIA**

Superorder **POLYCYSTINA**

Order **SPUMELLARIA**

Family **SPHAEROZOIDAE**. Colonial radiolarians of which the skeletons consist of numerous unconnected intracapsular spicules (van de Paverd, 1995).

Sphaerouzoum punctatum Müller 1858 [*Plagonium* cf. *sphaerouzoum* Haeckel; Benson, 1966, pl. 19, figs. 12-13]

Family **COLLOSPHAERIDAE**. Colonial polycystines, each individual has a single, thin-walled, spherical or subspherical latticed shell.

Acrosphaera murrayana (Haeckel) 1887 [*Choenicosphaera murrayana* Haeckel 1887; Benson, 1966, pl. 2, fig. 3]

Collosphaera sp. det. Benson 2003 [*Polysolenia* sp. Benson, 1966, pl. 2, figs. 1-2]

Siphonosphaera socialis Haeckel 1887 [*Siphonosphaera* cf. *socialis* Haeckel 1887; Benson, 1966, pl. 2, fig. 4]

Trisolenia megalactis megalactis Bjørklund & Goll 1979 [*Disolenia* cf. *variabilis* (Haeckel 1887); Benson, 1966, pl. 2, fig. 5]

Family **ACTINOMMIDAE**. Solitary species with latticed or spongy spherical, subspherical, or ovoid shells (not lenticular); with or without medullary shells. Surface of shell is often covered with spines, but not tubes. All actinommids possess either single or multiple, concentric spherical or ovoid shells. When several shells are present they are connected to each other by radial beams which pierce the cell.

Actinomma antarcticum (Haeckel) 1887 [*Diploplegma banzare* Riedel, 1958; Benson, 1966, pl. 3, figs. 2-3]

Actinomma boreale Cleve 1899 [*Sphaeropyle langii* Dreyer 1889; Benson, 1966, pl. 5, figs. 7-9]

Actinomma delicatulum (Dogiel and Reschetnjak) 1952 [*Actinomma* cf. *hystrix* (Müller) 1856; Benson, 1966, pl. 5, figs. 3-4]

Actinomma leptoderma (Jørgensen) 1900 [*Actinomma* sp.; Benson 1966, pl. 5, fig. 6]

Actinomma leptoderma longispina Cortese and Bjørklund 1998 [Benson and Bjørklund, 2003]

Actinomma medianum Nigrini 1967 [*Diploplegma banzare*; Benson 1966, pl. 2, fig. 14, pl. 3, fig. 1]

Actinomma sol Cleve 1901 [*Thecosphaera* sp.; Benson, 1966, pl. 2, figs. 12-13]

Actinomma sp. det. Benson 2003 [*Actinomma* sp.; Benson, 1966, pl. 5, fig. 5]

Actinosphaera acanthophora (Popofsky) 1912 [*Carposphaera acanthophora* (Popofsky); Benson, 1966, p. pl. 2, figs. 8-10]

Amphisphaera cristata Carnevale 1908 [*Amphisphaera* cf. *uranus* Haeckel; Benson, 1966, pl. 3, figs. 4-5]

Anomalacantha dentata (Mast) 1910 [*Anomalacantha dentata* (Mast); Benson, 1966, pl. 5, figs. 10-11]

Cenosphaera sp. det. Benson 2003 [*Thecosphaera* sp.; Benson, 1966, pl. 2, fig. 11]

Cenosphaera sp. aff. *C. perforata* Haeckel, Benson 1966 [*Cenosphaera* aff. *perforata* Haeckel; Benson, 1966, pl. 2, figs. 6-7]

Cladococcus abietinus Haeckel 1887 [*Cladococcus stalactites* Haeckel; Benson, 1966, pl. 6, figs. 2-3]

Cladococcus cervicornis Haeckel 1862 [*Elaphococcus cervicornis* Haeckel; Benson, 1966, pl. 6, fig. 1]

- Doryconthidium* sp. cf. *D. hexactis* (Vinassa de Regney) Benson 1983; [*Doryconthidium?* sp.; Benson, 1966, pl. 3, fig. 12]
- Drupptractus irregularis* Popofsky 1912 [*Drupptractus irregularis* Popofsky; Benson, 1966, pl. 7, figs. 7-11]
- Drupptractus variabilis* Dumitrica 1973 [*Drupptractus* cf. *pyrifomis* (Bailey); Benson, 1966, pl. 7, figs. 2-6]
- Heliosphaera radiata* Popofsky 1912 [*Heliosphaera radiata* Popofsky; Benson, 1966, pl. 5, figs. 1-2]
- Hexacontium arachnoidale* Hollande and Enjumet 1960 [*Hexacontium* cf. *heteracantha* (Popofsky); Benson, 1966, pl. 4, figs. 6-7]
- Hexacontium laevigatum* Haeckel 1887 [*Hexacontium laevigatum* Haeckel; Benson, 1966, pl. 4, figs. 4-5]
- Hexacontium melpomene* (Haeckel) 1887 [*Sylacontarium bispiculum* Popofsky; Benson, 1966, pl. 3, figs. 8-11]
- Hexacontium* sp. cf. *H. giganteum* det. Benson 2003 [*Hexacontium entacanthum* [sic.] Jørgensen; Benson, 1966, pl. 3, figs. 13-14, pl. 4, figs. 1-3]
- Hexacontium* sp. cf. *H. heracliti* (Haeckel) [*Hexacontium* cf. *hericlitii* [sic.] (Haeckel); Benson, 1966, pl. 4, figs. 8-10]
- Hexastylus triaxonius* Haeckel 1887 [*Hexastylus triaxonius* Haeckel; Benson, 1966, pl. 3, figs. 6-7]
- Spongosphaera streptacantha* Haeckel 1861 [*Spongosphaera streptacantha* Haeckel; Benson, 1966, pl. 6, fig. 4, pl. 7, fig. 1]
- Stylatractus cronos* (Haeckel) 1887 [*Xiphatractus cronos* (Haeckel); Benson, 1966, pl. 7, figs. 12-13]
- Stylatractus pluto* (Haeckel) 1887 [*Xiphatractus pluto* (Haeckel); Benson, 1966, pl. 7, figs. 14-17]

Family **COCCODISCIDAE**. Latticed discoidal or lenticular shell enclosing a single or double medullary shell, and surrounded by an equatorial zone of spongy or concentrically-chambered structures, or forms with an ellipsoidal cortical shell equatorially constricted enclosing a single or double medullary shell.

- Cypassis irregularis* Nigrini 1968 [*Spongoliva* cf. *ellipsoides* Popofsky; Benson, 1966, pl. 8, figs. 6-7]
- Didymocyrtis tetrathalamus* (Haeckel) 1887 [*Zygocampe chrysalidium* Haeckel; Benson, 1966, pl. 8, figs. 8-13, pl. 9, figs 1-2; text-fig. 10]

Family **PHACODISCIDAE**. Lenticular, biconvex, latticed cortical shell, not surrounded by spongy or chambered structures, within which a small, spherical single or double medullary shell is enclosed. The margin (but less commonly the surfaces) of the cortical shell may bear radial spines.

Circodiscus microporus (Stöhr) 1880 [*Ommatodiscus pantanellii* Carnevale; Benson, 1966, pl. 9, figs. 7-8; pl. 10, fig. 1; text-fig. 12]

Heliodiscus asteriscus Haeckel 1887 [*Heliodiscus asteriscus* Haeckel; Benson, 1966, pl. 9, fig. 3]

Heliodiscus echiniscus Haeckel 1887 [*Heliodiscus asteriscus* Haeckel; Benson, 1966, pl. 9, fig. 4]

Family **SPONGODISCIDAE**. Discoidal or cylindrical, spongy or finely chambered skeleton, with or without surficial pore-plate, often with radiating arms or marginal spines. The members of this family are characterized by possessing skeletons which are partly or entirely spongy in appearance. Spongodiscidae are not spherical. Their overall shape can be lenticular (biconvex discs), cylindrical, quadrangular or subquadrangular in outline, or Y-shaped. With the exception of the cylinders, all others are depressed or flattened (rather than circular in cross-section). Lenticular, quadrangular, and Y-shaped forms may be entirely composed of a spongy mass with no discernible structure (in which case the central part of the skeleton is often thicker and/or denser, and therefore appears darker in the light microscope; or may possess a small central chamber surrounded by concentric or spiral, continuous or interrupted bands. The surface of some forms may be partly or totally covered with a very thin, porous sieve-plate, which in lenticular forms may extend beyond the central spongy mass forming a delicate equatorial girdle around the periphery of the shell.

Amphirhopalum ypsilon Haeckel 1887 [*Amphicraspedum wyvilleanum* Haeckel; Benson, 1966, pl. 11, figs. 5-6]

Dictycoryne truncatum (Ehrenberg) 1861 [*Dictycoryne* cf. *truncatum* (Ehrenberg); Benson, 1966, pl. 15, fig. 1]

Dictycoryne profunda Ehrenberg 1860] *Hymeniastrum koellikeri* Haeckel; Benson, 1966, pl. 12, figs. 4-6]

Euchitonia elegans/furcata group Boltovskoy 1998 [*Euchitonia elegans* (Ehrenberg); Benson, 1966, pl. 14, figs. 1-2; text-fig. 17]

Euchitonia sp. Benson 1983 [*Euchitonia mülleri* Haeckel; Benson, 1966, pl. 14, figs. 3-4]

Euchitonia sp. cf. *E. furcata* Benson 1966 [*Euchitonia* cf. *furcata* Ehrenberg; Benson, 1966, pl. 13, fig. 4, fig. 5(?)]

Euchitonia triangulum (Ehrenberg) 1872 [*Euchitonia* cf. *echinata* Haeckel; Benson, 1966, pl. 12, fig. 7, pl. 13, figs. 1-3]

Hymeniastrum euclidis Haeckel 1887 [*Hymeniastrum euclidis* Haeckel, Popofsky; Benson, 1966, pl. 12, figs. 1-3]

- Spongaster tetras* Ehrenberg 1860 [*Spongaster tetras* Ehrenberg; Benson, 1966, pl. 15, fig. 2]
- Spongocore puella* Haeckel 1887 [*Spongocore puella* Haeckel; Benson, 1966, pl. 8, figs. 1-3]
- Spongodiscus biconcavus* Haeckel 1887 [*Spongodiscus biconcavus* (Haeckel) Popofsky; Benson, 1966, pl. 11, fig. 1, text-fig. 14]
- Spongopyle osculosa* Dreyer 1889 [*Spongopyle osculosa* Dreyer; Benson, 1966, pl. 11, figs. 2-3; text-fig. 15]
- Spongotrochus glacialis* Popofsky 1908 [*Spongotrochus* cf. *glacialis* Popofsky; Benson, 1966, pl. 11, fig. 4; text-fig. 16]
- Spongurus* sp. cf. *S. elliptica* Benson 1966 [*Spongurus* cf. *elliptica* (Ehrenberg); Benson, 1966, pl. 8, figs. 4-5]
- Stylochlamydium asteriscus* Haeckel 1887 [*Ommatodiscus* sp. [part.]; Benson, 1966, pl. 10, fig. 6 (not figs. 2-4, 5(?), 7)]
- Stylochlamydium venustum* (Bailey) 1856 [*Ommatodiscus* sp. [part.]; Benson, 1966, pl. 10, figs. 2, 4, 7 (not figs. 3, 5(?), 6)]
- Stylodictya tenuispina* Jørgensen 1905 [*Ommatodiscus* sp. [part.]; Benson, 1966, pl. 10, figs. 3, 5(?), (not figs. 2, 4, 6-7)]
- Stylodictya validispina* Jørgensen 1905 [*Stylodictya validispina* Jørgensen; Benson, 1966, pl. 9, figs. 5-6; text-fig. 11]

Family **LITHELIIDAE**. The lattice of the ellipsoidal, spherical or lenticular shell is totally or partially arranged along a bilaterally symmetrical spiral.

- Larcopyle buetschlii* group Dreyer 1889 [*Larcopyle bütschlii* Dreyer; Benson, 1966, pl. 19, figs. 3, 5, (not 4); *Larcopyle?* sp., Benson, 1966, pl. 19, figs. 1-2]
- Larcospira minor* (Jørgensen) 1900 [*Lithelius minor* Jørgensen; Benson, 1966, pl. 17, figs. 9-10; pl. 18, figs. 1-4]
- Larcospira quadrangula* Haeckel 1887 [*Larcospira quadrangula* Haeckel; Benson, 1966, pl. 18, figs. 7-8]
- Larcospira* sp. Bjørklund et al. 1998 [*Lithelius?* sp.; Benson, 1966, pl. 18, figs. 5-6]

Family **PYLONIIDAE**. The major part of the shell is composed of a series of successively larger elliptical latticed girdles in three mutually perpendicular planes, with the major diameter of each girdle being the minor diameter of the next larger one. In certain orientations the test appears as an internal single or double spiral and in others as a series of concentric ellipsoidal shells, thus obscuring the trizonal structure. The center is occupied by a small ellipsoidal structure—the microsphere.

- Dipylissa bensoni* Dumitrica 1988 [*Spirema* sp.; Benson, 1966, pl. 18, figs. 9-10]

Hexapyle dodecantha group Haeckel 1887 [*Hexapyle dodecantha* Haeckel; Benson, 1966, pl. 18, figs. 14-16; pl. 19, fig. 4; text-fig. 20; *Discopyle* ? sp.; Benson, 1966, pl. 18, figs. 11-13; text-fig. 19]

Octopyle stenozona Haeckel 1887 [*Octopyle stenozona* Haeckel; Benson, 1966, pl. 16, figs. 3-4]

Phorticium pylonium group Haeckel 1887 [*Phorticium pylonium* (Haeckel) Cleve; Benson, 1966, pl. 16, figs. 5-9, pl. 17, figs. 1-3]

Pylonium sp. Benson 1966 [*Pylonium* sp.; Benson, 1966, pl. 16, fig. 2]

Tetrapyle octacantha group Müller 1858 [*Tetrapyle octacantha* Müller; Benson, 1966, pl. 15, figs. 3-10; pl. 16, fig. 1; text-fig. 18]

Family **THOLONIIDAE**. Completely latticed shell, without larger openings, and with constrictions that define several (typically 6) dome-shaped protuberances.

Amphitholus acanthometra Haeckel 1887 [*Amphitholus acanthometra* Haeckel; Benson, 1966, pl. 17, figs. 4-7]

Cubotholus octoceras Haeckel 1887 [*Cubotholus* cf. *octoceras* Haeckel; Benson, 1966, pl. 17, fig. 8]

Order **NASSELLARIA**

Family **SPYRIDAE**. (=Trissocyclidae). The skeleton is represented by a well-developed D-shaped sagittal ring (median bar and anastomosed vertical and apical spines), either free or embedded into the latticed cephalic wall, in which case the cephalis is usually bilaterally lobed). Sometimes with thorax, abdomen always absent.

Acanthodesmia vinculata (Müller) 1858 [*Eucoronis nephrospyris* Haeckel; Benson, 1966, pl. 21, figs. 6-8]

Ceratospyris sp. cf. *C. borealis* Benson 1983 [*Eucoronis*? sp.; Benson, 1966,; pl. 21, figs. 9-10]

Clathrocircus stapedius Haeckel 1887 [*Clathrocircus stapedius* Haeckel; Benson, 1966, pl. 21, figs. 11-13; pl. 22, figs. 1-2]

Liriospyris reticulata (Ehrenberg) 1872 [*Amphispyris toxarium* Haeckel; Benson, 1966, pl. 20, figs. 2-7]

Lophospyris pentagona hyperborea (Jørgensen), emend. Goll 1976 [*Ceratospyris polygona* Haeckel; Benson, 1966 (in part), pl. 22, figs. 17-18 (not figs. 15-16)]

Lophospyris pentagona pentagona (Ehrenberg), emend. Goll 1969 [*Ceratospyris polygona* Haeckel; Benson, 1966 (in part), pl. 22, figs. 15-16 (not figs. 17-18)]

Lophospyris pentagona quadriformis (Haeckel), emend. Goll 1976 [*Ceratospyris* cf. *pentagona* Ehrenberg; Benson, 1966, pl. 22, figs. 19-21]

- Neosemantis distephanus distephanus* Goll 1979 [*Neosemantis distephanus* (Haeckel) Popofsky; Benson, 1966, pl. 19, fig. 18, pl. 20, fig. 1]
- Nephrospyrus renilla* Haeckel 1887 [*Nephrodictyum renilla* (Haeckel); Benson, 1966, pl. 21, fig. 5]
- Phormospyris* sp. det. Benson 2003 [*Patagospyris?* sp.; Benson, 1966, pl. 22, fig. 22; pl. 23, figs. 1-2]
- Phormospyris* sp. cf. *P. ophirensis* Ehrenberg 1872 [*Petalospyris* cf. *ophirensis* Ehrenberg; Benson, 1966, pl. 22, figs. 11-14]
- Phormospyris stabilis scaphipes* (Haeckel) 1887 [*Tristylospiris scaphipes* Haeckel; Benson, 1966, pl. 22, figs. 7-10; text-fig. 8A]
- Phormospyris stabilis capoi* Goll 1976 [*Rhodospyrus* sp.; Benson, 1966, pl. 23, figs. 3-5]
- Phormospyris stabilis stabilis* Goll 1976 [*Desmospyris anthocyrtoides* (Bütschli) Haeckel; Benson, 1966, pl. 23, figs. 6-8]
- Phormospyris tricostata* Haeckel 1887 [*Phormospyris tricostata* Haeckel; Benson, 1966, pl. 23, fig. 9]
- Tholospyris baconiana baconiana* Goll 1972 [*Tricolospyris kantiana* Haeckel; Benson, 1966, pl. 23, figs. 10-12]
- Tholospyris devexa* Goll 1969 [*Amphispyris* aff. *zonarius* (Haeckel); Benson, 1966, pl. 20, figs. 13-14; pl. 21, figs. 1-4]
- Tholospyris procera* Goll 1969 [*Amphispyris subquadrata* Haeckel; Benson, 1966, pl. 20, figs. 8-12]
- Tholospyris rhombus* Goll 1972 [*Zygocircus* sp.; Benson, 1966, pl. 19, figs. 16-17]
- Zygocircus productus capulosus* Goll 1979 [*Zygocircus productus* Hertwig (Bütschli); Benson, 1966, pl. 19, figs. 14-15]

Family **PLAGONIIDAE**. Skeletons restricted to a simple tri- or tetraxonic nassellarian spicule, or a well-developed system of main spines enclosed within a fully formed cephalis. The degree of development of the cephalis may vary from a few anastomosed bars to a well-developed, latticed or latticed/spongy chamber. Usually without postcephalic segments.

- Amphiplecta acrostoma* Haeckel 1887 [*Amphiplecta* cf. *acrostoma* Haeckel; Benson, 1966, pl. 32, fig. 2, (not fig. 1)]
- Amphiplecta* sp. Petrushevskaya 1971 [*Amphiplecta* cf. *acrostoma* Haeckel; Benson, 1966, pl. 32, fig. 1, (not fig. 2)]
- Arachnocorallium calvata* Petrushevskaya 1971 [*Peridium longispinum* Jørgensen; Benson, 1966, pl. 23, fig. 27; pl. 24, figs. 1-3]

- Archnocorys umbellifera* Haeckel 1862 [*Archnocorys umbellifera* Haeckel; Benson, 1966, pl.24, figs. 20-21]
- Callimitra emmae* Haeckel 1887 [*Callimitra emmae* Haeckel; Benson, 1966, pl. 25, fig. 12]
- Campylacantha cladophora* Jørgensen 1905 [Benson and Bjørklund, 2003]
- Ceratocyrtilis histricosus* (Jørgensen) 1905 [*Helotholus histricosa* Jørgensen; Benson, 1966, pl. 31, figs. 4-5, 7-8, (not fig. 6)]
- Cladoscenum* sp. cf. *C. tricolpium* Benson 1966 [*Cladoscenum* cf. *tricolpum* {sic.} (Haeckel) Jørgensen; Benson, 1966, pl. 25, figs. 10-11]
- Clathrocanium coarctatum* Ehrenberg 1860 [*Clathrocanium* cf. *coronatum* Popofsky; Benson, 1966, pl. 26, figs. 1-2]
- Clathrocorys murrayi* Haeckel 1887 [*Clathrocorys murrayi* Haeckel; Benson, 1966, pl. 25, figs. 13-15]
- Clathromitra pterophormis* Haeckel 1887 [*Clathromitra pterophormis* Haeckel; Benson, 1966, pl. 26, fig. 4]
- Lampromitra cracenta* Takahashi 1991 [*Lampromitra* cf. *coronata* Haeckel (partim.); Benson, 1966, pl. 30, figs. 9-10 (not fig. 8)]
- Lampromitra quadricuspis* Haeckel 1887 [*Lampromitra quadricuspis* Haeckel; Benson, 1966, pl. 30, fig. 11; pl. 31, fig. 1]
- Lithomelissa laticeps* Jørgensen 1905 [*Lithomelissa laticeps* Jørgensen; Benson, 1966, pl. 24, figs. 14-15]
- Lithomelissa pentacantha* (Popofsky) 1913 [*Lithomelissa hystrix* Jørgensen; Benson, 1966, pl. 24, figs. 6-9]
- Lithomelissa setosa* Jørgensen 1900 [Benson and Bjørklund, 2003]
- Lithomelissa thoracites* Haeckel 1862 [*Lithomelissa thoracites* Haeckel; Benson, 1966, pl. 24, figs. 10-12, not 13]
- Lophophaena hispida* (Ehrenberg) 1872 [*Acanthocorys variabilis* Popofsky sens. emend.; Benson, 1966, pl. 24, fig. 19]
- Lophophaena nadezdae* Petrushevskaya 1971 [*Lithomelissa* cf. *galeata* (Ehrenberg) ? Popofsky; Benson, 1966 (part.), pl. 24, figs. 16-17, (not 18)]
- Lophophaena variabilis* Petrushevskaya 1971 [*Lithomelissa* cf. *galeata* (Ehrenberg) ? Popofsky; Benson, 1966 (part.), pl. 24, fig. 18, (not 16-17)]
- Lophophaena witjazii* (Petrushevskaya) 1971 [*Lophophaena* cf. *capito* Ehrenberg; Benson, 1966, pl. 24, figs. 22-23; pl. 25, fig. 1]
- Peridium* sp. cf. *P. longispinum* Benson 1966 [*Peridium* sp.; Benson, 1966, pl. 24, figs. 4-5]

- Peridium longispinum* Jørgensen 1900 [Benson and Bjørklund, 2003]
- Peromelissa phalacra* (Haeckel) 1887 [*Lithomelissa thoracites* Haeckel; Benson, 1966, pl. 24, fig. 13, not 10-12]
- Phormacantha hystrix* (Jørgensen) 1900 [*Phormacantha hystrix* Jørgensen; Benson, 1966, pl. 23, figs. 24-26]
- Plectacantha* sp. Benson 1966 [*Plectacantha?* sp.; Benson, 1966, pl. 23, figs. 21-23]
- Pseudocubus obeliscus* Haeckel 1887 [*Pseudocubus obeliscus* Haeckel; Benson, 1966, pl. 22, figs. 3-6]
- Sethophormis pentalactis* Haeckel 1887 [*Lampromitra* cf. *coronata* Haeckel (partim.); Benson, 1966, pl. 30, fig. 8 (not figs. 9-10)]
- Verticillata hexacantha* Popofsky 1913 [*Verticillata hexacantha* Popofsky; Benson, 1966, pl. 26, fig. 3]
- Family **THEOPERIDAE**. Cephalis spherical or subspherical, relatively small, often poreless or sparsely perforate. It usually bears an apical horn. Internal spicule small and inconspicuous. With one or more, sometimes up to over 10, usually well-developed postcephalic segments. Generally, cap- or helmet-shaped, or conical in overall outline.
- Artopilium undulatum* Popofsky 1913 [*Lophocorys polyacantha* Popofsky; Benson, 1966 (partim.), pl. 34, figs. 1-2, (not 3)]
- Calocyclus monumentum* Haeckel 1887 [*Clathrocyclas?* sp.; Benson, 1966, pl. 31, figs. 2-3]
- Carpocanarium papillosum* (Ehrenberg) 1872 [*Dictyocephalus mediterraneus* Haeckel; Benson, 1966, pl. 29, fig. 13]
- Coracalyptra cervus* (Ehrenberg) 1872 [*Coracalyptra cervus* (Ehrenberg); Benson, 1966, pl. 30, figs. 3-5]
- Cornutella profunda* Ehrenberg 1854 [*Cornutella profunda* Ehrenberg; Benson, 1966, pl. 29, figs. 7-8]
- Cycladophora davisiana* Ehrenberg 1862 [*Theocalyptra davisiana* (Ehrenberg); Benson, 1966, pl. 29, figs. 14-16]
- Cyrtopera laguncula* Haeckel 1887 [*Cyrtopera laguncula* Haeckel; Benson, 1966, pl. 35, figs. 3-4]
- Dictyophimus crisiae* Ehrenberg 1854 [*Pterocorys?* sp.; Benson, 1966, pl. 28, figs. 4-6]
- Dictyophimus histricosus* Jørgensen 1905 [*Dictyophimus histricosus*(?) Jørgensen; Benson, 1966, pl. 31, fig. 6]
- Dictyophimus killmari* (Renz) 1974 [*Pterocorys* cf. *columba* Haeckel; Benson, 1966, pl. 28, fig. 7]

- Dictyophimus* sp. cf. *D. tripus* Benson 1966 [*Dictyophimus* cf. *tripus* Haeckel; Benson, 1966, pl. 25, figs. 2-3; text-fig. 8C]
- Eucecryphalus clinatus* Takahashi 1991 [*Eucecryphalus* sp.; Benson, 1966, pl. 30, figs. 6-7]
- Eucyrtidium annulatum* (Popofsky) 1913 [*Lithostrobos hexastichus* Haeckel; Benson, 1966 (partim.), pl. 34, figs. 13-14, (not 15-16)]
- Eucyrtidium anomalum* Haeckel 1861 [*Eucyrtidium anomalum* Haeckel; Benson, 1966, pl. 34, figs. 4-5]
- Eucyrtidium erythromystax* Nigrini and Caulet 1992 [*Lithomitra infundibulum* Haeckel; Benson, 1966, pl. 34, figs. 10-12; text-fig. 26]
- Eucyrtidium hexagonatum* Haeckel 1887 [*Eusyringium siphonostoma* Haeckel; Benson, 1966, pl. 34, figs. 6-9]
- Eucyrtidium hexastichum* (Haeckel) 1887 [*Lithostrobos hexastichus* Haeckel; Benson, 1966 (partim.), pl. 34, figs. 15-16, (not 13-14)]
- Lipmanella bombus* (Haeckel) 1887 [*Dictyoceras* cf. *pyramidale* (Popofsky); Benson, 1966, pl. 28, fig. 11]
- Lipmanella dictyoceras* (Haeckel) 1861 [*Dictyoceras acanthicum* Jørgensen; Benson, 1966, pl. 28, figs. 8-10]
- Litharachnium tentorium* Haeckel 1862 [*Litharachnium tentorium* Haeckel; Benson, 1966, pl. 29, figs. 5-6]
- Lithopera bacca* Ehrenberg 1872 [*Lithopera bacca* Ehrenberg; Benson, 1966, pl. 33, figs. 10-11]
- Lithostrobos hexagonalis* Haeckel 1887 [*Lithostrobos* cf. *hexagonalis* Haeckel; Benson, 1966, pl. 35, figs. 1-2]
- Lophocorys polyacantha* Popofsky 1913 [*Lophocorys polyacantha* Popofsky; Benson, 1966 (partim.), pl. 34, fig. 3, (not 1-2)]
- Peripyramis circumtexta* Haeckel 1887 [*Peripyramis circumtexta* Haeckel; Benson, 1966, pl. 29, fig. 4]
- Plectopyramis dodecomma* Haeckel 1887 [*Plectopyramis dodecomma* Haeckel; Benson, 1966, pl. 29, fig. 3]
- Pseudodictyophimus gracilipes* (Bailey) 1856 [*Dictyophimus gracilipes* Bailey; Benson, 1966, pl. 25, figs. 4-6]
- Pseudodictyophimus platycephalus* (Haeckel) 1887 [*Dictyophimus platycephalus* Haeckel; Benson, 1966, pl. 25, figs. 7-9]
- Pterocanium auritum* Nigrini and Caulet 1992 [*Pterocanium* sp.; Benson, 1966, pl. 26, figs. 5-6]

Pterocanium elegans (Haeckel) 1887 [*Pterocanium cf. elegans* (Haeckel); Benson, 1966, pl. 27, figs. 1-2]

Pterocanium praetextum eucolpum Haeckel 1887 [*Pterocanium prosperinae* Ehrenberg; Benson, 1966, pl. 27, figs. 3, 5 (not 4)]

Pterocanium praetextum praetextum (Ehrenberg) 1872 [*Pterocanium praetextum* (Ehrenberg); Benson, 1966, pl. 27, fig. 6; pl. 28, fig. 1]

Pterocanium trilobum (Haeckel) 1861 [*Lychnodictyum challengeri* Haeckel; Benson, 1966, pl. 27, fig. 4, pl. 28, figs. 2-3]

Theocorys veneris Haeckel 1887 [*Theocorys veneris* Haeckel; Benson, 1966, pl. 33, figs. 12-13]

Theopilium tricostatum Haeckel 1887 [*Theopilium tricostatum* Haeckel; Benson, 1966, pl. 30, figs. 1-2]

Family **CARPOCANIIDAE**. The small, rudimentary cephalis is usually totally immersed in the large and well-developed thorax. Abdomen absent or rudimentary.

Carpocanistrum sp. A (Nigrini) 1970 [*Carpocanium* sp.; Benson, 1966, pl. 29, figs. 11-12]

Carpocanistrum spp. (Nigrini) 1970 [*Carpocanium petalospyris* Haeckel; Benson, 1966, pl. 29, figs. 9-10; text-fig. 25]

Family **PTEROCORYTHIDAE**. Cephalis large, divided into three lobes by two lateral furrows directed obliquely and downward from the apical spine to the base of the cephalis. The upper unpaired lobe is located above the two smaller paired ones; these basal paired lobes are not always conspicuous. Many pterocorythids are two or three-segmented, lacking postabdominal segments.

Anthocyrtidium ophirens (Ehrenberg) 1872 [*Anthocyrtidium cineraria* Haeckel; Benson, 1966, pl. 32, figs. 6-9]

Anthocyrtidium zanguebaricum (Ehrenberg) 1872 [*Anthocyrtium oxycephalis* (Haeckel); Benson, 1966 pl. 32, figs. 3-5]

Lamprocyclas maritalis group Haeckel 1887 [*Lamprocyclas maritalis* Haeckel; Benson, 1966, pl. 32, figs. 10-12; pl. 33, fig. 1]

Lamprocyrtes nigrinia (Caulet) 1971 [*Conarachnium* sp.; Benson, 1966, pl. 33, figs. 2-3]

Pterocorys clausus (Popofsky) 1913 [*Theoconus zancleus* (Müller) Haeckel; Benson, 1966, pl. 33, fig. 4 (not fig. 5)]

Pterocorys hertwigii (Haeckel) 1887 [*Phormocyrtis fastuosa* [sic.] (Ehrenberg) Haeckel; Benson, 1966, pl. 33, figs. 6-7]

Pterocorys minythorax (Nigrini) 1968 [*Theoconus zancleus* (Müller) Haeckel; Benson, 1966, pl. 33, fig. 5 (not fig. 4)]

Stichopilium bicorne Haeckel 1887 [*Stichopilium bicorne* Haeckel; Benson, 1966, pl. 29, figs. 1-2]

Theocorythium trachelium trachelium (Ehrenberg) 1872 [*Calocyclas amicae* Haeckel; Benson, 1966, pl. 33, figs. 8-9]

Family **ARTOSTROBIIDAE**. Spherical or subspherical cephalis, usually with an apical tube directed obliquely upwards. The pores on all postcephalic segments, or at least on the last ones, are arranged in clearly defined transverse rows. Usually elongated, multisegmented forms.

Botryostrobos aquilonaris (Bailey) 1856 [*Siphocampium erucosum* (Haeckel); Benson, 1966, pl. 35, figs. 18-20]

Botryostrobos auritus-australis (Ehrenberg) group Nigrini 1977 [*Siphocampium cf. seriatus* Haeckel; Benson, 1966, pl. 35, figs. 12-13]

Phormostichoartus corbula (Harting) 1863 [*Siphocampium cf. polyzona* Haeckel; Benson, 1966,; pl. 35, figs. 5-8; text-fig. 27]

Siphocampe lineata (Ehrenberg) 1838 [*Siphocampium cf. cylindrica* Haeckel; Benson, 1966, pl. 35, figs. 10-11]

Siphocampe sp. (Benson) 1966 [*Siphocampium sp.*; Benson, 1966, pl. 35, fig. 9]

Spirocyrtilis scalaris Haeckel 1887 [*Siphocampium cf. cornutella* Haeckel; Benson, 1966, pl. 35, figs. 15-17 (not 14); text-fig. 28]

Stichocorys seriata Jørgensen 1905 [*Siphocampium cf. cornutella* Haeckel; Benson, 1966, pl. 35, fig. 14 (not 15-17); text-fig. 28]

Family **CANNOBOTRYIDAE**. Cephalis large, with several asymmetrical lobes (sometimes appearing as irregular bulges). Mostly 2-segmented forms (cephalis and thorax), but sometimes with post-thoracic segments.

Acrobotrys cribosa (Popofsky) 1913 [*Acrobotrissa cribosa* Popofsky; Benson, 1966, pl. 23, fig. 15; text-fig. 22]

Acrobotrys teralans Renz 1976 [*Acrobotrys cf. disolenia* Haeckel; Benson, 1966, pl. 23, figs. 13-14; text-fig. 2]

Botryocyrtilis quinaria(?) Ehrenberg 1872 [*Botryocyrtilis cf. caput-serpentis* Ehrenberg; Benson, 1966, pl. 23, fig. 17]

Botryocyrtilis scutum (Harting) 1863 [*Botryopyle sp.*; Benson, 1966, pl. 23, fig. 16; text-fig. 23]