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RADIOLARIA

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INTRODUCTION, HISTORY AND CLASSIFICATION

Meyen (1834) first described radiolarians from plankton tows taken from the Atlantic and China seas. Ehrenberg (1847) after producing a number of short papers (mainly on fossil radiolarians) produced the first classification of radiolarians which he called polycystina. Muller (1858) first called the group Radiolaria. Hertwig (1879) classified the radiolarians based on the nature of their unique feature the central capsule (that divides the protoplasm into endo and ectoplasm) and appears to be the first to truly recognize that radiolarians are protozoans. Haeckel, a contemporary of Ehrenberg, Müller, and Hertwig, published a monograph on radiolaria that essentially documented all known fossil radiolarians and included a new radiolarian classification (Haeckel, 1862). Haeckel (1881) further developed this radiolarian classification with the use of material from the CHALLENGER Expedition into a form that at least for the major subdivisions greatly resembled the radiolarian classification of Hertwig (1879). However, Haeckel's major radiolarian work is included as a number of volumes in the CHALLENGER Report (Haeckel, 1887), in which he not only reported on almost 3,000 new species but includes a monographic study of all radiolarians (living and dead) known to that date. Haeckel's classification, although "artificial" and not "natural" remained the classification for almost a century. However; during that 100 years a number of papers presented important information on radiolarian taxonomy. Rust (1885, 1888, 1892) studied radiolarians from European Mesozoic and Paleozoic rocks. Haecker (1906, 1907, 1908) Dreyer (1913), Popofsky (1904, 1906, 1908, 1912, 1913, 1917, 1920, 1926), and Borgert (1905-1913) described the living radiolarians collected on the German oceanographic expeditions of the time. Davis (1918) studied the Franciscan radiolarian charts of California. Campbell and Clark (1944a, b) and Clark and Campbell (1942, 1945) studied Cretaceous and Tertiary radiolarians from the California sections. Campbell (1954) wrote the Treatise volume on radiolaria which follows the Haeckelian system.

In the 1950's the modern period of radiolarian work began, led by W. R. Riedel of Scripps Institution of Oceanography. Riedel (1952) described Tertiary radiolaria in Pacific surface sediments. Riedel (1957) published the first radiolarian biostratigraphy, using material from piston cores from the western Pacific and other material including material from the original CHALLENGER Expedition. Riedel (1959) described two lineages of radiolarians and started to correlate his developing radiolarian biostratigraphy with the foraminiferan zonation of Bolli. In 1967 Riedel began to revise Haeckel's radiolarian classification, in an attempt to make it more "natural" and illustrated the geologic ranges of his radiolarian families (Riedel, 1967). A major radiolarian classification was produced by Riedel (1971) which included a number of revisions at the generic level. Petrushevskaya (1971a) produced another new radiolarian classification, which she further developed in two volumes of the Initial Reports of the Deep Sea Drilling Project (Petrushevskaya and Kozlova, 1972; and Petrushevskaya, 1975).

Currently either or combinations of Riedel's and Petrushevskaya's are used by radiolarian workers. Serious students of radiolarians should be familiar with these classifications. The "common name" classification presented herein (Appendix 1) follows the similar "common name" classification presented by Kling (1978), and extensive "class notes" used by Riedel over the years; and, is essential a "common name" (no formal family etc. names used) combination of the classifications of Riedel and Petrushevskaya.

DISTRIBUTION AND ECOLOGY

Anderson (1980) reviews and adds to the physiological and biochemical research on radiolarians in the second edition (volume 3) of Biochemistry and Physiology of Protozoa.

Radiolarians in the water column and sediments were first studied in detail by Haeckel (1887) using the H.M.S. CHALLENGER collections. Until recently, there have been few studies of living radiolarians and modern forms in the sediments. Studies by Casey (1971a, b ; 1977), Petrushevskaya (1971a), Renz (1976), McMillen and Casey (1978), Boltovskoy and Riedel (in press), King (1979) and Spaw (1979) are adding to our knowledge of radiolarian distributions in the water column. Recent papers by Petrushevskaya (1971b, c and d), Goll and Bjorklund (1971; 1974) and Nigrini (1967) have increased our understanding of radiolarian distributions in Holocene sediments. Recent studies of radiolarian distributions in the Gulf of Mexico are McMillen and Casey (1978), Leavesley et al. (1978), and Casey et al. (1979a, b, and submitted).

Our studies (Casey et al., 1979a) indicate that there are about 400 to 500 relatively common polycystine radiolarian species living in the present oceans. Approximately 200 of these species live in the shallow (0-200 m) central and tropical waters of the ocean ("warm water sphere"), 40 to 50 species in high latitude (poleward of the subtropical convergences) shallow (0-200 m) waters, and 100 to 150 in deep (greater than 200 m) water, and are tropical submergent shallow high latitudes and diving as tropical submergent or tropical avoidant forms).

Appendix 2 illustrates the niches that we believe that Radiolarians occupy, and also how these niches are distributed in a hypothetical ocean. A biogeographic zonation for radiolarians was erected by Casey (1971a) and later updated (Casey, 1977).

In a recent publication (Casey et al., 1979b) on radiolarian ecology and the development of the radiolarian component in Holocene sediments the following conclusions were made:

(1) Many polycystine Radiolaria appear to be endemic or indicative of specific water masses. However, radiolarians indicative of a certain water mass in one ocean basin may not necessarily be indicative of the counterpart of that water mass in another ocean basin; (2) Low densities and diversities characterize the living radiolarian faunas of the oligotrophic open Gulf of Mexico and the eutrophic brackish Texas shelf waters. Higher densities and diversities typify these assemblages in the olgiotrophic open ocean Sargasso Sea region and the mesotrophic western boundary current, the Gulf Stream. The greatest densities and diversities were recorded in samples from the eutrophic eastern boundary current off southern California; (3) Low density and diversity assemblages from eutrophic neritic waters (Texas shelf) are distinguished from low density and diversity assemblages of the open Gulf of Mexico by the dominance of spongy radiolarian forms in the meritic water assemblage; (4) The presence of more deep-living forms in the surface waters distinguishes radiolarian faunas from eutrophic eastern boundary currents from faunas from mesotrophic western boundary currents; (5) Eutrophic open ocean regions appear to produce more radiolarian tests that "find" their way to the bottom faster than in oligotrophic ocean regions; (6) Certain radiolarian species can be used to trace horizontal water movements such as the movement of Subtropical Underwater and Antarctic Intermediate Water into the Texas area. Vertical water movements were also indicated by certain radiolarian species. This included large-scale boundary current upwelling off southern California and small-scale upwelling on to the south Texas outer continental shelf; (7) Changes in the species composition of radiolarian populations in shelf regions and in eastern boundary currents (off southern California) reflect seasonal changes in the physical oceanography of the water column.

Reviews of other work on radiolarian distribution and ecology including studies on the seasonal distributions of radiolarians may be found in Casey (1971a, b and 1977) and Casey et al., (1979a, b, c and submitted).

PALEOECOLOGIC STUDIES

Significant research has also come from the use of radiolarians in paleoceanographic studies; such as the determinations of paleotemperatures (Casey, 1972; Dow, 1978; Johnson and Knoll, 1974; Moore, 1973; Nigrini, 1970; and others), paleowatermass and paleocirculation boundaries

(Maurrasse, 1979; Morley and Hays, 1979; Pisias, 1978 and 1979; Sancetta, 1978: and others), and the use of factor analysis and other computer aided studies have tried to interpret the radiolarian thanatocoenosis in the sediments (Molina-Cruz, 1977; Moore, 1978; Morley, 1979; Sachs, 1973; and others).

Casey and McMillen (1977) have suggested how radiolarians may have reacted paleoecologically to past biologic, tectonic and oceanographic events. Casey et al., (1979a and b) have suggested how radiolarians can be used to interpret paleoupwelling and paleoproductivity, (see Appendix 3 for paleoecologic information).

PRESERVATIONAL STUDIES

In the modern seas polycystine radiolarian skeletons occur only in the upper few centimeters of sediment over much of the mid and low latitude oceans (Casey and McMillen, 1977). Radiolarian oozes, however, are preserved mainly in the equatorial Pacific, and good preservation occurs in the Pacific especially under the boundary currents and in high latitudes. Radiolarians are poorly preserved in the Atlantic and Gulf of Mexico. Casey and McMillen (1977) suggest some conditions for optimum radiolarian preservation and optimum radiolarian dissolution. At times in the past, such as the Miocene siliceous shales of California and Baja California, there appear to have been pulses of siliceous sedimentation.

Radiolarian sedimentation and preservation studies are contributing to the understanding of chemical, geochemical and sedimentological cycles and regimes in the world's oceans. The use of man made (Takahashi and Honjo, in press; Berger and soutar, 1970) and natural (such as Santa Barbara Basin (Soutar and Crill, 1977; Casey et al., 1971, Pisias, 1978 and Kling, 1977) sediment traps have greatly increased our knowledge of the avenues, rates and imprints of radiolarian sedimentation. Preservation studies on radiolarian thanatocoenoisis (Johnson, 1974; and 1976a and b; Hurd and Theyer, 1975) and on individual radiolarians from the sediments (Hurd and Theyer, 1977; and Kunze, 1980) and live and dead from the water column (Kunze, 1980) etc. are illustrating the avenues of radiolarian sedimentation, preservation and dissolution. Studies by Weaver and Wise, 1972; and others, are contributing to our knowledge of the role of radiolarians in chert formation; and cherts are an important preservational media for many of the pre-Cenozoic radiolarians whose biostratigraphic potential for decipering complex stratigraphic sequences are well known (Pessagno, 1976). See Appendix 4 for preservation information.

BIOSTRATIGRAPHIC STUDIES

As previously stated Riedel (1957) published the first radiolarian biostratigraphy, and later (Riedel, 1979) the first lineages from the fossil record. Riedel and Sanfilippo (1970 and 1971) developed a tropical radiolarian zonation for the Tertiary which has become the standard.

The tropical radiolarian zonation of Riedel and Sanfilippo (1970 and 1971) has been modified (such as by Moore, 1971; Riedel and Sanfilippo, 1977; and Sanfilippo and Riedel, 1973), extended (Nigrini, 1971; Foreman, 1973; Sanfilippo and Riedel, 1973) related to the paleomagnetic time-scale (Theyer and Hammond, 1974a and b), compared by magnetostratigraphy to other microfossil zonations (Hays et al., 1969; Berggren and Van Couvering, 1974; Casey and Reynolds, 1980; and others), compared to the type sections (Sanfilippo et al., 1973), and to mid and high latitude oceanic (Many D.S.D.P. reports) and land-based sections (Casey, 1972; and others), and has also lead to attempts to develop a more cosmopolitan radiolarian zonation (Casey and Reynolds, 1980).

Although there have not been many workers involved in developing radiolarian biostratigraphies for the Mesozoic and Paleozoic a good introduction to work done on the Mesozoic can be found in Pessagno (1977), and the initiation of a Paleoozoic radiolarian zonation can be found in Holdsworth (1977), (see Appendix 5 for biostratigraphic schemes).

EVOLUTIONARY STUDIES

Radiolarians have also become a significant tool in evolutionary studies and will become even more important with the continued use of the hydraulic piston core. Evolutionary lineages have been suggested by many authors such as the "closed" theoperid lineage of Sanfilippo and Riedel (1970). Examples of allopatric speciation, phyletic "gradualism" (Kellogg and Hays, 1975) character displacement (Kellogg 1976), and hybridization (Goll, 1979) have all been suggested. Distributional studies have detected relict and expatriated radiolarian populations (Casey et al., 1979c), and suggested that deep living radiolarians are evolutionarily conservative (Casey et al., 1978).

THE ESSENTIAL "TOOLS" FOR A RADIOLARIAN WORKER

LITERATURE Foreman and Riedel (1972) produced a catalogue of polycystine radiolarians similar to the catalogues of foraminifera and ostracoda from the American Museum of Natural History. This radiolarian catalogue can be obtained from the American Museum of Natural History and consists of two volumes that contain all the original descriptions and genera, subgenera, species, and taxa below the rank of species described for the first time and subsequent references to these taxa which contain new information for the period of 1834 to 1900. However, the catalogue in its "final" form (up to 1930 I believe) is just now available on microfiche (this can be obtained for about $300, I believe) from Fran Roberts, 5285 Port Royal Road, Springfield Virgina U.S.A. 22161). To obtain this catalogue ask for the Polycystine Radiolaria Catalogue on microfische #PB-281 000 when ordering. Riedel has compiled the most extensive collection of radiolarian reprints in the world, converted them to microfiche and will sell these sets for $375 (currently) if you send a personal check made out to W. R. Riedel for that amount and ask for a microfiche copy of his Radiolarian Reprint Collection (send to W. R. Riedel, Scripps Institution of Oceanography A-012, University of California, San Diego, La Jolla, California U.S.A. 92093). The third essential source (especially for biostratigraphic work) are the Initial Reports of the Deep Sea Drilling Project. These too may be obtained on microfiche by writing Barbara Pinkston, Deep Sea Drilling Project A-031, Scripps Institution of Oceanography, University of California San Diego, La Jolla, California U.S.A. 92093. Currently the microfiche set of all volumes, 1-44, costs $164.80. So for about $1,000 (which includes the price of buying a microfiche reader and a couple extra bulbs) a person can be well set up in literature for radiolarian work. From then on a keen eye should be kept for new radiolarian literature. In the past Riedel has sent lists of new literature that he has acquired and reproduced on microfiche, and which he has made available for an extremely reasonable amount. In the United States most of the new radiolarian papers are published in the Deep Sea Drilling Reports, Marine Micropaleontology, Micropaleontology, Journal of Paleontology, and Quaternary Research. The American Museum of Natural History publishes a Bibliography and Index of Micropaleontology that lists current worldwide publications arranged by microfossils groups. This publication is very useful for keeping up to date and may be obtained by contacting Micropaleontology Press, The American Museum of Natural History, Central Park West at 79th Street, New York, New York U.S.A. 10024 (prices are different for students, institutions etc., and inquiry should be made stating the potential subscribers affiliations, (microfiche copies may be available, I do not know). Lastly in recent years there have been a number of symposium etc. volumes that contain significant radiolarian literatures. A few of these are: The Micropaleontology of Oceans B.M. Funnell and W.R. Riedel eds.; Stratigraphic Micropaleontology of Atlantic Basin and Borderlands F.M. Swain ed.; Proceedings of the II Planktonic Conference, Roma 1970 A. Farinacci edl; and Oceanic Micropaleontology vol. 2 A.T.S. Ramsay ed.

EQUIPMENT AND LABORATORY A good quality binocular-light transmission-research microscope is a must for working on radiolarian slides and thin sections. This microscope should be equipped with 4, 10, 20, 40 and perhaps oil immersion objectives. Wide field 10x eyepieces are good. The microscope should have a graduated mechanical stage and it would be advantageous to have a microscope set up so that microphotography is possible at any time (it is good to use a Polaroid camera set up for routine use and a regular film camera that can replace the Polaroid for manuscript work). For some work such as hydrofluric extraction of radiolarians from Mesozoic and Paleozoic cherts a good reflecting microscope will be needed for picking the radiolarians from the washed and dried residue as is used for picking foraminiferan samples. For Mesozoic and Paleozoic chert work the best results (for publishing illustrations of the radiolarians) are obtained with the use of the scanning electron microscope. Other special microscopes may be needed for special types of radiolarian research such as inverted or plankton microscopes for working on radiolarians taken from plankton tows. An essential and time saving device for use with the microscopes having a mechanical stage is the England Finder which is a slide with a grid etched on it so that one can record the exact position of a radiolarian on a permanent glass slide and return to that specimen easily. England Finders are commonly used in indicating the locations of type specimens and may be obtained from Graticules Limited, Sovereign Way, Tonbridge, Kent England - Tel. Tonbridge 359061 (I am not aware of the current price but suggest you buy more than one for they can get broken for they are usually in constant use).

Basic laboratory equipment for preparing radiolarian slides for work on sediments and sedimentary rocks should include: variable heat hot plates that can range in temperature from about 70 to over 500 degrees centigrade; slide dryers; drying ovens that can be maintained at about 70 degrees centigrade; stainless steel mesh sieves of various sizes but at least a few with a mesh size of 62 microns; a large wash basin (sink) with running distilled water if possible; an ultrasonic cleaner; and Pyrex beakers (250 or 500 ml.), stirring rods and asbestos gloves for picking up hot beakers. The actual heating of samples and use of acids etc. should be done under a laboratory hood.

Special equipment will be needed for processing radiolarian samples from other than the normal sediments or sedimentary rocks and the techniques and equipment suggested in the papers cited herein in the section on extracting and processing radiolarians should be consulted. This equipment may range from lapadary wheels and polishing wheels for thin section preparation to acid traps for the use of hydrofluric acid in chert extrations.

SAMPLING, EXTRACTING AND PROCESSING RADIOLARIANS

SAMPLING - Procedures for sampling radiolarians can be found De Wever and Riedel et al., (1979). This publication is also excellent for procedures on extracting and processing radiolarians from samples.

EXTRACTING AND PROCESSING RADIOLARIANS - The above publication is excellent for these procedures (De Wever and Riedel et al., 1979). Herein I will only mention a common procedure for processing radiolarians from Recent sediment and sedimentary rock samples exclusive of cherts etc. Take about 5 cc of sample and break into pea-sized particles; soak sample in distilled water, about 100 ml water in a 250 or 500 ml Pyrex beaker (overnight if possible); put beaker on hot plate (under hood) and boil; add small amounts of 30% hydrogen peroxide (carefully) until effervescence stops; wash over a 63 micron screen with distilled water (tap water if no distilled water); look at the sample as it may be ready; if still dirty or containing calcareous microfossils add 100 ml water to the sample in beaker, boil, add more 30% hydrogen peroxide and drop in a small amount of sodium pyrophosphate (careful it may boil over) then wash again over 62 micron screen (this is to be done if there are no calcareous microfossils or if you wish to keep the calcareous microfossils (if you wish to remove the calcareous microfossils use the next step); add 100 ml distilled water to sample in beaker and add drops of concentrated hydrochloric acid (under a hood) until effervescence stops, wash with water over a 62 micron screen. If the sample is not clean, dry sample in drying oven and repeat above until sample is clean.

PREPARATION OF RADIOLARIAN SLIDE - Remove radiolarians from bottom of beaker (distilled water in beaker) and place drops of water with radiolarians on a glass slide sitting on a hot plate of about 70 degrees centigrade. Allow slide to dry and add more drops until you have a dense concentration of radiolarians on the slide. Remove slide and radiolarians, allow to cool, place a few drops of toluene on the radiolarians so they are visibly wet and immediately place a few drops (at least 6) of Permount on the wet radiolarians and cover with a number 1 cover slip. Label slide and allow slide to remain flat for a number of days at least. The same procedure can be done using other mounting media such as balsam etc. and the appropriate solvents for such media. Radiolarian slides so prepared should always remain flat. Moore (1973) describes a technique for quantitatively distributing the radiolarians on a glass slide.

Other procedures such as thin section and hydrofluric acid streat may have to be used with cherts or very hard sedimentary rocks. Some techniques for these rocks may be found in De Wever and Riedel et al., (1979), and an excellent technique for the use of hydrofluric acid on cherts may be found in Pessagno (1972).

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COMMON NAME CLASSIFICATION OF POLYCYSTINE RADIOLARIANS (NATURAL GROUPS)
POLYCYSTINES (skeleton of opalina silica)
SPUMELLARIANS (polycystines that are generally spherical or based on sphere)

BELOIDS = skeleton of scattered spicules that are usually circular in outline, beloids can be distinguished from sponge spicules because beloids do not possess a central canal as sponges do

range = Paleozoic to Recent
environment = cosmopolitan

ENTACTINIIDS - skeleton spherical to ellipsoidal with a latticed wall structure, distinguished from other groups by bars running to the center of the skeleton

range = Ordovician to Carboniferous
environment = ?

OROSPHAERIDS = a large spherical or cup shaped skeleton with a coarse, polygonal lattice and commonly club shaped spines, distinguished by large size of complete speciments (a few mm) but in sediments usually find only pieces of lattice or whole spines

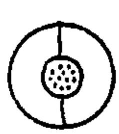
range = Eocene to Recent
environment = probably all deep sea or cold water sphere, occur in red clays as one of the few preserved fossils

COLLOSPHAERIDS = single spheres with usually more inter-pore area than pore area, many times with internal or external tubular or spiney projections, can be distinguished from similar forms by the above characteristics and usually frail (not robust nature)

range = Lower Miocene (or Upper Oligocene) to Recent
environment = warm water sphere, dominate the oligotrophic anticyclonic gyres, colonial as lives and possessing symbiotic algae (zooxanthellae), a few more robust forms appear to be cold water forms (cold water sphere?)

ACTINOMMIDS = a catch all polyphyletic group containing generally spherical forms (some rough subgroups below)
range of "group" = Paleozoic?, Triassic to Recent

SATURNALINS = spherical latticed skeleton possessing a circular outer ring connected to a latticed or sometimes spongy shell



range = Triassic to Recent, forms with ornamented outer ring appear to be restricted to the Mesozoic
environment = warm water sphere

STYLOSPHAERIDS = latticed shells with polar spines, one or two (the saturnulins are probably a subgroup of this group)

range = Paleozoic? to Recent
environment = cosmopolitan

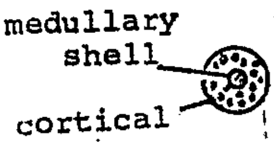
CUBOSPHAERIDS = latticed shells with polar and equatorial spines (six) (tripospherids = 3 spines, staurosphaerids = 4 spines, pentasphaerids = 5 spines)

range = Paleozoic to Recent
environment = cosmopolitan

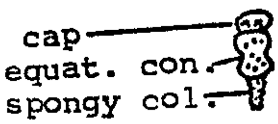
ASTROSPHAERIDS = latticed shells with numerous spines

range = Paleozoic to Recent
environment = cosmopolitan

CENODISCIDS = lattice shell (single) without obvious spination, can usually be distinguished from collosphaerids by having less inter-pre area, thicker skeleton, and no tubes
range = Paleozoic to Recent
environment = wide range of environments but great abundance in sediment samples usually means the sample reflects cold surface waters or has undergone considerable dissolution



LIOSPHERIDS = lattice shell (multiple) without obvious spines
range = Paleozoic to Recent
environment = cosmopolitan



ARTISCINS = elliptical outer (cortical) latticed shell many times with an equatorial constriction and caps and or spongy columns
range = Oligocene to Recent
environment = warm water sphere, symbiotic algae

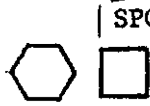
PHACODISCIDS = discoidal, biconvex latticed outer shell
range = Mesozoic to Recent
environment = warm water sphere

COCCODISCIDS = lens shaped with a latticed center and spongy chambered girdle or arms
range = Mesozoic to Oligocene
environment = ?

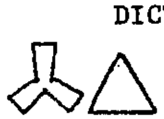
SPONGODISCIDS = a polyphyletic group of generally discoidal and spongy nature, group range = Devonian to Recent (sub-groups below)

SPONGOTROCHINS = spongy lens (sometimes with evidence of "rings") and many times with large numerous spines
range = Mesozoic (maybe Paleozoic) to Recent
environment = commonly cold water sphere, good indicators of upwelling

SPONGOPYLINS = spongy lens without spines but with a pylome
range = Mesozoic to Recent
environment = cold water sphere



SPONGASTERINS = spongy disk with margins faceted and radiating
range = Eocene to Recent (K?) thickenings internally
environment = warm water sphere, tolerant of nearshore conditions (indicator of such), with symbiotic algae



DICTYOCORIINS - spongy disc with three arms (chambered or spongy)
range = Mesozoic to Recent
environment = mainly warm water sphere, common in eutrophic environments (indicative of such), some with symbiotic zooxanthellae (there are cool and warm morphotypes)

STYLODICTIDS or PORODISCIDS = disk with rings of lattice, may be a subgroup of spongodiscids
range = Permo-Triassic - Recent
environment = appear to be mainly subsurface warm water and cold water forms

SPONGURINS = spongy cylinder
range = Mesozoic to Recent
environment = cosmopolitan, cold and warm morphotypes

HAGIASTRIDS = flat "disk" with spongy-rectangular mesh and 2 to 4 (usually three) radial arms (large) that may possess spines
range = Mesozoic
environment = ?

PSEUDOAULOPHACIDS = lens like or more commonly triangular spongy and triangular mesh, usually with a few prominent marginal spines
range - Mesozoic
environment = ?

PYLONIDS = shell an ellipsoid of girdles with gates (holes)

range = Eocene to Recent
environment = mainly warm water sphere

THOLONIDS = outer (cortical) shell elliptical with bulb like extensions of the shell and some spines

range = Pliocene to Recent
environment = deep and or cold water sphere (in intermediate waters)

LITHELIIDS = coiled latticed shell (includes larcospirins and sphaeropylins)
range = Carboniferous to Recent

environment = cosmopolitan with cold water morphotype tightly coiled and warm water sphere morphotype loosely (more open) coiled

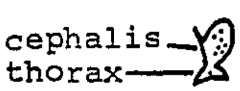
NASSELLARIANS (polycystines that are generally cone shaped)

PLAGONIIDS = polyphyletic group of simple forms, spicule to two joints

PLAGIACANTHINS = thorax and sometimes walls of cephalis reduced, sometimes to the extreme of only spicules remaining; these "spicules" can be distinguished from beloids in that the plagiacanthins usually possess; faceted spines and the beloids round spines

range = Miocene to Recent
environment = cosmopolitan in surface and subsurface

LOPHOPHAENINS = cephalis and thorax about equally developed, usually two lobes (or three) in cephalis; apical, dorsal and primary spines usually obvious and extending beyond lattice shell

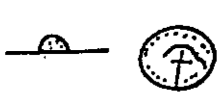


range = Cretaceous to Recent
environment = cosmopolitan, mainly shallow but also deep members

SETHOPERINS = cephalis and six latticed plates extending from cephalis, or modified as a "basket" like thorax

range = Cenozoic
environment - warm water sphere

SETHOPHORMINS = cephalis large, hemispherical with a flattened umbrella shaped thorax

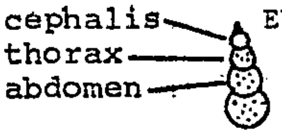


range = Cretaceous to Recent
environment = cosmopolitan

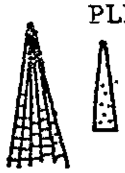
CRYTENTACTINS = looks like "cross" between entactinid (spumellarian) and lophophaenin (nassellarian) · may be earliest nassellarian
range = Devonian
environment = ?

CARPOCANIDS = cephalis small and recessed into the thorax, thorax usually elongate and usually with longitudinally arranged pores
range = Eocene to Recent
environment = warm water sphere mainly

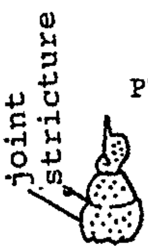
THEOPERIDS = small spherical, usually poreless cephalis, with one or more postcephalic chambers, usually only one small apical spine on top of cephalis



EUCYRTIDINS = usually more than one postcephalic chamber (joint), and pores not quadrangular
range = Mesozoic to Recent
environment = cosmopolitan but mainly in warm water sphere

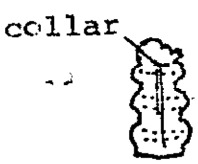


PLECTOPYRAMINS = usually only one postcephalic joint, and this joint cone shaped and usually with longitudinally arranged quadrangular pores
range = Mesozoic to Recent
environment = cosmopolitan but mainly deep or cold water sphere



PTEROCORIDS or PTEROCORYTHIDS = large elongate cephalis with one or more postcephalic chambers; cephalis usually consists of a main lobe (eucephalic) and two lateral lobes separated by furrows; the cephalis is pored and usually bears a large vertical spine (apical) that emerges from the side of the cephalis
range = late Cretaceous to Recent
environment = warm water sphere

AMPHIPYNDACIDS = small spherical, usually poreless cephalis with several postcephalic joints; cephalis divided into two vertical segments by transverse internal ledge
range = Cretaceous to lower Tertiary
environment = ?

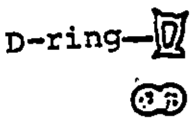


ARTOSTROBIDS = cephalis of eucephalic lobe, other lobes and sometimes tubes; many postcephalic joints usually with latitudinally arranged pores; spines may sometimes be seen protruding from the collar structure into the postcephalic chamber innerarea
range = Cretaceous to Recent
environment = cosmopolitan, warm water and cold water (and deep water) morphotypes can be distinguished

CANNOBOTRYIDS = cephalis of eucephalic lobe, other lobes which may extend as tubes; usually only one or two postcephalic joints; pores commonly appear to be randomly arranged
range = Eocene (K?) to Recent
environment = cosmopolitan but more diverse in warm water sphere; cold (deep) and warm water morphotypes can be distinguished

ACANTHODESMIIDS = D shaped ring or latticed, bilobed chamber with internal D shaped sagittal ring

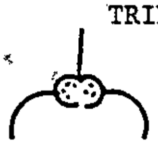
ACANTHODESMINS - D shaped ring or modification of such, or sagittal ring (D-ring) surrounded by two latticed lateral lobes; apical and basal poles not obvious



range = Eocene to Recent

environment = mainly warm water sphere, usually shallow and apparently with symbiotic algae

TRIPSYRINS = sagittal ring (D-ring) surrounded by two latticed lateral lobes, apical and basal poles obvious; commonly with basal feet and apical spines (sometimes very long)



range = Paleocene to Recent

environment = mainly warm water sphere

ROTAFORMIDS = lens shaped, central area enclosing what appears to be a nassellarian cephalis, this central area is connected to an outer ring by radial bars

range = Cretaceous

environment = ?

RADIOLARIA INCERAE SEDIS (PROBABLY NASSELLARIAN LIKE)

ALBAILLELLIDS - skeleton consisting of three spines in a plane forming a triangle, rib-like elements may protrude from the spines giving the skeleton a jointed appearance, may be oldest nassellarian

range = Silurian to Carboniferous

environment = ?

PALAEOSCENIDS = skeleton consisting of four diverging basal spines with rib-like elements protruding, topped by two or four "apical" spines

range = Devonian to Carboniferous

environment = ?

APPENDIX 2, RADIOLARIAN NICHES AND HYPOTHETICAL OCEAN
(the figures produced here and on the next page
are from Casey etal., 1979b)

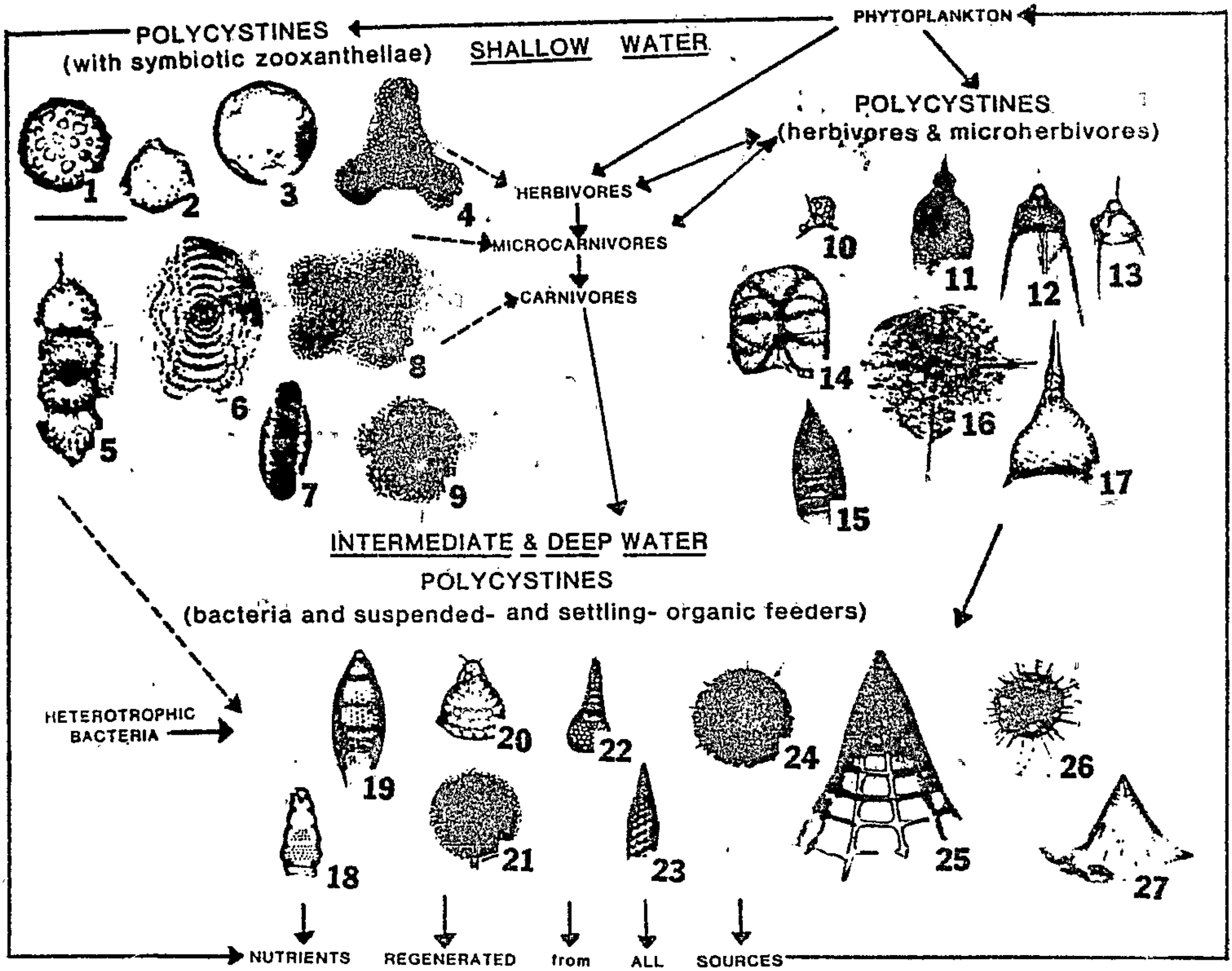


Figure 5. Polycystine radiolarian niche diagram. The inferred niches, the species number on the figure and the names figured are: polycystines with symbiotic zooxanthellae (usually in shallow water but to depths of 2000 m) are, 1-3) collosphaerids, 4) *Dictyocoryne profunda-truncatum* group, 5) *Ommatartus*, 6) *Amphirhopalum ypsilon* Haeckel, 7) *Spongocore*, 8) *Spongaster tetras* Ehrenberg, and 9) *Spongaster pentas* Riedel and Sanfilippo; polycystines mainly representing the herbivore and micro or nannoherbivore niches (usually in the upper 200 m of the water column) are, 10) *Peridinium spinipes*, 11) *Theocorythium trachelium* (Ehrenberg), 12) *Pterocanium praetextum praetextum*, 13) *Pterocanium praetextum eucolpum* Haeckel, 14) *Liriospyris reticulata* (Ehrenberg), 15) *Eucyrtidium hexagonatum* Haeckel, 16) *Spongosphaera streptacantha* Haeckel, and 17) *Anthocyrtidium ophirense* (Ehrenberg); polycystines mainly representing the bacteria (bactivore) and suspended and settling organic feeder (detritivore) niches are, 18) artostrobids, 19) *Eucyrtidium calvertense*, 20) *Theocalyptra bicornis*, 21) *Spongopyle osculosa*, 22) *Cyrtopera laguncula-Stichoformis cornutella* group, 23) *Cornutella profunda*, 24) *Spongotrochus glacialis*, 25) *Peripyramis circumtexta*, 26) *Lithelius nautiloides* Popofsky, and 27) *Litharachnium tentorium* Haeckel. The scale bar under number 1 is 100 µ.

APPENDIX 2 CONT'

Table 1. A comparison of the microplankton collected from the eutrophic California Current (a eutrophic eastern boundary current), the Gulf Stream (a mesotrophic western boundary current), the open ocean Gulf of Mexico (an oligotrophic open ocean region), and the Galveston shelf (a eutrophic neritic environment) from samples collected with the DUCA high speed plankton net. All numbers are in numbers/m^3, except for radiolarian richness.

	California Current	Gulf Stream	open ocean Gulf of Mexico	Galveston shelf
nassellarian radiolarians	391	50	4	0
spumellarian radiolarians	96	62	15	0
total polycystine radiolarians (nassellarians plus spumellarians)	487	122	19	1
planktonic foraminiferans	332	68	44	1
benthonic foraminiferans	0	0	0	13
pteropods, shelled	12	121	6	181
radiolarian richness	43	17	8	0
microplankton standing crop	77,500	29,600	5,500	128,000
dominant phytoplankton	pennate diatoms	trichodesmium	trichodesmium	pennate diatoms

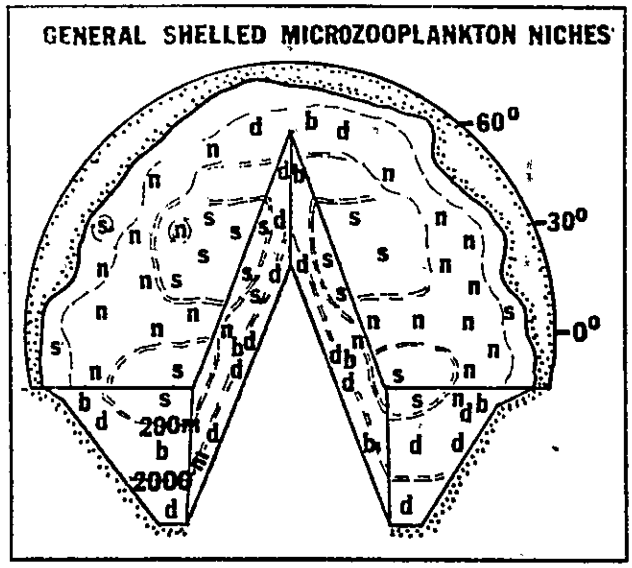


Figure 6. General shelled microzooplankton niches. On the hypothetical dissected ocean figured the letters represent the four basic niches referred to in the text (n = nannoherbivore, s = symbiotic algae associated, b = bacterivore and d = detritivore). The density of the packing of the letters represents the density of the individuals representing those niches. Major oceanographic faunal boundaries are represented by double broken lines and lesser boundaries by single broken lines. General trends that can be seen are: nannoherbivores are restricted to the upper 200 m of the water column and are most common in the upwelling areas (boundary currents and equatorial currents); symbiotic algae associated forms are mainly restricted to the open ocean gyral systems but may occur nearshore in low latitudes; both detritivores and bacterivores are found at depth and in shallow high latitudes (they also shoal in upwelling areas and especially underneath eastern boundary current systems and are of greater abundance under areas of higher productivity). Populations may move shoreward or oceanward from boundary currents via entrapment in cyclonic or anticyclonic rings broken from these currents (shown as s and n with arrows around them). Polycystine radiolarians fill all the niches but planktonic foraminiferans are mainly nannoherbivores or associated with symbiotic algae and pteropoda (shelled) appear to be mainly nannoherbivores or planktivores. The slice from the middle of the hypothetical ocean basin illustrates not only what is at depth but also such features as the thickening of the central gyral systems and their incorporated faunas and niches in midlatitudes, *etc.*

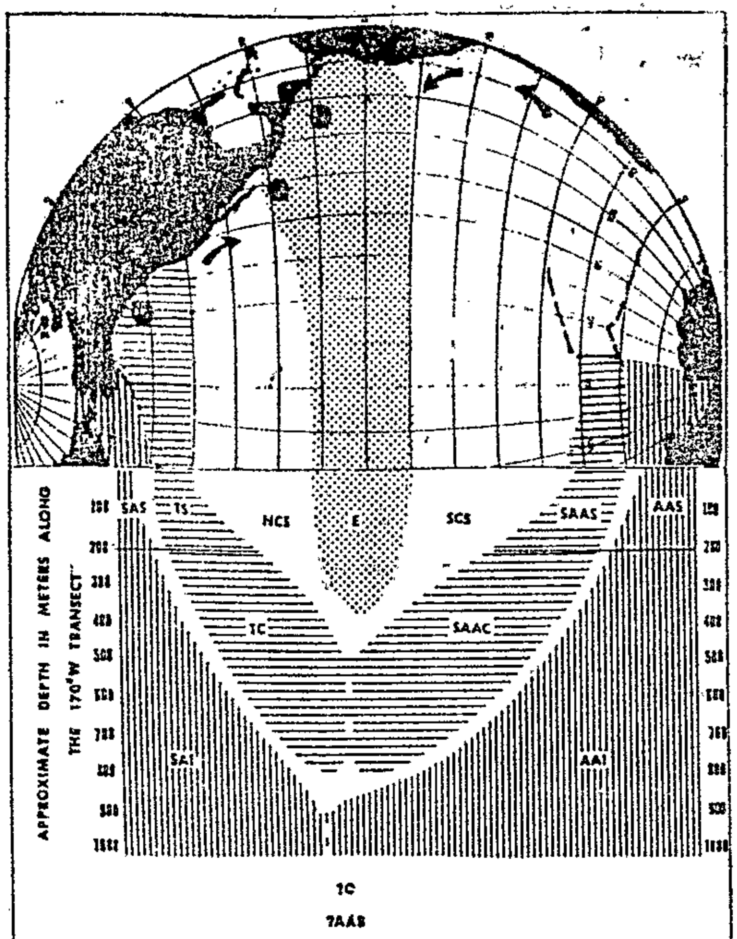


FIG. 5. Biogeographic zones for polycystine radiolarians in the Pacific Ocean (from Casey, 1971a). AAS, Antarctic Shallow Faunal Zone; AAI, Antarctic-Intermediate Faunal Zone; SAAS, Subantarctic Shallow Faunal Zone; SAAC, Subantarctic Central Faunal Zone; SCS, South Central Shallow Faunal Zone; E, Equatorial Faunal Zone; NCS, North Central Shallow Faunal Zone; TC, Transition-Central Faunal Zone; TS, Transition Shallow Faunal Zone; SAI, Subarctic Intermediate Faunal Zone; SAS, Subarctic Shallow Faunal Zone.

(Perhaps a C, Common Faunal Zone may exist below the Intermediate Zones, and an AAB, Antarctic Bottom Faunal Zone below the Common Zone. The large dots represent subzones which appear to be oceanographically stable areas which allow the development of slightly different faunas within the major zone.) SAS and AAS faunas are restricted to high latitudes whereas SAI and AAI faunas are tropical submergent faunas.

(from Casey and McMillen, 1977)

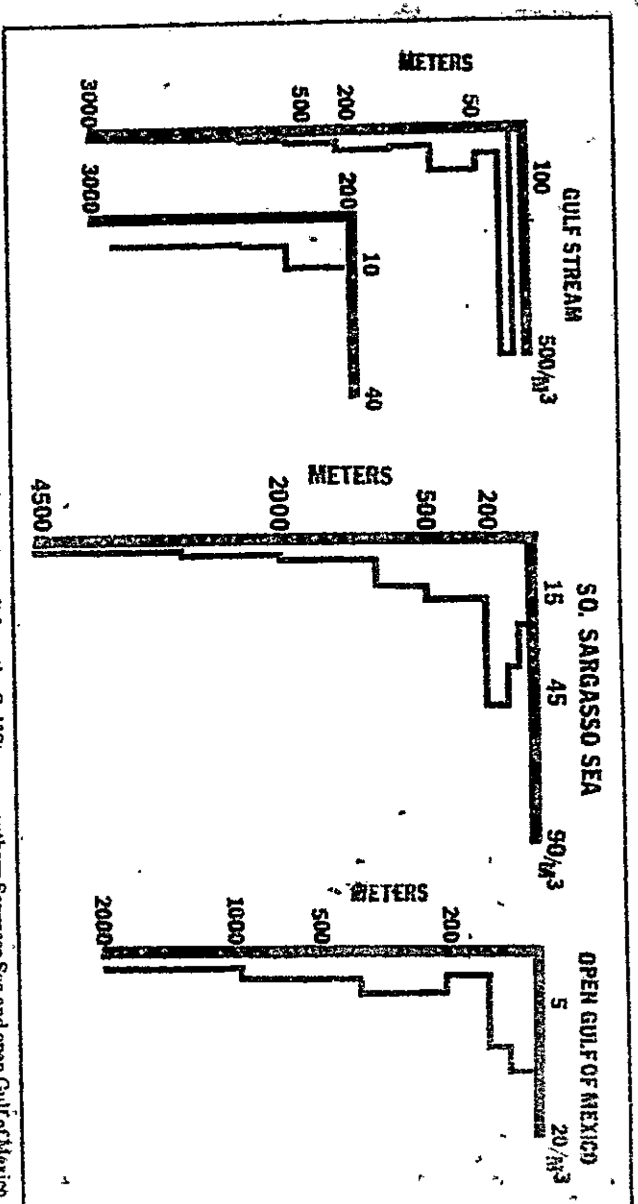


Figure 2. Densities of live radiolarians (stained with rose bengal) from the Gulf Stream, southern Sargasso Sea and open Gulf of Mexico. Samples were taken with vertically stratified Nansen closing nets. Note that the scales differ for each station. Of special interest is that the radiolarian populations are best developed (denser) under eutrophic conditions (the Gulf Stream) than under oligotrophic conditions (the southern Sargasso Sea and open Gulf of Mexico). (from Casey etal., 1979a)

APPENDIX 3, RADIOLARIAN PALEOECOLOGIC INFORMATION

Figure 1 TECTONIC AND OCEANIC EVENTS IN THE ATLANTIC AND THEIR POSSIBLE EFFECTS ON RADIOLARIANS AND SILICEOUS SEDIMENTATION

EVENT	POSSIBLE EFFECT
1. Development of diatoms and rapid increase in diversity and "abundance" during the Cenozoic	1. Radiolarians adapt to development of diatoms and competitive pressure for silica by using less silica in test.
2. Separation of Australia and Antarctica about Late Paleogene (about 35 m.y.a.) (Kennett et al., 1972)	2. Development of a circum-Antarctic current resulting in thermal isolation of Antarctica and increased glaciation in Antarctica. Paleogene "Antarctic Bottom Water" formed and flows into Atlantic through newly-formed pass in the Rio Grande-Walvis Ridge changing the mid and low latitude Atlantic from a carbonate sink or lagoonal-type basin (that it had been during most of the Paleogene) to a silica sink or estuarine-type basin (with both silica and carbonate being deposited) similar to the present day Pacific. This persisted until early Miocene.
3. Closure of eastern Tethys (Africa-Arabia joined to S.W. Asia in early Miocene about 18 to 20 m.y.a. and closure of western tethys (Europe-Africa join at Gibraltar) in mid-Miocene about 12-14 million years ago (Berggren and Van Couvering, 1974) and elevation of Panamanian block to about 1500 meters (Sandy and Casey, 1973)	3. Atlantic isolated from equatorial Indian Ocean and considerably restricted from the equatorial Pacific, resulting in the development of Neogene water mass regimes and radiolarian faunas endemic to these water masses (such as those referred to in the living radiolarians in this paper). Periods of glaciation due to development of meridianal circulation and periods of production of Mediterranean intermediate water resulting in saline waters reaching the Antarctic and lowering the freezing point depression and resulting in "interglacials" and periods of no generation of Mediterranean Intermediate Water resulting in Mediterranean evaporites and "freshening" of Antarctic waters and resulting "glacials". This period is the period of change from an Atlantic silica sink (estuarine type basin) to a carbonate basin (lagoonal type) which has persisted to the present. (Ryan, et al, 1974)
4. Elevation of the Panamanian Block to effective sill, stopping communication between the equatorial Atlantic and Pacific completely at about the Miocene-Pliocene boundary (4 to 5 m.y.a.)	4. Development of provincial radiolarian faunas in the low latitude oceans with "leaking" of low latitude Pacific and Indian Ocean faunas into the Atlantic around the Cape of Good Hope and the retention of a relict radiolarian fauna in the equatorial Atlantic and its marginal seas (Gulf of Mexico and Caribbean). The almost complete closure at Panama intensifies the Gulf Stream, carrying warm water to high latitudes, allow island hopping of vertebrate faunas between North and South America, and results in increased precipitation and the development of northern hemisphere glaciation at about 3 m.y.a. Increased glaciation in the Pleistocene may result from the more complete restriction through Panama at that time.

(from Casey and McMillen, 1977)

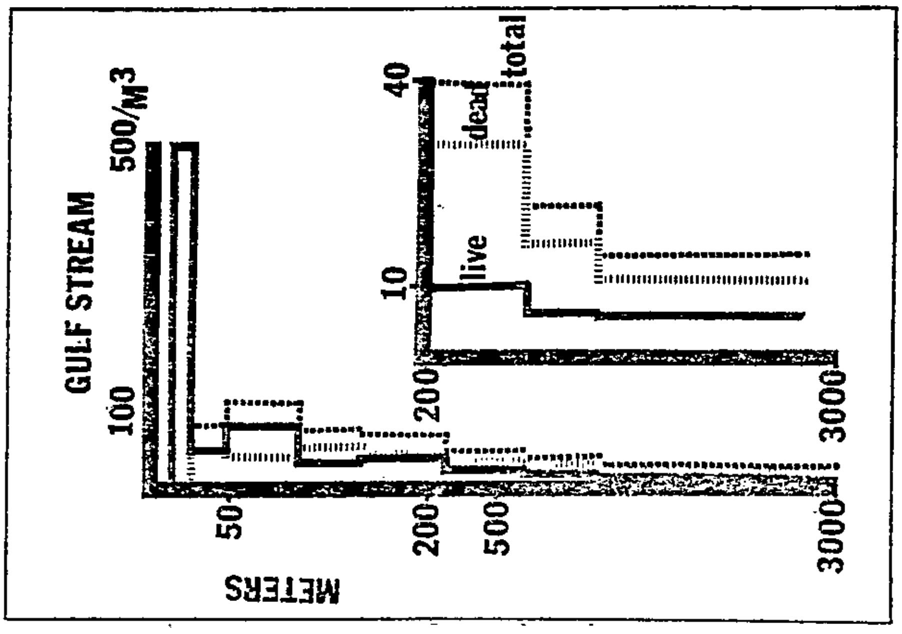


Figure 4. Densities of dead (empty tests), live (stained with rose bengal), and total (both dead and live) in Gulf Stream station mentioned in the text. Of special interest are the absence of polycystine radiolarians in the upper 10m of the water column and a density peak between 10 m and 20 m. (from Casey etal. 1979a)

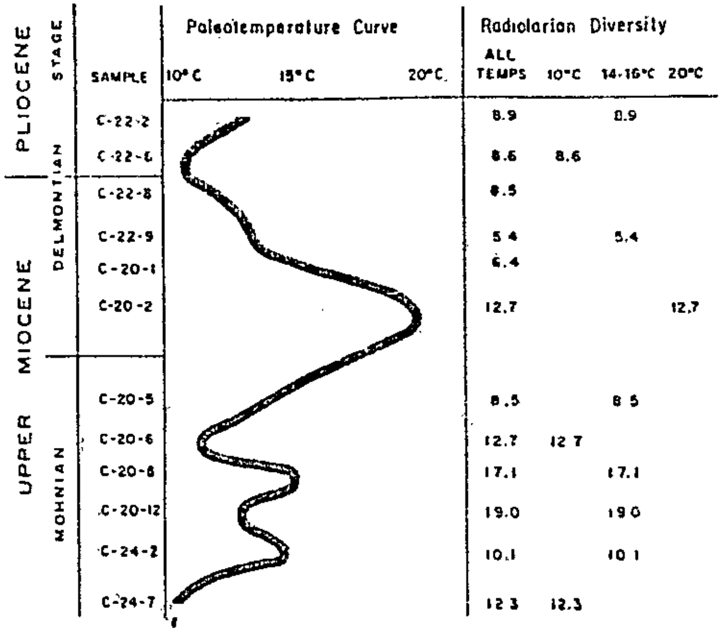


FIG. 7. Palaeotemperatures and radiolarian diversities within the Monetery Formation, Malaga Cove, Palos Verdes, California (from Casey, Price and Swift, 1972). The palaeotemperature curve was developed by the method mentioned in the text and the palaeodiversities were determined by the method as described in the caption to Fig. 2.

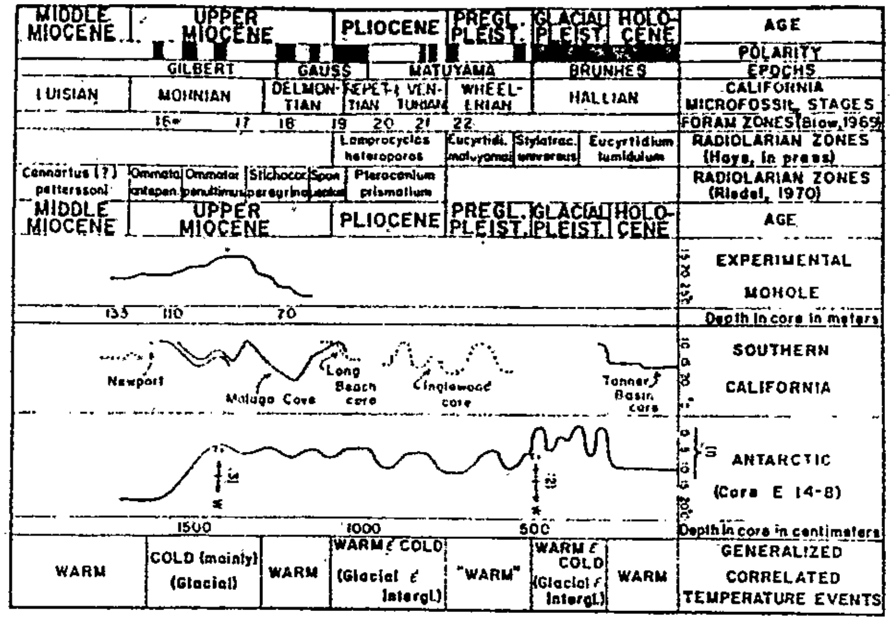


FIG. 6. Correlated palaeotemperature curves are correlated with each other biostratigraphically and temperature-wise. The palaeotemperature curves were derived in the manner described in the text, as an example the method for evaluating the Antarctic palaeotemperatures (Core E14-8) is given below.

Palaeotemperature variation, Core E14-8. There are three levels of temperature-related groups. (1) The first represents temperatures of less than 5°C and is based upon the ratio of the Antarctic *Spongotrochus glacialis* and *Lithelius nautiloides* to the Subantarctic *Lithamphora furcaspiculata* and *Theocalyptra bicornis* (these four species are illustrated on Plate 1). When the ratio of the Antarctic to Subantarctic group is about 9:1 or more, the surface temperature is 0°C or less than 0°C. When the ratio is about 1:1, the surface water temperature is about 5°C. (2) Added to the criteria used in (1) are fluctuations in the abundance of temperate radiolarians *Eucyrtidium acuminatum*, *Lamprocyclas maritalis*, and *Saturnulus planetes*; fluctuations in these temperate species suggest variations in surface water temperatures from about 5°C to about 15°C. Where they are very common the temperature approaches 15°C; where they are rare the temperatures are considered to be about 10°C; and where this group is very rare the temperatures are thought to be near the lower limit of about 5°C. (3) Subtropical temperatures of about 20°C are represented by the influx of the collosphaerid radiolarian group (from Casey, 1972). The polarity scale has been changed.

(from Casey, 1977)

APPENDIX 4, RADIOLARIAN PRESERVATIONAL INFORMATION

ABUNDANCE OF RADIOLARIA
IN CORE 75-G-10,11 (CARIB.)

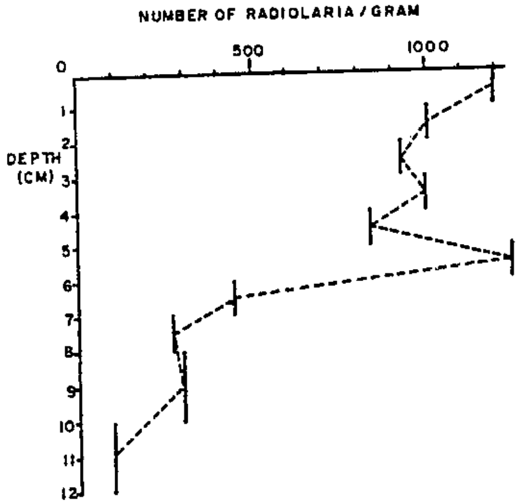


TABLE 3. The abundance rankings (1 most abundant and 11 least abundant) for radiolarians from southern California plankton and sediment samples. (From Casey *et al.*, 1971.)

Sediment abundance ranking (1 = most abundant)	Plankton abundance ranking (11 = most abundant)
1. *Siphocampe erucosa*	1. *Spongopyle osculosa*
2. *Spongosphaera streptacantha*	2. *Pterocorys zancleus*
3. *Spongopyle osculosa*	3. *Eucyrtidium hexagonatum*
4. *Spongotrochus glacialis*	4. *Siphocampe erucosa*
5. *Pterocorys zancleus*	5. *Spongotrochus glacialis*
6. *Eucyrtidium hexagonatum*	6. *Spongosphaera streptacantha*
7. *Cornutella profunda*	7. *Lithomelissa monoceras*
8. *Pterocorys hirundo*	8. *Pterocorys hirundo*
9. *Lithomelissa monoceras*	9. *Periphyramis circumtexta*
10. collosphaerids	10. Collosphaerids
11. *Peripyramis circumtexta*	11. *Cornutella profunda*

Figure 2 CONDITIONS FOR OPTIMUM RADIOLARIAN PRESERVATION AND OPTIMUM RADIOLARIAN DISSOLUTION

OPTIMUM PRESERVATION

Low Latitudes
1. High Productivity (Upwelling areas, under boundary currents and equatorial divergences)
2. Low Dissolution Potential of waters (Estuarine type waters)
3. Rapid radiolarian sedimentation (fecal pellet sedimentation)
4. Relatively low benthonic activity per unit time
5. Low dissolution potential in sediments (high silica content in sediments and interstitial waters plus low pH)
6. High rate of terrigenous sedimentation

High Latitude
1. Medium productivity (away from polar divergences)
2. Rapid radiolarian sedimentation (fecal pellet sedimentation)
3. Relatively low benthonic activity per unit time
4. Low dissolution potential in sediments (high silica content in sediments and interstitial water plus low pH)
5. High rate of terrigenous sedimentation

OPTIMUM DISSOLUTION

Low Latitudes
1. Low Productivity (within mid-latitude gyres)
2. High dissolution potential of waters (lagoonal type waters)
3. Low radiolarian sedimentation (individual test sedimentation)
4. Relatively high benthonic activity per unit time
5. High dissolution potential in sediments (low silica content in sediments and interstital waters plus high pH)
6. Low rate of terrigenous sedimentation

High Latitudes
1. High productivity (development of centric diatoms to exclusion of shallow radiolarians (at polar divergences) or low productivity)
2. Low radiolarian sedimentation (individual test sedimentation)
3. Relatively high benthonic activity per unit time
4. High dissolution potential in sediments (low silica content in sediments and interstital waters plus high pH)
5. Low rate of terrigenous sedimentation

(from Casey and McMillen, 1977)

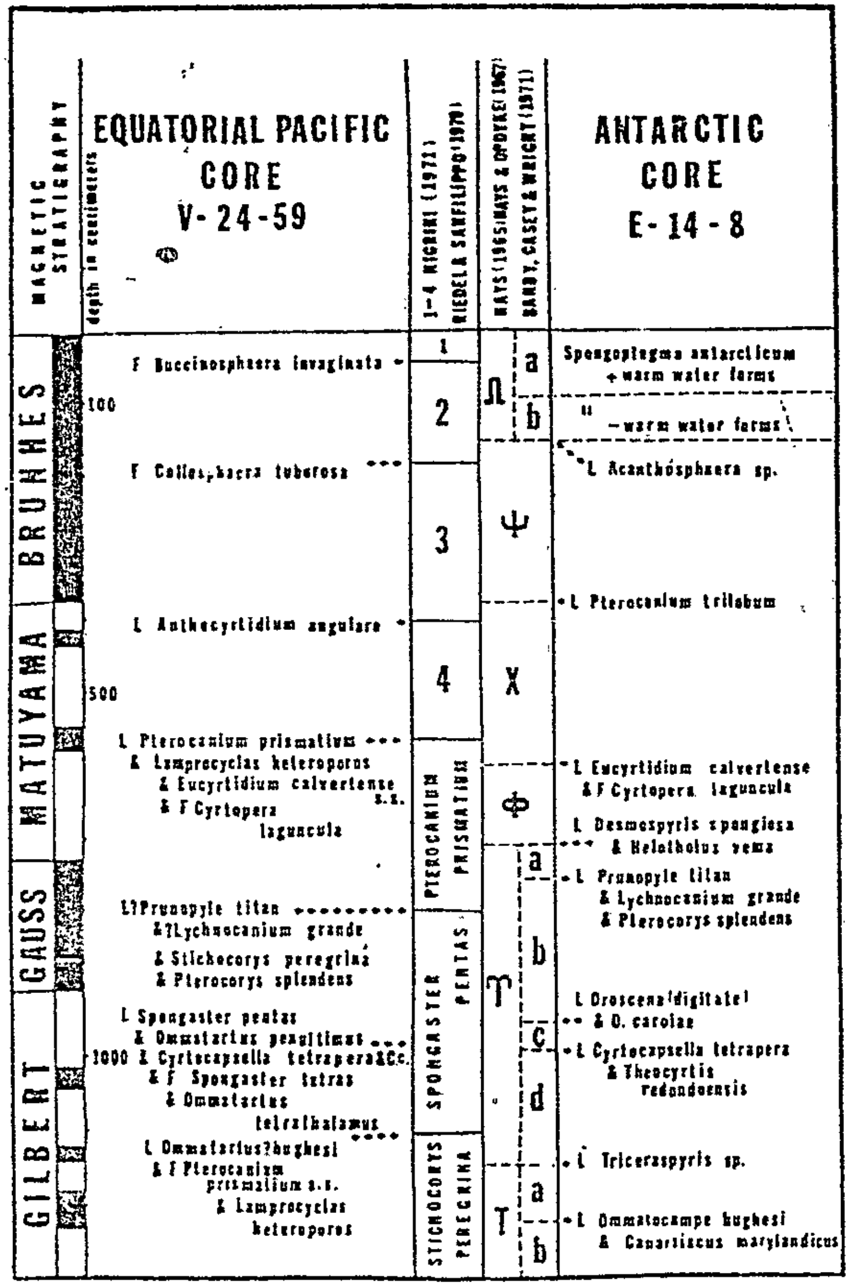


Fig. 4. Radiolarian biostratigraphy.

(from Casey and McMillen, 1977)

Figure 3 RIEDEL AND SANFILIPPO'S ZONATION RELATED TO MAGNETOSTRATIGRAPHY

EPOCHS		RIEDEL AND SANFILIPPO (IN PRESS) ZONES	RADIOLARIAN EVENTS	THEYER AND HAMMOND (1974) ESTIMATED AGE (M.Y.) AND POLARITY POSITION
QUAT.		LAMPROCYRTIS HAYSI	L. NEOHETEROPOROS TO L. HAYSI	1.6-1.7 top of Olduvai
PLIOCENE		PTEROCANIUM PRISMATIUM	L.O. STICHOCORYS PEREGRINA	2.5-2.6 latest Gauss
PLIOCENE		SPONGASTER PENTAS	S. BERMINGHAMI TO S. PENTAS	4.5-4.6 Gilbert "c2" event
MIOCENE	LATE	STICHOCORYS PEREGRINA	S. DELMONTENSIS TO S. PEREGRINA	6.2-6.3 Epoch 6, above event "a"
MIOCENE	LATE	OMMATARTUS PENULTIMUS	L.O. OMMATARTUS HUGHESI	8.6-8.7 base of Epoch 8
MIOCENE	LATE	OMMATARTUS ANTEPENULTIMUS	C. PETTERSSONI TO O. HUGHESI	10.7-10.8 top of Epoch 11
MIOCENE	MID	CANNARTUS PETTERSSONI	F.O. C. PETTERSSONI	11.3-11.4 base of Epoch 11
MIOCENE	MID	DORCADOSPYRIS ALATA	D. DENTATA TO D. ALATA	15.5-15.6 late Epoch 16
MIOCENE	EARLY	CALOCYCLETTA COSTATA	F. O. CALOCYCLETTA COSTATA	about 18 early Epoch 17
MIOCENE	EARLY	STICHOCORYS WOLFFII	F.O. STICHOCORYS WOLFFII	
MIOCENE	EARLY	STICHOCORYS DELMONTENSIS	L.O. THEOCYRTIS ANNOSA	
MIOCENE	EARLY	CYRTOCAPSELLA TETRAPERA	F.O. C. TETRAPERA	
MIOCENE	EARLY	LYCHNOCANOMA ELONGATA	F.O. L. ELONGATA	
OLIGOCENE		DORCADOSPYRIS ATEUCHUS	TRISTYLOSPYRIS TRICEROS TO D. ATEUCHUS	
OLIGOCENE		THEOCYRTIS TUBEROSA	LITHOCYCLIA ARISTOTELIS GROUP TO L. ANGUSTA	
EOCENE	LATE	THYSOCYRTIS BROMIA	F.O. CARPOCANISTRUM AZYX	
EOCENE	LATE	PODOCYRTIS GOETHEANA	F.O. PODOCYRTIS GOETHEANA GOETHEANA	
EOCENE	LATE	PODOCYRTIS CHALARA	PODOCYRTIS MITRA TO P. CHALARA	
EOCENE	MID	PODOCYRTIS MITRA	PODOCYRTIS SINUOSA TO P. MITRA	
EOCENE	MID	PODOCYRTIS AMPLA	PODOCYRTIS PHYXIS TO P. AMPLA	
EOCENE	MID	THYRSOCYRTIS TRIACANTHA	F.O. EUSYRINGIUM LANGENA LAGENA	
EOCENE	EARLY	THEOCAMPE MONGOLFIERI	F.O. THEOCAMPE MONGOLFIERI	
EOCENE	EARLY	THEOCOTYLE CRYPTOCEPHALA CRYPTOCEPHALA	THEOCOTYLE CRYPTOCEPHALA NIGRINIAE TO T. CRYPTOCEPHALA CRYPTOCEPTHALA	
EOCENE	EARLY	PHORMOCYRTIS STRIATA STRIATA	F.O. THEOCORYS ANACLASTA	
EOCENE	EARLY	BURYELLA CLINATA	BURYELLA TETRADICA TO B. CLINATA	
EOCENE / PALEOCENE		BEKOMA BIDARFENSIS	F.O. BEKOMA BIDARFENSIS	

(from Casey and McMillen, 1977)