

## PLANKTONIC MICROFOSSILS AND THE RECOGNITION OF ANCESTORS

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### *Abstract*

*Prothero, D. R., and D. B. Lazarus (Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York 10024 and Lamont-Doherty Geological Observatory of Columbia University, Palisades, New York 10964) 1980. Planktonic microfossils and the recognition of ancestors. Syst. Zool. 29:119-129.—Many cladistic systematists consider hypotheses of ancestor-descendant relationship untestable in fossils. Although fossil preservation is never complete enough to know which fossil population is actually ancestral, theoretically it is possible to sample the ancestral population. If all potentially ancestral populations were sampled, then some members of the actual ancestral population must be contained in the sample.*

Preservation of most vertebrate and macroinvertebrate fossils is notoriously spotty. However, marine microfossil sequences are the most complete available in the fossil record. Since most planktonic microorganisms have biogeographic distributions that closely correspond to the extent of major water masses, it is possible to sample each population by sampling the water masses. Lack of preservation due to non-deposition, erosion, or dissolution can generally be recognized. We can tell if absence of a form from an area is real or due to lack of preservation. Piston cores from the entire world ocean are available for all the water masses since the late Miocene. Their stratigraphy can be carefully worked out by at least three independent means of correlation, and in some cases these cores faithfully record events spaced only hundreds of years apart. Thus, in certain pelagic microfossils it is possible to sample all populations that have existed through millions of years, and be confident that no forms of interest remain unsampled. Therefore, the marine microfossil record can meet the criteria necessary to recognize ancestors. An example from the Radiolaria is discussed. [Biogeography; microfossils; ancestor/descendant; Radiolaria; stratigraphy; cladistics; phylogeny.]

The problem of recognition of ancestors in the fossil record has been the subject of much recent debate. Opinions have ranged from complete rejection of ancestor-descendant hypotheses as unfalsifiable (Engelmann and Wiley, 1977; Cracraft, 1974) to the assertion of the testability of such hypotheses in both the cladistic (Szalay, 1977) and traditional (Gingerich, 1976, 1979; Bretsky, 1975, 1979; Harper, 1976) frameworks of phylogeny reconstruction. The argument can be reduced to its simplest form as follows: Can a fossil population which is primitive in all features with respect to its putative descendant, and older than it, be labeled ancestral? Many cladists have asserted that it cannot. In their opinion, the hypothetical common ancestor reconstructed from the nodes of a cladogram must always remain hypothetical. Others have disagreed, saying, in effect, that if a fossil

population conforms to the hypothetical common ancestor in every feature and occurs in the right time and place, why not call it ancestral? We feel that this line of debate has reached an impasse, and further discussion along these lines seems fruitless.

Part of the problem seems to be semantic. Ancestor-descendant hypotheses in the fossil record are by nature inferential, since we can never observe fossil A giving rise to fossil B. Therefore, the assertion that a particular fossil specimen is the actual ancestor of any other fossil specimen is clearly untestable. In our experience, few paleontologists would stand by such a narrow and trivial definition of ancestor. A more commonly-held concept of ancestry could be phrased as follows: specimen A is a member of the population that gave rise to the population that includes specimen B.

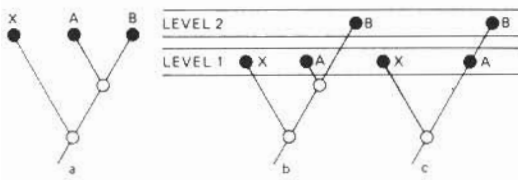


FIG. 1.—A. A statement of relationship between three taxa, X, A, and B. B. The same phylogenetic relationships with superpositional relationships between samples indicated. C. The same superpositional relationship with the assumption that A and B share an ancestor-descendant relationship. After Engelmann and Wiley (1977).

This reduces the argument to a question of sampling populations represented by fossils.

In discussing the concept of ancestry, Engelmann and Wiley (1977:9) have outlined several conditions which must be met for stratigraphic recognition of ancestors. In brief, their argument runs as follows:

Suppose there are three phenotypes hypothesized to be related to one another as in Figure 1A, and whose stratigraphic relations are shown in Figures 1B and 1C. Phenon A can therefore be hypothesized to be ancestral to phenon B (Fig. 1C) or not ancestral to phenon B (Fig. 1B). But if A is not ancestral to B (Fig. 1B), then the ancestor of B must have existed at the time of level 2. Thus, the hypothesis that A is ancestral to B appears to be more parsimonious, since it invokes no unsampled taxa. Engelmann and Wiley criticize this reasoning because it makes several assumptions they feel are untestable:

- 1) The direct ancestor of B was available for sampling at level 1.
- 2) The direct ancestral form was included in our sample.
- 3) Two genetically isolated taxa can or cannot be distinguished by the criteria we used to define phenon A and B.

Let us first discuss assumption 3. As taxonomists, we can set up a homogeneous population of observable morphologies and delimit it by characters which define phenon A. In this sense, phenon A is a minimally diagnosable group. How

many genetically isolated subsets make up phenon A? Obviously, such information is no longer available in fossil populations. But in the reconstruction of the phylogeny of fossils, we can only use observable morphology and stratigraphic information. Subsets of phenon A cannot be distinguished by the types of characters used to define phenon A, or phenon A would not be minimally diagnosable. Since these are the only characters used in the phylogenetic analysis, even if we knew which subset of phenon A is actually ancestral, it would not alter our phylogenetic hypothesis.

So far, this argument could apply to any fossil group. To recognize the ancestral morphology, we must be able to state that phenon A does contain, somewhere within it, the ancestral population. This point, and Engelmann and Wiley's first two points, are thus questions of sampling.

We feel that the assumptions listed above become testable under the following conditions:

- 1) The hypothetical ancestor must be older than its descendant.
- 2) No potentially ancestral population remains unsampled.

If such strict criteria could be met, ancestor-descendant hypotheses become testable. We therefore propose an example of such an hypothesis, and test it below.

#### THE PLANKTONIC MICROFOSSIL RECORD

We readily admit that, in most cases, the fossil record cannot meet the criteria outlined above. Preservation is notoriously spotty, time control is often difficult, and most importantly, most fossils sample only a very small part of once extensive and heterogeneous geographic ranges. Thus most fossil collections are a very minute and possibly unrepresentative sample of life at that time. Statements about ancestor-descendant relationships in most fossilized groups are indeed untestable.

A notable exception to this difficulty is the deep-sea microfossil record. Piston core suites from the entire world ocean

contain continuous sequences of marine microfossils, spanning millions of years. They have time control from isotope stratigraphy, biostratigraphy, and magnetic stratigraphy. To demonstrate the quality of the marine microfossil record, we have chosen the evolution of one particular radiolarian, *Eucyrtidium matuyamai*, because it has been previously studied (Hays, 1970). Just about any well-studied marine microfossil would suffice, however. A brief review of the nature of the deep-sea microplankton and their record follows to document our conclusions about the quality of the marine microfossil record.

The pelagic realm supports many groups of microplankton. Some forms possess hard parts formed of calcium carbonate or opaline silica and are commonly preserved as fossils on the sea bed. Diatoms, coccolithophorids, and silicoflagellates constitute the major phytoplankton groups, while foraminiferans, radiolarians, and pteropods are the important fossilizable zooplankton. With the exception of pteropods, these groups are all small, unicellular life forms, only a few tens of microns in size. Their abundances can be staggering—a single cubic meter of sea water may contain a million or more individual living cells (Lisitzin, 1972), while sediments on the ocean floor are often primarily composed of their remains.

The distribution of these organisms in the ocean is not uniform. Most groups are confined to the vertically well-mixed, sunlit surface waters—generally the upper 50 meters or so. Although radiolarians are most common in the upper waters, significant numbers are also found living at great depths. The depth zones of radiolarians correspond closely to the distribution of subsurface water masses (Casey, 1971, 1977). The distributions of all microplankton, including the Radiolaria, are also controlled by circulation patterns in the upper waters. These are the large, wind-driven surface current gyres, shown in Figure 2A. The major pelagic biogeographic provinces of

the ocean are shown in Figure 3. As one can readily see, the patterns are extremely similar to the water masses shown in Figure 2B. Thus, on a broad scale, it can be said that planktonic biogeography is controlled largely by the same forces that maintain the large-scale structure of the oceans. These forces—e.g., the earth's rotation—are primarily geophysical and have not changed significantly in the recent geologic past.

Similar broad patterns can be deduced for land biotas. Terrestrial provinces, of course, are quite heterogeneous, with many relatively stable subprovinces and local ranges. This is not the case in the oceans. Other than the large-scale features just mentioned, there are no stable subregimes in the ocean. There are several reasons for this. Unlike the land, the ocean is a fluid medium. Lateral or vertical variations in physical parameters such as temperature or salinity result in changes in water density. These differences create circulation patterns which stratify, advect, and eventually mix the oceanic waters. Thus, the ocean is a self-mixing environment of relatively great homogeneity. In fact, based on chemical considerations it can be shown that the entire ocean may be considered well-mixed on time scales of a few thousand years (Broecker, 1974). Secondly, the oceans are stably stratified. Water of a specific density may spread great horizontal distances before becoming mixed. Oceanographers have studied this phenomenon, and have determined that the oceans are made up of a relatively small number of water types, which slowly mix into one another as they flow laterally over each other. This behavior is called thermohaline circulation and controls deep water flow. Any biota contained within such a water mass, as one of these layers is called, would therefore be expected to be relatively homogeneous and laterally widespread. This is what is seen in the Radiolaria, which include deep-dwelling forms. Third, the motions of surface waters are not controlled by density differences, as in the deep ocean.

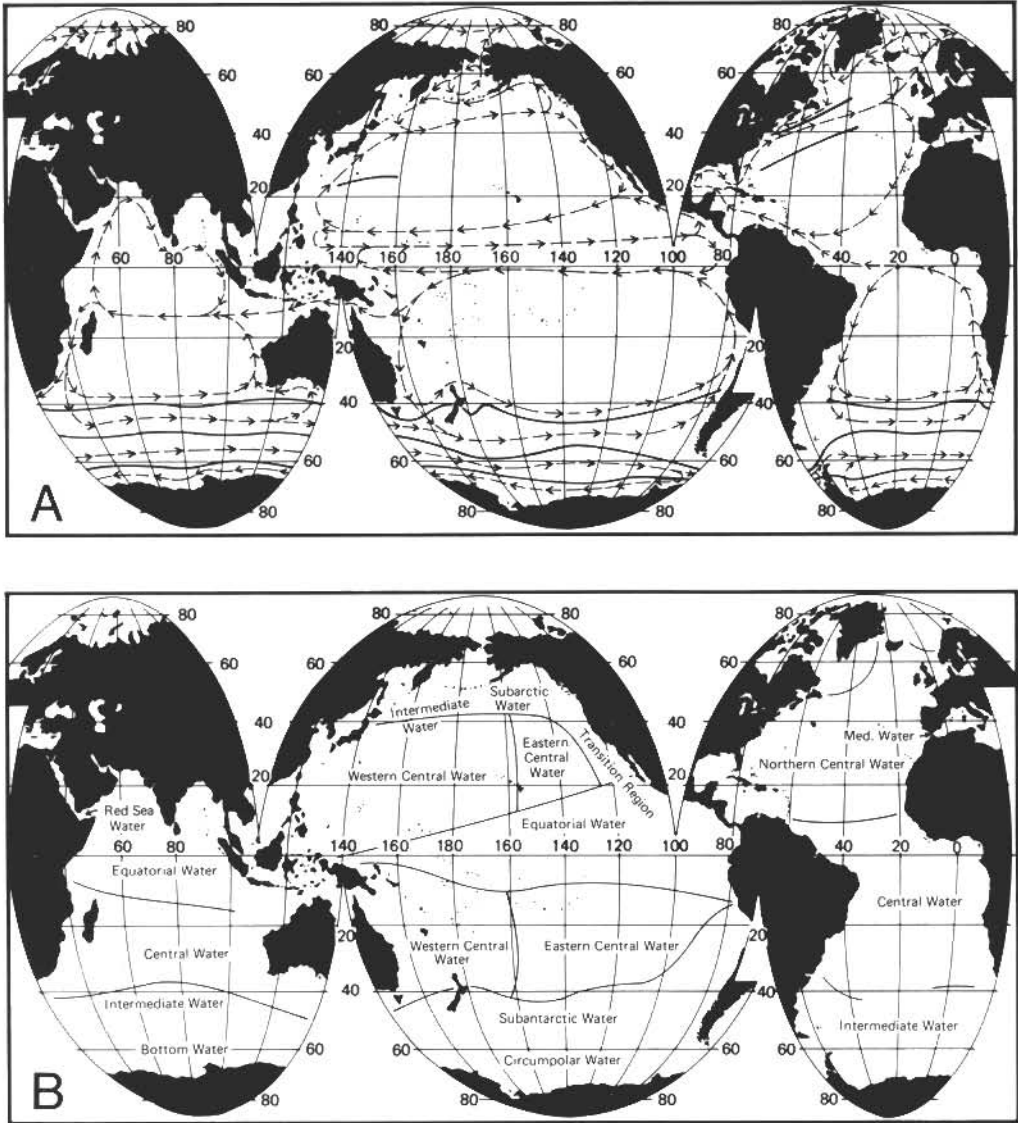


FIG. 2.—A. Generalized flow patterns in the surface ocean. Details of motion in any area are considerably more complex. B. Intermediate and surface water masses. Modified from Sverdrup, Johnson, and Fleming (1942).

Here winds are the dominant driving force. The large gyres mentioned above (Fig. 2A) are permanent oceanic features. But, on a smaller scale, no such long-term structure exists. Instead, turbulent motion is observed. Some of these eddies may persist for many months, but no evidence of longer-term stability has been

observed. Although the oceans are highly structured vertically, they are much more homogeneous laterally. The distribution pattern of individual planktonic species demonstrates that the biotas are equally homogeneous. Planktonic net tow data (Funnell and Riedel, 1971) show no species that has less than province-wide

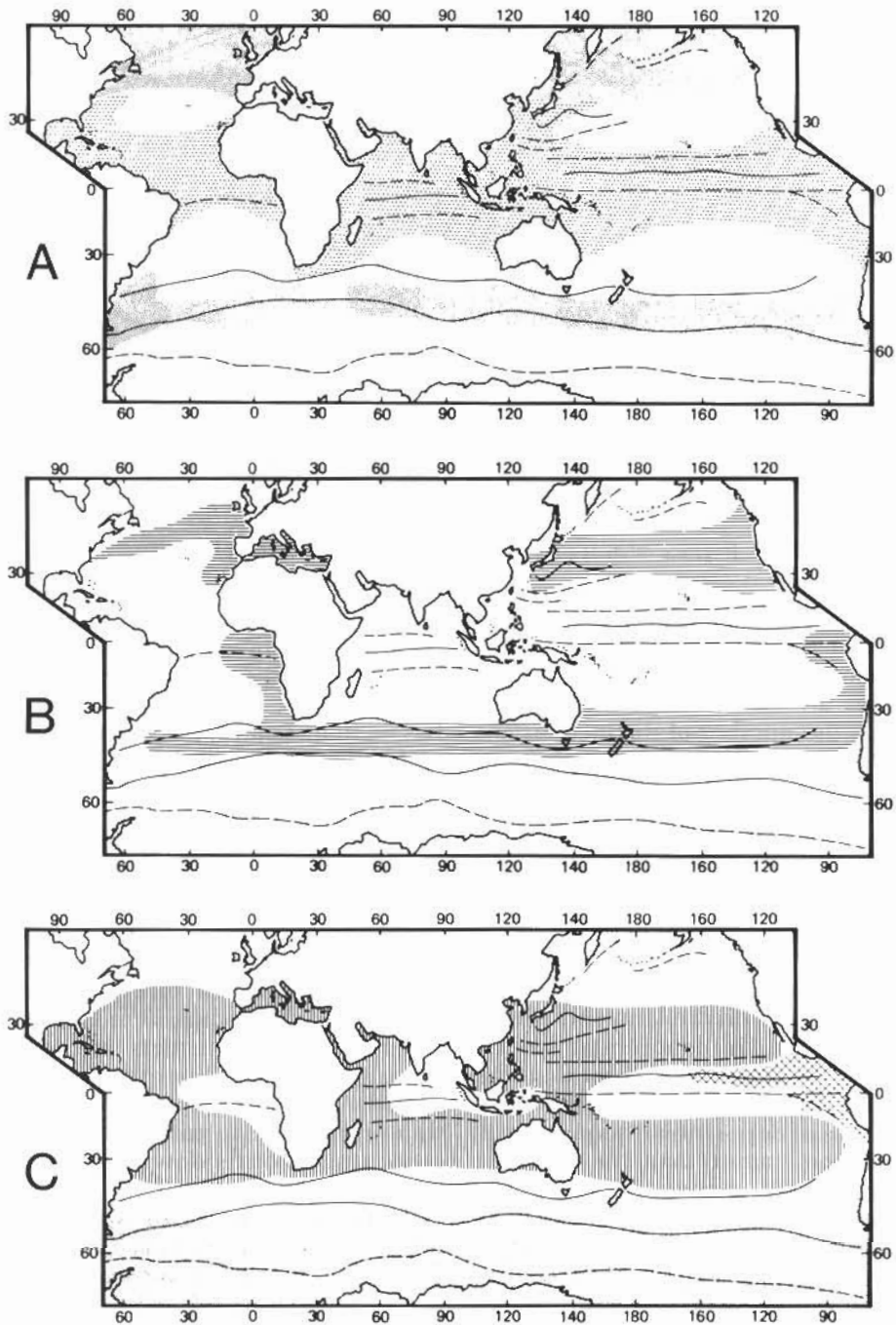


FIG. 3.—Planktonic biogeographic provinces. A. Fine stipple = Subarctic and Subantarctic; Coarse stipple = Equatorial. B. Transitional. C. Stipple = Arctic and Antarctic; Hachured = Central; Cross-hachured = eastern equatorial Pacific. Solid lines indicate oceanic convergences, broken lines are regions of upwelling; after Goll (1976).

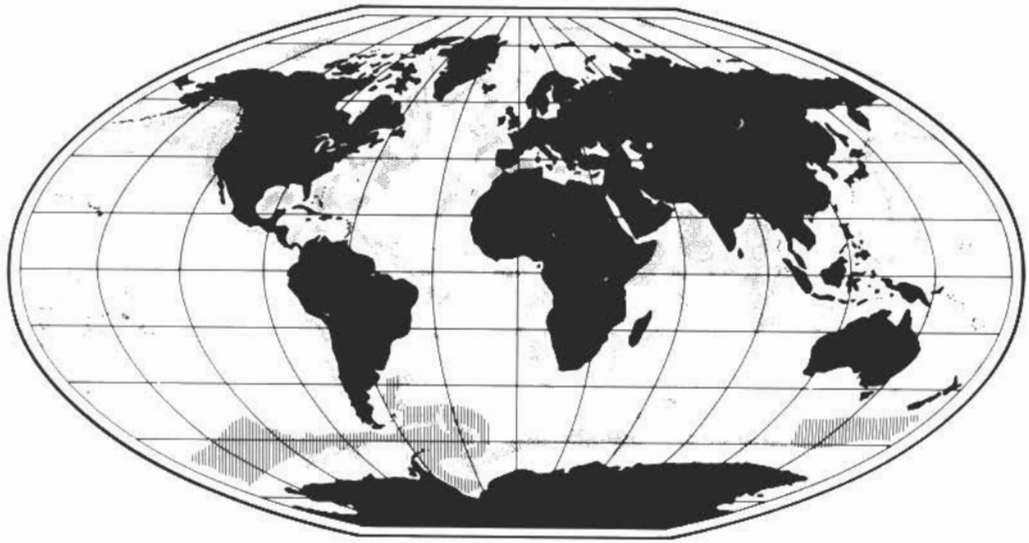


FIG. 4.—Regions of strong bottom-current activity. After Ruddiman (1977).

distribution. Therefore we conclude that the number of laterally distinct 'panmictic' demes are very few in number, no more than the number of distinct surface water provinces. All demes can be sampled by a data set consisting of only a few well-chosen vertical plankton tows. It is possible to extend this reasoning to fossil forms, due to the nature of oceanic sedimentation and preservation.

#### DEEP-SEA SEDIMENTATION

Oceanic depositional processes differ greatly from those on the land and in epicontinental seas. On continental blocks, the output of sediment is greater than the input, and the net effect is denudation. Preservation of depositional sequences is the exception, rather than the rule, on land (Ager, 1973; Shaw, 1964). In the deep sea, this is not possible. Because water output from the oceans occurs in the gaseous phase, no sediment can be removed from the ocean by water transport. Instead, sediment is removed by tectonic processes which operate only along the edges of oceanic plates. Further, because these removal processes operate slowly and predictably, their effect on the deep-sea record is easily

quantified. Since the beginning of the Pliocene, for example, approximately three percent of the area of the sea floor has been lost and replaced by subduction and ridge spreading. This figure is quite negligible, considering the distribution of the biogeographic provinces (Fig. 3). At most, only a few percent of the sedimentary record of a given province has been subducted in the last five million years.

In areas close to the continents, episodic deposition of turbidites supplies the bulk of the sediment to the sea floor. Where turbidity currents are less common, another sedimentary mechanism dominates. Throughout the ocean, a continuous rain of fine particles, often of biogenic origin, drifts down toward the sea bottom. This rain contains within it the record of the biotas which produced it. Although a large fraction of these particles is dissolved, a substantial portion remains undissolved and is incorporated into the deep-sea record.

Locally there are interruptions in the record. Bottom currents can destroy or jumble the stratigraphic sequence in a given area. However, these processes are important only over restricted regions of

the sea floor (Fig. 4). Such reworked sediment can be identified by lithologic and other criteria. Further, a sufficient number of cores is available that the effect of these processes on the overall quality of the deep-sea record of a given province is negligible. Bioturbation, or the mixing of bottom sediment by burrowing organisms, blurs the record slightly. It has been shown, however, that extremely high temporal resolution is still possible. Events only hundreds of years apart are often easily resolved (Ruddiman and Glover, 1972). Under exceptional circumstances, even annual events are clearly discernable (Schrader et al., 1979).

Dissolution of microfossils is the primary reason for their non-preservation within sediments. It is possible to quantify dissolution by the use of dissolution indices (Berger, 1967; Johnson, 1974; King, 1976; McIntyre and McIntyre, 1971) and make empirical statements about the relative susceptibility to dissolution of various forms. By examining the sediment it is possible to determine the amount of dissolution that has occurred. As susceptibility to dissolution is a taxonomic character, the intermediate members of an ancestor-descendant lineage cannot show markedly different dissolution characteristics, or they would be autapomorphic. It is possible, therefore, to determine whether the absence of a given form from a sample is of primary origin, and when it may be due to problems of preservation. Preservability is an intrinsic, measurable character of marine microfossils.

Of course, not even the most thorough study can hope to exhaust all the potential microscopic, submicroscopic, and biochemical characters in a single microfossil test. Thus, the hypothesis that certain forms are ancestral can be rejected when more subtle characters are examined. The existence of these unexamined characters adds a further dimension of falsifiability to ancestor-descendant hypotheses. In any case, specifying which part of the putative ancestral population is actually ancestral is beyond the limits

of our resolution. We can only assert that it has been preserved, and can be sampled, but we will never know when we have it.

#### SAMPLING

Because the deep-sea record is of such high quality, it is possible to develop extremely precise methods of correlation. Three completely independent stratigraphic tools are commonly available: biostratigraphy, magnetic stratigraphy, and isotope stratigraphy. The latter two often provide isochronous global time planes on which paleogeographic reconstructions can be based. Geographic control for these reconstructions is excellent for relatively recent sediments, and becomes somewhat less so for earlier intervals of geologic time. More than 20,000 piston cores have been taken by various institutions from all parts of the ocean (Fig. 5A). As these cores sample only the upper 10–20 meters of sediment, older sediments are progressively underrepresented. Due to drilling disturbances, Deep Sea Drilling Project cores do not provide as high a temporal resolution as piston cores. Nonetheless, these drill cores represent an additional data set, one with relatively great temporal penetration. Some 500 sites, ranging from the Late Jurassic to present, have now been drilled. Figure 5B shows the location of some of these sites. The coverage of the world ocean is complete in the sense that all biotic provinces are represented by continuous or nearly continuous sections as far back as the early Cenozoic; piston core records are presently limited to the late Miocene. Recent development of the hydraulic piston corer (Curry et al., 1979) should provide improved temporal resolution for earlier periods of earth history.

#### AN EXAMPLE FROM THE RADIOLARIA

To illustrate the concepts mentioned above, we review a published study of radiolarian evolution (Hays, 1970) that shows how the conditions necessary to recognize ancestors may be met in the

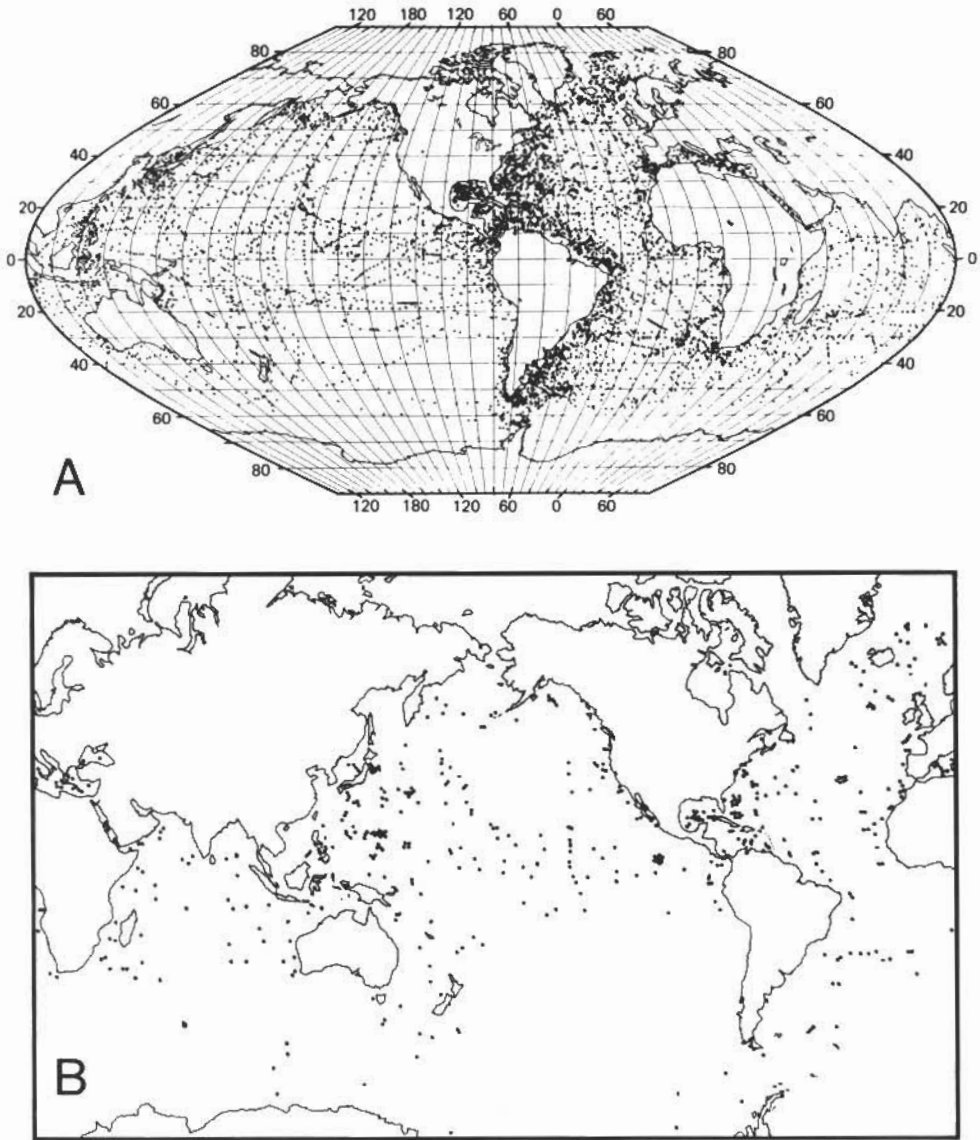


FIG. 5.—A. Distribution of Lamont-Doherty Geological Observatory piston cores (approximately 8,000 sites). National Geophysical and Solar-Terrestrial Data Center map. B. Distribution of Deep Sea Drilling Project sites (through Leg 64). Modified from map prepared by Geologic Data Center and Deep Sea Drilling Project.

deep-sea record. In this study, Hays noted the presence of a stratigraphically-restricted species of radiolarian, *Eucyrtidium matuyamai*, in North Pacific

sediments of Pleistocene age. Early forms of this species intergrade with another species, *Eucyrtidium calvertense*, which ranges throughout the Plio-

FIG. 6.—Morphological development of *Eucyrtidium matuyamai* (large species) from *Eucyrtidium calvertense* (small species) in core V20-105 (North Pacific Transitional Province); after Hays (1970).



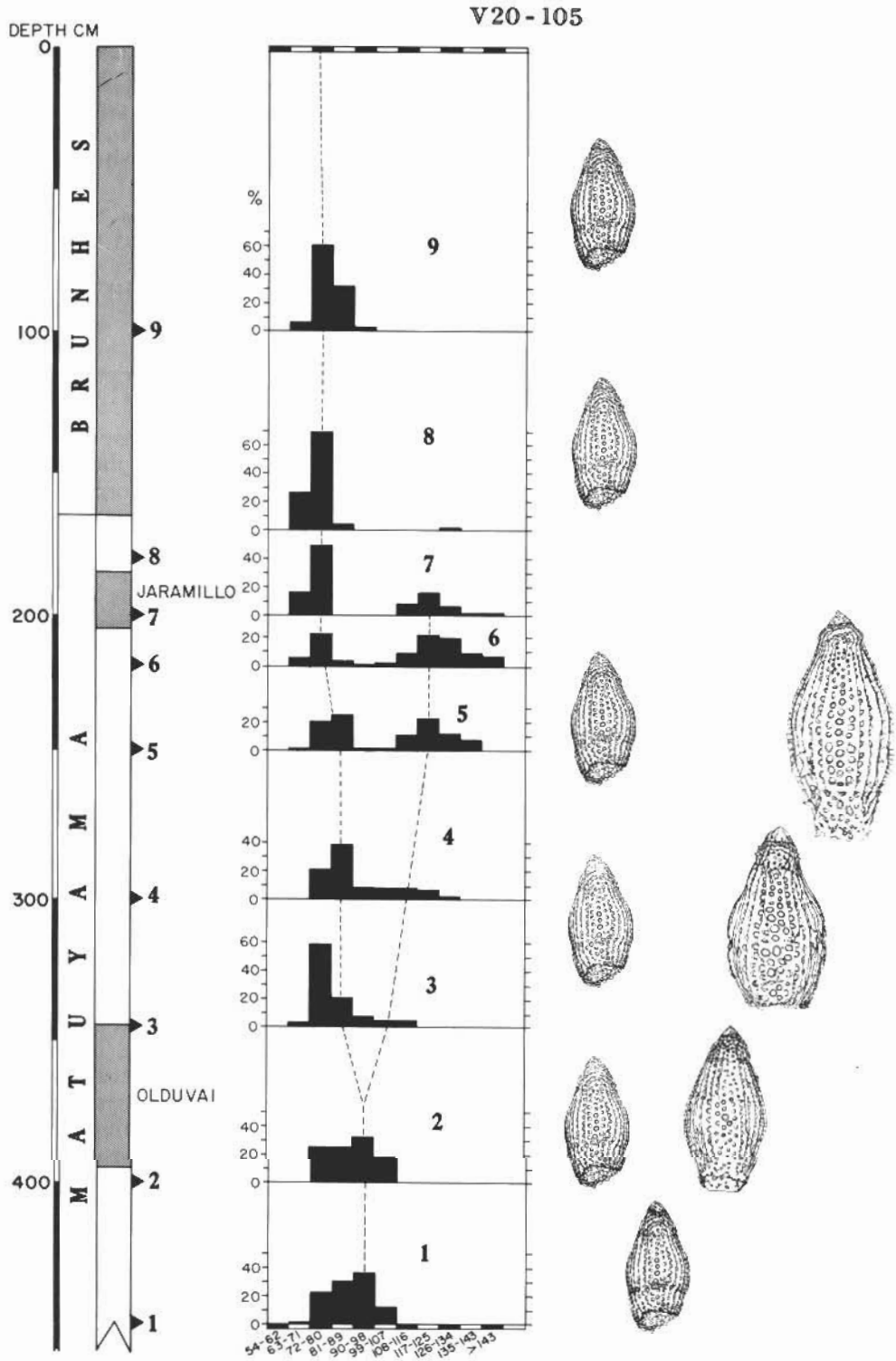


TABLE 1. CORES EXAMINED IN THE *EUCYRTIDIUM* STUDY.

Late Pliocene Cores	Biogeographic Province(s)	Location	Reference
V16-132-4,66; V18-72	Antarctic	Antarctic	Opdyke et al., 1966
E13-3; E14-8	Antarctic	Antarctic	Hays and Opdyke, 1967
V19-169-171	Equatorial	Indian	Opdyke and Glass, 1969
V29-40; RC14-22	Equatorial	Indian	Burckle and Opdyke, 1977
V24-58-60,62	Equatorial	Pacific	Hays et al., 1969
Several	Subarctic	North Pacific	Hays, 1970
Sites 341, 348	Arctic	Norwegian Sea	Bjørklund, 1976
Site 173	Central and Transitional	North Pacific	Kulm et al., 1973
RC8-52	Subantarctic and Transitional	South Indian	Unpublished data*
Site 157	Equatorial and Transitional	East Pacific	van Andel et al., 1973

\* We wish to thank Dr. N. D. Opdyke for allowing us to use his unpublished paleomagnetic data on this core.

cene and Pleistocene. The occurrence of *E. matuyamai* is restricted to sediments of the North Pacific. Because of these observations, Hays concluded that *E. calvertense* gave rise to *E. matuyamai* at the beginning of the Pleistocene in the North Pacific. These relationships are shown in Figure 6.

Table 1 gives a partial list of examined cores of the appropriate ages. This table also shows the stratigraphic control available, and lists the biogeographic provinces represented by the cores. Reference to Figure 3 shows that coverage is virtually complete. Dissolution is minimal in these cores, and is insignificant in the context of this problem. *E. matuyamai* is therefore originally absent from all provinces except the North Pacific. Thus, as *E. calvertense* is the morphologically closest to *E. matuyamai* of all known *Eucyrtidium* species that existed during the time in which *E. matuyamai* evolved, *E. calvertense* must be the ancestor.

In summary, we have used the criteria established above to test the hypothesis that *E. calvertense* was the ancestor of *E. matuyamai*. Since this hypothesis passes these tests, we have established the testability of ancestor-descendant hypotheses in at least some fossil groups.

#### DISCUSSION

Well-corroborated hypotheses of ancestor-descendant relationships have implications beyond those of phylogeny reconstruction. Specifically, the resolu-

tion of such fossil records preserves 'speciation level' evolutionary phenomena. Deep-sea records can therefore be used to study patterns of microevolutionary change and processes previously considered to be entirely the province of neontologists. Topics such as character displacement, parapatric/sympatric/allopatric speciation patterns, and rates of change during speciation may be studied using paleontology's unique historical view. Neontologic theories may be tested rigorously against these long temporal sequences, despite the limitations imposed by purely phenotypic data. We feel that as more ecologic and genetic information is acquired on living members of the different microplankton groups, the usefulness of the deep-sea sediment record in evolutionary studies will be greatly increased. Eventually, the fossils of these microscopic plankters may come to mean to paleontology what *Drosophila* has meant to the field of genetics: 'laboratory animals' for evolutionary study, whose evolution will provide the standard data upon which an original paleontologic theory of evolution may be based.

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