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CURRENT PROBLEMS IN RESEARCH

Ecology, Paleontology, and Stratigraphy

Understanding of the habits of living organisms aids interpretations of fossiliferous sediments.

Harry S. Ladd

Ecology deals with the relations of living organisms to each other and to the environments in which they live. The word thus expresses man's interest in the living habits of the diverse forms of life that share the earth with him. Paleoecology extends the field backward in time; it deals largely with plants and animals that lived on earth before man arrived. Human beings became interested in ecological matters long before the term "Oecology" was defined, nearly one hundred years ago. An innate curiosity about the activities of other forms of life probably was found in early man—along with a selfish desire to use such information for his own benefit. Ecology is now recognized as a broad field in which some workers study the life of the land, with its lakes and rivers, while others study the life and environments of the sea. Many paleoecologists are chiefly interested in marine life because most of the fossils that make up the paleontological record are contained in sediments that were deposited in the sea.

Paleontology is concerned with fossils, the remains of organisms that lived in the past. The fossil record is diverse and discontinuous—a record that was not fully understood until the theory of evolution was formulated. It is a remarkable record in spite of its imperfections. The list of fossils includes animals that range in size and organic complexity from the shells of microscopic protozoans to the frozen bodies of elephants. Paleontology includes tests of microscopic plant-like organisms (diatoms) and trunks of forest trees. Even bacteria have been preserved and, in rare instances, the impressions of soft-bodied forms such as jellyfish. One of the basic truths discovered by early paleontologists and confirmed by later work was that, in general, the fossils from the upper (younger) rock layers more closely resemble living forms than do those from the lower (older) strata.

Stratigraphy deals with sedimentary rocks and their order of superposition (chronological sequence) and with maps showing the geographic distribution of sediments. Early stratigraphers discovered that the fossils in the same bed or formation remained essentially unchanged when the bed or formation was traced laterally. Before the close of the 18th century, William Smith, the founder of stratigraphy as we know it, had demonstrated that in England isolated outcrops could be tied together by their contained fossils regardless of distance, elevation, or the attitude of the beds. Thus, from the start, paleontology and stratigraphy were—and they still are—as inseparable and interdependent as Siamese twins.

In any stratigraphic investigation the first task is to set up a standard section. In this process lithologic features and sedimentary structures are used to supplement data on the occurrence of fossils. It then becomes possible to fit sections from other areas into the established sequence and to make a geologic map. On such a map each recognizable sedimentary unit is given an identifying color or pattern. William Smith colored his first geologic map in 1794. This map covered only a small area in the vicinity of Bath, but a geologic map of England appeared in 1815. Though evidence of several sorts is used in preparing a geologic map of areas of sediments, the value of fossils cannot be overemphasized. Without usable fossils, only the first step is possible. A stratigraphic sequence for a given locality may be set up, but sections from widely separated localities cannot be accurately tied together without fossil control. Thus, the ancient and largely barren sediments of the Grand Canyon or the Black Hills cannot be correlated with the ancient and equally barren sediments of the Lake Superior region. All of the barren sediments older than the richly fossiliferous Cambrian beds are now, by general agreement, simply recorded as Precambrian. The Cambrian began about 500 million years ago, and fossils have been abundant in the rocks ever since.

The assemblages of animals and plants that live in the sea at intertidal levels differ from those found on the continental shelves, and the shelf assemblages are entirely different from those found at greater depths. These fairly obvious distinctions were noted by many early workers, including Edward Forbes (1815–1854), who suggested names for bathymetric and biogeographic zones (*1*). Some of the names that Forbes suggested are still in use (*2*, pp. 1, 2). The major subdivisions in the sea are subdivided into smaller units (Fig. 1), and both large and small units are referred to as *facies*. Thus, an ecologist can refer to a deep-water assemblage as a *bathyal facies* or to one from the shelf seas as a *neritic facies,* to an assemblage from the inner shelf as *inner neritic*, and so on (*2*, p. 18).

Paleontologists and stratigraphers apply the word *facies* to fossiliferous beds. Indeed, the word was coined by a paleonotologist, Amaz Gressly, more than 100 years ago (*3*). Any section of beds that differs in lithologic character or

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fossil content from other beds believed to be of the same age may be called a facies (sedimentary facies). The recognition of facies is a matter of fundamental importance to paleontology and stratigraphy, and it is in this field that ecological studies make their greatest contribution. Ecological observations on conditions in the existing seas can be applied to fossiliferous rocks formed in ancient seas. Many factors are involved, including depth of water, type of bottom, nearness to land, agitation, turbidity, temperature, and salinity. The fossils of a given sedimentary facies tell only a part of the story. Equally important evidence comes from the rocks containing the fossils—from their composition, texture, and sedimentary structures such as ripple marks, cross bedding, and graded bedding (*4*).

Conflicting Stratigraphic Interpretations

Throughout the 19th century paleontology and stratigraphy progressed steadily. Geologic periods and their systems of rocks were recognized in Europe and America, and their limits were defined. Paleoecology received some attention in that facies were recognized and mapped in many areas, but major efforts were directed toward describing fossils and using them to correlate geologic sections.

In America, starting at the turn of the present century, a new trend of thought was set in motion by those studying the older (Paleozoic) rocks. It was a trend that ignored ecology and facies interpretation, and it profoundly affected paleontologic and stratigraphic thinking for several decades. A group of geologists propounded new conceptions of the environmental conditions that prevailed in Paleozoic times. These conceptions were fully set forth by E. O. Ulrich in his "Revision of the Paleozoic systems" (*5*). Though well aware of the diversity of shore and bottom conditions in the seas of today, some geologists did not believe that comparable conditions existed in Paleozoic times and held no belief in lateral changes in synchronous deposits (*6*). It was explained that the world today is in an emergent stage, with no environments comparable to the shifting seas that lay between low lands in the Paleozoic (*7*). It was contended that conditions in the epicontinental seas were uniform and that the animals living in them, where not confined by barriers, could migrate over enormous distances in no time at all, geologically speaking. Life zones and facies changes were not considered important, and evolution was largely relegated to the margins of the continents.

Under these conditions, most differences between similar fossils were explained as differences in age. If the differences were minor it was postulated that the forms in question lived in basins separated by a barrier, usually a land barrier. In stratigraphically complex areas, such as the Appalachian region in the eastern United States, it became necessary to postulate the existence of longitudinal troughs in which somewhat different faunas lived under somewhat different conditions and perhaps at slightly different times. As information about these faunas and their distribution accumulated, it became necessary to break the troughs into short segments by postulating zigzag transverse axes. The resulting picture of Paleozoic seas was complicated indeed. Some of the complications were more imaginary than real. The failure to recognize facies deposits as such made it necessary to imagine a great hiatus in an area where none actually existed (*8*).

The above-described trend was in full

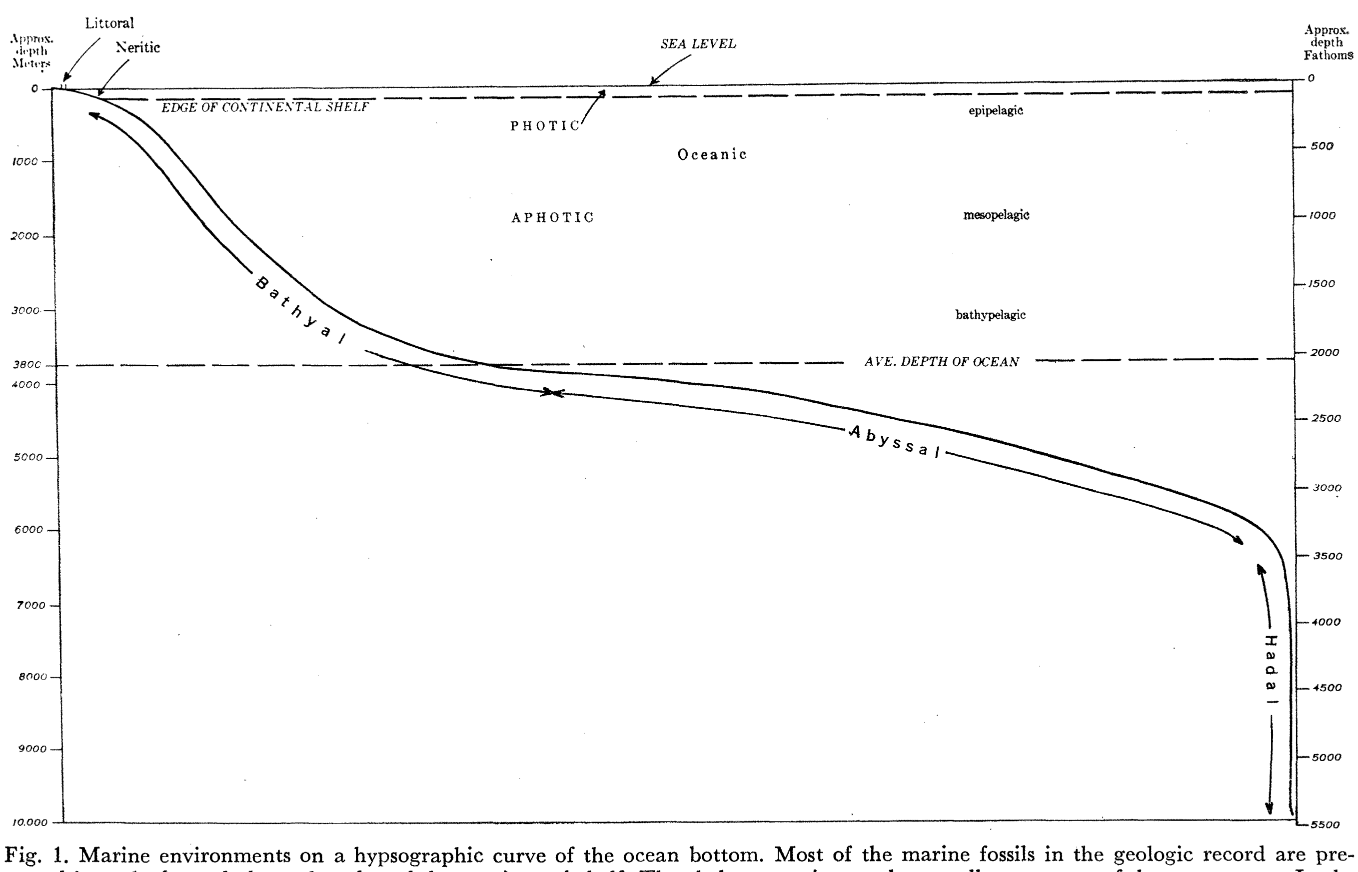

Fig. 1. Marine environments on a hypsographic curve of the ocean bottom. Most of the marine fossils in the geologic record are preserved in rocks formed above the edge of the continental shelf. The shelves constitute only a small percentage of the ocean areas. In the past, shelf seas have sometimes covered as much as half of the North American continent. [After Hedgpeth, 1957]

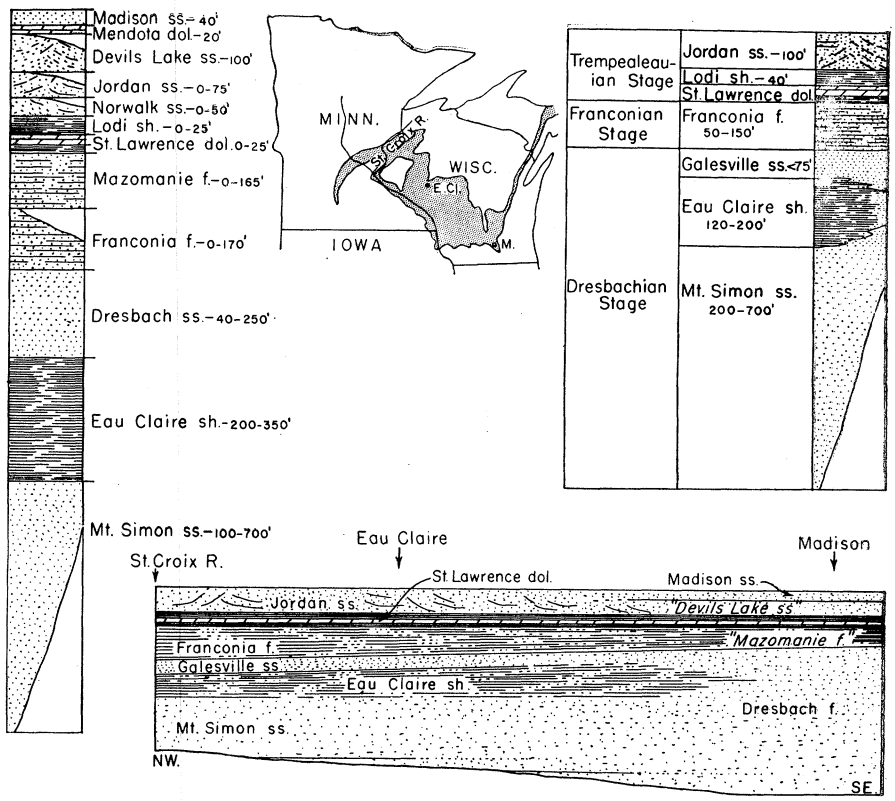

Fig. 2. Upper Cambrian correlations in the upper Mississippi Valley. (Left) Composite section, 1924; (right) composite section as now generally accepted; (top center) outcrop area of the Cambrian formations; (bottom) stratigraphic section across the area (*68*). [Reprinted, with permission, from C. O. Dunbar and J. Rodgers, ***Principles of Stratigraphy*** (Wiley, New York, 1957)]

swing at the time I was introduced to paleontology and stratigraphy. At a university in the Midwest I heard about a debated area in Wisconsin where these early interpretations had complicated what others thought was a fairly simple regional picture. The section according to the older concept and the currently accepted stratigraphic section are shown in Fig. 2. Facies changes, both lateral and vertical, are clearly brought out in this figure. The book from which it was taken contains information about other and more complicated instances.

Opposition to these older interpretations mounted, and few now follow them. One of the remaining defenders, a paleontologist, complained recently to me about the activities of a younger man who once had worked with Paleozoic fossils. "Why," he exclaimed, "that fellow now spends most of his time looking at the ocean!"

A line of reasoning somewhat similar to that of these early stratigraphers was followed by many students of ancient reefs. Reefs of the Paleozoic were said to be fundamentally different from structures now existing in the tropical seas. It was pointed out that the ancient reefs were built by tetracorals, members of an extinct subclass, that might have had habits and ecologic requirements quite different from those of the hexacorals, which are main contributors to existing reefs. The fact that Paleozoic reefs were more widespread and the fact that they all grew in the waters of shallow epicontinental seas were cited as other distinguishing features. Direct comparisons between ancient and modern reefs were made with caution or were avoided altogether.

One of the first to disagree with this line of reasoning was T. Wayland Vaughan, who contended that the habits of reef-building corals had always been much the same and that Paleozoic reefs grew under conditions like those found in reef areas today (*9*). We now know from intensive studies of the distribution of reef facies that ancient and modern reefs do have much in common. An understanding of the ecology and facies distribution of existing reefs has been of great practical value to petroleum geologists, who, with the help of drill cores, have worked out the regional relations of buried Paleozoic reefs, some of which have been major oil producers. The Scurry reef of western Texas, for example, has been described as the largest oil-producing limestone reservoir in the Western Hemisphere (*10*).

Metal mining has also benefited from studies of reef ecology. In the extensive underground workings of the Southeast Missouri Lead District, Ohle and Brown (*11*) have shown by geologic mapping that Paleozoic algal reefs constitute an important ore control. In a large part of this district these reefs have served as host structures for ore deposition.

Recent Developments

For the past 25 years most American paleontologists and stratigraphers have paid some attention to ecological considerations, and their interest in ecology seems to be growing. In addition to the recognition of facies, already mentioned, there are other aspects that concern them. One is fundamental, as it involves species discrimination. Students of living marine animals are able to collect specimens from all parts of the environment inhabited by a given species. Since size, shape, or growth form may be greatly influenced by environmental conditions, this is helpful in determining the range of variation in a given species.

Many attached animals, like corals and some mollusks, vary greatly. On Bikini reefs, for example, it was noted that the same species of coral might assume several growth forms; the form assumed depended primarily upon exposure to strong surf and on the depth of water at low tide. At the seaward edge of the reef, where coral growth was exposed to heavy surf at low tide, the species was found as a living carpet, or veneer, lining shallow depressions in the reef pavement and rising to cover low elevations. One colony exceeded 30 feet in length! Back from the reef edge, where wave action was less vigorous but where the water at low tide was still very shallow, low stubby fingers were found rising from the flat surface of the colony. Still farther landward, in tide pools below the reef flat and beyond in the quiet waters of the lagoon, the same species would assume the fragile form of "staghorn" coral. Many such growth forms have been described as distinct species and each has been given its own name. John W. Wells, who reported on the extensive Bikini collections, was able to combine many such forms and greatly reduce the number of specific names (*12*). Likewise the size and shapes of mollusk shells, such as those of oysters, vary greatly in accordance with the nature of the foundation to which they are attached, the degree of crowding (*13*), and perhaps other ecological factors such as salinity. Variation in the size and shape of shells also occurs in mollusks that are not attached. A paleontologist who has become familiar with the variability exhibited by living species will be cautious in attaching distinct names to shells or other fossils that differ only in size or proportions.

Ecological studies of the distribution of living assemblages in the existing sea have been applied to the interpretation of fossil faunas in a number of areas. Natland, in his pioneering work in 1933 (*14*), used data on the bathymetric and temperature ranges of some Recent species of Foraminifera off the California coast, and he described five temperature-depth zones. These were correlated with fossiliferous beds in the Hill's Canyon section that were thought to range from lower Pliocene to Pleistocene. He showed that dissimilar faunas may be contemporaneous and stated that the resemblances between two assemblages indicate a similar environment but do not necessarily indicate contemporaneity.

Investigations by oceanographers of newly discovered turbidity currents have ecological aspects that bear directly on paleontology and stratigraphy. Daly (*15*) was the first to suggest that mud-laden currents ("density currents") might be responsible for the carving of the enigmatical submarine canyons known to cross the continental shelves. Kuenen (*16*) obtained experimental support, and a whole series of investigations was started. It is now generally recognized that turbidity currents as well as several types of landslides can transport sediments carrying shallow-water organisms into deeper waters. Ecological studies of cores taken from such transported sediments lend strong support to the postulated movement if, for example, they show concentrations of shallow-water organisms between layers containing deeper-water forms. The student of submarine cores must depend upon ecology (or paleoecology) to reveal the degree of mixing involved, and a knowledge of paleontology may be needed to determine the exact geologic age.

Critical data obtained from the study of marine cores have been applied effectively to sediments outcropping on the land. Natland and Kuenen (*17*) used Foraminifera and sedimentary criteria to show that the coarse sandstones between shales in the Tertiary rocks of the Ventura Basin in California were deposited by turbidity currents of high density and that the conglomerates in the same section were emplaced by submarine slides.

In many parts of the geological record fossils are scattered sparsely through the rocks, but in other parts they are densely concentrated on one or more bedding planes. The numbers of fossils may be so great as to suggest abnormal conditions, possibly a catastrophe of some sort. Such an example was described by D. S. Jordan from the Miocene of California. Enormous numbers of the herring *Xyne grex* were found (Fig. 3, top) crowded on a bedding plane in the "Monterey shale" (*18*). Jordan estimated that more than a billion fish, averaging 6 to 8 inches in length, died on 4 square miles of bay bottom. Catastrophic death in the sea on a comparable scale occurs today, due, in many instances, to the development of "red water." Studies of ecologic conditions in the existing seas again bear directly on paleontologic studies.

A good example to cite in this connection is the upwelling of cold waters from the depths along certain existing coasts (especially along the western margins of continents). The upwelling waters do not come from great depths, as was formerly supposed, but from depths not exceeding 200 to 300 meters (*19*). They are rich in nutrients, and this condition may lead to the development of noxious "blooms" of microscopic flagellates and dinoflagellates, commonly referred to as "red water" or the "red

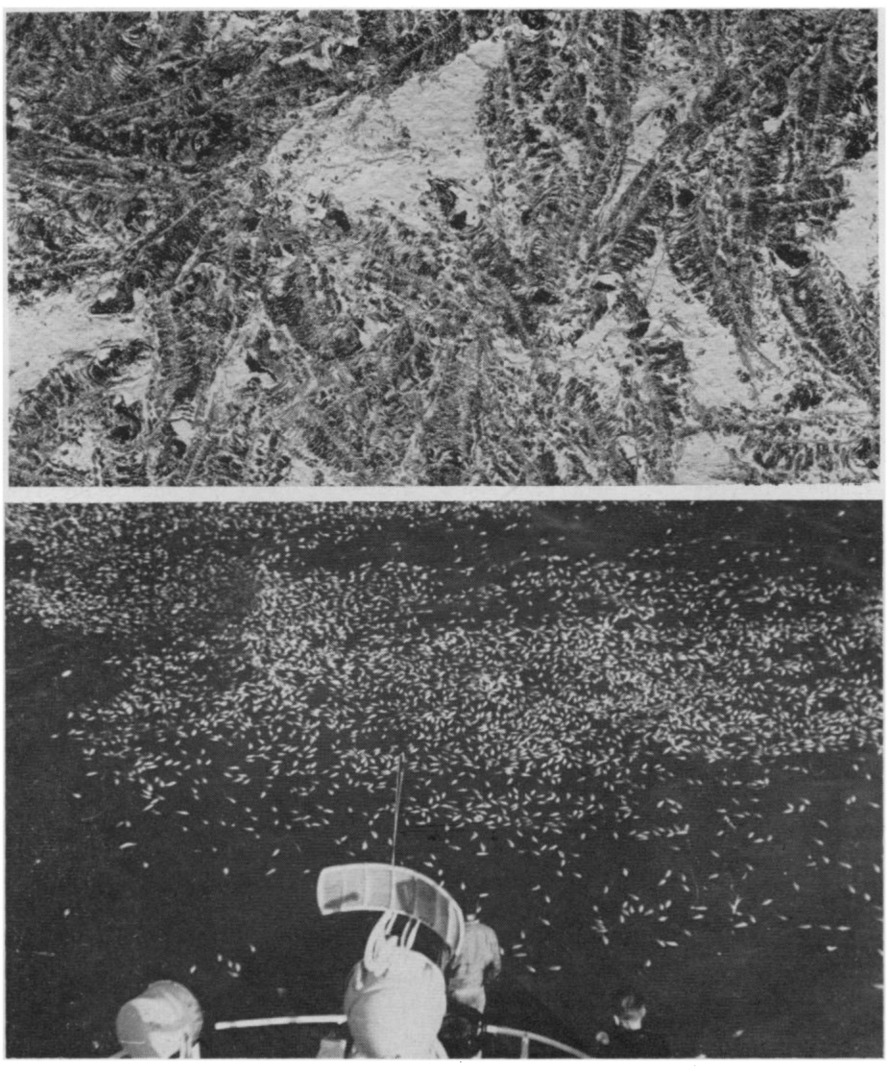

Fig. 3. (Top) Catastrophic death in the Miocene skeletons of herring preserved on a bedding plane of diatomaceous earth in the Monterey shale of Lompoc, California. The skeletons are 6 to 8 inches long. [Photograph, from *Geol. Soc. Am. Mem. No. 67* (1957), vol. 2, by A. B. Cumings, Johns-Manville Company]. (Bottom) Catastrophic death in the sea today. Fishes killed by the "red tide" in the Gulf of Mexico as seen from the research vessel "Alaska" of the U.S. Fish and Wildlife Service. View 5 miles south of Sanibel Island in November 1953. Predominant forms shown are pinfish, grunts, and pigfish. [Photograph, from *Geol. Soc. Am. Mem. No. 67* (1957), vol. 2, by Kenneth Marvin]

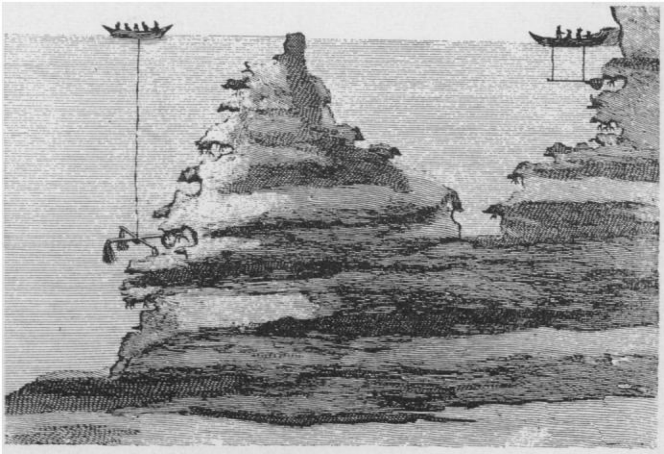

Fig. 4. Sampling, past and present. (Left) Fishing for coral in the shallow waters of the Mediterranean in the early years of the 18th century. [After Louis Ferdinand Compte di Marsilli, *Histoire physique de la mer* (Amsterdam, 1725)]. (Right) Fishing at great depths with modern equipment. Three zoologists of the "Galathea" expedition examine material brought up from a depth of 10,120 meters in the Philippine Trench. Even from such depths, living organisms of several sorts were recovered. The man on the left has his hand on one of two 25-kilogram weights that had to be attached to the jaws of the 0.2 m^2 grab above the lead brick that normally is adequate to insure closure. [Photograph courtesy of Anton Brunn]

tide." Such blooms may be directly responsible for catastrophic death among fishes (Fig. 3, bottom). Incidents of this sort have been recorded since biblical days and are known to occur in many parts of the world, yet they are so spectacular that they make newspaper headlines each time they strike a home shore.

Not all instances of "red tide" are due to upwelling, but it is a controlling factor in many areas, and this particular ecological setting has a most important bearing on paleontology. M. Brongersma-Sanders assembled information on upwelling in the existing seas and concluded that similar conditions in the geologic past may have been responsible for the formation of sediments rich in fish remains. She cited specifically the Monterey shale occurrence mentioned above, pointing out that the fossiliferous layer appears as an exact equivalent to a layer formed by a "red water" catastrophe off Africa in 1924 (*20*). She also compared the sediments formed as a result of upwelling to certain types of sediments looked upon as source beds of petroleum (*21*).

Development of "red water" is only one of the several phenomena that may bring about mass mortality in the sea today and that may have been responsible for the preservation of crowded layers of fossils in the past. Other well-documented causes include volcanic eruptions, tidal waves, and rapid changes in temperature or salinity. Not all crowded fossil layers, of course, record sudden catastrophes. Some such layers are covered by dead shells or skeletons brought peacefully to their final resting place by normal wave or current action. Other layers record the burial—dead or alive—of gregarious forms preserved at a site of their own choosing.

Upwelling waters do more than stimulate development of "red water." They are appreciably cooler than the surface waters they displace, and this fact seems to be chiefly responsible for the paucity of coral reefs off the western sides of large land masses in the tropical seas of today. Individual colonies of coral may live in such areas, but the ecological situation is unfavorable to prolific growth over an area large enough to form a reef. From what is known of the distribution of older reefs, similar conditions prevailed in Tertiary times.

In areas affected by upwelling, the fauna and flora may contain genera and species that are indicative of cool waters —that is, cooler than those found in adjoining areas. By means of a temperature survey in the upper 200 feet of the coastal waters off Baja California, Dawson (*22*) demonstrated the wide occurrence of upwelling. He found that the marine flora in the areas of upwelling contained many cool-water forms. Because of upwelling these are found far south of their latitudinal range.

Valentine (*23*) reviewed the thermally anomalous distribution of Pleistocene molluscan faunas in California and suggested that upwelling of cold waters during the glacial period might be partly responsible. As has long been known, the Pleistocene faunas contain a mixture of species that are now found widely separated geographically. Species that today live far to the north of a given fossil locality may be found with others that now live far to the south. Valentine suggested that during some stages of the Pleistocene, warm-water species spread northward, and that simultaneously increased upwelling of colder waters permitted northern species to range southward. Thus the shells of the two types could become mixed in a single deposit. In commenting on this proposal, Woodring (*24*) expressed doubt that the anomalous distribution could have been entirely controlled by Pleistocene events because similar anomalous features also characterize preglacial Pliocene faunas. At the same time he urged further exploration of the potential role of upwelling.

New Instruments and Techniques

The floors of the oceanic basins and the oceans themselves are currently being investigated on a scale not previously attempted. Shore lines, estuaries, and inland seas are sharing in this stepped-up program. New and improved instruments and new techniques are being used, and many of the ecological data obtained bear directly on paleontology and stratigraphy.

Earlier conceptions of life in the deep sea are being radically altered. More efficient trawling and more extensive dredging (*25*) have shown that life is more widespread and that its pattern is more complicated than was formerly supposed. In 1950–1952 the Danes sent the "Galathea" on a round-the-world marine biological expedition. The primary purpose was to explore the deep ocean trenches and learn more about the life found there (Fig. 4). In this, the expedition was markedly successful. Anton Bruun, a member of the "Galathea" expedition, has recently published a summary of the "Hadal fauna" that inhabits the deep trenches. Including some forms obtained by Swedish and Russian expeditions, the total is now more than 50, representing a wide variety of types—sponges, coelenterates, worms, echinoderms, mollusks, arthropods, and fish (*26*). In the Acapulco Trench off Central America, at a depth of 3590 meters, the "Galathea" dredged a living monoplacophoran mollusk, a type previously thought to have become extinct during the Devonian period.

The deeper waters are also being explored with a new diving instrument, the bathyscaphe, developed by Jacques Piccard and his father, with later improvements by the French Navy. The possibilities of the "underwater blimp," whose steel cabin has walls 3½ inches thick, have recently been discussed by Jacques Piccard under the intriguing title "The Oceanographer Must Now Go Down Himself" (*27*). The record manned dive made to date exceeds 13,000 feet. The bathyscaphe is complicated and expensive, but its possibilities for exploration of the deep sea appear to be limitless (*28*).

Quantitative ecological data on the life of bottom communities are being obtained from all depths by a wide variety of instruments (*29*) (Fig. 5). Methods of taking bottom photographs are being improved (Fig. 6), and in shallow waters television has been used to a limited extent to record activities of marine life. The shallow-water marine environments are now also being explored in all parts of the world by divers using the aqualung. Eventually this self-contained diving apparatus will reveal much about living conditions at depths down to about 40 fathoms. Information on the shallow waters is, of course, particularly interesting to the paleontologist and stratigrapher because most of the known fossiliferous marine sediments were deposited in shallow waters.

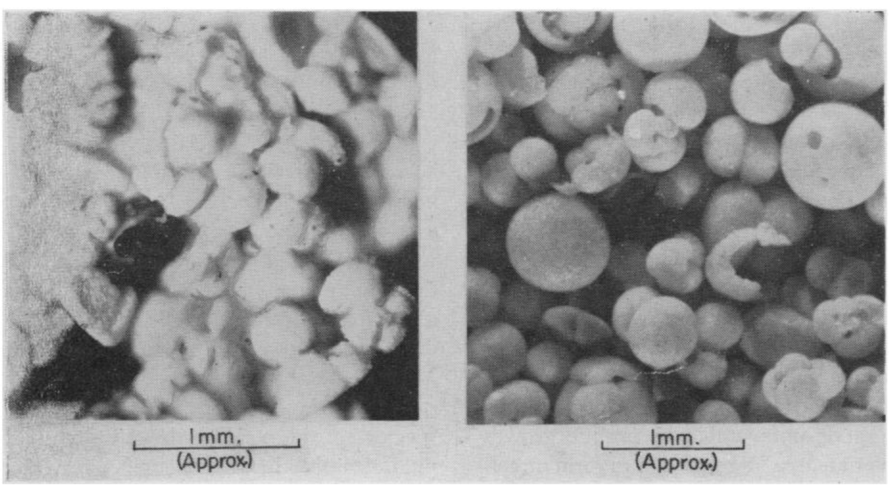

Fig. 5. Eocene and Recent pelagic Foraminifera from the surface of the same flat-topped seamount. Though environmental conditions may have changed but little during the passage of some 40 million years, the assemblages of genera and species are distinct. The sample at left is a partially phosphatized *Globigerina* ooze from cracks in a manganese nodule (*69*) from the surface of Sylvania Guyot in the Marshall Islands; the sample was dredged near the northwest edge at 800 to 1000 fathoms. The sample at right is unconsolidated *Globigerina* "sand" from the surface of the same guyot, about 30 miles to the southeast, at 680 fathoms. The Eocene nodule was not deeply buried by the rain of pelagic shells.

"Living Fossils"

The collection of living organisms from the beach to the deep sea has brought in new finds for the systematist that have had profound significance for the paleontologist and the paleoecologist. Several such cases have occurred in recent years.

The first of these "living fossils" was the coelacanth (*Latimeria chalumnae* Smith), a fish with two pairs of vertebrate limbs, belonging to a group thought to have become extinct at the end of the Cretaceous period, about 90 million years ago. The first specimen was trawled in the Indian Ocean off the African Coast in December 1938; an announcement stressing the significance of the find appeared the following month. A second specimen was taken in 1952, and a total of nine are now preserved in Paris. These are large fish, 4 to 5 feet in length (*30*). Living in the uniform conditions of the "twilight zone" (140 fathoms at night, possibly still deeper by day), this primitive fish has been able to retain its ancient form and structure.

In the same year that the first coelacanth was caught, in fairly deep water, a series of primitive crustaceans (*Derocheilocaris typicus*) was found inhabiting the interstitial waters of beach sands in New England (*31*). The average length of the adults was less than 500 microns. *Derocheilocaris* was assigned to a new order, Mystacocarida, and was regarded as the most primitive living crustacean yet discovered. It held this significant position only until 1953, at which time a still more primitive crustacean was dredged from the mud beneath the shallow waters of Long Island Sound (*32*). This newest relative of ancestral crustacean stock (*Hutchinsoniella macracantha*) was small enough to crawl through the eye of a needle. It possessed such primitive features that a new subclass was set up to receive it. Its closest known relative, *Lepidocaris*, lived in Middle Devonian time, some 300 million years ago.

The latest "living fossil" is a mollusk, *Neopilina galatheae* Lemche, dredged by the "Galathea" expedition off the west coast of South America in 3590 meters

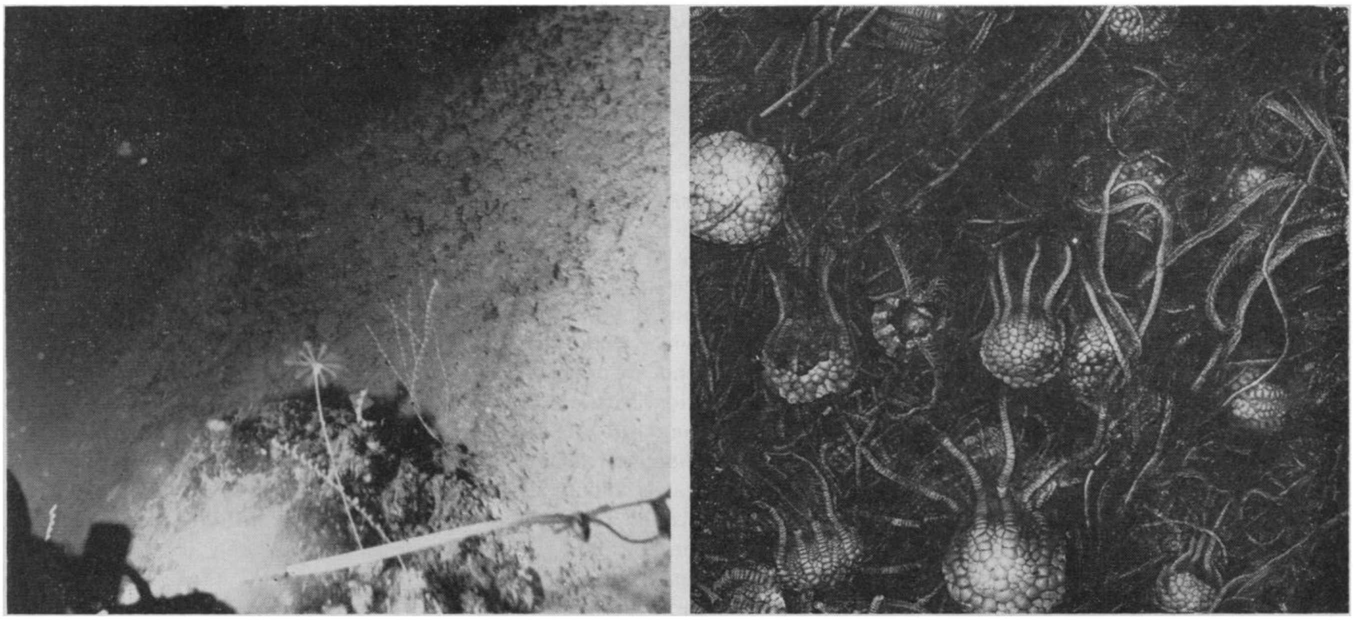

Fig. 6. Crinoids, living and fossil. (Left) A solitary stalked crinoid ("sea lily") at a depth of 1200 fathoms in the Gulf of Mexico. The stem is about 1 foot long. [Photograph, from *Geol. Soc. Am. Mem. No. 67* (1957), vol. 2, by D. M. Owen, Woods Hole Oceanographic Institution]. (Right) Gregarious, free-swimming crinoids (*Uintacrinus socialis*) from the Cretaceous rocks of Kansas. Rounded cups are 1½ to 2½ inches in diameter. [Photograph, from *Geol. Soc. Am. Mem. No. 67* (1957), vol. 2, courtesy of the Smithsonian Institution]

of water. This abyssal form superficially resembles modern shallow-water limpets, and, though a new genus was created for it, it fitted nicely into larger taxonomic units designed to include fossils that lived in the Paleozoic from Cambrian to Devonian times (*33*). This discovery was of great importance to paleontologists as well as zoologists. Although it proved certain paleontological assumptions regarding primitive gastropods to be erroneous, it offered strong support to others (*34*) and greatly clarified the phylogeny of the entire phylum Mollusca.

Subsurface Exploration

New and greatly improved methods of drilling on the land and beneath the sea have been developed in recent years, penetrating new sections of fossiliferous sediments for stratigraphic, paleontologic, and paleoecologic analysis.

On the land, 1¾ million holes have been drilled for oil and gas. The records of these wells have contributed much to the knowledge of ecologic conditions of sedimentary deposition and petroleum accumulation—of, for example, the "shoestring" sands of Kansas; reef structures in Illinois, Texas, and elsewhere; and sedimentology of the Berea sandstone in the northern Appalachian oil and gas fields. A number of holes have been drilled by oil companies to depths of more than 20,000 feet. In recent years the "deepest hole" has shifted about the country, each new hole being a little deeper than the previous record-breaker. At the time of this writing (July 1958) a new record of 23,500 feet has been established in Texas, and the hole is still being deepened.

In oil fields where extensive subsurface exploration has been done, quite a number of geologic formations, unknown from surface outcrop, have been recognized and named. Many fossils, both large and small, are known only from drill cores and cuttings. Drill samples likewise lend themselves to paleoecologic analysis. On Eniwetok Atoll in the Marshall Islands, for example, two widely separated 4000-foot holes were drilled through Tertiary limestones to the volcanic basement (*35*). One of these holes penetrated shallow-water reef limestones from top to bottom, but the other passed through 1000 feet of fine chalky material whose high content of pelagic Foraminifera clearly indicated that the sediment was accumulated off the reef edge in deeper waters that were open to the sea (*36*).

For several decades oil has been produced from horizons lying far below shallow bodies of water, such as Lake Maracaibo in Venezuela. The stratigraphic section beneath Lake Maracaibo is as well known to the oil companies as are the sections that outcrop on the land surrounding the lake. Extensive drilling in shallow waters open to the sea has been done off the coast of California and in the Gulf of Mexico. All such drilling has been done from towers firmly anchored to the bottom. A new technique has recently been developed, by a group of oil companies in California (*37*), that permits drilling from a barge anchored in waters as deep as 1500 feet. Some of the drilling was done despite strong currents and high waves. This is a revolutionary step that should lead to the exploration of many of the submerged continental shelves. Future drilling should reveal their structure, their age, and something about the environments under which their sediments were deposited. It could lead much farther and make possible a drill hole through the sediments that blanket the floor of the deep ocean.

Much information about the uppermost layers of sediment beneath the deep sea has been obtained in recent years. New coring devices, such as the Kullenberg piston corer, have brought up undisturbed cores of up to 70 feet in length, and the Russians report that they have obtained cores exceeding 100 feet (*38*). Stratigraphic boundaries have been carried back into the Tertiary, and much has been learned about the environments in which the contained organisms lived.

Ecologic studies of value to paleontology and stratigraphy are being actively carried on in various marine, brackish, and fresh-water environments by geologists, biologists, oceanographers, and geochemists. Some of the ecological problems are outlined below, together with some indication of how they are being tackled.

Carbonate Deposition in Shallow Waters

The Bahaman region has long interested marine scientists because of the richness of marine life on its reefs and because of the extensive shallow banks covered by a deposit of finely divided calcium carbonate that adjoin the reefs. As early as 1946 Cloud and Barnes (*39*) suggested that the conditions on the Bahama Banks were analogous to those that prevailed in the Llano region of Texas in a part of early Paleozoic time. More recently Cloud has devoted much time to field and laboratory studies of materials from the Bahama Banks west of Andros Island, concentrating on the conditions that seem to favor the chemical deposition of calcium carbonate (*40*).

The finely divided calcium carbonate of the Bahama Banks consists mainly of minute aragonite needles. Lowenstam has compared the Bahaman needles and needles from sediments in other areas, finding them similar in habit and dimension to aragonite needles secreted by common marine calcareous algae. He believes that algae living today and in the past are a source of such needles and that they may be responsible for part or most of the bank deposits (*41*).

Norman Newell and a number of his students made detailed studies of the reef and bank ecology in the Bahamas (*42*) before undertaking a comprehensive study of the Permian (Paleozoic) reef complex in the Guadalupe Mountains of Texas and New Mexico. The ecologic findings in the Bahamas were applied with marked success (*43*).

Intensive ecological studies of existing reefs and the surrounding sea floor on a scale not heretofore attempted were carried out in connection with the testing of nuclear weapons in the Marshall Islands, starting in 1946. Many of the results have appeared in the numerous chapters of *U.S. Geological Survey Professional Paper No. 260.* These data—assembled by biologists, oceanographers, and geologists—are being used in paleontologic and stratigraphic studies of the thick geologic sections drilled beneath atolls in the Marshalls and elsewhere. The ecologic findings have also been used in a variety of paleontologic and stratigraphic studies in other parts of the world.

Sedimentary Structures in Shallow Waters

Shallow-water environments — tidal flats, beaches, reefs, estuaries—are being studied by ecologists in many parts of the world (*44*). Much information that can be applied to paleontology and stratigraphy is being obtained, but not even a cursory review can be attempted here. Special mention must be made, however, of one area where notable studies have been and are being made. This is the area of tidal flats (waddens) extending along the coast of Europe from Denmark to the Netherlands. The extensive areas of sands and muds are cut by tidal channels and present a variety of environments that support equally varied assemblages of animals and plants. The easily accessible flats, with their diversified sedimentary structures and organic markings, appealed to the late Rudolph Richter, and in 1920 he began to study the tidal-flat phenomena and seek for their counterparts in older sediments. Richter's work led to the establishment of the institution known as Senckenberg-am-Meer on the shore of Jade Bay at Wilhelmshaven, Germany. The detailed studies carried out there by Richter, Walter Häntzchel, W. Shäfer, and others have been invaluable to paleontologists. They are published as beautifully illustrated papers in *Senckenbergiana.* The Dutch have carried on similar studies from headquarters in Groningen.

In most shallow-water areas physical forces seem to influence, if not actually control, the bottom communities that live there. Ginsberg and Lowenstam (*45*) have recently reviewed this subject in the light of work done in Florida Bay, pointing out that living communities are capable of modifying water circulation sufficiently to produce sediments recognizably different from those deposited without organic influence. Growth of blue-green algae binds sediment, other types of plant growth trap sediment, and organic structures like barrier reefs produce quiet lagoonal waters in which distinctive types of sediments may be laid down over long periods of time.

Biochemical Studies

Some of the most interesting and exciting studies in marine paleoecology are biochemical in nature, involving determinations of the temperatures and salinities of ancient seas. Other geochemical studies of fossil shells have led to improved methods of dating the younger fossiliferous beds.

Work on a geologic thermometer involving the temperature-controlled ratio of O^{16} to O^{18} in calcareous fossils as compared with the ratio in shells of organisms living today was started in 1947. The studies have been markedly successful, and oceanic temperatures have been determined—in the case of a belemnite —as far back as the Jurassic (*46*). The distribution of magnesium in skeletal carbonate is also being investigated, and it offers promise as a geological thermometer (*47*). Abelson's determinations of amino acids in a variety of fossils extending back into the Paleozoic have opened up an entirely new field of study, and it appears that alanine may also serve as a geological thermometer for sediments (*48*).

The effect of temperature on the mineral composition of skeletal carbonate is being investigated by Lowenstam (*49*), who determined the aragonite-calcite ratios of the shells of living species by x-ray analysis. Temperature differences were found in some organisms in which the ratio of aragonite to calcite increased with a rise in temperature. Some warm-water species that in low latitudes secrete a skeleton composed entirely of aragonite develop traces of calcite at higher latitudes near the margins of their ranges. In some cases the aragonite content was temperature-sensitive at the species level; in others, at a much higher level. Examination of the aragonite-calcite ratio in growth series collected locally revealed some evidence of seasonal variation. All of these studies promise to have applications to phylogeny and to be of interest to paleontology in other ways.

Geochemical studies of the strontium cycle have been coupled with determinations of the occurrence of strontium in fossil shells (*50*). Turekian (*51*) has concluded that salinity is an important factor in determining the strontium-calcium ratio in shells and sediments and believes that it may be used in determining changes of salinity in past times.

Ecological Aspects of Deep-Sea Cores

The amount of information about earth history obtained from the first of the deep-sea cores that were brought up in 1936 was gratifying. Since then, longer cores have been obtained, and the amount of information extractible from the cores has increased in even greater proportion. Comprehensive reports on the cores collected by deep-sea expeditions (*52*) give much information about the stratigraphy, composition, age, and rate of accumulation. From the start, ecological data have played a vital part in all interpretations, particularly the important ones involving past climatic changes. Many of the faunas preserved in the cores consist largely of minute Foraminifera, some benthonic (bottom-dwelling), others pelagic (floating). Many of the fossil species are identical with still-living species, and the habits and distribution of the latter are of great importance to the stratigrapher. Some of the fossils are shallow-water forms, others suggest deeper waters; some suggest cool waters, others warm waters. The occurrence of a shallow-water assemblage in the sediments of the deep sea far from shore lends strong support to interpretations involving turbidity currents or some form of landslide. The stratigrapher, attempting to recognize the deposits of glacial (cold-water) epochs and of the interglacial (warm-water) epochs in deep-sea cores, is guided by the ecologist.

Among the core studies of great interest to stratigrapher and micropaleontologists are those being made of the oxygen-isotope ratios of the shells of fossil Foraminifera. Samples for analysis are taken from cores obtained in areas where the bottom sediments appear undisturbed. Some of the cores already studied penetrate the Pleistocene into Tertiary beds as old as middle Oligocene—some 30 million years (*53*). Shells of benthonic and pelagic Foraminifera are, of course, studied separately. Results to date give information about oceanic temperature changes through the late Cenozoic and reveal facts about circulation in the ocean in past times (*54*). Temperature variation in Pleistocene deep-sea cores from the Caribbean and Atlantic has been studied, by means of the relative abundance of certain planktonic Foraminifera (*55*). Results of temperature and age analyses have been summarized by Emiliani (*56*).

Foraminifera, however, are not the only fossils in deep-sea cores. The list includes microscopic diatoms, ostracodes, mollusks, and—smallest of all—the discoasters and other forms related to the coccolithophores. Bramlette and Riedel (*57*) have recently shown the stratigraphic value of discoasters. Their interest in them was aroused when, in the course of examining bottom sediments from the Pacific, they noted that those in the cores that penetrated the Tertiary were strikingly different from those in Recent sediments in the same area. The fossils measure only 3 to 15 microns in diameter and are thus close to the size limits between clay and fine silt particles. They can be transported more easily and for greater distances than Foraminifera or larger diatoms. Ecology at the present time contributes little to studies of extinct groups such as that including *Discoaster* because, as Bramlette and Riedel point out, little or nothing is known about their ecologic controls. The discoasters and their relatives seem, nonetheless, to provide one of the most promising leads in the expanding field of micropaleontology.

Determinations of the exact ages of the organic materials in stratigraphic units of deep-sea cores have been made by several methods. The radiocarbon method is the best known and the most widely used, but others involving the ionium-thorium ratio (*58*) and the ionium-uranium ratio (*59*) are being investigated. This work will make accurate correlations possible in the youngest beds of the geologic section. Fossil identifications alone mean little in these beds, because most of the shells are identical with still-living species. Another method of estimating geologic age, under investigation at the University of Wisconsin, consists in measuring the thermoluminescence exhibited by limestone sediments. Results to date are distinctly encouraging (*60*).

Present Status and Outlook for Future

A comprehensive summing up of the present status of invertebrate paleontology is well underway at the present time. The treatise will be a monumental work, sponsored by several paleontological societies, supported by the Geological Society of America, and edited by Raymond C. Moore (*61*). It is designed to summarize existing knowledge, in a score of volumes for which more than 100 authorities are preparing reports on individual taxonomic units. Seven of these units have already appeared. This work will replace the single-volume *Text-book* of Zittel-Eastman that has been the standard reference work for more than 40 years. The new treatise will equal half a dozen Zittel texts, and this ratio gives some indication of the progress that has been made in describing and classifying fossil invertebrates.

A volume entitled *Principles of Stratigraphy,* illustrated by many examples from the geologic record, has recently been published by Carl O. Dunbar and John Rodgers (*62*). This readable volume is the first over-all stratigraphic summary to appear in this country since A. W. Grabau published a book with the same title in 1913. Stratigraphy is presented as a growing science, still in possession of interesting unsolved problems.

Marine ecology and paleoecology, too, have recently been appraised in two volumes, with more than 100 contributors, issued as *Geological Society of America Memoir No. 67* (*63*). This work was prepared under the direction of a committee of the National Academy of Sciences–National Research Council. Volume 1, under the editorship of Joel W. Hedgpeth, summarizes the broad field of marine ecology in the light of the special needs of the paleontologist. Volume 2, edited by H. S. Ladd, deals specifically with paleoecology.

In the last chapter of the "Treatise on Paleoecology," G. Evelyn Hutchinson considers the "Future of marine paleoecology" (*64*). Though the author modestly refers to "uninspired prophecy," his summary contains many interesting speculations about what we may learn, through geochemical studies, concerning the history of the oceans (paleo-oceanography) and about what biochemical studies of living assemblages and statistical studies of fossil assemblages may reveal concerning the animal communities of the past (paleobiocoenology).

I am interested primarily in marine studies, and I am aware that nonmarine organisms and environments have been rather shamefully neglected in the present summary. I would be remiss indeed, however, not to call attention to the outstanding *Treatise on Limnology* by G. Evelyn Hutchinson. This work aims to present—for the biologist, geologist, and oceanographer—as complete an account as is possible of the physical, chemical, and biological conditions that obtain in lakes. Volume 1, issued in 1957 (*65*), deals primarily with geography, physics, and chemistry. A second volume will cover ecological and stratigraphic problems of lake development.

A continuation of basic studies in ecology will be of benefit to paleoecologists. It will not be possible to interpret fossil assemblages fully until more is known about the living habits of existing species. For example, careful collecting reveals the niche or niches occupied by certain species of living mollusks at a given time and place, but it does not tell anything about changes in the habits of these same species over a period of time —about migrations or cycles that may affect their distribution in a given area. Continuing ecologic investigations in the same area are urgently needed. This sort of information about living forms will be of real value to paleoecologists.

A continuation of paleontologic and stratigraphic investigations on the land should continue to yield data having paleoecologic implications. Not all of the land areas have yet been fully surveyed, either on the ground or by means of the drill. It is the sea, however, that seems to promise the greatest rewards. Mention has already been made of the "living fossils" that have been collected in recent years. As more and longer cores are obtained from the sea—particularly from the deep sea, where sedimentation has been uninterrupted for long periods —more will be learned about biological and climatological changes back to early Tertiary and Mesozoic times.

If, as many geologists believe, the deep-ocean basins have been in existence since early geologic times, it might be possible by drilling and sampling the submerged marine section to obtain an uninterrupted record of the development of early life. I myself think that such a project will prove feasible. The proposal, first suggested by the American Miscellaneous Society and now being seriously studied by a committee of the National Research Council, to drill through the sediments of the deep sea and the underlying basalt to the Mohorovicic discontinuity (*66*) and thus obtain a sample of the earth's mantle is not as fantastic as it sounds (*67*).

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