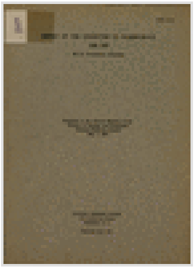

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REPORT OF THE COMMITTEE ON PALEOECOLOGY

1936 - 1937

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REPORT OF THE COMMITTEE ON PALEOECOLOGY

Introduction

W. H. Twenhofel

All biologists agree that organisms and the environments in which they live are so adjusted as to seem to have been especially created each for the other, and before the formulation of the doctrine of evolution something like this was generally believed. The idea is still more or less true but not in the original sense. The doctrine of evolution explains the adjustments as due to gradual selection and elimination and shows the struggle that organisms must make to keep pace with an ever changing environment, since at about the same time as the presentation of the doctrine it was learned that the "Everlasting hills" and the "Hills, rock-ribbed and ancient as the sun" are but figments of the imagination, that no environment on the earth's surface remains the same for long, but is constantly in a state of change, and that this has been so since the dawn of recorded geologic history and probably will continue for aeons into the far distant future.

Students of fossil organisms have been mainly interested in morphology and classification, and stratigraphers have been mainly interested in the use of organisms for correlation and the building of sequences. Neither branch of geology greatly concerned itself with the conditions under which the fossil organisms had lived and the relations and adaptations of the organisms to these conditions. Thus, there are thick tomes with profuse illustrations giving descriptions of fossils and equally thick tomes describing sequences and presenting correlations. This is not said in depreciation as these works have been of immense importance, but they state nothing or very little with respect to the conditions under which the organisms lived and the meaning of the sequences of fossils that change in association and in character from bed to bed.

Stratigraphers and paleontologists have more or less generally assumed that organisms migrated freely from sea to sea and that within any epicontinental or marginal shelf sea the same organisms had rather general distribution. It has also been rather generally assumed by some paleontologists and stratigraphers that the fossil organisms of any given body of water, if not generally distributed during life for some cause or other, attained that distribution after death through transportation by waves and currents. Others have tended to assume that fossil organisms are close to, if not at, the places of life and that there was little transportation after death. Neither of these assumptions can be entirely correct. It is doubtless true that from time to time a few organisms may have existed which, like the ubiquitous dandelion of today, lived nearly everywhere on all bottoms of each epicontinental and marginal water, but

It should be remembered that even the dandelion does not live everywhere and that it is not probable that plants and animals with such general adaptations to environments often lived in the past, and that most plants and animals of the past were restricted in distribution just as most plants and animals of the present are.

While paleontologists and stratigraphers were thus occupied, ecological biologists concerned themselves with qualitative and quantitative adaptations of organisms to their environmental conditions, and produced a wealth of data showing the mutual adjustments of organisms to each other and how both in kind and quantity each environment contains organisms in adjustment to the places in which they live.

The problems of existing environmental impacts are extremely complex, and perhaps the feature that is given least concern by ecologists is the possible geologic record that each individual factor and the combined environmental factors leave in the sediments and sedimentary materials upon which the organisms dwell. But this record is all important to paleoecologists, paleontologists, and stratigraphers since upon this record must be based any interpretation of past conditions, as direct observations of rainfall, humidity, temperature of the air, depth and temperature of water, etc. cannot be made. The records of these various factors are preserved in the textures, structures, and materials of sedimentary rocks and every student of past environments should be primarily a sedimentationist, or at least versed in the significance of sedimentary processes and informed as to the meaning of sedimentary structures. The significance of ripple mark of the various kinds, the meaning of cross lamination, mud cracks, etc. should be understood. Unfortunately this is all too frequently not the case. As an example may be cited the otherwise excellent paper by Romer and Groves on the "Environment of the Early Vertebrates"[1] in which they state that "invertebrates may be numerous during life but their shells are rapidly destroyed by a solution of calcium carbonate" (p. 807). Unfortunately, solutions of calcium carbonate do not increase solubility for additional calcium carbonate. Again it is stated, "We find puzzling the fact that in the case of the Cleveland shale, for example, remains are found not only of the bones and cartilages of fishes, but also exceedingly delicately preserved muscle fibers and kidney tubules" (p. 808). The "difficulty" seems to be in the absence of the shells of invertebrates, but there is no difficulty if the significance of the high organic content of the shales and the presence of pyrite nodules are understood. The missing organisms are largely benthonic; those present are planktonic and nektonic. The blackness shows reducing conditions, the pyrite or marcasite the presence of hydrogen sulphide, and both indicate a paucity of oxygen so that benthos could not live on the bottom or in the bottom materials. The plankton and nekton evidently lived in overlying waters in the equivalents of the epilimnion and thermocline where oxy-

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[1] Am. Midland Naturalist, vol. 16 (1935), 805-856.

gen was plenty. These on death ultimately sank to the bottom where the absence of scavenger organisms made preservation easily possible. In another place it is stated that "Horizontal gradations of sediments and cross-bedding are generally indicative of deltaic or aeolian conditions" (p. 809), but every student of sediments has known for years that these features are equally, if not better, developed under shallow water marine conditions, and that lateral gradation is found in every deposit made by aqueous or eolian transportation and that cross-lamination is developed wherever sediments are transported by traction. Cross-lamination is fully as abundant in shallow water marine deposits as the deposits of any delta. It is also stated that "mud cracks, ripple marks, and rain drop impressions indicate shallow water exposed at times to the air, but without additional criteria may range from tidal flats to lake margins in their origin." (p. 809.) Mud cracks and rain drop impressions develop under the conditions postulated but they probably develop best on the playas of deserts and on the flood plains of rivers, but ripple marks do not indicate exposure to the air at all and they are known to develop on the bottoms of waters hundreds of feet in depth, and it is probable that current ripple mark forms as deep in the ocean as currents exist. It has been known for many years that these extend to depths of at least 2000 meters. There are other statements in this paper that indicate ignorance of the significance of sedimentary features.

Marine biologists and ecologists continue to produce evidence showing the importance of the environment. One of the most important contributions of recent years has been made by Professor G. E. MacGinitie in his studies on the distribution of organisms in Elkhorn Slough, a tributary of Monterey Bay, California.[1] Studies were made of the physical geography of Elkhorn Slough, the tides therein, bottom materials, plant life, temperatures of the waters, oxygen supply in the waters, salinity, light penetration, pollution from sewage, food supply, etc. These factors form the physical and chemical background of the environmental conditions existing in the Slough to the sum total of all factors of which the animals are adapted. The food chain of the animals dwelling in the Slough was studied and an excellent diagram showing this chain from plants to final decomposition, elimination, or burial is given. There are also considered the associations, zoning, and density of the bottom and burrowing population.

The conditions in the Slough are shown to be rather uniform. Nevertheless, the animals tend to segregate in groups and may be placed in associations in which one animal is predominant. The activities of this animal regulate to a greater or less extent the activities of the animals associated with it and provide the set of conditions which to some extent determines "what animals may live within the boundaries of the association." The associations are by no means permanent and apparently change within

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[1] Ecological Aspects of a California Marine Estuary, Am. Mid. Nat., vol. 16, (1935), 629-765.

relatively short periods of time to give place to other associations with another animal predominant. This is the condition one finds in the geologic column in which beds succeed each other with different assemblages of organisms. On the other hand there are associations with no predominant animal, for which parallels may also be found in beds of the geologic column. Among other matters considered are parasitism, commensalism, trophism, nocturnal activities, migrations from water to land, and geological indications. Under the last topic it is pointed out that there is considerable movement of bottom materials, and from the age of shells of clams it is shown that in certain places the bottom has remained stable for definite periods of time. It is also shown how erosion of the bottom may lead to removal of fine materials originally deposited around shells, thus leading to concentration to make a layer composed entirely of shells. Attention is called to tracks, trails, fecal pellets and borings.

This article contains a wealth of material of great value to sedimentationists, stratigraphers, and paleoecologists and it is particularly important in that it shows the distribution and associations of organisms existing in a body of shallow water not subject to strong waves or tides and, in general, one subjected to rather uniform conditions where variations of distribution are commonly considered not to be present.

Another study by a marine biologist is that by W. G. Hewatt[1]. This study was made on the more open waters of Monterey Bay, to which bay Elkhorn Slough noted above is satellitic. The studies were made on the southern margin of Monterey Bay on a transect 108 yards long and 1 yard wide. The animals dwelling on this area were studied in detail. The area studied is rocky and on the whole it is characterized by apparent monotony with respect to most of the physical and chemical factors of the environment. Nevertheless, the studies show that there is a definite zonation in the distribution of the animals dwelling on the area. Among factors governing the zonation it was found that the relative lengths of the periods of tidal exposure are important and that the limits of ranges of some of the animals are biological rather than physico-chemical, a fact long ago pointed out by Petersen as being the case in Danish water (See report of this committee for 1935-36.)

Two diagrams of the food cycle or chain are given, one of the animals found on the exposed littoral of Cabrillo Point and the other on protected littoral at the same place ("littoral" is defined as the area between the mean higher high water and the mean lower low water lines of spring tides.) The study loses in importance for paleoecology and sedimentation as there is only the most remote chance that a coast like the one studied will leave a record in the geologic column, but the study indicates that shores upon which sediments are in process of deposition and sediment-covered bottoms in the neritic life zone may also be expected to show zonation, but from other causes among which it is probable that light,

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[1] Ecological Studies on Selected Marine Intertidal Communities of Monterey Bay, California, Am. Mid. Nat., vol. 18 (1937), 161-206.

depth, pressure, and circulation have importance. When it is remembered that stratigraphers and sedimentationists as yet have little on which to base a determination of depth of the seas of the past it should be obvious that the paleoecological characteristics and relations shown by the zoning of animals should be of great importance once their significance has been determined.

The Danish Biological Station continues to contribute ecological data of great importance as this phase of biology is particularly pertinent to the objectives of the station in its studies of the food for fish. A report[1] published during the past year contains two items bearing on ecology that are of interest. The vegetation in Dypsø Fjord is arranged in three different communities, designated the *Chara*, *Ruppia*, and *Zostera-Fucus*. The *Chara* community covers the largest area, the *Zostera-Fucus* second, and the *Ruppia* third. These communities are so arranged that the *Chara* covers something more than the eastern three-fourths, and then in order westward, the *Ruppia* and the *Zostera-Fucus*. Reasons for this distribution are not apparent.

A second fact of interest, and one that shows the great difficulty in determining what is the factor (or the factors) in an environment that controls the presence or absence of a species, relates to the little neck clam *Mytilus edulis*. The waters and the bottoms of Dypsø Fjord seem suited to the clam and it should be common there, but it has been found only along the western half of the northern side of the Fjord. The waters over the other parts of the Fjord do not seem to be greatly different and there seem no reasons why it should not be generally present. The reason for the limited distribution is not known.

On the other side of the world about the Japanese Islands, S. Nomura and K. Hatai during the past several years have given attention to the ecological problems connected with the distribution of organisms in the outlying waters, and they conclude that studies need to be made of the distribution and kinds of organisms in the various aquatic environments and that information is needed as to how far a shell may be moved after death and the places to which it may be carried.[2]

Bearing on the transportation of shells and showing the extent that transported shells may give to an interpretation of such shells from the point of view of ecology, if it is not realized that the shells are transported, is the following: A half pound stone was picked up on the coast of New Zealand on which several individuals of *Boltenia pachydermata* were

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[1] K. Larsen. The distribution of the invertebrates in the Dypsø Fjord, their biology and their importance as fish food. Rept. Danish Biol. Sta., vol. 41 (1936).

[2] The geologic significance of the recent Mollusca from the vicinity of Isinomake, Rikujen, Jour. Geol. Soc. Japan, vol. 43 (1936), 808-813.

growing. The stone had evidently been transported buoyed up by the ascidians and to the stalks of these were attached Hydrozoa, Bryozoa, and other marine organisms.[1]

Other papers by students of marine biology could be cited but the need for such is not apparent. Marine biologists are fully cognizant of the influence of the environment on the distribution of organisms and the modifications that environments produce, and are aware of the fact that this influence applies to both plants and animals from the most complex to the most simple forms. Paleontologists and stratigraphers need to become ecologically minded and to fully appreciate that there are no places, unless it is the bottom of the deep sea, that the environment does not differ over very limited areas. The view expressed by one eminent paleontologist that the epicontinental seas of the Paleozoic at any particular time were of such uniformity in the physical and chemical factors as to make possible uniform distribution of organisms in kind and perhaps in quantity from shore to shore, should be totally abandoned. The statement is one that is impossible of occurrence in any shallow body of water.

This report brings the work of the Committee on Paleoecology to an end. Specialists have presented in a previous report consideration of the Paleoecological relations of the Porifera, Arthropoda, Trilobita, Vertebrata, and Paleozoic plants. On following pages there are considered the Brachiopoda, Gastropoda, and Pelecypoda, Cephalopoda, and Protozoa. No consideration has been given to the Echinodermata as no one has been found willing to undertake the task. Little or nothing seems to be known of the environmental conditions controlling distribution of living bryozoans, and less seems to be known of the environmental conditions of those of the past. The Coelenterata have been given much consideration in previous publications by Dr. T. Wayland Vaughan and a forthcoming paper by him and Dr. J. A. Wells will explore the field to a greater degree.

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[1] C. Chilton, Trans. and Proc., New Zealand Jour., vol. 56 (1926), 523-524.

PALEOECOLOGY OF THE FORAMINIFERA

J. A. Cushman

Although foraminifera are now known throughout the fossil series from the Cambrian to the Recent oceans, very little has been written in regard to their ecology or about the controls of their distributions. Our growing knowledge as to the ecology of this group must be based largely, as in other groups, on the living species, their associations and environmental conditions of life. For convenience in discussion, the foraminifera may be divided into bottom-living and pelagic groups. The latter group is the more specialized and later in its development and will be considered first.

Pelagic Foraminifera

Peculiar characters have developed in the foraminifera to adapt them to pelagic existence. They occur only in comparatively warm waters so far as is known. Owing to their floating life in which there is little need of the development of dorsal and ventral sides for attachment or protection of the aperture and the extended protoplasm, a generally rounded form is developed. This is carried to its perfection in Orbulina which in the adult consists of a test in the shape of a perfect sphere. In order to float in the water the protoplasm is extended from the test and becomes filled with gas so that the whole mass is many times the size of the original test. In order to support this greatly enlarged protoplasmic mass spines are developed on the exterior of the test, in some species longer than the diameter of the test itself. These make useful supports for the protoplasmic mass and may provide a certain amount of protection for the animal itself against enemies. In other groups such as Globigerina, Globigerinoides and Globigerinella the chambers are themselves subspherical and the whole mass of the test is more or less globular. Other genera, of the Globorotaliidae, for example, have developed a more flattened form and much shorter spines but yet meet the conditions of a pelagic environment so that they appear in enormous numbers but with only a few species.

As a rule the pelagic foraminifera exist in the warm surface waters of the Gulf Stream and the similar warm currents of the other oceans. They exist until they meet cold currents and then apparently die quickly, and their tests form the Globigerina-ooze of the ocean bottom. Their empty tests are also rained down upon the ocean bottom beneath these warmer currents of all the oceans. In such areas the tests of pelagic forms make up a very large percent of the entire ocean bottom.

In certain other very specialized genera such as Tretomphalus a pelagic existence may develop during the adult stage only. The test in this genus is a bottom living form of coral-reefs but at the final stage in its development produces a large globular chamber which is gas-filled and sends the test to the surface where it apparently reproduces by zoospores. This is a very specialized development and has apparently occurred only in late Tertiary time. At certain seasons or under certain conditions which we do not understand there must be an enormous development of these forms, as they have been reported as forming definite "windrows" along the beach in the Australian regions so numerous are the tests at certain times.

The more normal pelagic forms are know to occur as early as the Lower Cretaceous and in the Upper Cretaceous form a large portion of the fauna in some formations. Many of the same pelagic genera developed in the Cretaceous exist in the present oceans, and it seems rather warranted to infer that conditions at the two periods were more or less similar as to the temperature of the ocean surface. That warm ocean currents existed at those and later periods seems safe to infer as in the depositional series pelagic forms may dominate in some layers and then for a time give way to those of more shallow or colder waters just as they do in cores recently taken from the present ocean floor. During Tertiary times masses of pelagic foraminifera were deposited in "Globigerina-oozes" comparable in most features with those which are developed today. The distribution of such deposits should indicate rather closely the areal extent of the warm ocean currents of those periods, and when more is known of the distribution perhaps even the directions of the currents may be determined.

Bottom-living Foraminifera

The foraminifera which now live on the ocean bottom may first of all be divided into brackish water and truly marine forms. The former which compose a specialized group will be discussed first.

Brackish-water Foraminifera—In certain regions such as Lake Maracaibo, Venezuela, the southern extension of San Francisco Bay and other regions, are developed faunas which are restricted in number of species and genera. Moreover, the same sort of grouping exists in widely separated brackish-water area. As might be supposed, these consist partly of arenaceous foraminifera which are especially fitted to withstand acidic conditions but strangely enough some of the highly calcareous forms also appear. The Miliolidae are represented by a few species of Quinqueloculina and Triloculina and the Nonionidae by certain species of Elphidium. Very similar restricted faunas consisting of the same genera are known in the latter part of the Tertiary and undoubtedly also represent brackish-water conditions. It should be possible in the future when the distribution of these faunas is better known to predict the position of the shore line and that of the open ocean from the restriction or addition to the faunas in one direction and the other. It should also indicate something of the relative salinity of the water at the time these faunas were deposited.

Marine Foraminifera—Of the foraminifera living in the present oceans under marine and non-brackish conditions it is convenient to divide the faunas into three groups just as is done with other animals, making three groups; (1) those of littoral or comparatively shallow waters, (2) those of the

Continental Shelf, and, (3) those of abyssal depths. While there are genera which are found under all three of these different conditions very few species, if any, occur in all three.

Littoral Foraminifera. The faunas of shallow waters, under 50 fathoms vary greatly according to temperature and bottom conditions. For example, there are probably no species existing in 5-10 fathoms on the coral reefs of Jamaica or Cuba that exist at the same depths off the Coast of New England. The clearness of the water is a decided factor in the tropics, and where muddy water is brought in (or perhaps the lowered salinity may also be a factor) the fauna is rapidly changed. Off the coast of Jamaica it was found that various species lived on the short eel-grass (Posidonia) and were very abundant where that plant flourished. Some of the larger foraminifera of coral reef regions such as Marginopora, etc., have associated with them certain algae in a commensal relation. As these algae are limited in their vertical range by the depth of penetration of sunlight necessary to photosynthesis they also limit the distribution of the foraminifera in the association. There is a considerable fauna in the tropics limited in this way, and it may be rather safely inferred that some of the later Tertiary faunas of similar association indicate like environmental conditions. One thing at least to be watched for is that such forms may be carried out into deeper water by wave and current action and occur with other than their normal association. Such specimens are, however, usually rather obviously worn and their association through mechanical means can usually be ascertained.

In temperate and arctic regions the bottom conditions, whether sandy or muddy may change very suddenly, as in Vineyard Sound and Buzzards Bay, and it has been found that many constituents of the foraminiferal fauna change likewise. These associations have not yet been worked out in detail as they should be and until this is carefully done it will be impossible to apply this data in the study of fossil faunas which probably lived under similar conditions. In general there are certain genera and species which are characteristic of comparatively shallow waters and those which should be much more definitely known than at present.

Foraminifera of the Continental Shelf. From 50-500 fathoms off the continental shelves there is developed a very rich fauna in which the Lagenidae, Polymorphinidae, Buliminidae, Rotaliidae and some of the arenaceous foraminifera are very characteristic and abundant. The range in depth is less restricted as temperature seems to be the most definite control. As temperatures at these depths are less variable and have less seasonal range the environmental conditions are more uniform, and as a result the species are widely distributed. That such conditions have prevailed during the Tertiary, at least, is shown by the Eocene, Oligocene and Miocene deposits of the Gulf and Atlantic Coastal Plain regions of the Southeastern United States where the faunas of apparently the same ages change as one goes toward the present shore line just as the faunas of the present ocean change in passing out from shore line.

Abyssal Foraminifera. Due to the solvent action of water under pressure most of the calcareous foraminifera disappear at about 2000 fathoms and the resulting fauna is largely composed of arenaceous foraminifera which are not greatly affected by these conditions. The statement sometimes made that arenaceous foraminifera live best under abyssal conditions is probably not true as they are often much more abundant in littoral dredgings and the fact of their apparent abundance in abyssal dredgings is due solely to the absence of the calcareous forms.

The occurrence of typical abyssal deposits is not, so far as I am aware, known at all in the fossil series.

Factors to be Eliminated in Correlation

Two faunas with much the same elements would naturally be considered of the same age. One must take under consideration, however, that faunas migrate or live on in one region when from ecologic changes they disappear in others. As an example, a number of species of the lower Oligocene of Mississippi now exist, or at least very closely allied ones, in the Indo-Pacific region. Miocene species of the area about the Eastern Mediterranean are found living today about Australia and adjacent areas while they are apparently extinct in the Mediterranean itself.

Re-working of faunas is evident in the case of the foraminifera and should always be held as a possibility. Where highly fossiliferous sediments are borne away by rivers or by wave action, the contained foraminifera may be carried some distances and redeposited with living faunas. There are numerous known instances of this and many more will undoubtedly be discovered.

Criteria for the Study of Ecology of the Foraminifera

One of the most certain methods of getting basic data for a study of the distribution of living foraminifera and the part that ecologic factors play in that distribution is an intensive study of the occurrence of species in definite regions. At present a study of the foraminifera of Monterey Bay, California, has been carefully made. Studies are under way on a number of lines of samples taken along our Atlantic Coast from Florida to the Gulf of Maine. These lines were taken from shallow water well out onto the slope of the Continental Shelf and have been carefully taken with bottom temperatures and depths. A qualitative and quantitative study of those samples is under way, and it is hoped the results will give basic data for the study of at least late Tertiary sediments with considerable accuracy as to the ecologic conditions under which they were deposited.

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AN ECOLOGICAL CROSS-SECTION OF THE LOWER PART OF FLORIDA BASED LARGELY UPON ITS MOLLUSCAN FAUNA

Paul Barsch*

Paleoecology, probably more than any other phase of earth history—or shall I say science—is an intriguing subject. It is not only that but fascinating, since it offers a challenge to all minds whether these be simple, complex or profound. Here each searcher can find a subject that will expand and keep pace with the growth, width and breadth of his paleobiological knowledge. For this reason there is probably no field of human endeavor, unless it be theisms, in which more thobbing[1] is indulged in than in Paleoecology.

The factors that govern the distribution of existing life are not completely known. We have only the broader phases within our grasp. The infinite details which determine the to be or not to be of this or that vary frequently even with the extremes in the distributional range of a single species and often very widely so when one considers the members of a single genus.

I have always felt that paleontologists, before entering this specialized branch of science, should have a thorough basic training in Botany and Zoology, and in the latter field stress not the histo-physiological phase, but the field studies, Ecology, the adjustment of organisms to their fellow creatures as well as physical environment.

It would be interesting to know how many of America's paleontologists would qualify under the above requiremtns, which to me appear as an absolutely necessary prerequisite to Paleoecology.

To one so versed, a tray of Tertiary fossils, fresh from the field, unassorted, brings to mind visions of habitats where similar associations hold forth today, and his mind's eye quickly pictures conditions paralleling those in which he found the living forms. His assumption of a definite range of depth, temperature, salinity, bottom characteristics, turbidity, light, current or wave action, and food supply, will probably be almost correct, certainly more so than it would be if this yardstick had not been applied.

In sections of certain silt deposits of bygone lakes, it has been possible to pin out the annual increments as definitely and easily as the counting of tree rings. This, unfortunately, is never the case in shallow seas free from river freight of silt and teeming with life. Here there is a constant intermingling of the living with the dead; the quick seek-

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* Published with permission of the Secretary of the Smithsonian Institution.

[1] Proving preconceived notions.

ing shelter among the bones of things gone by mix todays with yesterdays to an extent that forces us to abandon days, years, decades and centuries and employ geologic reckoning, Recent, Pleistocene with the Glacial and Interglacial signposts—and these as ill defined as the symptoms of most maladies.

I am hoping that when the Everglades National Park will have become a reality, which is soon to be, that some arrangement will be made for a summer course, parallel to the Woods Hole seasons, when qualified students under qualified guidance may have an opportunity to become acquainted with living marine organisms in their native habitat, and see the many wonderful peculiar, synchronous associations which this region affords. Such an ecologic study on the part of Paleontologists translated into their fossil assemblages, should, I believe, reduce many things assigned different vertical distributional positions on account of the diversity in faunal assemblages to a horizontal field, in which space rather than time constitutes the dominant factor.

Once again let me present a cross section of this region, let us say from the center of the Everglades eastward to the Florida Strait. In presenting this picture I shall people my field largely with the creatures that have been my favorite subject for study, the Mollusks; they still play a dominant role in paleontology.

Everglades

The glades, immense stretches of shallow water with good stands of saw grass that makes wading from point to point a somewhat painful, or at all events, a not altogether delightful enterprise. The uninitiated can picture it by conceiving a partially submerged, luscious meadow, miles upon miles in extent, played upon by the varying breezes and the lights and shades produced by the passing clouds.

Here in season we may see in places, Sandhill Cranes, a dozen species of Herons, Ibises in flocks, the Limpkin, and tilting overhead, or combing the field, Turkey Buzzards, and in spots even now, Everglade and Swallow-tailed Kites.

Paleontologically considered, the glades proper with their feet of muck composed of vegetable detritus and such animal remains as can be preserved in such places, should prove of interest to the Paleontologist.

Here we find a peculiar molluscan assemblage:

Stagnicola cubensis (Pfr.)
Helisoma trivolvis intertextum (Sby.)
Helisoma scalare (Jay)
Helisoma duryi seminole Pils.

Helisoma duryi intercalare (Pils.)
Helisoma duryi preglabratum (Marshall)
Helisoma duryi eudiscus (Pils.)
Menetus dilatatus (Gld.)
Gyraulus parvus (Say)
Physella heterostropha peninsulae (Pils.)
Ferrissia peninsulae (Pils.)
Musculium partumeium (Say)
Eupera cubensis (Prime)
Pisidium abditum Hald.

Leads and Channels in the Everglades

Should one fly over the region he would see an endless number of slender liquid threads, usually combining into larger leads, which eventually form channels of canoeable size, but the land is so flat that often as not they are mere slender openings in the shallow fields without current or flow. Where tidal influence is felt, as well as in the more elevated reaches of the area, we do have pulsating or more or less steadily flowing streams. The edges of these are particularly favorable habitats of the Apple Snail, Pomacea depressa, the sole food of the Everglades Kite and to a great extent that of the Limpkin. Here, too, we find fish of many kinds and sizes, which will at least contribute their scales, and bones, where these are not destroyed in the acid peat, to future paleontologic records.

Peopling these deeper reaches we may find the following fresh-water mollusks:

Pomacea depressa (Say)
Stagnicola cubensis (Pfr.)
Helisoma trivolvis intertextum (Sby.)
Helisoma scalare (Jay)
Helisoma duryi seminole Pils.
Helisoma duryi intercalare (Pils.)
Uniomerus obesus paludicolus (Gld.)
Micromya papyraceus (Gould)
Cyrenella floridana (Dall)

Lakes in the Everglades

Here and there in these large stretches of submerged meadows we find open bodies of water, lakes of shallow depth where the same molluscan association listed for the channels holds forth, but here also the Manatee still maintains its precarious existence and so do Alligators.

Cat-tail Association

In places great stretches of these plants (*Typha angustifolia*) form almost pure dense stands, harboring an associated avian and batrachian fauna.

Cypress Swamps

Bordering the glades we may have immense stands of Bald Cypress. These are also wading in the shallow waters with their breathing knees lifted above the surface, shedding pollen, leaf and cone year by year, to form a field for the Paleobotanist. Nor is this all, for here the Crocodilians, the Turtles and Snakes, as well as a host of Batrachians, find a suitable home in which they may enjoy life, little disturbed even by man. Bear, Panthers and Raccoons aplenty, as well as many birds, make this their home, and in passing add their bones to the geologic contributions of today.

Flying over lower Florida brings plainly into view, how the land graudally slopes southward, how barring the hurricane rampart at the southern edge of the mainland, we see to the northward a continuation of the keys that characterize the "Bay of Florida," but gradually lifting above the water. Once clear of water we cease to call them keys; they now become "hammocks," which, botanically considered, must be separated into several associations.

Palmetto Association

This consists of dense stands of Palmettos with small shrubs and grasses as a ground cover. Here some forms of *Liguus* and *Chondropoma dentatum* may be found.

Palmetto-Deciduous Association

In this the deciduous trees usually predominate, with only a sprinkling of the former. This will contain the mollusks common to the Deciduous Tree Association.

The Deciduous Tree Association

This frequently forms dense tangles interlaced with vines and shrubs to form almost impenetrable thickets. The branches of the trees are frequently covered with mats of Orchids, Bromeliads, or Ferns. Here on the trunks of the tall trees we may find some of the members of the 17 named forms of *Liguus fasciatus*, or of the 9 subspecies of *Liguus crenatus*, as well as *Oxystyla undata* (Bruguière) or *Oxystyla floridensis* Pilsbry, or *Drymaeus multilineaus* (Say), *Drymaeus dormani* (W.G.B.) or *Drymaeus dominicus* (Rue.). While occupying a less elevated position, we may see *Cepolis* *varians* (Menke), *Chondropoma dentatum* (Say) or *Helicina orbiculata clappi* Pils and still lower in the shrubbery *Bothriopupa variolosa* (Gld.) and *Pupisoma dioscoricola* (Ads.), while on the ground, tucked away among the rocky nooks and crannies, or when showers have moistened the ground, crawling over the vegetable detritus we may find a whole molluscan faunula as the following list will proclaim:

Chondropoma dentatum (Say)
Helicina orbiculata clappi Pils.
Polygyra uvulifera (Shuttl.)
Praticollela jejuna (Say)
Lobosculum pustula (Fér.)
Thysanophora plagioptycha granum (Streb.)
Thysanophora selenina (Gld.)
Opeas octonoides (Ad.)
Opeas gracillima (Pfr.)
Euglandina rosea minor Pils.
Holospira poeyana (Orb.)
Holospira jejuna (Gld.)
Macroceramus pontificus (Gld.)
Macroceramus floridanus Pils.
Gastrocopta contracta peninsularis Pils.
Gastrocopta pentodon (Say)
Gastrocopta rupicola (Say)
Gastrocopta pellucida hordeacella (Pils.)
Pupoides modicus (Gld.)
Sterkia rhoadsi (Pils.)
Strobilops hubbardi (Brown)
Retinella dalliana (Simpson)
Retinella indentata paucilirata (Morelet)
Euconulus chersinus (Say)
Guppya gundlachi (Pfr.)
Guppya miamiensis (Pils.)
Hawaiia minuscula alachuana (Dall)
Zonitoides arboreus (Say)
Vaginulus floridanus (Binn.)
Carychium exiguum (Say)

Prairies

These are the low flat dry treeless reaches covered by short grass, the favorite haunts of the meadow lark, where at times we may find the ground fairly swarming with:

Succinea floridana Pils.
Polygyra septemvolva volvoxis (Pfr.)
Polygyra cereolus (Mühlf.)
Polygyra carpenteriana (Bld.)

Pines

To the east we find some of the wavelike north and south ridges covered with a stand of scattered pines, or pines and mixed deciduous trees and shrubs, and grass, but with pine dominance. This is poor picking ground for the mollusk student, for pines proclaim acid soil, which is not conducive to shell life. Here Cerion incanum Binney may frequent the open spaces.

Mangrove Flats

To the southeast, the Everglades pass by imperceptible stages into the mangrove flats; here low bushes of scraggly mangroves try in vain to gain a foothold. Bayward they gradually grow more luxuriant and form large clumps, lifting their main trunks above the water by their outreaching roots or root stems that anchor them in the ground below the water. Here Littorina angulifera and Ostrea floridensis enjoy an airing with each ebbing tide, or the former may prefer the air for a longer period.

The Mainland Hurricane Rampart

At the southern end of the peninsula, stretching westward from Flamingo City through East, Middle and West Cape Sable, we have a huge sand dune varying in width from a dozen yards to the length of a city block. This represents the wave combings from the shallow floor of the Bay of Florida piled high and dry by Hurricanes and other winds. It consists of ground-up bits of the Bay's life, embodying the skeletons of about everything that has withstood the wave-grinding process.

Lagoons and Swales behind the Hurricane Rampart

On the landward side of the hurricane rampart we are sure to find a depressed area filled with brackish water, usually in communication by narrow channels with the Bay. Places like these are usually bordered by trees or shrubs, in which Oxystyla and Liguus hold forth, and in the button bushes at the water's edge, Florida Red-winged Blackbirds and Boat-tailed Grackles makes their nests, while among the decaying leaves in the pools Haminoea elegans Gray finds a favorable home.

Salt Pans

In the northern edge of the Bay of Florida are some keys struggling hard to rise from the sea, or more probably to return to it at present. These frequently are barren rings with a slight central depression. These pans are sufficiently submerged at each high tide to admit a new influx of salt water through narrow channels to the shallow basin. Warm breezes and the sun's rays evaporate a great part of the water during the emergence of the rim with the result that the contents of these pans become hypersaline, and not infrequently deposit layers of salt. In such salt pans we find a curious faunal assembly of Brine Shrimps and

Cerithidea scalariformis Say
Cerithium minimum Gmel.
Anomalocardia cuneimeris Conr.
Cyrenella floridana Dall
Mulinia lateralis Say
Pteria atlantica Lam.
Mytilus exustus L.
Tellina

Black Mangrove Association

Bordering the southern end of Biscayne Bay, on the mainland, we have quite a stand of Black Mangrove trees, south of, and here and there among these, stretches of fine sharp sand mixed with vegetable detritus and the combing of the waves; here under old decaying logs or boards when these are turned over, we are sure to find caches of thousands of specimens of the beautiful, small, *Truncatella caribaeus* Rve. and *Truncatella bilabiatus* Pfr. and *Melampus floridanus* Shuttl. and *Melampus lineatus* Say.

Next we mist consider the Bays, for lying off the mainland we have a series of shallow expanses of water known as Biscayne Bay, Barnes Sound, Card Sound and Little Card Sound, which occupy the trough between the mainland and the string of keys offshore. Later we shall speak of a second trough between these keys and the edge of the outlying reef known as Hawk Channel.

Brackish Water Channels

In the bays and sounds we have numerous flats and shoals, some laid bare at low tide, cleft by narrow or wider channels to give access to the pulsating sea.

Where these channels communicate with the rivers such, for example, as Miami River, we get mingling of salt and fresh water, producing a brackish condition where *Cerithidea scalariformis* Say and *Cerithidea iostoma* Pfr. are at home with *Cyrenella floridana* Dall and *Congeria (Mytilopsis) leucophaeata* Conr.

Pilings and Docks

On the piles in the harbor region and the stakes throughout the bays where these have not been protected by heavy creosoting, we may find a heavy incrusting with Barnacles, Ascidians, Bryozoa and *Modiolus demissus* (Dillwyn) and *Pinctada radiata* (Leach), while the wood where not protected or sufficiently protected, may be riddled with Teredo floridana Bartsch and Bankia gouldi Barsch, or chewed away by Sphaeroma destructor

Deep Channels Leading to Sea

These now are dredged places as straight as the configuration of the bay will permit, but in the days gone by they were not laid out by rule and compass, but sinuous natural passages winging their way to sea through low flats, usually steep-sided. Here Oysters and Pholads found a desirable habitat.

Ostrea virginica Gmelin
Barnea costata Linnaeus

Halimeda Association

Some of the shallow water flats are covered by an almost pure stand of the calcareous alga Halimeda, which crunches under foot as one walks across. The segments of this form dense patches of considerable thickness.

Porites Association

Under conditions apparently the same as those under which Halimeda occurs, frequently only separated by a lead of a few feet in width from this, other flats are characterized by a dominance of Porites furcata, the small branched coral easily held in the palm of a hand.

KEYS

The Mangrove Fringe of the Keys on the Bay Side, under water

On the bay side of the keys we usually have a moderately deep channel fringed by mangroves whose sprawling, outreaching roots repel all approach to the key from this side. On these roots below low tide we find clusters of Melina alata (Gmel.), while a little higher in the inter-tidal reaches Ostrea floridensis Sby. forms dense masses that completely cover the roots and at low tide, when out of water, furnish plain proof the oysters here grow on trees. Here, too, we can find specimens of the beautiful Cowry, Cypraea exanthema L., under water.

The Mangrove Fringe of the Keys, out of water

On the mangrove roots, sometimes a yard or more above high tide level, Littorina angulifera Lam. is found abundantly, while on the beach among the drifted flotsam and jetsam Melampus coffeur (L.) and Auricula pellucens Mke. may be found in abundance, and Strobilops hubbardi stevensoni Pils. occurs under the bark of dead limbs.

Interior of Keys

Here where avaricious man has not destroyed the native forests we still find heavy stands of Gumbo limbo, Mahogany, Poison Tree, Wild Tamarind, West Indian Birch, Darling and Coco plums and many others freighted with epiphetic orchids, Ferns and Bromeliads. On their boles and branches a sprinkling of Liguus can be found, and not infrequently their center harbors a little prairie with an abundance of Cerion incanum Binney, Polygyras and Succineas.

Cuts, Ripraps

The harbor improvements of Miami have wrought many changes in Biscayne Bay; mud flats have been changed into islands by pumping the dredged material upon them, and in many places where Halimeda or Porites reefs held forth we now find luxurious homes surrounded by or buried in a mass of floral glory. Here the landscape architect has had an opportunity and he has used it in bringing here things beautiful from everywhere.

The shallow cuts which in days of old made you wait for a high tide to slip across the bar, even in a moderate-draft boat, have been widened and deepened to admit shipping of all kinds, and that these channels may not be filled by the ever southward shifting sharp sands of the outer beaches, long ripraps with stone facing have been placed on the north side of the cuts to shunt the sands eastward into deep waters.

These jetties or sea walls are not only favorite places for the disciples of Izaak Walton, but have made a paradise for certain mollusks, which in the past found it difficult to locate a suitable place of attachment. Here we now find abundantly:

Tectarius muricatus (L.)
Ceratozona rugosa (Sby.)
Siphonaria lineolata (d'Orb.)
Nerita peloranta L.
Nerita versicolor Gmelin
Thais floridana (Conr.)
Fissurella alternata Say

The Sea Side of the Keys

This presents another hurricane rampart where wind and waves, combing Hawk Channel, pile the product of their labors high and dry. This may present long stretches of loose, more or less shifting sand, where Cenchrus tribuloides, the devilish sandspur, makes walking a misery, or equal reaches of loose sand held down by the long runners of the Goatsfoot Morning Glory, Ipomaea pes-caprae and Ipomaea bona-nox (L.). Still other places where the long stolons of the gracefully swaying Bermuda Grass are more or less successful in checking the wind-blown sand. On the inner edges the funereal Tournefortia holds sway, and forming the outer edge of the woods, the sea grape with its leathery, shining, kidney-shaped leaves and pendant racemes of fruit, makes a characteristic setting enjoyed by Cerion incanum Binney.

Shallow-water Sandy Stretches beyond the Keys

When these are present they enable the burrowing mollusks to dig in, while the predatory members of the phylum hunt them out and devour them. Where the wind-swept waves roll up on such beaches we frequently see myriads of the lively Coquina clams swept on the beach by each oncoming wave, right themselves, and dig in before the wave recedes. While small, they are so abundant that they furnish an element of commerce. To the knowing one, Coquina broth brings pleasant memories to the palate. Their abundance in the region in the past is vouchsafed by Coquina Rock, of which Donax contributes the chief element.

Here also we will find:

Donax variabilis Say
Olivella floralia Duclos
Olivella Mutica Say
Marginella apicina Menke
Terebra dislocata Say
Terebra protexta Conrad
Mitrella lunata (Say)
Epitonium angulatum (Say)
Laevicardium mortoni (Conrad)
Polinices duplicata (Say)
Tellina alternata Say
Dosinia discus Reeve
Busycon perversa (L.)
Alectrion vibex (Say)
Strigilla flexuosa Say

Shallow water (Hard pan) beyond the Keys

Off the keys on the sea side we have streaks of hard pan where Corallines, Foraminifera and Algae encrust the bottom. Here Chama sarda Reeve and Glycimeris americana Defrance and the following find a suitable habitat:

Anachis avara (Say)
Cantharus tincta (Conr.)
Leucozonia cingulifera (Lam.)

Clathrodrilla ostrearum (Stearns)
Thais haemastoma (L.)
Fissurella alternata (Say)
Phos parvus C. B. Ad.
Tritonalia cellulosa Conrad
Ischnochiton limaciformis Sby.
Murex pomum Gmelin

Shallow waters (Mud flats) beyond the Keys

Here and there in Hawk Channel we find mud flats in shallow water where among other creatures the following mollusks are at home:

Acteocina canaliculatus (Say)
Mangelia cerina K. & S.
Epitonium lineatum (Say)
Cerithium ferrugineum Say
Cerithium muscarum Say
Tagelus gibbus (Spengler)
Cardita floridana Conrad
Pyramidella crenulata Holmes

Coral Reef Walls

Offshore, beyond Hawk Channel, which stretches outside of the keys from Miami south to Key West, is another submerged ridge, which at intervals bears a series of lighthouses. This ridge supports a thriving coral reef, which extends even farther south past the Marquesas and the Tortugas. Here we find walls of corals exposed to the surf, with leads between them, or at times just coral patches.

These massive builders, embracing *Orbicella annularis* (Dana), Porites astrerides Lamarck, *Siderastria siderea*, *Meandria strigosa* (Dana) and *Meandra labyrinthiformis* (Linnaeus) produce veritable walls of coral limestone, which contain an endless number of grottoes, caves and caverns in and among which dozens of species of fish seek shelter, fish ranging from the huge Sea Bass weighing at times several hundred pounds to the tiny exquisite Iridio. Here brilliant leisurely Angel and Butterfly Fishes search for food, while schools of hundreds of Gray Snappers stay put and sway all day long under sheltering ledges, in the pulsating surge, waiting for the close of day to begin their foraging. Schools of hundreds of Yellow Tails and Carangids will pass in review as they cover their beat, while the Banded Schoolmasters play about the summit of the blocks, enjoying the varying lights and shades occasioned by the wave lens surface of the sea, or swift and dangerous Baracuda move leisurely about, singly or in pairs. To here list the whole fish assemblage would take more space than is allotted to me, and to adequately record the scene requires not pen or pencil or even brush, but a diving helmet and water-tight moving picture camera, using color film to do justice to the view.

Tucked away here among the nooks and crannies, we find all the nestling and burrowing mollusks. Gorgeous *Lima scabra* Born tucked away in small crevices displays its bright tentacles, while sombre *Chama congregata* Conrad and *Vermetus nigricans* Dall are fixed to the solid rock.

Sandy Stretches between the Coral Walls

Between the solid walls of coral are flat stretches of white sand, comminuted bits of coral and shell with small lumps of detached corals usually furnishing attachment for the purple and yellow fan coral and various other species of Gorgonians. Here the Hog fish and various species of garishly colored Parrot Fish and Slippery Dicks and the burrowing *Gnathops* and the *Stingaree* and sometimes *Manta birostris* find a suitable habitat, and the long-spined Black Sea Urchin, *Centrechinus antillarum* Phil., whose contact one should avoid, may live singly or in bunches of several dozens. At home here also are:

Dosinia elegans Conrad
Anodontia alba Link
Oliva sayana Ravenel
Polinices duplicata Say
Natica canrena L.
Sinum perspectivum Say
Tonna galea L.

Stag-Horn Coral Association

Even among corals we have associations, as exemplified by the stag-horn coral, *Acropora cervicornis*, which in places forms dense stands covering considerable space. To a somewhat lesser extent this is also true of the Palmate Coral, *Acropora palmata*.

Gorgonian Field

In the flats inside of the other reef we find extensive fields of Gorgonians, forming the so-called "Sea Gardens," composed chiefly of various species of *Plexaura*, *Xiphigorgia*, *Gorgonia*, *Muricea*, *Eunicea* and *Pterogorgia*. Museum specimens give little idea of the real beauty of these so-called "Sea Garden" denizens where the half-inch investment of slender zooids that characterizes them in life is shrunken into a thin animal film. Wading among them with a diving helmet, or viewing them through a water glass from above, certainly justifies the novices' name "Sea Garden" for they sway and bend to currents, the surge of waves or the pulsation of the sea as do plants on shore which their forms resemble.

These colonial animals contribute largely to the reef deposits by adding their spicules upon their demise. Among them, on the sea fans our molluscan friends, *Simmia uniplicata* (Sowerby) and *Cyphoma gibbosa* (L.), find their favorite habitat.

Grassy Patches

Betwixt the Coral walls and the Gorgonian fields we may have long stretches of grass covered sand bottom, composed of the Sea Grass, *Thalassia*, among which the trunklike Cowfish, Pipe Fishes, and the Sea Horses dwell. This, too, is the favorite habitat of the red Giant Star Fish, *Oreaster reticulata* L., and *Tripneustes esculentus* L., and the Giant Horse Conch, *Fasciolaria gigantea* Kiener, the largest Gastropod of the Atlantic, and *Fasciolaria tulipa* L., as well as the King and Queen Conchs, *Cassis madagascarensis* Lam., *Cassis tuberosa* L., and above all the Pink Conch, *Strombus gigas* L., whose delicious flesh has gained the name "Conch" for those devoted to this fish. Mixed in with these are Holothurians, while among the lesser folk may be listed the soft Sea Hare, *Aplysia willcoxi* Heilprin, *Conus pealii* Green and *Nassarius ambiguus* Monts.

The Continental Shelf, 5-100 fms.

Passing the reef area we come to a gradually sloping submarine plain of varying width, the so-called Continental Shelf, which we may say ranges down to 100 fathoms. This is a rich molluscan field; here among many others the following species hold forth:

Tellina lintea Conrad
Acteon punctostriatus C. B. Ad.
Drillia ebur Reeve
Maculopeplum junonia Hwass.
Xenophora conchyliophora Born
Polinices uberina d'Orb.
Epitonum hellenica Forbes
Eulima carolii Dall
Niso interrupta Sby.
Pyramidella candida Mörch.
Calliostoma euglyptum A. Ad.
Calliostoma jujubinum Gmel.
Cadulus quadridentatus Dall

Pourtales Plateau, 90-300 fathoms

By far the richest marine mollusk field is the Pourtales Plateau to the east of the Continental Shelf, whose varied bottom teems with all sorts of life.

As a modest representative selection of the fauna we may mention:

Arca glomerula Dall
Euciroa elegantissima Dall
Acteon exilis Jeffreys
Protocardia peramabilis Dall
Modiola Polita Verrill & Smith
Leucosyrinx verrillii Dall
Leucosyrinx subgrandifera Dall
Ancistrosyrinx elegans Dall
Ancistrosyrinx radiata Dall
Genota viabrunnea Dall
Mangilia cerina Dall
Mangilia comatotropis Dall
Marginella succinea Conrad
Aurinia dubia Brod.
Aurinia gouldiana Dall
Fusinus benthalis Dall
Phos candei d'Orb.
Murex beaui Fisch. & Bern.
Coralliophila deburghiae Rve.
Pedicularia decussata Gould
Omalaxis nobilis Verrill
Amalthea benthophila Dall
Xenophora conchyliophora Born
Pyramidella candida Mörch
Microgaza rotella Dall
Calliostoma bairdii Dall
Solariella ottoi Phil.
Liotia bairdii Dall
Haliotis pourtalesii Dall
Dentalium antillarum d'Orb.
Dentalium laqueatum Verrill

Bed of Florida Straits

Still further east than the Pourtales Plateau come the Florida Straits, ranging from 350 to 800 fathoms in depth, from which we may list:

Glyphostoma gratula Dall
Mangilia serga Dall
Pleurotomella chariessa Dall
Fusinus benthalis Dall
Leptothyra induta albida Dall
Margarita (Bathymophila) euspira Dall
Solariella ottoi Phil.
Dentalium perlongum Dall
Dentalium callithrix Dall
Daphnella lunacina Dall

Plankton

This presents still another phase of life that we have so far completely ignored, but which is of immense importance to the marine animal world. The Phytoplankton, the microscopic ~~free-swimming~~ plants have been aptly called the grazing grounds of the sea. The large protozoan admixture, as well as eggs and larval stages of animals, and the pelagic creatures that prey upon them found in this liquid habitat, constitute an immense element of marine life. Among mollusks, we may mention the Squids, Spirula, the Pteropods and Heteropods; among the shelled Protozoa, Foraminifera on dying, drop enough skeletons to form an ooze known by this name, while others, like the Peridinae, at times are present in such countless numbers as to smother life in the region invested, requiring a restocking of the fauna of the place. This killing off occasionally is also due to the presence of Pseudomonas, likewise a flagellate protozoan whose contribution of ammonia to the sea causes enough disbalance to produce sufficient chemically precipitated ooze, suspended in the water and on the bottom also, to choke all life.

In this brief account I have purposely avoided mentioning the numerous minute species of the families Epitoniidae, Melanellidae, Pyramidellidae, Caecidae, Rissoidae, Tripheridae, Cerithiopsidae, Vitrinellidae and others, since these are not the obvious things of the fauna. I have selected those mollusks which force their attention upon the observer in each habitat; they, therefore, represent the striking element of each association.

In closing, may I express the hope that this brief account will arouse the interest of students of Ecology in this, the most marvelous field for such studies known to me.

U.S. National Museum,
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BRACHIOPOD ECOLOGY AND PALEOECOLOGY

G. Arthur Cooper*

Introduction

Life for most organisms is a struggle against adverse physical conditions and inimical neighbors. Nowhere is this struggle against environment more severe than in the sea. Any seashore will show windrows of dead shells, the victims of storms or rapacious enemies. Although the strife is unceasing and cruel, life itself has survived this uncompromising environment through countless ages. Eons of struggle have lead to the spinning of an amazingly complicated web of life in which all contemporary species in any given environment are more or less remotely involved. The enemy of one organism may be the unwitting friend of another and the welfare of one or more species may depend on the prosperity of other forms. The study of the complicated relationships of organisms to one another and to their physical environment is Ecology.

The generalities of historical geology are now common knowledge. Most informed people know that many sedimentary rocks are solidified sea-bottoms. It is also well known that these petrified sea-bottoms have entombed many luckless molluscs and other animals. The sedimentary rocks and their contained fossils thus have a story of their own to tell, but the tale is told in no simple language. Fossils and sediments are the characters that must be read to understand the earlier stages of the struggle of life against its environment. It has taken millions of years to weave the web of ecology about us. Fossils and sediments are the documents of Paleoecology, or the study of ancient ecology.

An amazing quantity of data dealing with fossils and sediments has been accumulated during the last century. Yet with this mass of information relating to these special subjects it is painfully disconcerting to learn that few investigators have concerned themselves with the subject of Paleoecology. The study is new and when seriously pursued should lead to results of distinct benefit to the geological and biological sciences.

Although data bearing on the ecology of many groups of animals has been gathered, the ecology of modern brachiopods, as well as their paleoecology, has been neglected. The various treatises on modern brachiopods yield little direct information bearing on their habits, their relationships to contemporary organisms, their embryology and life history. The reason for this gap in our knowledge is not difficult to understand. Brachiopods are now rare animals and usually difficult to secure. Moreover, the study of this group is still in the qualitative and descriptive

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stage. Zoology, embryology and biology have long since practically abandoned qualitative research. It is no longer a vogue to describe the life history of a species, consequently many years may go by before some of the foremost questions concerning brachiopods and their ecology will be answered.

This present discussion of brachiopod ecology and paleoecology is admittedly incomplete, because time did not permit an exhaustive search of the voluminous brachiopod literature. The appended bibliography by no means exhausts the papers having ecological information. There are undoubtedly many data buried in descriptive papers, which only future study will bring out.

Brachiopod Anatomy

In the most general terms the brachiopod may be described as bilaterally symmetrical, inequivalved bivalves. The larger shell as a rule is on the ventral side of the animal and the smaller one on the dorsal side. The valves are held together more or less tightly by teeth and sockets (articulate brachiopods) in some forms, but only by muscles in others (inarticulates). The brachiopod is either sessile or sedentary. When sessile it may be cemented by the ventral valve to some object such as a shell or piece of coral or may be fastened by a fleshy pedicle which protrudes from an opening in the beak of the ventral valve. A few forms have the ability to burrow in sand and mud and to move about with difficulty.

Inside the valves the body proper occupies the body cavity at the posterior or beak region. The body cavity contains the gullet, stomach, intestine and liver, as well as other vital organs, and is traversed by a complicated set of muscles which open and close the valves and turn the animal on its pedicle. The mouth opens into the mantle cavity which contains the lophophore or brachia, a cirrate loop or horseshoe-shaped organ. Movement of cirri on the lophophore create the currents of water necessary to bring to the mouth the tiny animals and plants on which the brachiopod feeds.

Brachiopods in Past and Present Faunas

Brachiopods have existed from early Cambrian time to the present. Now their numbers are greatly reduced but the past has seen a great array of these animals. Many bizarre and little understood types lived in bygone eras and the evolution of the class is now nearly complete. This great group of animals with its glorious past is thus an ideal one to study in order to learn the laws of evolution and ecology. The brachiopod by its very nature is intimately tied to its environment but as will be seen below the race is a hardy one, resisting many changes in external conditions and persisting since the known dawn of life. The meaning of all brachiopod adaptations is by no means clear; some suggest the impress of environment but others indicate that initiated trends continued beyond usefulness to extinction.

Today but a handful of genera and species remain to represent the lineages of the past. However, these few modern brachiopods are of utmost importance to the biologist and geologist, because they yield the only first-hand knowledge of the life processes and habits of these animals. Unfortunately, the brachiopods occupy a very subordinate position in the seas today, consequently the class has been neglected by modern zoologists and biologists.

Except in a few instances living brachiopods form a small percentage of the fauna at any given place. At most stations they are rare prizes but in a few localities species occur in considerable abundance. At the present writing a few more than 200 species distributed among 61 genera are known. It is likely that this number will be materially increased with time but the list of living brachiopods will never attain very imposing proportions.

Distribution of Recent Brachiopods

Modern brachiopods are world-wide in their distribution. In general they are located along the coastal margins of the continents and oceanic islands. They may occupy tidal regions or shallow marginal waters or they may live in deeper waters on the continental slopes or in the deep waters margining the oceanic islands. Several important centers of brachiopods have been found. The Mediterranean, northwest coast of Africa, Spain, and the British Isles are inhabited by a group of species whose nearest relatives are found in the West Indies. The West Indian brachiopod fauna extends from the southern tip of Florida to Trinidad. A few species are known from the New England coast to Labrador and Greenland. These are related to Arctic forms.

In the Pacific a few species are known from the Hawaiian Islands and the Philippines but the waters about the Japanese Islands contain one of the most prolific modern brachiopod faunules. The Hawaiian and Japanese brachiopods are related to those found along the west coast of North America from southern California to Alaska. In the southern Pacific the waters along the southeastern shore of Australia and New Zealand contain brachiopods of types similar to those found along the shores of southern South America. The cold waters off the Antarctic Continent also contain related austral genera.

Modern brachiopods occupy all bethymetric zones of the sea. Some species are confined to shallow water[1] but others have been found only in deep water. Many species are found in both deep and shallow water.

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[1] Shallow water is from the tide zone to 100 fathoms.

The bathymetric range of *Frieleia halli* Dall, for example, is from 21 fathoms to 1,059 fathoms. Of the known recent species, numbering a little more than 200, those confined to shallow water comprise 59 species or about 33 percent.[1] In this group occur all known species of *Lingula* (11) and *Glottidia* (5). Other genera confined to shallow water are *Cnismatocentrum*, *Megerlina*, *Coptothyris*, *Bouchardia* and *Neothyris*. A few other genera have one or more species confined to shallow water: *Discinisca*, *Crania*, *Hemithyris*, *Terebratulina*, *Terebratalia*, *Terebratella*, and *Magellania*.

A still larger percentage of brachiopods occupies water deeper than 100 fathoms. Sixty-three species or 36 percent of known species with data occupy this realm. *Pelagodiscus*, *Abyssothyris*, *Neorhynchia* and *Macandrevia americana* Dall have been dredged from water deeper than 2000 fathoms. *Abyssothyris wyvillei* (Davidson) has been taken from 2900 fathoms, and *Pelagodiscus atlanticus* (King) from 2737 fathoms. Other genera taken from deep water are *Basiliola*, *Hispanirhynchia*, *Chlidonophora*, *Eucalathis*, and *Dyscolia*.

The remaining 55 species or 27 percent of recent brachiopods with bathymetric data are found in waters ranging from the tide-zone to the deeps. Some of these species are able to endure amazing differences of pressure and temperature. Some of the genera having a wide bathymetric range are: *Crania*, *Frieleia*, *Terebratulina*, *Gryphus*, *Argyrotheca*, *Platidia*, *Campages*, *Laqueus* and *Dallina*. Sixty percent of brachiopod species thus occupy shallow water but only a little more than half of this percentage is actually confined to shallow water. The above figures thus allow no generalization other than the well known fact that *Lingula* and its close relative *Glottidia* are confined to the shore zone.

It will be noticed that these figures do not agree with those published by Professor Schuchert in 1911.[2] Two reasons account for the discrepancy. (1) Many new genera and species have been described since 1911. A large percentage of these new species are deep water forms proposed by Dall in 1924. (2) Many old genera have been drastically revised. The eleven species of *Hemithyris* noted by Schuchert have been distributed among four genera. It is obviously impossible at the present time to generalize on the bathymetric range of the brachiopods. Too little is now known of these rare animals and future dredging will alter the present figures.

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[1] This percentage was obtained by eliminating 25 living species on which no data were available. The figures arrived at are based on 177 species with data.

[2] The writer's figures were taken from Thomson's "Brachiopoda Morphology and Genera", and from the Annotated list of Recent Brachiopoda in the U. S. National Museum (Dall, 1920).

Brachiopods are often very abundant where they live, which is to be expected of sessile animals. If one were to judge by the superb collection of recent brachiopods in the U. S. National Museum he might be led to believe that shallow water brachiopods were more abundant as to individuals than deep water brachiopods. This is also misleading because the shallow water forms are easier to obtain. Deep sea forms may be very numerous at any given place but the dredge actually samples only a minute portion of the bottom.

Habitats of Recent Brachiopods

The life habits of *Lingula* and *Glottidia* are perhaps the best known of all brachiopods. The species of these two genera live near the shore from tide zone to about 17 fathoms. Some have been found near the mouths of rivers. The animal has a long pedicle which is capable of considerable motion. Ordinarily the *Lingula* lives fastened in burrows by its pedicle. The anterior third protrudes from the sand or mud. If *Lingula* is taken from its burrow and thrown on the sand it will bury itself again. It is thus capable of motion which it accomplishes by means of lateral movements of the dorsal valve, movements of the lateral setae and a *wiggling* motion of the pedicle. *Lingula* fixes itself in its burrow by secreting mucus which agglutinates sand grains or mud to form a tube. The pedicle permits protrusion from the burrow and instant withdrawal when alarmed. The mantle edge at the front of the shell is provided with numerous setae, which, when the animal is feeding, are so arranged as to form three elliptical channels. Movement of the cirri causes water to be drawn into the two lateral canals and expels it from the central one which is a little longer than the others.[1]

Discinisca is structurally related to *Lingula* but leads an entirely sessile life after fixation. The shell is attached to rocks or other objects by a short stout pedicle.

The terebratulids are the most abundant group of brachiopods living today, forming a little less than seventy percent of the known genera. The majority of terebratulid species possess a short pedicle by which they are tightly fixed to the substratum. In general the ventral value lies obliquely over the dorsal valve. Thus the dorsal valve may occupy the lower position when the animal clings to the upper surface of a stone, but the ventral valve may occupy a lower position if the brachiopod fixes itself to the under side of a stone.

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1. Morse, E. S. "Observations on Living Brachiopods", Mem. Boston Soc. Nat. Hist., vol. 15, no. 8, p. 319, 1902.

Numbers of Brachiopods

Modern brachiopods are mostly rare and little known animals, but in past geological periods they were an abundant form of life. The Paleozoic Era might be termed the age of brachiopods. They were so abundant that some of the Paleozoic rocks are literally made up of their shells. During this vast stretch of time many stocks of brachiopods rose to ascendancy only to decline and be replaced by new forms. During the Paleozoic, types of brachiopods were produced which were never again duplicated by later stocks of brachiopods. The Paleozoic ascendancy was brought to a tragic close during Permian time. A few Paleozoic types survived into the Triassic period and still fewer into the Jurassic. After Jurassic time two stocks, the rhynchonellids and the terebratulids, flourished while a few inarticulates straggled on.

Throughout time there has been a gradual decline of brachiopods but at the same time a gradual rise to dominance of the Mollusca, chiefly pelecypods, cephalopods and gastropods. In the early Paleozoic the Mollusca occupied a position numerically subordinate to the brachiopods. The Devonian witnessed an advance in the numbers of pelecypods and gastropods, which became still more apparent in the Carboniferous and Permian periods. This increase in Mollusca continued steadily through the Mesozoic to recent times. The snails and ammonites, together with increasing numbers of vertebrates, by their voracious habits, may have played an important role in overwhelming the brachiopods.

History of Brachiopod Stocks

The earliest brachiopods are still shrouded in obscurity. Chapman[1] has described two genera, *Protobolella* and *Fermoria* from the Pre-Cambrian of India, but the characters of these forms are very indefinite. Fenton and Fenton[2] have described *Lingulella* from supposed Pre-Cambrian strata in Montana but most authorities agree that the age of these beds is very questionable. The earliest undoubted brachiopod genera in North America are *Obolella* and *Rustella*. The former is a somewhat advanced type with a pedicle foramen but *Rustella* is the most primitive form known and is a member of Thomson's Palaeotremata. *Rustella* with its calcareous shell and *Obolella* with its specialized pedicle opening are both actually advanced types. Not long after these two forms there appear several more advanced types: *Nisusia*, *Kutorgina* and two undescribed genera, one with strong ribs and looking somewhat like the Ordovician *Platystrophia*; the other with fine ribs but a deeply sulcate ventral valve. *Paterina*, which is a

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1. Rec. Geol. Surv. India, vol. 69, pt. 1, pp. 114-118, 1935.
2. Bull. Geol. Soc. Amer., vol. 47, no. 4, pp. 609-620, 1936.

chitinous inarticulate genus, occurs with the genera named above. Paterina is regarded by some as the most primitive brachiopod but it is actually of a quite advanced and specialized type. Nisusia appears to be the oldest and most primitive known articulate brachiopod, but it has features of a specialized nature. It is apparent, therefore, that a long evolution of brachiopods preceded the genera named. After these forms the Lower Cambrian stocks persist with little change until the Upper Cambrian, when a number of new types appear.

A brief survey of the rise and decline of the major stocks of brachiopods will serve as a background for the ecological discussions to follow. The linguloid brachiopods, to which may be added the oboloids, which are chitinous, elongate or oval, compressed animals, appeared in the Lower Cambrian with Lingulella. The linguloids have persisted from then until present time. They are hardy animals which have, through most of geological time, endured the vicissitudes of the shore-region.

The Neotremata are chitinous forms with specialized pedicle openings. They flourished in Cambrian time but declined rapidly in the Ordovician. From then on the order has straggled along to Recent time and is represented by three genera today; Discinisca, Pelagodiscus, and Discina.

The Protremata were a great stock of brachiopods having an open delthyrium or one modified by a calcareous plate, the deltidium. In general it may be said that this order was represented by six major stocks: Syntrophids, clitambonitids, orthids, dalmanellids, pentamerids and strophomenids. The syntrophids had medianly folded shells with a spondylium simplex. They appeared in late Cambrian time and flourished in the Canadian but declined and disappeared in the Silurian. The clitambonitids were wide-hinged forms with a spondylium simplex. The stock lived from the Middle to Upper Ordovician. The orthids which had impunctate, wide-hinged shells, appeared in the early Cambrian and persisted to early Devonian time. The dalmanellids were punctate orthids which appeared first in Chazyan time and existed until late Permian. The true pentamerids mostly had large shells with a spondylium duplex. They appeared in the Middle Ordovician and died out in Upper Devonian time. The strophomenids, including the Sowerbyella-Chonetes stock, the productids, and the strophomenids proper, all had a deltidium and a pseudo-punctate shell. The strophomenids appeared in the late Canadian and persisted through the Permian. The Sowerbyella-Chonetes stock originated in the late Canadian and persisted into the Permian. The productids originated in Middle Devonian and lived through Permian time.

The Telotremata are characterized by the presence of deltidial plates restricting the delthyrium and consist of three major stocks: rhynchonellids,spiriferids, and terebratulids or loop-bearers. The rhynchonellids appeared in the Chazyan and have persisted to the present.

Impunctate spiriferids appeared in Chazyan times and lived into the Triassic, but the punctate spiriferids appeared possibly in late Ordovician, but certainly in early Silurian time, and died out in the Jurassic. The terebratulids appeared doubtfully in Middle Silurian time but are definitely known in the Late Silurian and exist at the present time.

The critical times of brachiopod evolution appear to be late Cambrian, Late Canadian, Permian, Triassic and Jurassic times. These periods all saw the disappearance or appearance of important stocks. A few inarticulate stocks were very persistent, particularly the linguloids. Among the articulate brachiopods it is interesting to note apparent survival value of punctae. The punctate dalmanellids outlived the impunctate orthoids and the punctate spiriferids persisted into the Jurassic after the impunctate forms had died out in the Triassic. The punctate loop-bearers or terebratulids are today the most abundant types of brachiopods forming about 70 percent of the known members of the class, thus far outnumbering the rhynchonellids.

Except for bizarre types and unusual forms there is nothing to indicate that the brachiopods lived in the past in a manner different from that followed today. In the past they were very abundant; these hosts must have used vast quantities of food and must also have furnished the principal diet of many carnivorous invertebrates, fish, and marine reptiles.

Methods of Paleoecology of Animals

In studying the paleoecology of any group of animals the paleontologist follows several lines of inquiry. The easiest and perhaps most accurate is comparison of fossils with recent animals of similar form and structure. The original position of the fossil in the rock often yields a clue to its life habits. Associated fossils may help in explaining the environment of certain forms. The type of enclosing sediment may tell in what kind of environment the fossil lived. A study of Paleogeography is also another resort in studying ancient environments. To these lines of study may be added the adaptations of form, ornamentation, and structure of the animals under consideration. Experience has shown that certain types of animals are customarily found in definite environments. All of the methods stated have dangers that must be considered. Before an ancient environment can be regarded as established all lines of inquiry must be investigated.

Analogy with modern animals.--Comparison of fossil forms with Recent ones is the most direct method of paleoecological research. With brachiopods, unfortunately, the method is of very limited application and is hazardous when applied to Paleozoic brachiopods. Comparison of Recent and Tertiary brachiopods is helpful, but when the strange and aberrant forms of the Paleozoic are compared, analogy becomes strained. The method is applicable only to types related to or structurally like modern brachiopods, such as, lingulids, discinids, craniids, rhynchonellids, and terebratulids. The Protremata includes few forms suggestive of modern types. A few modern species, however, have adaptations of form suggestive of ancient genera. *Argyrotheca*, for example, has the same wide-hinged form as *Cyrtina* of the Devonian. *Argyrotheca* lives with the beaks closely attached to some object of support. Specimens of *Cyrtina* from the Devonian attached to other shells in their position of growth indicate that this genus had the same habit of life. Although the two genera are thus believed to have had essentially the same habit the structure of their foramina shows that their pedicles were completely unlike. The terebratulids and rhynchonellids of the Paleozoic are close structurally to the recent representatives of these two groups and all evidence points to the fact that ancient forms lived in the same manner as the modern ones live.

"*Lingula*" of the Paleozoic is structurally very close to modern *Lingula*. This fact taken with the kind of sediments in which "*Lingula*" is usually found and the fact that these sediments on paleogeographical evidence can often be shown to be close to an old shore, indicates that this genus must always have inhabited the shore zone. No other fossil and Recent brachiopod stock yields such clear and reliable evidence.

The bathymetric range of many recent species is so great as to preclude their usefulness in paleoecology. *Lingula* is the only brachiopod type known to be restricted to a definite zone. Other brachiopod species now known to be restricted to shallow water are of types that range into deeper water or the abysses. This makes the use of any terebratulid or rhynchonellid of the modern seas dangerous in studies of ancient bathymetry. Furthermore, brachiopods that dwell in shallow waters of a cold region may live also in the deeper waters of a region with a milder climate. This condition has been indicated by species of *Gryphus* and other modern genera that are now found in the deep waters of the Atlantic. In Miocene time these species inhabited the Mediterranean. These facts have been taken to indicate that in Miocene time the Mediterranean received cold waters from the Atlantic (Fischer and Oehlert, 1890).

Position of the fossil in the rock.—When the student can be sure that a fossil has been found in its original position of growth, such a discovery gives definite knowledge of life habits. But it is difficult to be sure that a fossil has actually been entombed in its natural position of growth. Waves and currents play many tricks in sorting and arranging fossils. In the Upper Devonian of New York the writer has seen large lenses of brachiopod shells consisting almost wholly of the ventral valves of *Cyrtospirifer*. Most brachiopods are heaviest at the beak end or posterior of the shell, hence many dead brachiopod shells will lie on the bottom with their beaks on the mud but with the anterior portion off the bottom. However, when a hinged brachiopod is found with its interarea horizontal or parallel to the bedding planes it is suggestive evidence that the shell is in its original position of growth.

The sandy shales of the Hamilton group of New York have yielded *Lingulas* in an upright position with the anterior margin up and the posterior margin down. The occurrence of *Pseudolingula* in this position in the Dubuque beds at Dubuque, Iowa, is also well known. These and other similar occurrences of lingulids have made it clear that the life habits of this group have probably not changed throughout time.

Sardeson (1929) has described interesting occurrences of brachiopods in their position of growth in the Black River sediments of Minnesota. Here *Valcourea*, a convexi-concave brachiopod, occurs in a nearly upright position with the convex dorsal valve lying obliquely over the ventral valve. *Hesperorthis* is found in the reverse position, with the convex ventral valve lying obliquely over the flat dorsal valve. In each instance the animal rested on its broad interarea and was anchored by a pedicle. In the same layers Sardeson discovered countless numbers of a certain species of *Strophomena* lying on the bedding planes. These resembled *Valcourea* in form but had a small, thread-like pedicle. From this evidence Sardeson concludes that *Valcourea* was a bottom-dweller but *Strophomena* may have led a pseudoplanktonic existence.

Most wide-hinged forms with a broad interarea that have been found in position of growth, lived with the interarea closely appressed to the object of support. *Cyrtina*, *Platystrophia* and *Hesperorthis* are examples.

Teichert (1930) has shown, in his study of *Porambonites*, that incomplete filling of a brachiopod by matrix may yield a clue as to its former life-habits. Teichert illustrates a large *Porambonites* filled with mud at the posterior end but by clear calcite at the front, the junction between the two types of filling forming a sharp line. When this line is brought into a horizontal position, the life posture of the shell is indicated, which in this instance showed the animal to have lived in an almost upright position. Teichert's evidence, however, might have been interpreted as indicating a dead shell held upright by gases of decomposition with the light anterior up and heavy posterior down.

The habit of growth of cementing forms has long been known. Craniids are often found attached to corals, bryozoans or other shells. Cementing strophomenids, young and old, have been found clinging to corals or other objects. *Schuchertella* has been found in clusters in the Hamilton of Ontario and Michigan. Other shells, such as *Strophalosia* may show a cicatrix of attachment. Often this scar shows the plication pattern of the supporting shell with sufficient clearness to allow identification of the host.

Associated fossils.—Not infrequently the associates of a brachiopod or group of brachiopods indicate the nature of the environment. The association of brachiopods with large corals is an obvious example. In the Alpena formation of Michigan a great variety of brachiopods occurs in and about the giant Prismatophyllum reefs. Such reefs are an ideal habitat for brachiopods because the waters are warm, aerated, and lighted. Caves and grottoes in the corals give ample protection from the waves.

In certain layers of Devonian and Carboniferous rocks brachiopods have been found associated with abundant thin-shelled clams, ostracodes, and plant fragments. This association suggests very close-shore deposits and probable brackish-water environment. As clear as such evidence seems, the student must beware the possibility of the brachiopods having been drifted into position with the other shells and plants. Waves and currents may bring many animals after death into an association which did not, or could not, have existed in nature.

Enclosing sediments.—To deduce the brachiopod habitat from enclosing sediments is a task fraught with difficulties and dangers. Geologists are not all agreed on the conditions of deposition of certain types of sediments. Furthermore, the point at which a brachiopod is found may not be the one at which it lived, nor necessarily near its actual abode. It is also well known that the gradation of sediments away from shore, classically assumed to be from coarse to fine, is more complicated than once supposed. The grade or degree of coarseness of a sediment is not a reliable clue to its environment of deposition. From paleogeographical considerations it would also appear that old ideas regarding limestone and black shale deposition must be revised. Some limestones by their geological relationships indicate that they were rapidly deposited near shore.

In general brachiopods in a coarse sandstone suggest a near-shore, perhaps littoral zone. The entombed brachiopods may not have lived near the shore but may have been cast up by currents and waves from habitats farther offshore. Lingulids are a common form in sandstones, particularly in the late Cambrian, and from their habits today would be expected to be the commonest forms in the near-shore zone.

Heavy-shelled brachiopods have been commonly regarded as shore forms. The Oriskany fauna has been pointed out as a fine example. The Oriskany sandstone by its lithologic features and paleogeographic distribution is probably a far better indicator of shore conditions than the thick-shelled animals found in it because the Oriskany fauna is one of large, strong-shelled individuals regardless of its sedimentary environment. The same heavy-shelled species are found in the fine-grained Little Saline limestone of Missouri and the Grande Grêve and Percé limestones of Gaspé.

A favorite habitat of many modern brachiopods is the rocky shore where individuals live in hollows and sheltered places on and about the stones. In Puget Sound, Washington, and at Eastport, Maine, brachiopods live in the tide zone, where they are left out of water at low tide. This sort of environment would be represented by conglomerates, but it is rare indeed to find brachiopods preserved in such a matrix.

Brachiopods are abundant in the finer sediments in most Paleozoic formations. The ecologic relationships of brachiopods found in the fine muds cannot be determined without difficulty. It might be thought that these muds represent off-shore deeper-water sediments but paleogeographic evidence often determines them to be of near-shore origin. Often such muds are found on the flanks of reefs in shallow water. Corals associated with brachiopods in very fine muds point to shallow water.

Much has been written on the environment of deposition of black shale. Most authors agree that the bottom conditions were not hospitable to normal faunas, but few authors agree on the depth at which the shales were deposited. Were they off-shore deep-water deposits or near-shore sediments? It is probable that no generalization will suffice for all black shales; the bathymetric level and conditions of each one must be determined by its own paleogeographic distribution, contained faunas and any other evidence available.

Most Paleozoic black shales contain at least a few brachiopods, mostly lingulids, discinids, or thin-shelled rhynchonellids. The black shale fauna has been regarded by Ruedemann (1934) as chiefly planktonic, but two of its important forms, by analogy with modern brachiopods of the same type, are bottom dwellers only, the lingulids and rhynchonellids. The presence of lingulids, which could not possibly have lived in the plankton, is a most forceful indication that these shales were deposits in shallow water and probably near the shore.

Limestones are usually fine-grained sediments and have been conventionally regarded as deep-water or off-shore deposits. But the presence in some limestones of pebbles of quartz or igneous rocks, and intraformational conglomerates argue for shallow-water deposition, at least for those deposits. Here again each occurrence of limestone must be weighed individually, with all available evidence, before the environment it represents can be determined.

Some limestones are composed almost wholly of broken shells, rolled corals and other animal debris. These may have been formed at times when the bottom was so stirred by waves and currents that fine material could not settle and was carried away, but the heavier shell debris remained. The Tichenor and Portland Point limestones of the Hamilton group of New York, which are composed chiefly of shell debris, are examples.

The environment of deposition of most Paleozoic deposits seems to have been in water less than 100 fathoms deep. Most authorities agree that the Paleozoic seas did not exceed this figure and some maintain that the seas were not deeper than 200 feet (Elias 1937). Most Paleozoic deposits crop out on the margins of uplifts which have brought up only the near-shore regions, but even where Paleozoic off-shore zones can be demonstrated, their fossils, current and wave-markings usually indicate shallow water.

Paleogeographic features.--Paleogeography is often a great aid to studies in Paleoecology because it enables a student to outline a basin of deposition, locate its probable shores and oceanic connections. If the study of fossils and sediments is inconclusive or yields conflicting evidence, report to paleogeographic data may indicate the ancient environment. For example, thinning of the Hamilton shales westward in Erie County, New York, and the development of layers of concretions and shell breccia, point to a shoal or land on the site of Lake Erie. This ancient positive area was called the Buffalo Axis by Grabau. This region of the Hamilton sea was formerly regarded as a deep-water environment but the facts as now interpreted point to shoal water deposition of the Hamilton black shales and blue calcareous shales of western New York.

Brachiopod Adaptations

Anyone who has studied bachiopods or collected them will be impressed by the fact that different stocks at different times develop the same or similar forms. This homeomorphy has been interpreted in some quarters as adaptation to environment, but study indicates that adaptation is not the whole story. Another school favors an orthogenetic process as an explanation for the phenomena. It has also been suggested that such parallelisms are entirely fortuitous. Only a few combinations of characters are possible in brachiopods. Therefore it is inevitable that many characters will be reinvented.

Many of the developmental trends to be discussed below may be interpreted as more or less directly tending to improve or maintain the animal's ability to bring currents of water into the shell. This is the most important function of a brachiopod because the currents bring life-maintaining food and oxygen. Brachiopods that live above the bottom on stones or corals have no great problem in bringing in the necessary currents, but brachiopods that live free or anchored on the mud have the problem of keeping the margin away from the bottom. If the margin is covered by mud the animal is likely to perish from suffocation or starvation. Thus many adaptations to keep the margin above the mud and to facilitate entrance and exit of currents are known.

By their form many brachiopods are adapted to keep their margins above the mud if they are torn free from the place of attachment. The posterior or umbonal portions of one or both valves are very heavy and thick when compared to the anterior portion. If the shell sinks in the water it will fall with the beaks down and will lie on the mud with the heaviest or ventral valve on the mud and the front margin oblique to the bottom. Round or ovoid shells like *Gryphus vitreus* can be rolled about on their posterior by currents, and the front margin will never touch the mud. Some shells, *Davieselia* and *Gigantella*, must have relied mainly on the weight of the posterior part of the ventral valve for anchorage. The dorsal valve then serves as a lid. The development of a ponderous ventral valve was carried to extremes in the genera *Richthofenia* and *Prorichthofenia*.

It is impossible at the present time to say why certain types of brachiopod shells were developed. The modern brachiopods show only a few of the known trends of the Paleozoic. Many Paleozoic types, therefore, cannot be compared with any recent forms, hence remarks on their ecology must be regarded as tentative until more positive data can be collected. In discussing some of the known adaptations of the brachiopods the writer has selected the published views that seemed most reasonable to him. The adaptive trends here considered are as follows: folding, lobation, plication, cementation, alation and mucronation, elongation, compressed form, resupination, reversion, spinescene, geniculation and punctation.

Folding.—All stocks of articulate brachiopods tend sooner or later to develop a strong median fold. In the Paleozoic the fold usually takes the form of a strong median plica that undulates the anterior commissure or line of valve junction. The folding of the commissure may take place either in a ventral direction or in a dorsal direction. The prevailing condition is a dorsal fold, but a ventral fold occurs in a few genera.

In young brachiopods or in early genera of certain stocks the ventral valve is gently folded in a ventral direction. Later development, as in *Finkelnburgia*, leads to loss of the ventral fold and dorsal sulcus to produce a secondarily rectimarginate or straight commissure. In many brachiopods, however, the sulcus is present in the dorsal valve in young stages but as growth continues a well-marked fold develops from the sulcus. Examples are *Eridorthis* and *Virgiana*.

Two types of folding are now recognized: an opposite fold and an alternate one. In the former type a fold or sulcus on the ventral valve is opposed by a fold or sulcus on the dorsal valve. The anterior commissure thus remains rectimarginate but the ventral or dorsal profiles become lobate. Examples of opposite folding are: *Pentamerus*, *Phipidium*, *Zeilleria*, and *Digonella*. Alternate folding is produced when a fold in one valve is opposed by a sulcus in the other. This is the more common type, of which Platystrophia or Enteletes will serve as good examples. In instances of alternate folding the anterior commissure is thrown into one or more folds.

Orton (1914) has presented the view that development of a median fold produces a trilobate shell, thus facilitating the ingress and outgo of the water currents that aerate the mantle and bring in food. The incoming currents in spiriferids enter by the median fold of the shell and the unclean water leaves by the lateral flanks.

Folding apparently had little to do in determining the life position of a shell except where the brachiopods lived in mud. This was not true, however, of shells folded in a ventral direction. These must have been attached with the dorsal valve below because in most known sulcate (anterior commissure folded ventrally) brachiopods the ventral beak is more or less curved over the dorsal umbo.

Lobation.--This trend, which is of distinct value in separating the incurrent from the excurrent streams is usually incipient in all folded brachiopods but has been carried to extremes in a few instances. Lobation develops in oppositely and alternately folded brachiopods. Pentamerus and Rhipidium tend to develop an elongate central lobe at the front of the valves which thus brings the excurrent channel well forward of the receding flanks of the shell where the water enters. In Spirifer, according to Orton (1914, p. 295), the condition is reversed, the currents containing oxygen and food enter the front, medial portion of the shell and the currents containing the products of metabolism leave by the flanks.

The most extreme instances of lobation occur in Pygope and Pygites. In young stages of Pygope a strong fold develops on the ventral valve, producing a deep, wide sulcus and flaring flanks. In Pygites the flanks are greatly elongated with growth, and often grow together anteriorly to leave a hole in the center of the valves. The ventral fold of these "keyhole brachiopods" is directed obliquely ventrally, thus directing the incurrent canal far above and posterior to the excurrent lobes.

Plication.--By plication is meant the development of major folds in the shell. This tendency has developed in many different brachiopods, the punctate orthids, strophomenids, and terebratulids. Late-derived members of the strophomenids and orthids in the Pennsylvanian and Permian periods developed strongly plicated shells. Examples are: Enteletes, Kiangsiella and Meekella. No other advantage than increased shell strength appears to the writer to have accrued from this development. The widespread and nearly simultaneous development of plications in these stocks may be an expression of phylogerontism because all of them disappeared with the Permian. The trend may, perhaps, have been induced by world-wide adverse conditions such as a slight increase in salinity due to removal of water from eperic seas to form the growing Pennsylvanian and Permian glaciers.

Cementation.—When one mentions cementation in connection with brachiopods he naturally thinks of the craniids. The various genera of this family have been cementing forms as far back as they have been found—in the Middle Ordovician. Their ecology apparently has not changed and need not be further considered. A number of secondarily attached genera are known which may be divided into two groups: one that is attached throughout life, and another which in later life may break free and lie on the sea-bottom.

Beginning with Liljevallia in the Silurian, strophomenids cementing by the entire ventral surface of the ventral valve persist into the Devonian, where they are represented by Irboskites and Davidsonia. With the advent of Productella in the Middle Devonian two aberrant genera appear and persist into the early Mississippian. These genera are Leptalosia and Etheridgina, and the two are characterized by cementation of the ventral valve by its ventral surface to corals or other objects. In addition to this means of attachment peripheral spines also serve to anchor these little shells. Etheridgina often grows on crinoid stems in such a manner that the anchoring spines appear to wrap around the stem.

Many genera are known that are cemented in early stages of growth but, because of their large size, later break from their attachment and lie free on the bottom. Schuchertella, Derbyia, Strophalosia and Oldhamina are examples of this group. In much the same category are brachiopods having the form of cup corals, such as Richthofenia. These types were only evolved in Pennsylvanian and Permian times. They were derived from strophomenid ancestors at the twilight of the Protremata.

Alation and mucronation.—Lateral extension of the hinge to form wings or ears is a tendency developed in many different groups of brachiopods. It may occur as an adult character or in youthful forms only. Argyrotheca johnsoni Cooper, from the West Indies, has a wide-hinged, alate form in its young stages, but the adult has almost rectangular cardinal extremities. Many strophomenids of the Ordovician and Devonian developed alate shells. The development of a wide hinge is uncommon in modern brachiopods but among the spiriferids this development reached its maximum.

It is apparent from the structure of the strophomenids that some were attached by a slender pedicle but others, such as Stropheodonta which has no functional pedicle opening, lived free on the bottom. Such forms would be able to develop the hinge to its limit. For prone shells auriculation or mucronation would readily serve to keep the animal on the surface of the mud and from sinking into depressions. It would also serve to prevent currents from upsetting the shell.

The development of symmetrical alate forms could not have taken place in shells tightly affixed to a hard and irregular substratum. Spirifer mucronatus is one of the most mucronate brachiopods known. This and allied species may be collected in New York, Ontario, and Michigan. The writer has collected many hundreds of them but has seen comparatively few unequally developed or distorted individuals. This leads to the belief that these brachiopods were not attached closely to a hard substratum. Not only the symmetry of the shell but the strongly incurved beak would make close attachment to a hard substratum difficult. Because the animal possessed a functional pedicle opening it is believed that Spirifer mucronatus was attached by a pedicle of moderate length anchored in soft mud, with the umbo of the dorsal valve resting on the mud and leaving the extremities free to develop laterally. These spirifers may have lived where currents were active. The mucronate form would tend to serve in the same manner as a weathervane, always turning the shells on their pedicles so that their long axis was parallel to the direction of the current. Thus the force of the current working against the narrow side of the shell would be unable to uproot the animal and the mucronate extensions would prevent the shell from being driven into the mud.

Mucronation or alation may be an orthogenetic trend, because many different stocks of spiriferids have developed the character. Most of these have received generic names. Thus we have Mucrospirifer, Fusella, Cyrtospirifer, and Rastelligera, a mucronate development of Spiriferina, the punctate spiriferid.

Elongation.—This is an adaptation developed by a few brachiopods having delicate pedicles. Onychotreta and Terebrirostra are the two most extreme examples. The two genera are widely separated by time, the former having lived in the Silurian and the latter in the Cretaceous, yet they have developed identical external forms. Both genera lived in fine lime muds.

It has been suggested by Yakovlev (1908), that Terebrirostra lived with the beak in the mud and the extremely long ventral valve kept the anterior margin well above the surface of the mud. Dacqué (1921) has suggested that elongation is an aid to stiffening the pedicle. These forms lived with the ventral beak in the mud, anchored, perhaps, by a fine pedicle split into many fibers at its extremity.

Compressed form.—According to Lamont (1934) water immediately in contact with a mud surface is normally very poor in oxygen. Hence, brachiopods of compressed form, like Strophomena or Radinesquina, have a maximum of oxygen-gathering tissue exposed to the water. This condition enables the animal to get the greatest amount of oxygen from a small amount of water. The early representatives of these brachiopods were provided with a functional pedicle and probably lived lying on the bottom or attached in the usual manner. The later compressed brachiopods, such as *Stropheodonta*, had no pedicle. *Stropheodonta* was more or less deeply concave and may have lived[1] with its ventral surface stuck tightly on the sticky clay in which it is usually found. The mud is sufficiently tenacious to prevent the shells from being overturned. If overturned, it is possible that *Stropheodonta* and other compressed forms, like *Chonetes*, may have had setae strong enough to have been useful in restoring the animal to its normal position.

Resupination.—Everyone familiar with brachiopods has been impressed by the phenomenon of resupination, in which the young shell possesses a convex ventral valve and a flat or concave dorsal valve, but in maturity the condition is reversed, the anterior of the ventral valve becoming more or less deeply concave and the dorsal valve becoming strongly convex. This appears to have been a derived tendency, because brachiopods more commonly have a deeper ventral valve. Examples of resupinate brachiopods are *Strophomena*, *Schucheretella* and *Chonostrophia*.

Resupination would be an advantage to compressed types that lived free on the bottom, lying on their ventral valves. The anterior margin would be lifted well above the surface of the mud and the hollow on the ventral valve just anterior to the beak would effectivly prevent the valve from being overturned. According to Lamont (1934, p. 167), radial ornamentation, but more particularly concentric rugae which are commonly developed in compressed shells, would prevent slipping in the mud and sinking of the lateral margins into the mud when the valves were opening during feeding.

Reversion.—This term is applied to the rare instances in which the anterior commissure is folded in a ventral direction, producing a fold on the ventral valve. This condition is rare but a number of genera are known which are reversed counterparts of more common genera. Examples are: *Brachymimulus* of the Silurian, *Anabaia* of the Devonian, *Parenteletes* in the Pennsylvanian, *Enteletina* and *Camerophorina* in the Permian, *Norella* in the Triassic, *Nucleatula* in the Jurassic, and *Neorhynchia* and *Abyssothyris* in present day seas.

Although all of the genera named would be difficult to separate on the basis of an examination of the exterior, the animals probably did not all live in the same manner. *Brachymimulus* has a minute foramen situated at the apex, suggesting that this little brachiopod was attached with the dorsal valve down, thus bringing the anterior margin well above the bottom. The other genera were undoubtedly attached to shells or other objects by a short pedicle in the usual manner of rhynchonellids and terebratulids. No particular advantage to its possessor seems to be apparent in the known instances of reversed fold and sulcus.

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[1] This idea was suggested by Dr. J. P. E. Morrison of the U. S. National Museum.

Spinescence.—Spines have been developed independently in many different stocks of brachiopods from Cambrian time to the Recent. Spines in some forms, such as Squamularia, are developed as a part of the ornamentation and play no apparent part in the life of the animal. On the other hand, hinge spines and long, strong spines scattered over the surface, as in the productids, appear to have played an important role in the habits of the animal. Nowhere among the brachiopods has evidence been discovered to prove that spinescence indicates a phylogerontic stage. The Chonetids and productids, once initiated had a long and flourishing career.

Hinge spines appear first in Eochonetes, which must have developed from Sowerbyella in late Ordovician time. The spines on the hinge of Chonetes were developed to all degrees, some are short and blunt but others, as in the group of Chonetes emmetensis, are exceedingly long. Such long spines could have served to anchor Chonetes by becoming entangled with submarine seaweeds. Shorter spines have been explained as anchors to hold the shell upright in the mud, but most of them seem too short to have been effective holdfasts. Chonetes may have lain on the sea-bottom on its convex ventral valve, and the oblique spines may have been an important aid in preventing the shell from being overturned by currents.

Productella and the later productids have the common feature of spines scattered over the body of the ventral valve as well as along the posterior margin. Many genera of productids have been separated on the basis of their ornamentation. The many types of ornament naturally suggest that these shells had different habits of life. Many of the productids are not well known but a study of a few types will give some ideas as to their mode of life.

Silicified specimens of Productella from the Devonian of Nevada are ornamentated along the hinge of the ventral valve by long spines that curve in an antero-dorsal direction over the concave dorsal valve. Spines along the anterior border curve postero-dorsally to overhand the dorsal valve. Such spines curved over the dorsal valve and towards the center of the animal will keep the shell above the surface of the mud regardless of the position of the valves. If the shell is thrown up off the bottom by a current, it will make no difference to the animal it settles with the ventral or the dorsal valve down. The curved spines will keep the shell off the bottom as the legs of a water-strider keep their owner's body on the surface. The dorsal valve of Productella carries no spines, consequently it is free to open regardless of the position of the animal on its spines. In the U. S. National Museum a specimen shows many individuals of Productella entangled by their spines. Even in this tangled mass the dorsal valve had no difficulty in opening. Thus some productids may have lived on the sea-bottom as a spongy mass of shells held together by interlocking spines.

Many of the later productids have a construction similar to that of Productella and are provided with similarly situated spines. Muir-Wood (1928, p. 26) states that Dictyoclostus lived with its ventral valve lying over the dorsal valve. Moore (1929, p. 469) supports this contention. It seems likely that the productids seen by Muir-Wood and Moore were supported above the muddy bottom on which they lived by spines in the manner described above. If they were not, the animal must surely have perished because it could not have functioned with its entire margin in the mud.

In productids with long hinge-spines only it is possible that the animal lay on the bottom on its ventral valve which was by far the heavier. Long hinge-spines extending posteriorly would prevent the creature from being tipped over onto its dorsal valve. Marginal frills, such as those of Atrypa, may have served their possessor in the same manner as spines to keep the valves out of the mud.

Geniculation.--Various degrees of geniculation have been developed in all stocks of the thin-bodied or compressed brachiopods, such as Rafinesquina, Leptaena, and Productus. Most of these compressed forms live on mud. Thus the geniculation seems to be a necessary development to keep the margins of the shell above the surface of the mud. In the productids geniculation is carried to an extreme, the front of the valve being produced into a sort of siphon, as in Proboscidella.

Punctation.--The function of punctae in the inner layers of a brachiopod shell is still problematical. However, it seems clear that punctate branches of the articulate brachiopods were more vigorous and long-lived than the impunctate lineages. The earliest known punctate brachiopods are dalmanellids, which appear in the Chazyan or lower Middle Ordovician. These dalmanellids flourished throughout the remainder of the Paleozoic, outliving the impunctate orthids by several periods.

It is not possible to prove whether punctae developed once or several times. It is possible that the dalmanellids gave rise to all other punctate forms and that these developed series paralleling those of the impunctate stocks. The punctate spirifers outlived the impunctate ones and today the terebratulids are the dominant race of brachiopods, with the rhynchonellids represented by only a few genera and a handful of species.

Form and Size of Pedicle

Among recent articulate brachiopods nearly all species have a short pedicle. The pedicles vary slightly in length but even the long-beaked forms are anchored tightly by short pedicles. Of all modern brachiopods only Chlidonophora, an abyssal species, is noteworthy because of its unusually long pedicle. Chlidonophora is a small, subcircular brachiopod with a lenticular profile, suggesting a Paleozoic dalmanellid by its form. The pedicle is almost as long as the animal and its end is divided into many long, slender fibers. These entwine foraminifer shells and anchor the animal in the same manner as the roots of a plant. It is likely that many bottom-dwelling brachiopods of the Paleozoic may have had such a pedicle. For example, some of the brachiopods having small foramina may have had pedicles with divided distal ends. Such a pedicle could have effectively anchored most brachiopods to a muddy bottom.

Brachiopod enemies

There is little direct evidence to indicate that Paleozoic brachiopods served as food for such animals as the fishes, cephalopods and trilobites. However, if one considers their enormous numbers in the Paleozoic they must have been a prolific source of food, if not in the adult form, certainly their eggs and larvae must have yielded many a feast. Direct evidence indicates that snails equipped with a radula, actually bored brachiopod shells and devoured the succulent tissues within. The earliest example of this molluscan habit known to the writer was found in the Richmond (Fenton and Fenton 1931). This early custom is still in vogue because Jackson (1918) and Dall (1895) record instances of modern brachiopods having been bored by snails. In modern times man has added himself to the list of brachiopod enemies. The natives of the Japanese and Philippine Islands relish the pedicle of Lingula.

Embroyology and Distribution

The young of brachiopods have a free-swimming stage before they finally settle to the bottom for life. Very little is known of these young stages, in fact, they are known in detail in only four genera, Argyrotheca, Lacazella, Terebratulina and Lingula. Each of these genera represents a different large major division of the brachiopods. Observations have been made on a few other genera, but too little is known to permit much generalization on them.

It has been long recognized that the chief means of dispersal of brachiopods is by currents during the free-swimming stages. But there are difficulties in the way of a complete understanding of the process. It has been discovered that the known larvae of the inarticulates differ from the larvae of the articulate brachiopods. In the former the pelagic larvae are provided with a mouth and functioning stomach, allowing them to live for some time in the free-swimming stage. Larvae of Discinisca and Pelagodiscus have been recognized in the plankton. The known larvae of the articulates do not swim after the development of a functioning stomach. Their free-swimming period is thus short, 10 to 12 days in Terebratulina, and they settle not far from their place of origin.

Two obstacles to dispersal are, therefore, apparent. In the articulates the free-swimming stage is short, thus limiting dispersal. In the inarticulates, although the larvae are better adapted to longer free-swimming existence, most of the species live in shallow water only. Therefore, deep water and consequent cold temperatures are a barrier to their distribution.

In the Paleozoic the seas were probably shallow, and there were probably no great depths in the geosynclines to form a barrier to dispersal. Nevertheless, there is evidence to show that species were localized then as now. In the Devonian the equivalent Hamilton (Centerfield) faunas of western New York, Ontario, Michigan, and Indiana contain species peculiar to these areas. In Michigan and Indiana many of the rare species dwelt on and about the coral reefs. Adjustment to the peculiar conditions of reef life may have been the controlling factor in their localization. In all periods of the Paleozoic, local areas characterized by definite assemblages are known and contemporaneous faunas nearby may contain many different species. The reasons for such localization will make interesting ecological material.

Allan (1937) has published a note on an overlooked phase of brachiopod migration. He has discovered the young of two species of brachiopods attached to the free-swimming _Chlamys_ _radiatus_ (Hutton). This is a member of the Pectenidae which contains species known to make migrations. Although the point is not proved, Allan suggests that this may have been a means of distribution. Paleozoic brachiopods have been found attached to mobile forms such as cephalopods, and trilobites, but it is usually difficult to prove whether or not the brachiopods were attached during the life of the swimmer or after the creature had died. The latter seems the more likely.

Color

Anyone seeing a large collection of recent brachiopods for the first time will be struck by the beauty and high color of some of the species. Perhaps the most beautiful species is _Argyrotheca_ _barrettiana_ (Davidson), with its straw yellow costae and crimson interspaces. The terebratulids are the most highly colored modern brachiopods, the colors ranging from pale yellow through salmon to pink and crimson. The recent rhynchonellids are drab shells of brown, pale bluish-gray and black. Some linguloids are highly colored by bright or dark green mixed with rich brown.

Most colored brachiopods are dwellers in shallow water, a feature that is true of other groups of animals as well as the brachiopods. It is generally true also that, as deeper water is approached, colored shells become fewer and fewer in number. Most shelled invertebrates of the deep waters have thin, white or translucent shells. Forbes (1854) has stated that, "In the Mediterranean only one in 18 of the shells taken from below 100 fathoms exhibited any markings of colour, and even the few that did so, were questionable inhabitants of those depths. Between 35 and 55 fathoms, the proportion of marked to plain shells was rather less than one in three, and between the sea-margin and 2 fathoms the striped or mottled species exceeded one half of the total number".

In studying the recent brachiopods in the U. S. National Museum the writer has found that most of the colored species were collected from shallow waters. A few colored species are recorded, however, from considerable depth. One specimen of Argyrotheca barrettiana (Davidson) was taken from 805 fathoms but it is not known whether the animal was alive or dead when dredged.

Color-marked fossil brachiopods are of very rare occurrence. A few specimens have been taken from the Paleozoic and a few from succeeding periods. The oldest known specimens of color-marked brachiopods are from the Middle Devonian in Europe and the United States. Most fossil brachiopods showing traces of color are terebratulids and the usual pattern is one of radial bands with or without a gentle curve towards the front margin. Davidson[1] has figured specimens of Dielasma showing the more common type of color mark. Living Laqueus rubellus (Sowerby) from Japan and Hawaii is similarly marked. The usual traces of color in fossil brachiopods show the pattern in light or dark gray and usually give no hint as to the original color.

Brachiopods showing traces of original color are known from the Cedar Valley of Iowa and Illinois. The writer and Preston E. Cloud, of the U. S. National Museum, collected several specimens of Cranaena having four or six straight red stripes radiating from the beak to the front margin. Other specimens taken from the same deposits and those figured by Cleland[2] have the same pattern but do not show the red color. The red-marked fossil species and predominant red colors in recent terebratulids suggest that this color prevailed also in the fossil forms.

Richter (1919) has pointed out by analogy with recent forms and on the basis of Forbes' remarks that, colored brachiopods in ancient sediments are excellent indicators of shallow, sunlit waters.

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[1] Brit. Foss. Brach., pt. V, Carboniferous Brachiopoda, Palaeontographical Soc., London, p. 13, pl. 1, 1858-1863.

[2] Wisc. Geol. Nat. Hist. Surv., bull. 21, p. 73, pl. 13, figs. 8, 9, 1911.

Pathology

Pathologic brachiopods have been recorded many times, but most of the figured specimens that have been interpreted to be pathologic appear to have attained their distorted condition by accidents during growth or unfavorable conditions of growth. Distorted brachiopods are common and are produced under crowded conditions of growth. Brachiopods often grow in clusters or in crannies in corals so that growth of one side or the other may be seriously impeded. Speciments of spiriferids may be found with the mucronate points of only one side developed. Rhynchonellids of the Paleozoic and Jurassic often are unequally developed on one side or the other. These malformations appear to have been produced by crowding. One extreme instance is shown by a specimen of Rafinesquina from Cincinnati, Ohio, in the U. S. National Museum. The front margin of this specimen had impinged against a branch of a small bryozoan and had grown completely around it.

Only one example of a diseased brachiopod is known to the writer. This is a specimen of Cariniferella tioga (Hall) from the Chemung of south central New York, now in the U. S. National Museum, showing only half of the muscle scars normally developed. One adductor and the large diductor and adjustor scars are represented only by a small irregular spot. The exterior of the specimen is perfect, indicating that some internal cause must have been responsible.

Commensalism and Parasitism

Many instances of commensalism are known in fossil brachiopods. Modern Terebratulina is often found encased by a brown sponge. Bryozoans, worms and other animals often are attached to brachiopod shells. Yakovlev (1926) claims that encrusting Aulopora served its host advantageously by the presence of sting cells which protected coral and brachiopod alike.

Fenton (1932) described a brachiopod, Terebratalia transversa caurina (Gould) living inside the shell of a large gastropod, Argobuccinum oregonense (Redfield). The brachiopod larva had entered through a rent in the mantle of the shell and grown to considerable size in this unusual environment. Although Fenton regarded this association as parasitic it seems rather to have been accidental.

Conclusions

Brachiopods are a minority element of modern faunas, but in the Paleozoic and Mesozoic they were very numerous and at times the most abundant form of life.

With the exception of the lingulids, modern brachiopods have too wide a bathymetric range to be of use in determining the depth of seas older than the Tertiary.

Life habits of groups represented by fossil species and by forms now living probably did not differ throughout time. Life habits ascribed to extinct forms, unless these forms have been found in their living positions, must be regarded as speculative.

Aids to the study of Paleoecology are: (1) Analogy with Recent forms; (2) position of the fossil in the rock; (3) associated fossil forms; (4) the nature of the enclosing sediments; and (5) paleogeography.

Some trends of adaptation during past time appear to have been in the direction of increasing the ability to get food and oxygen.

Too little is known of brachiopod embryology to permit generalizations on distribution of free-swimming larvae.

Colored brachiopods in general indicate shallow, warm waters.

Brachiopods are not known to have been truly parasitic but instances of commensalism are well known.

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PALEOECOLOGY OF THE PALEOZOIC CEPHALOPODA

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The host of tetrabranchiate cephalopods that inhabited the Paleozoic seas are today represented by only three closely related species, all of which belong in one genus, Nautilus. The habitat of these three species is very restricted, their habits are not well known, and they represent an archaic type. Therefore, it is not possible to draw general inferences in regard to the paleoecology of the ancient cephalopods from a comparison with their modern relatives.

Forms with heavy unornamented coiled shells, like Nautilus, have existed since Early Paleozoic times, and the lithology and faunal characteristics of the rocks in which their remains occur as fossils indicate that they lived in a variety of habitats. However, the shells of dead cephalopods, after the fleshy bodies had decayed and dropped out of them, must have drifted widely much as do those of modern Nautilus. That is, all three of the existing nautiloid species live only in the shallow waters about the shores and coral reefs of the South Pacific from the Malay region to the Philippine and Fiji islands; their empty shells, however, drift to such remote places as Japan, Africa, and New South Wales. Obviously the character of the sediments in which drifting shells finally come to rest can yield no information in regard to the ecology (or paleoecology) of the species represented. The local abundance of "Orthoceras" sociale Hall in the Maquoketa formation at Graf, Iowa, to which Twenhofel (1936) has recently called attention may well be due to a concentration of drifting shells by eddies or currents. The shells of the goniatites were even lighter in weight than were those of the nautiloids, and presumably therefore they must have drifted very readily—their relatively fragile construction, however, may have kept them from drifting as far as those of the nautiloids. It would seem then that we can not draw reliable inferences from the associations of isolated fossil cephalopods, and that in only those cases where we find an abundance of adolescent and mature specimens in close association are the lithologic, faunal, and other characteristics of the inclosing rocks likely to give us trustworthy data in regard to the paleoecology of the species represented.

There is so much uncertainty as to the affinities of the structures which are believed to be goniatite anaptychi by some paleontologists and crustaceans by others that it is hardly possible at present to discuss them intelligently. However, it should perhaps be noted that Matern (1931) believes that the anaptychi were lost with the bodies soon after the death of the animals that bore them, whereas the empty shells drifted into other regions before settling and therefore are found in different lithologic facies.

It is generally recognized that the chances of preservation of a marine shell are indeed small, and our present knowledge is not sufficient to give us a satisfactory understanding of the relationships of fossils and lithology. Since the shells of modern Nautilus, and presumably those of fossil nautiloids and ammonoids, are composed almost entirely of aragonite their chances of preservation were even less than average. It is conceivably possible therefore that conditions in the normal habitat of many of the ancient cephalopods were such as to be almost prohibitive to preservation and that only when shells were washed into an abnormal habitat were they preserved.

Insofar as is now known, cephalopods, both fossil and recent, are exclusively marine, and the nature of the rocks in which the fossil forms occur as well as the faunal associations indicate that the vast majority of them lived in shallow water. From a study of the color markings preserved on certain fossil nautiloids Foerste (1930) has found additional evidence to support the conclusion that they lived in shallow water. He states that evidently there "is an intimate connection between the presence of color markings on shells and their access to light during the life of the animal. Forbes (1844, 1854) has called attention to the fact that in shallow waters shells present more varied colors and more distinct color designs. At greater depths the colors tend to become uniform over the entire surface of the shell, so that color patterns disappear. Moreover, at these depths the variety of colors is restricted more and more to various shades of dull red or of reddish brown. Newton (1907) stated that in the Mediterranean only 1 out of 18 shells showed colors below the 100-fathom line; between 35 and 55 fathoms, 1 out of 3; and at depths of only 2 fathoms or less, more than half. From the vividness of the color patterns of the Carboniferous limestone specimens studied by him, Newton concluded that the Carboniferous limestone was deposited in water less than 50 fathoms deep. The relatively numerous species of gastropods with color patterns found by J. Brookes Knight in a single horizon of the Pennsylvanian division of the Carboniferous, in the vicinity of St. Louis, Missouri, suggests deposition in an equally shallow sea. By a similar line of reasoning, it seems probable that the portion of the Alpena limestone which retained color markings in a species of cephalopod and also in a species of brachiopod ... was deposited in relatively shallow waters." Modern nautiloids are confined to the tropics and the fact that many of the Paleozoic forms possessed rather brilliant color markings suggests that they also lived in warm waters.

Many of the Early Paleozoic nautiloids were large and their shells were heavy. The majority of these forms were straight and circular or broadly elliptical in cross section, but some of them were subcircular, subtriangular, or even lenticular in cross section. The latter types were of course adapted for life on the bottom, and it has been suggested that the lenticular types, for example, Gonioceras and Lambeoceras, were mud grovellers. Although the shells that were circular or nearly so in cross section were undoubtedly rolled over by storm waves, many of them like the endoceratoids possessed large heavy (secondarily weighted) siphuncles which were ventral in position and therefore served to right and stabilize them.

The available information in regard to color markings, hyponomic sinuses, etc. seems to indicate that the straight cephalopods lived in a horizontal position, and the view expressed by Jaekel and Clarke that some of them lived vertically attached to the bottom never had many adherents and now seems to be entirely rejected (See Teichert, 1933, pp. 196-197). Most of the large straight heavy-shelled forms were almost certainly benthonic, and we agree with Ruedemann (1921) that in all probability "the conchs, buoyed up by gas in the air chambers [camerae], were lightly dragged over the soft mud by the sluggish animals." Judging these forms by their modern relatives we conclude that they could move forward by crawling on their tentacles or backward by jetting water out of their mantle cavity through a hyponome. Since no trace of a hyponomic sinus is present on the shells of most of the early forms like the endoceratoids, it seems probable that at first progression was accomplished chiefly by crawling and that only later in the history of the race was the jet-propulsion method of locomotion perfected.

The Silurian strata of the Upper Mississippi Valley contains numerous nautiloids, and in many cases they are particularly abundant along the flanks of bioherms. Most of the seventy-five species of cephalopods recently described by Foerste from the Port Byron formation came from the flanks of a single large bioherm. Presumably we should picture these animals as rather inactive or sluggish creatures which spent most of their lives in the shallow waters on the flanks of the bioherms where we find their remains today. However, the large cephalopod fauna described from the near shore facies of the Upper Ordovician of the Northwest probably did not live precisely where we find its remains today. That is, most of the cephalopods described from the Wind River Mountains and the Black Hills, for example, came from what appear to be littoral deposits, and the shells are almost invariably somewhat worn and broken. Presumably the creatures that secreted these shells lived in the shallow waters beyond the littoral zone, and when they died their shells were distributed by waves and currents. The large straight forms, belonging in the genera Endoceras and Cyclendoceras, are far more abundant in these littoral deposits then elsewhere in the same formation, indicating again that they flourished rather close to the shore.

In his recent study of the actinoceratoids, Teichert (1933, 1935) concluded that some of the known genera must have been almost entirely benthonic as they had large heavy siphuncles, strongly developed inter cameral deposits, and a distinctly flattened ventral side; some "may have been capable of swimming, but perhaps mainly inclined to a benthonic life;"

and the curved forms, "all of them conspicuously lacking a distinct flatness of the ventral side, may have been mainly swimming." He continues with the conclusion that the "benthonic forms, however, were the more or less persistent ones. The last representation of the Actinoceroids is the genus Rayonnoceras in the Mississippian of Oklahoma and the lower Carboniferous of England. It is by far the largest Actinoceroid we know of and at the same time its endosiphuncular and intercameral deposits show such a hypertrophical development, that a benthonic life of that animal can be assumed with certainty."

When color markings are preserved on the breviconic Paleozoic nautiloids, they are as a general rule equally well developed on all sides of the conch, indicating that the shell was carried more or less vertically rather than horizontally. Therefore forms of this type probably rested on the bottom of the sea like certain gastropods with the aperture of the shell down; of, if the weight of the animal was more than counterbalanced by the buoyancy of the gas in the phragmacone, when the creatures came to rest they may have been suspended in the water head downwards like modern Spirula. Rapidly expanding conchs form large apertures which facilitate crawling, whereas constricted apertures interfere with the protrusion of the body from the conch and therefore tend to retard crawling. Since many of the breviconic nautiloids possessed rapidly expanding conchs which only at maturity developed constricted apertures, it seems likely that during adolescence these creatures were primarily crawlers, but that as maturity was approached and the number of camerae increased the shell tended to be used more and more as a float and the tentacles were protruded almost exclusively for the purpose of obtaining food and not for locomotion. Hexameroceras and Phragmoceras can be considered as typical examples of this type of development. However, other breviconic forms, like Westonoceras, which had relatively long fusiform conchs were, as Teichert (1935) has recently pointed out, more active swimmers and presumably they were normally oriented with the long axis of the conch more or less horizontal. In the breviconic nautiloids with greatly restricted apertures, typified by Hexameroceras, there is a well developed hyponomic sinus, and therefore one might conclude that these forms were not entirely floaters. However, it is possible that they had lost their ability to swim effectively and that they had retained their hyponome merely as part of their respiratory apparatus. Modern Nautilus and presumably most fossil nautiloids can move vertically by protruding or retracting their fleshy bodies and thereby varying the amount of water displaced. However, forms with greatly restricted apertures, like the genera cited above, apparently had no such provision, and presumably they were relatively inactive and were feeble swimmers.

The habits of coiled nautiloids, whether or not they were involute, must have been comparable to those of modern Nautilus. Although comparatively little is known about the details of the life habits of Nautilus, almost certainly representatives of that genus are not particularly good swimmers. The weight and general configuration of their shells would be prohibitive to rapid locomotion. They are believed to spend a considerable portion of their time hovering over beds of crustaceans upon which they feed.

During adolescence the mixochoanitic cephalopods developed long slender conchs, which would seem to indicate that they were crawlers. These conchs were curved longitudinally and therefore it would have been almost impossible for the animals which bore them to have swum backwards by jet propulsion and controlled the direction of their progression. However, when the animals reached maturity they are believed to have broken off the early stages of the phragmacone and thus removed much of the impediment to rapid and straight progression. Such truncation however necessitated the development of a few large camerae or gas chambers next to the living chamber to serve as buoys, and this will perhaps account for the globular form assumed by the early mixochoanites. Perfection was not attained however by these early forms for they apparently had two serious handicaps: first, when the animal came to rest its conch must naturally have assumed a vertical position with the aperture down (cf. modern *Spirula*); and, second, its globular form must have retarded its passage through the water. The first of these handicaps was surmounted by the development of long, deep dorsal saddles in the adoral septa (the ones that were retained after truncation), so that the phragmacone (buoy) was extended all along the dorsal part of the conch and the weight of the animal's body was distributed all along the ventral. The second handicap was overcome by what superficially appears to be a reversal in evolution in that the conch tended to become long and narrow again, but this time it assumed a spindle-like or fusiform shape, which is particularly advantageous for subaqueous progression.

The shells of the Paleozoic ammonoids were relatively light in construction, which seems to be an adaptation for swimming. The septa of these forms were crenulate, which strengthened the shells greatly without the addition of much weight. Strength achieved in this way would allow the creatures to withstand the varying pressures encountered with changes of depth--it would not, however, protect them against concussions, and therefore it seems probable that these animals lived in the zones that were relatively free from wave-action. As Schindewolf (1930) has pointed out, there seems to be no good reason to believe that E. Perna was correct when in 1915 he assumed "für evolute Goniatiten eine nektoplanktonische Lebenweise, für involute eine benthonische."

It should perhaps be noted that almost no Paleozoic cephalopods lost their bilateral symmetry, as did certain of the Mesozoic forms, and therefore presumably none of them became immobile. Uncoiling forms like *Lituites* probably represent a reversion from swimming to crawling habits.

In many cases we can derive considerable information in regard to the paleoecology of any group of organisms from a study of the associated faunas. In the Early Paleozoic deposits cephalopods are commonly found associated with heavy-shelled benthonic animals, indicating that the entire fauna lived in relatively shallow water. Foerste (1936) has recently stated that where Early Paleozoic cephalopods are abundant so are the mobile gastropods but not the sedentary brachiopods, corals, and bryozoans. However, it has been our observation that in the Upper Ordovician of northwestern United States the remains of nautiloids, mobile gastropods, and corals are all very common and all occur together. This association is particularly noticeable in the near-shore deposits like the Lander sandstone member of the Bighorn formation, and it may well be that the abundant fauna of this thin sandstone epresents a heterogeneous mixture of forms which lived near the shore and those which lived farther out but whose remains washed into the near-shore zones. However, in the Middle Silurian rocks of the Upper Mississippi Valley both cephalopods and corals are common, and as stated above the cephalopods are most abundant on the flanks of certain of the bioherms where the remains of many types of sedentary animals are to be found in quantity. Ruedemann (1934) has noted that nautiloids occur in Silurian graptolite shales in both this country and England. Also, in certain of the Devonian rocks of Iowa, for example, in the Cedar Valley formation, cephalopods, brachiopods, corals, etc. occur in close association. Relatively recently Troedsson (1926) has stated that in "several horizons of the Baltic Orthoceras limestone the bedding planes are crowded with straight cephalopods thrown together parallel to each other. Sometimes they are even weathered before embedding. In one *Endoceras* from Kinnekulle, now kept in the collections of Stockholms Högskola, the camerae are filled with mud and the dorsal side weathered down to a plane surface; this is overgrown by sessile animals, among others two basal parts of a crinoid (similar to *Aspidocrinus*), indicating that the mud filling was consolidated before the last embedding of the fossil. Briefly speaking, a great many observations show that the Orthoceras limestone is not only a shallow water deposit but also that the depositing of the rock ceased at times on account of upheaval..... In the Gonioceras Bay limestone [of northern Greenland] most cephalopods are weathered on their dorsal side before embedding, as is seen in *Leurorthoceras* and *Gonioceras holtedahli*. The same weathering has also been found in the Cape Calhoun [northern Greenland] specimens, for instance, in *Gonioceras angulatum*. In most instances this weathering cannot be definitely stated because the fossils are almost free from rock."

In America Devonian goniatites are much less common than in Europe, and we are not any too familar with the details of many of the European occurrences. However, it can be stated that in the thick Devonian limestones of central United States goniatites are almost entirely absent, whereas in certain of the shaley rocks of the Appalachian Geosyncline, from New York south to Virginia, they are relatively common. For the most part the prolific ammonoid faunas of the uppermost Devonian of Europe do not occur in North America. Their absence here may be due in part to the fact that over much of our continent the uppermost Devonian is represented by a black shale facies. The Kinderhook goniatite faunas of North America, like those of the lower Upper Devonian (zone of Manticoceras), are, however, surprisingly like those of Europe.

In the Northern Mid-Continent Region the Late Paleozoic goniatites occur in association with shallow water deposits which seem to have been formed fairly close to the shore. In some cases these goniatites occur in limestone but it is generally argillaceous or arenaceous, and apparently it represents a shallow-water deposit which was formed sufficiently close to the shore that it received a considerable amount of land-derived or terrigenous material. In many places in United States and Mexico, at least, where goniatites are found in carbonaceous marine shales they occur in calcareous concretions, in which they are particularly well preserved. It has been suggested that many shells were deposited along with these concretionary shales, but that only those inside the concretions were preserved. In the Cherokee shales of Henry County, Missouri, John Britts Owen has found that cephalopods (both nautiloids and ammonoids) are abundant in the calcareous concretions which locally occur at several horizons, and that only rarely are good specimens to be found outside the concretions. It seems reasonably certain that the presence of the animals was directly or indirectly responsible for the formation of the concretions. The occurrence of some shells outside the concretions and some concretions in which there are no shells might be taken to indicate that it was the fleshy bodies of the creatures that caused the concretions to form. That is, fossils found outside the concretions would then be regarded as shells which were empty when they were buried, and concretions which contain no shells would be explained by assuming that they formed around fleshy bodies which contained no hard-parts. In the Coffeyville formation of Oklahoma the camerae of the cephalopods, which occur in calcareous concretions, are in many cases filled with black viscous petroleum, and ammonoids which contain petroleum have been found in the Union Valley sandstone of Oklahoma.

In many places the faunas of Late Paleozoic carbonaceous shales are composed almost entirely of goniatites. It seems probable that in these areas the bottom of the sea in which the containing beds accumulated was inhospitable and that therefore only nektonic and pelagic organisms are represented. Of course it is possible that the cephalopods did not live in these areas but that their empty shells floated into them after the death of the animals which bore them. However, in many of these cases we find numerous adolescent as well as mature shells which would indicate that the forms were indigenous to the areas in which we now find their remains. In the Caney and Wewoka formations of Oklahoma and in the Sabden shales of northern England many adolescent and mature goniatites occur in close association and along with them we get an abundant molluscan fauna. In general it can be said that goniatites occur in association with molluscan faunas and Professor G. Delépine has informed us that the same is true for European occurrences and that there pelecypods are particularly abundant in goniatite-bearing beds. Only rarely do goniatites and fusulinids occur in direct association though quite commonly they are to be found in the same formation. However, we have studied one small block of limestone from the Permian of Sicily that contains both cephalopods and fusulinids and Dr. G. A. Doutkevitch has observed the same association in rare instances in the Permain of the Urals and Central Asia. It seems apparent that in general fusulinids and ammonoids represent distinct facies and that the few exceptions are probably due to specimens being washed into an environment in which normally they did not live. Nautiloids also are rare in Late Paleozoic goniatite faunas and are generally limited to a few ubiquitous types like Metacoceras and Coloceras. The fact that ammonoid and nautiloid faunas generally do not occur together may be explained by assuming that the two types require different ecological conditions or by assuming that the ammonoids are more active than the nautiloids and either ate them or ate the food on which they otherwise would have subsisted. This lack of general association of the two groups is well emphasized in the Late Paleozoic of the Mid-Continent Region for in Texas ammonoids are abundant whereas in Nebraska and Wyoming they are almost entirely lacking though nautiloids are fairly common. The fact that nautiloids and not ammonoids were able to thrive in the northern portion of the Mid-Continent Late Paleozoic seas may have been due to a subnormal salinity of those seas. This conclusion would be entirely in harmony with the general belief that nautiloids were always less specialized and therefore better able to adapt themselves to changing conditions than ammonoids.

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