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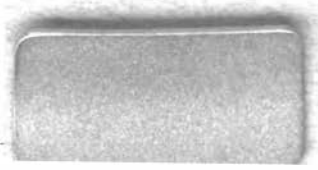
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DIVISION OF GEOLOGY AND GEOGRAPHY

WASHINGTON, D. C.

REPORT OF THE COMMITTEE ON PALEOECOLOGY

1935-1936

(Appendix J of Annual Report of Division)

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REPORT OF THE COMMITTEE ON PALEOECOLOGY

ORGANISMS AND THEIR ENVIRONMENT

By

W. H. Twenhofel
(University of Wisconsin)

Every organism lives where it does because the combined impact of all the environmental conditions permits it to live there. The relations thus existing between an organism and its environment constitute that division of biological science termed ecology. It can not be doubted that environmental or ecologic relations have influenced organisms since their first appearance. Past environmental relations are termed paleoecology. Existing ecologic relations have received considerable study, but the field is still essentially unexplored. Not a great deal is known of the ecologic relations of past organisms.

The matter of ecology is extremely complex and the factors that compose the physical and chemical environment are very numerous. Each grade of the temperature range has its influence on the distribution of organisms; likewise light, cloudiness, humidity, moisture, elevation, composition of the medium, character of the substratum, and other factors are equally important. On plants the acidity and alkalinity of the soil have great influence. Certain plants require soils with a low P_h before they will live; others must have soil of high alkalinity. As plants constitute the fundamental food of animals, the soil characters thus ultimately influence the distribution of animals. In waters temperature, depth, clearness, agitation, character of the bottom and the quality and quantity of the dissolved materials have large influence. In addition there are biologic factors which are almost as numerous as there are kinds of organisms. With this great number of variables, it follows, of course, that there are hosts of combinations - to each of these within the limits of life some organisms are adapted. When the combinations change, either because of the appearance of a new factor, or the dropping out of one, the consequences are immediate reactions in the organic associations to meet the new conditions. The ultimate result may be a complete change in the constitution of an organic group.

The statement given in the first sentence of this paper should have the validity of an axiom. Nevertheless, until recently, little attention has been given to paleoecologic relations by American paleontologists and stratigraphers. Correlations have not been made between certain formational units because of the absence of common species, or because of only a few. This inability to correlate did not necessarily prove unlike time relations, as was generally assumed, but just as likely unlike environments. In some instances the percentage basis has been used in the attempt to correlate in bland disregard of the fact that, if this basis were used in correlation of deposits of the present sea-bottom, it could readily be proven that the sediments and associated organisms on two different areas of the sea-bottom, which are known to be of the same age, are not of the same age; a reasoning as fallaceous as that of the algebraic problem by which it can be shown

- 2 -

that 2 is equal to zero. Many occurrences are known where closely adjacent areas of the sea-bottom have almost totally different populations and in some instances these areas are remarkably close together on the present bottom. When two deposits of the geologic column have been found to hold pretty much the same organisms it has been assumed that the two deposits have synchronous time relations. It is equally, if not more, valid to assume that the two deposits were laid down in similar environments and may actually be somewhat different in age.

Animals of the sea, like plants on the land, organize themselves into communities of which the individuals are adapted to each other so that each constitutes a definite cog in the economy of the association. The principle of animal communities was strongly emphasized in 1914 by Petersen on the basis of work done by him and his associates in Danish waters, the principle applying specifically to the waters about Zealand and in the Kattegat and Skagerrak. Petersen (1) distinguished at least eight well-defined animal communities of which each was differentiated from the others by "characteristic animals" belonging to the mollusks and the echinoderms.

Among the physical factors found important by Petersen were the character of the bottom, clearness of the waters, temperature, salinity, and depth. Some of these factors are not independent, as for instance, temperature to some extent is dependent upon depth. Some organisms and some animal communities seem to be essentially independent of the physical factors of the environment and yet these were not found to have general distribution. The answer was found in the biological factor whereby certain animal communities can not exist in the face of competition of other animal communities and in the illustration given by Petersen it is stated that the Macoma animal community is essentially independent of many physical conditions, but, nevertheless, it does not have general distribution over the bottom. Its boundary limits are determined by the competition of the Venus community against the pressure of which the Macoma community must retreat. When the distribution of the animal communities in Danish waters was placed upon a map it was found that these communities form belts more or less parallel to the shore as descent is made from shallow to deep water, thus showing that distance from the shore and depth are two of the fundamental factors controlling distribution and that these in turn determine or modify the intensities of such other factors as temperature, turbidity, and character of the bottom.

It is doubtful if all of the environmental factors that bear on any marine animal community are at all well understood or even known. The factors are obviously many in addition to the more apparent ones of depth, salinity, temperature, turbidity, and character of the bottom. It seems probable that no one is fully informed relatively to all the environmental factors that impinge upon any marine animal organism. The oysters and edible clams may form possible exceptions. The same statement may be made relatively to the undomesticated animals and plants of the land.

Slight physical changes are often adequate to totally eliminate growth of plants at a place. Each plant serves as the protector and food supply of

(1) Petersen, C.G.J., The animal communities of the sea-bottom and their importance for marine zoogeography, Rept.Danish Biological Station, vol.21 (1913), pp.1-68; The sea-bottom and its production of fish food, vol.23 (1918), pp. 1-62.

- 3 -

other organisms of which each in turn serves other organisms in a similar ca-
pacity. If any plant of a land community is eliminated a long chain of con-
sequences is initiated which may ultimately lead to complete transformation
of the animal community supported by a plant community into another of quite
different personnel. The chain of consequences leads from one organism to
another and ultimately to the submicroscopic organisms so that the impact of
an initial single elimination may ultimately affect the elimination of every
organism in the community. While this may be an exaggerated statement, it is
felt that in some way the welfare of every organism in any community is to some
degree tied up with that of all other members of the community. Thus, the
modification of an animal community may ultimately be caused by some non-appar-
ent factor that vitally affected an insignificant member of an adjacent plant
community. Eliminate the gooseberry and currant from a region, the white pine
blister is at the same time eliminated, and the white pine thrives and it may
thus set up a white pine forest with submergence of other forest trees and
develop a fauna dependent upon the white pine and its associates. Many plants
can not grow in soils unless these contain certain fungi with which the plants
have symbiotic relationships.

It seems probable that a somewhat similar setup exists for every an-
imal community, that the presence of each member in some way affects every
other member and that the various members of the community exist in the re-
lationship they do because a condition of equilibrium has been reached with
respect to the biological relationships, the physical characters existing in
the medium in which they live, and the character of the substratum. This con-
dition of equilibrium is one that may easily be disturbed and when such takes
place an entirely new setup may be produced.

The more important generalizations that may be drawn from the work of
Petersen and his associates were assembled by Miss Elles (1) which in summary
with some modifications are as follows:

1. Certain characteristic animal communities exist under certain phys-
ical conditions with the community coextensive with the same physical condi-
tions unless restricted by biological factors.

2. Changes in physical conditions are accompanied by changes in the
character and composition of the animal community.

3. The important physical changes correlated with changes in the animal
communities are those of temperature, salinity, clearness of water, and depth.
Depth seems to be important chiefly in that it serves as a factor in control of
temperature, light, character of the bottom, and quietness of water. There
are few of the physical factors that are not more or less related to changes
in other factors.

4. Certain organisms may be found in more than one community.

5. The characteristic animals of communities living in waters of

(1) Elles, G. L., Evolutionary palaeontology in relation to the Lower Paleo-
zoic rocks, Rept. Brit. Assoc. Adv. Science (1924), pp. 83-107.

- 4 -

different depths are so greatly different that few or none of these animals are common to two communities.

Petersen distinguished five animal communities in the North Kattegat in depths ranging from 7 to 50 meters which with depth, character of the bottom and temperature of the water are as follows:

Echinocardium community, 7 meters, fine sand.

Echinocardium-Turritella, 12-19 meters, dark sand with fine detritus.

Brissopsis-Turritella-Echinocardium, 24.5 meters, fine sand, 14^OC.

Brissopsis-Turritella, 35 meters, gray clay, 13.4^OC.

Brissopsis-Nucula, 50-52 meters, light clay, $8-6^O$C.

In another section were found these communities:

Macoma, 8 meters, pure sand, 18.5^OC.

Calcarea, 18 meters, light clay and sand, 10.1^OC.

Modiola-Echinoderm, 18 meters, coarse gravel with sand, clay and pebbles, 10.3^OC.

The geographical distribution of the various animal communities on the nearly level bottom is:

Macoma, on all southern coasts of Denmark and in Baltic.

Abra, especially in the belt sea and in the fiords.

Venus, open sandy coasts of the Kattegat and the North Sea.

Echinocardium-Filiformis, at intermediate depths in the Kattegat.

Brissopsis-Chiajei, deepest parts of the Kattegat.

Brissopsis-Sarsii, deeper parts of the Skagerrak.

Amphilepis-Pecten, deepest water of the Skagerrak.

Haploops, locally in southeastern Kattegat.

It is stated that transition stages between the successive communities are doubtless found, but that they seem to be narrow.

After organisms are dead, the shells and tests are inorganic sediments and are thus subject to the fates to which inorganic sediments may be subjected. If the shells and tests contain gases of any kind or are buoyed up

by other means they may be floated and ultimately sink to the bottom and become entombed in sediments of environments to which they are in no way related. Such not infrequently must have happened to the shells of the ancient cephalopods and protozoans. The very small and very fragile tests with large surface to volume as exemplified by the ancient graptolites and modern radiolaria must frequently have been entombed in places where their owners could not have lived. If the builders of the skeletal structures lived in waters agitated by waves and currents there is strong likelihood that these skeletal structures would be carried to other bottoms less agitated by waves and currents. This to some extent might integrate the faunal complex, but it would also carry the shells to environments when the shell builders did not live.

That conditions like those of the present sea-bottom existed over every sea-bottom of the past can hardly be doubted. That parts of the ancient sea-bottoms of unlike physical and chemical characters held animal communities totally different must also have been the case. There should also be ready acceptance that sea-bottoms alike as to depth, temperature, and other physical and chemical factors, may have had different animal communities because of variations of the biological factors. Little seems to be known of the biological factors of the existing marine environments and essentially nothing of those of ancient environments. It is a field that invites research. There needs to be assembled an overwhelmingly convincing array of facts proving that organisms of the past were controlled by the physical and chemical ecological factors and relationships just as it is known that most modern organisms are. This should be so completely done that stratigraphic problems can not be seen except through the inlet of ecology. As essentially nothing is known of the biological factors in the ancient environments, it follows, of course, that there is little information to assemble and only the future may show what may be done in this field. There also needs to be assembled information showing the extent to which the waves and currents distribute dead shells so that this factor in the distribution of fossil shells may be placed on some basis other than that of surmise.

In a recent study of the Lower Devonian Reefton Beds of New Zealand Allan (1) has attempted to apply the teachings of Petersen to the solution of some of the problems of Lower Devonian stratigraphy. He has adopted the principle of animal communities with "characteristic members" as having application to the marine faunas of the past as well as to those of the present and he has decided that the "characteristic animals" of the animal communities of the present are represented in the past by the characteristic animals of a fauna. He states "All attempts in the past to delineate Lower Devonian provinces have failed to take into consideration the fundamental factor of the physical environment, and its resultant impress upon the sediments, and upon the contained faunas." He suggests "that facies has been the dominant element in the distribution of the marine faunas of this period. The evidence points to a cosmopolitan fauna, which, as today, would vary with such factors as temperature, light, salinity, food conditions and so on" and that it is "possible to state that the Reefton fauna is most closely related to that of the same age in Western Europe not because of geographical station,

(1) Allan, R. S., The fauna of the Reefton Beds, Geol. Surv. New Zealand, Pal. Bull., no. 14 (1935), pp. 1-72.

- 6 -

but because in both areas the same physical conditions were identical, and
that those parts of the cosmopolitan fauna inhabiting those areas being sub-
jected to, or stimulated by, a similar set of environmental controls, are
therefore closely related in their characteristic fossils." He further
states that "the Reefton fauna differs in its characteristic members from
those of the Bokkeveld beds in South Africa not because one area is isolated
from the other, but because the environment was dissimilar in the two areas."
The above quotations give a clear statement of the application of the rela-
tionship of paleoecology to the problems of stratigraphy, a relationship
to which most stratigraphers have given general acquiescence and almost as
fully have generally ignored. In other connections the writer has called
attention to the need for consideration of the environment in connection
with sedimentation and stratigraphy and has given illustrations supporting
the relationship (1). There is no need to repeat these illustrations beyond
stating that on Anticosti Island, where the entire section can be seen on
opposite sides of the island - on the north side from 10 to 35 miles nearer
the coasts of the Silurian and the Ordovician seas than on the south, the
case is clear and the close connection of the organisms contained in the
sediments with the environmental conditions as portrayed in the character
of the sediments is excellently shown. Limestones on the south side carry
one fauna or animal community and equivalent sandstones on the north side
have a different fauna or animal community. Something of like relations may
be seen in the Gotland section of the Baltic Sea where there is a close re-
lationship between faunas and the sediments in which they are contained.

With respect to fauna and lithology, which is pretty much the same
thing as fauna and physical environment, Allan states as a general conclu-
sion that "Apart from certain cosmopolitan groups, the characteristic fossils
of this age (Lower Emsian, Lower Devonian) differ according to the facies of
the strata containing them. Four main Lower Emsian communities are recog-
nized - viz., the fauna of the Oriskanian of Maryland in calcareous strata;
the gaspensis-fauna of the Moose River sandstone of Maine in arenaceous
strata; the antarcticus-fauna of South American in argillaceous strata; and
the hercyniae-fauna of western Europe in psammo-pelitic strata.

"The chief condition governing the distribution of these Lower Emsian
faunas appears to have been the degree of clearness of the water. It is,
however, impossible to assess the value of such factors as salinity, temper-
ature, and competition."

"Where the physical conditions are identical, even in widely separ-
ated areas, the characteristic fossils of the same age are identical or
closely related."

"Certain Lower Devonian types appear to have had a wide range of
physical stability, and occur in strata of various facies." "These types
....are of great importance in that they allow correlation from facies to
facies."

Some of the problems of the New York Devonian stratigraphy have been

(1) Twenhofel, W. H., Environment in sedimentation and stratigraphy, Bull.
    Geol. Soc. Am., vol. 42 (1931), pp. 407-424.

attacked in recent years on the basis of differing environmental conditions
with somewhat surprising results. It has been shown that some of the Devon-
ian units previously considered sequential to other units are lateral there-
to. Chadwick (1) states "As, on any sea-coast sector, unlike societies co-
exist at different depths, so each faunal assemblage of this upper Devonian
terrane embraces several contemporaneous congeries, straying at times (lat-
erally) into each others door-yards, and all holding the same definite time
value." Cooper (2) has shown that the Devonian Hamilton of western New York
changes lithology when traced eastward from black shales in the west to ul-
timately pass into red beds, largely sandstones, formerly assigned to the
Catskill. The change in lithology is accompanied by a very great increase
in thickness. With the changes in lithology, that is, expressions of the
changes in the environment, there are corresponding faunal changes. Chad-
wick (3), in addition, states that the Chemung instead of being above the
Portage is really a part of it and that in proceeding northwestward from
southeastern New York one passes from the continental sand facies of "Pocono"
lithology into the red muds and sands of the Catskill. These lose the red
color in the presence of much organic matter and become the Chemung with a
marine fauna of brachiopods. Passing into the region farther northwestward
where the conditions of deposition were those of deeper water the Chemung
changes into the fine muds of the Naples with a molluscan fauna of fossil
shells. Farther northwestward this passes into the black shales of the
Geneseo. Caster (4) (after Clarke) has shown that the Naples shale fauna
of the Geneseo Valley is the equivalent of the lighter colored shale fauna
of the Ithaca region (Ithaca shale) and that into this there is inserted
in the Chenango Valley the tongue of sandstone containing the Oneonta fauna.

It is suspected that when the application of paleoecology to the other
parts of the New York section and also other Appalachian region sections has
been fully made that many of the various troughs and barriers so much in
vogue in the later decades of the nineteenth century and the first two dec-
ades of this century will vanish into the discard and in their place will
come explanations based on paleoecology. It is also thought that there will
be some modifications of the sections of the Cincinnati Arch and the Nash-
ville Dome when application of paleoecology has been made to interpretation
of these strata and it is suggested that it may ultimately be shown that
some units now placed in sequence to others will be found to be lateral there-
to. Other places where paleoecology should be given serious consideration

(1) Chadwick, G. H., Faunal differentiation in the Upper Devonian, Bull.
    Geol. Soc. Am., vol. 46 (1935), p. 307.

(2) Cooper, G. A., Stratigraphy of the Hamilton Group of New York, Am. Jour.
    Sci., vol. 19 (1930) pp. 116-134, 214-236; Stratigraphy of the Hamilton
    Group of eastern New York. Ibid., vol. 26 (1933), pp. 557-551.

(3) Chadwick, G. H., Chemung is Portage, Bull. Geol. Soc. Am., vol. 46
    (1935), pp. 343-354.

(4) Caster, K. E., Guide Book, no. 4, XVIth Intern. Geol. Cong. (1932),
    p. 46.

- 8 -

is about the Wisconsin Arch, the Ozark Dome, the Central Mineral Region of Texas, the Arbuckle Region, and in any other region where it seems obvious that different conditions of environment were probable.

The work of Philip King and the petroleum geologists (1) in unraveling the geology of the Permian strata of southwest Texas has shown that salt, gypsum, dolomite, shale and sandstone are lateral to each other and were all deposited in the Permian sea at the same time, each representing a different environment of deposition. "The faunal assemblage varies from one rock type to another." "Each faunal aggregate appears to have been adapted to a limited environment, the influence of which is also expressed by the nature of the rock laid down at the time" (P. B. King). There are deposits of lagoons, the confining barriers, the open sea and the coastal plain, the range being from continental deposits to deposits more or less typically marine.

There is much to be learned and hardly a beginning has been made. The ancient methods and doctrines of stratigraphy are so deeply ingrained that one almost instinctively tends to correlation by comparison of fossils with little or no attempt to see what the fossils really mean and what may have been the relations on the ancient sea-bottom. Deposits have been identified as estuarine, lagoonal, or of some other environment with little appreciation if such were the case that there must have been marginal deposits of another environment. Lately, Foerste (2) has stated that in the Paleozoic strata "as far as present observations permit it appears that wherever cephalopods are abundant the mobile gastropods also are relatively common, while the sedentary brachiopods, corals, and bryozoans are less common than elsewhere. On the contrary, where the brachiopods, corals, and bryozoans are common, cephalopods usually are rare."

"Possibly segregation is due occasionally to violent storms resulting in strong ocean currents which sweep along the mobile forms into areas where sedentary life is less abundant, overwhelming these mobile forms with muddy and arenaceous deposits. This might account for local segregations of cephalopods and gastropods, but would not account for their relative absence over large areas." It is suggested by the writer that there may have been some competitive biological relationship whereby the presence of the mobile forms is connected with the absence of the sedentary forms. At Graf, Iowa, in a rather well-known section of the Maquoketa, there are a half dozen feet of impure limestone in the middle of the section that are literally jammed with Orthoceras socialis, but this is the only place in the upper Mississippi Valley known to the writer where this species is abundant. It is rare elsewhere. Almost no other organisms are present.

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(1) King, P. B., and King, R. E., The Pennsylvanian and Permian stratigraphy of the Glass Mountains, Univ. Texas Bull., 2801 (1918), p. 139; Lloyd, E.R., Capitan limestone and associated formations, Bull. Am. Assoc. Petroleum Geol., vol. 13 (1929), pp. 645-659; King, P.B., Permian stratigraphy of of trans-Pecos, Texas, Bull.Geol.Soc.Am.,vol. 45 (1934), pp. 720-723.

(2) Foerste, A. F., Silurian cephalopods of the Port Daniel Area on Gaspé Peninsula, in eastern Canada, Bull. Denison Univ., vol. 31 (1936), p. 26.

What is the meaning? The abundance or rarity can only be ascribed to the paleoecologic relations of the time.

The foregoing is intended to be a brief introduction to this report of the Committee on Paleoecology. It is hoped that each great group of organisms may be considered in detail. In the articles that follow there are considered the paleoecology of the vertebrates by E. C. Case of the University of Michigan; the arthropods by P. E. Raymond of Harvard University, with an appendix on the habits of the trilobites by W. E. Schevill; the sponges by M. W. de Laubenfels of Pasadena Junior College of Pasadena, California; and the paleoecology of the Paleozoic plants by C. A. Arnold of the University of Michigan. It is hoped that the paleoecology of the other great groups may be considered in a later report.

PALEOECOLOGY OF THE VERTEBRATES

By

E. C. Case
(University of Michigan)

Paleoecology deals with life in relation to its environment; this relation is so far reaching and inclusive that it necessarily includes any connotation of the term paleobiology. The environment of any organism is the sum of its contacts with the external world, either organic or inorganic. Whether the environment be determinant in any degree of the development of life, or simply selective of forms whose development has been otherwise determined, it is dominant among the factors that influence and control life. No phase of biology, neo- or paleo-, can be considered without reckoning with the environment.

The paleoecology of the vertebrates must deal with much the same environment which governed the associated invertebrate animals and plants. The response was conditioned by factors inherent in the vertebrates themselves. Any discussion that would even approach a satisfactory content would be far too extended for a report of this character. The following is therefore cast in outline form with very limited amount of explanatory and illustrative material included.

The environment of extinct vertebrates must be inferred from so much of the morphology as is revealed by the skeletons or such part of them as is recovered; from the associated remnants of life; and from the matrix in which the fossils are found.

All such questions as may involve interpretation of the physiological response (function) must necessarily be answered by our ability to make such an interpretation and at present this is so limited that any definite conclusions are distressingly meagre.

All such questions as may depend upon a psychological response, which become increasingly important with the development of the nervous system, are unanswerable and at present no path is open which could lead to any answer.

The three categories of interpretable material, the morphology of the animal considered, the associated fossils (representing the organic environment), and the matrix in which the skeleton is found (representing the inorganic environment), are briefly considered below.

Morphology

The utterly fallacious idea that from a single bone the expert can restore a complete skeleton lingers with as much persistence and with as disastrous results as does the fallacious Biogenetic law. In both the

seductive elements of truth are present, expressed in broad generalities
which lead the uninstructed and the incautious to faulty and incongruous
conclusions.

Certain structures are commonly correlated and it is usually possible
to infer from the structure of tooth, limb or foot something of the habits
of an animal and hence something of its environment. The hooves and char-
acteristic teeth of a grazing or browsing animal are commonly associated
and from these and less obvious characters of the skeleton the paleoecol-
ogist may infer broad grass lands, sparsely watered, and enemies that demand
speed for escape, things to be checked by the remains of associated animals
and by the nature of the matrix in which the skeleton is entombed. For ex-
ceptions to such correlation one has but to recall Moropus or Agriochoerus
in both of which the teeth, limbs and axial skeleton suggest a grazing or
browsing ungulate but in which the toes terminate in efficient claws. Either
we must imagine an animal strange to the environment and present by chance,
or an animal capable of living in the environment of grazing creatures but
controlled by an, at least, partially different set of factors; both ex-
planations have been made, the latter being the most probable.

In South America the limbs and hooves of the Miocene Thoatherium are
almost identical with those of the horse and are even more specialized along
the same line being "absolutely single toed, more completely monodactyl than
any horse" (W. B. Scott, Land Mammals of the Western Hemisphere, p. 248) but
the animal belongs to a different order of mammals. "If the proterotheres
were not perissodactyla, as I am convinced they were not, they offered one
of the most remarkable examples of convergent evolution among mammals yet
made known." (W. B. Scott, idem).

It is obvious that this last instance may be taken as a lesson in
at least two ways. Similar correlation with the environment produced struc-
tures almost identical in animals so different that they must be placed in
separate orders, and both indicate a hard, grass land. Secondly, such cor-
relation has not produced similarity in more than the limbs; the structure
of the teeth and skull are radically different in the North American and
South American forms. Only the broadest deductions as to the nature of the
environment could be drawn from the form and proportions of the limbs.

An example drawn from living marsupials will emphasize the diffi-
culties and possibilities of misinterpretation. The arboreal kangaroo,
Dendrolagus, of New Guinea and Queensland differs from the ground kangaroo,
Macropus, only in the proportions of the limbs and minor structures of the
posterior feet. Waterhouse says the two differ in no "essential part of
the structure." Macropus lives on the "arid, withered savannahs and prairies
of Australia" (Vogt) and feeds upon harsh vegetation such as the herb called
"kangaroo grass." Dendrolagus is entirely arboreal, living upon "leaves,
bark and fruit" in the "dense, tropical forests" (Flower and Lydekker).
Surely no such radical difference of environment could be inferred from an
inspection of the skeleton.

As an illustration from another group, suffice it to say that the

- 12 -

author identified one described genus and species of Stegocephalian and two
described genera and three species of Phytosaur in the first complete denti-
tion of the lower jaw discovered; so different we e the teeth in different
portions of the jaw that different names, taxonomic position and inferred
habits were excusably assigned to isolated teeth.

Any assured inference as to food or habits of feeding is impossible
from the form of the teeth in such animals as the well-known Diadectes of
the Permian, or the very imperfectly known Trilophosaurus, a cotylosaurian
reptile, or Colognathus (Xenognathus), a fish, both from the Triassic.
Instances such as these could be cited in large numbers; these are suffi-
cient to make evident that beyond certain very broad lines no inference as
to habit or habitat may be drawn with certainty from the fragmentary, or
even complete, remains of the extinct vertebrates.

Associated Fossils

To the paleontologist whose interests are at all directed to the study of
his material as once living forms, the collection of any specimen involves
a study of every phase of its occurrence that may reveal something of its
oecological relations during life. The author in his desire to obtain such
information attempted to place upon paper in categorical form a list of such
observations as he should make upon the discovery of a specimen and in the
course of its excavation. This statement with the necessary explanatory
matter grew to a manuscript of 87 typewritten pages with over eighty cita-
tions to literature, later published as the "Elements of a Paleogeographical
Problem," in Publication 283 of the Carnegie Institution of Washington, 1919.

It is evident that if a reasoned list of necessary observations can
grow to such a length anything of the kind in this report must be a mere
reference to other material. There are, however, certain major points that
may well be called to attention.

The position of the specimen with regard to its natural habitat.

This must in part be considered in relation to the enclosing matrix
but must also be considered with relation to associated animals and plants.

A moment's consideration will make apparent the fact that many verte-
brate animals can hardly be preserved in their natural habitat. Petrefaction
requires burial under water or in water-bearing layers and for arboreal,
aerial, dry land, and any but benthonic forms of aquatic life, this requires
that bones found petrified must have been transported from their natural
habitat to a region of radically different conditions.

The transportation of a cadaver, distended by the gases of decomposi-
tion, by moving water is the simplest and most obvious of many means by which
such a change of locus can be accomplished. It is surely rather idle to spec-
ulate upon the habits and habitat of a fish whose structure implies a nectonic

- 13 -

life from the mud in which the cadaver was buried. Posthumous movement, perhaps horizontally by moving current, and certainly vertical by sinking to the bottom, have brought the remains into a position and relation which were entirely foreign to the activities of its life. Much inconsequential literature has been based on just such relations, notably the discussions concerning the fish found in the black shales of Triassic and Permian age.

The author may here cite his own rather extensive, rather hopeless, and certainly fruitless efforts to discover some morphological structure or combination of structures which would enable him to determine whether a fish was marine, brackish, or fresh-water in habit. Much futile discussion has gathered around just this point - the fish were fresh-water forms washed out to sea by flood either before or after death, were marine forms killed by sudden influx of fresh-water, were estuarine and destroyed by an untoward degree of salt concentration in the water. Knowing as we do how closely some fish are restricted to a definite salt content in the water and how tolerant are others, it is evident that we are here dealing with a problem of physiological response, not reflected in structure, which at the present is beyond the possibility of solution.

> "By the hoof of the Wild Goat up-tossed
> From the cliff where She lay in the sun,
> Fell the stone
> To the tarn where the daylight is lost."

Changes as great in degree and by causes as accidental have certainly occurred to many a residuum of life.

Who can doubt that the bones of the bison and western Pronghorn Antelope lie buried in the delta of the Mississippi River associated with the debris of marine life, and how much more frequent must be such occurrences at the mouths of shorter and more impetuous streams on abrupt coast lines.

Dr. Carl Wiman of the University of Upsala has described Stegocephalians from marine shales in Spitzbergen. By every implication of the physiology modern amphibians, both in ovum and after hatching, are intolerant of sea water even in extreme dilution. It is true that at least two cases of tolerance have been reported but one of these is discredited. The author was assured in conversation by Dr. Wiman that the specimens were apparently found in their natural habitat, i.e., they were marine stegocephalians, but there is so much against this, and the possibility of posthumous transportation so great, that the author cannot give credence to Dr. Wiman's position.

If the amphibia and certain fishes are fresh-water aquatic forms their distribution is fully as acceptable evidence of land connections as is that of any terrestrial animal.

The tests of whether a specimen is preserved in its natural habitat are in part in the matrix, discussed below, in part in the associated fossils,

- 14 -

and in part in the condition of the specimen. If the skeleton is complete
or approximately complete it may safely be assumed that it has been buried
where it died, or if isolated bones are found unworn it may be assumed that
they have not been transported a great distance. In general all fossil ma-
terial of any locality is apt to be of the same character and with the same
history, but this is not necessarily true. Instances may be cited of the
two conditions.

In fossiliferous areas or localities such as the Big Badlands of
South Dakota, the Agate Spring bone beds of Nebraska, or the bone beds at
Pikermi in Greece, the nature of the bones indicates preservation in or near
the place of death. In the growing river flood-plain of Oligocene time,
which is now the Big Badlands, the carcasses of the animals commonly found
burial in the river beds or mud holes which were an integral part of their
habitat. In the other two cases the large assemblage of unworn material
has been explained as due to the destruction of a herd of animals of one or
more kinds which were fleeing in stampede, perhaps before a grass fire.

A different condition occurs in the Permo-Carboniferous beds in the
Karroo area of South Africa and in north-central Texas. In the first the
skeletons of the great Pareiasaurians are mostly commonly found complete or
nearly so, with the bones in normal relation. In the same zone and area the
great Deinocephalians are represented by imperfect skulls and isolated bones
frequently in bad condition. In the Texas region the skeletons of certain
reptiles and amphibians are not uncommonly complete, or with a considerable
portion in association. One form, Edaphosaurus, with high dorsal spines
provided with lateral knobs or branches, is rarely found except as isolated
bones or fragments of the easily recognizable spines. The suggestion has
been made that the Deinocephalians and Edaphosaurians were upland forms,
and that their bones reached the swamps, lagoons and river beds only after
prolonged transportation and consequent disintegration. The only locality
in which there is a close association of the two groups of American Permian
forms is the Archer Creek Bone Bed which has every suggestion of having been
something like a salt lick where animals gathered from long distances, or
the sole surviving pool in a very considerable area, the last resort of
animals of every kind for the necessary water.

A similar illustration occurs in the Pleistocene deposits of Michigan
and adjacent states. The author has records of over eighty Mastodons and
only seventeen elephants from Michigan, this is perhaps a quarter of all that
have been found, but the proportions would probably remain approximately the
same. The records of Mastodons show them to have been found in areas or
deposits that were swamps or lowlands. The Mastodon was a browsing animal,
at home in such a habitat. The Elephant, a grazing animal with teeth adapted
to grinding hard grasses and grains, was of the upland and its remains were
destroyed by subaerial and organic processes before they could be buried and
preserved. A single specimen of an elephant is known which approaches com-
pletion, this was found on a layer of sand beneath eight feet of marl. One
imagines a sick or wounded animal seeking and dying upon the bank of an
expanding glacial lake. Other traces of the elephant are isolated, and

- 15 -

generally fragmentary, teeth or bones usually found in gravel pits, indicating transportation of the elements of disintegrated skeletons.

If it is determined that a group of animals has been preserved in its natural habitat the paleoecologist is concerned with the balance of the organic elements of the habitat, the adjustment of the herbivorous, carnivorous, carrion-eating, malacophagous, durophagous, and other forms to their food supply. Any suggestion as to diet must be checked by evidence of the presence of such a food supply. The form of the teeth indicates much but only too often the indications are vague or erroneous and only too often the form of the teeth leaves but a question. The teeth of Diadectes, of Trilophosaurus, of Ptilodus, among many instances, give but the vaguest hints of the habitual food. The author has fed a certain mule, whose teeth were adapted to grazing, soft watermelon rind and has had his tarpaulin chewed by the same mule. He has fed a squirrel soft peppermint candy and his family cat soft, boiled peas. These are abnormalities and would be absurd if they were not facts; I doubt if they are more absurd than some attempts to interpret food habits from the form of the teeth, unchecked by other evidence.

The unending strife for food, the battle between the eater and the eaten, can be, must be, read by the paleoecologist. Defense may be by active or passive resistance. Flight or 'offensive defense,' or passive donning of armor, may all be employed but any method implies a reason for its adoption, and every advance in either method implies increased power of attack from the eater. The process of such adjustment is continuous and leads to a specialization that is the shortest road to extinction. In the case of armored forms versus armed forms, it has led invariably to but one result; in every group and in every age the story has been repeated. As the armor grew heavier, the projectile and propulsive force grew stronger. Tooth and claw and muscular power have been balanced against ever heavier and more complete armor. The invariable result has been the extinction of both. The same history has been written and is being written by warring men, one dares prophecy the same result.

A most interesting fact has been demonstrated by the process of paleontological discovery. The progress of the plant world to modern types has consistently outdistanced the animal world. The modern deciduous trees shaded the Mesozoic reptiles in their later days. The Permian plants sheltered the late Pennsylvanian fauna and the suggestion of plant precedence is carried back even to Devonian time. The paleobotanist and the paleozoologist have been at variance as to the boundaries of eras and periods. The paleoecologist who would see rightly must not flinch from the vision of a Tyrannosaurus stalking through a forest of modern aspect. Certainly if such a vision were granted the paleoecologist would give thanks for the towering height of the elm or the sturdiness of some giant oak.

There is ample evidence of bacterial decay; there is, except in more recent forms, little evidence of bacterial disease. We can not doubt that bacteria, protozoans and parasites were present early in geological time and wrought help and hindrance as they do today. Evidence of such things is blind or lacking. The bacteriologists and pathologists the author has consulted

- 16 -

are reluctant to recognize these things from the effect produced or from
such evidence as can be presented. Dr. Novy refuses to recognize bacteria
"until I can see them divide." It is, however, a suggestive coincidence
that the blood of living reptiles is abundantly supplied, "swarms," with
protozoan forms, various forms of which are the cause of communicable dis-
eases of virulent and fatal character, and that the blood-sucking flies
which are the usual carriers of such protozoans appeared in the Jurassic,
preceding by a reasonable interval the extinction of highly specialized
reptiles at the end of the Cretaceous.

The attitude of the skeleton is frequently of significance. In the
case of the dinosaurs at the Dinosaur National Monument in Utah the heavier
body dragging on the bottom of the moving waters permitted the long neck and
the long tail to advance with the current. This not only gives the direction
of the current but explains in many cases the peculiar attitude in which many
long-necked and long-tailed forms are found, an attitude which has been in-
terpreted as due to an opisthotonic death spasm such as occurs in fatal cases
of tetanus and in poisoning by strychnine. The later explanation has not
received much support but is mentioned here as one of the ramifications of
paleobiology and paleoecology.

Another illustration of the attempt to read function from form is
the suggested explanation of the common specialization of giantism which
occurs in almost every group near the time of extinction. The term giant-
ism is, of course, used relatively. Normally minute animals may have giant
species or individuals, as well as normally much larger animals. It has
been noticed and commented upon that in giant forms of vertebrates the seat
of the pituitary gland is relatively enlarged, even to monstrous size. This
suggestion has been followed by the late Doctor Nopsca who has shown a very
probable relation between this endocrine gland and the size of the animal.
He has brought forward evidence to show that giant forms have uniformly a
pituitary gland of large size and that the structure of the animal shows ab-
normalities of proportionate growth such as occur in cases of enlarged pitu-
itary in humans, the condition called acromegally. That such a condition may
be endemic in a population of vertebrates is shown by the discovery that a
considerable number of the skeletons excavated on the site of one of the long
lost and forgotten early colonies of Northmen in Greenland, showed obvious
evidence of acromegally. The cause of acromegally is obscure, but if it
shall turn out to be due to some lack or excess of material in the food sup-
ply, as the thyroid is affected by lack of iodine, the relation of giantism
to the environment is obvious. This may seem a far fetched hypothesis but
to those who have paid any attention to the conditions of growth it is very
conceivable that such a small thing as ionic concentration in the water
which the animal inhabits or imbibes may be the determinant factor in its
development and fate.

An instance of the many attempts to translate form and form rela-
tions into terms of biology is the constant effort to arrange series in the
different groups by the proportions of the body. Such efforts have culmi-
nated in Osborn's Monograph upon the Titanotheres and Gregory's recent ef-
forts to generalize upon the development of the vertebrate skull. These

gentlemen have arranged various homologous skeletal elements according to
proportions and have assumed that their assemblage is in accordance with
the true course of phylogenetic development, and have finally attempted an
explanation of their series based upon genetic principles.

It is admitted that the series selected are plausible and are sus-
ceptible of explanation upon biological principles, but it remains to be
proven that the series formed are phylogenetic and not morphological, that
the serial differences are the result of phylogenetic change and not acci-
dental similarities. It remains to be proven that sufficient material has
been recovered to justify the generalizations pronounced or that other
characters than those selected might not lead to entirely discordant re-
sults. It is but another and perhaps more sophisticated attempt to read
the processes of life, physiology, from the form of but a single region of
the animal body. The difficulties in the path of the various attempts to
bridge the gap between the dead remains and the living animal is reflected
in the abundant coinage of new terms which, one and all, have a decided
morphological connotation, "budding," "reduplication," "metamerism," "rec-
tigradation," "aristogenesis," "polymerism," "differentiation," "allometry,"
"heterogony," "acceleration and retardation," "anisomerism." (The terms
are quoted from a late paper by Gregory). One has the uneasy sensation
of viewing a brittle, artificial edifice lacking the elasticity and re-
silience of life.

The assemblage of incidents and suggestions in the preceding pages
is not, and is not intended to be, even approximately, definitive or ex-
haustive but merely serves to direct attention to a few of the innumerable
factors of paleoecology which influence life.

The Matrix

For the vast majority of land animals and for all fish except
benthonic forms, the matrix of entombment is radically different from the
normal environment of the animal. As a generality it may be said that the
matrix of the aquatic amphibia most nearly represents the environment of
the living thing, but even this is subject to exception.

The only cases in which terrestrial vertebrates are preserved in
a matrix directly picturing the environment is where forms are buried in
the sand dunes of a desert, or covered by other local material, as in the
miring of animals in swamps and quicksands. In other cases the animal
either perishes in some body of water or the carcass or bones are washed
into it. Deposits in a body of water are composed of material which only
secondarily and imperfectly records the character of the adjacent land.
Even in the quick deposition in a pond or lake the rills and streams which
carry the material to it have exercised a sorting and selective action,
leaving behind the coarse and conveying the finer, in various degrees de-
pendent upon the velocity of the current and the volume of the stream.

In larger streams, as rivers, the sorting and selection is more ef-
fective. It is obvious that the carcass of a bison carried miles from the

- 18 -

place of death and cast upon a sand bar of the Missouri River, or floated far out upon the flood plain in time of high water and buried in the silt of some slough or backwater will leave the skeleton in a position where the matrix gives no hint of the normal environment. Knowing the bison and the Missouri River and its course, the situation is clearly understood, but given even the perfect skeleton of an unknown Eocene animal with generalized structure and found in a small exposure of what was perhaps, or probably, an Eocene river bed, the realities of the situation as a problem are more apparent.

Within a few square yards of exposure of uniform clay in the Big Badlands, the author recovered remains of a rhinoceros, a three-toed horse, a hawk, a mouse-like rodent, and a catfish. Any accurate interpretation of the assemblage would be difficult.

The salmon migrate far up the streams emptying into the Pacific and penetrate to the utmost sources of the waters. Thousands die of exhaustion after spawning or from injury. The skeleton of a salmon far above sea level in the muck of an upland forest is understandable. Knowing nothing of the habits of a Paleozoic or Mesozoic fish, the peculiarities of the matrix and the associated fossils might be very puzzling and lead to sad misinterpretation.

In younger deposits the matrix may in most cases be taken to be what it was, in color, texture and content, when deposited. In more ancient deposits the chances that the matrix is unchanged are far less. It would be a most serious error to assume habits and habitat from the appearance and condition of the matrix in many cases.

Take the classic example of the red beds which have been so often, so brilliantly and so inconclusively explained. The color has been explained by original deposition of ferric oxide, by secondary infiltration, by dehydration due to the pressure of incumbent beds, by change in ground water level. It has even been assumed that red beds mean some definite condition and that red beds are uniformly red, instead of yellow, green, blue, purple and all intermediate shades. Any interpretation based on the assumption that the matrix has remained unaltered in all its characters since first deposited is the first error of the veriest tyro.

The black shales, recurrent in several geological periods, are equally difficult. Explained in many ways by different authors, they have been but recently reinterpreted by Doctor Ruedemann.

A recent examination of the various possible processes of pyritization shows how undependable is any assumption that pyritized fossils, or fossils accompanied by pyrite in the matrix, mean foul bottom conditions during the life of the fauna; or that the sulfides were derived from the decay of the animal bodies, or indeed, that the pyrite is in any way necessarily connected with the life of the animals preserved fossil.

The chemical, mineralogical and physical character of any matrix is

subject to change and possibly profound change without destroying the evidence of life. The author possesses fragmentary remains of Baculites and Placenticeras shells and Plesiosaur bones from the Cretaceous of southwestern Minnesota which are completely converted into bright red haematite. Metamorphism (in the sense of Van Hise - "any change in any rock") and structural changes are responsible for a part of the peculiar conditions. It may be truly said, and it has certainly been true with the author, that a vertebrate paleontologist can not write of his faunas without a copy of Van Hise's Metamorphism, Clark's Data of Geochemistry, Twenhofel's Treatise on Sedimentation, near his hand.

As the remains of terrestrial animals are most commonly found in subaqueous deposits, the environment can only be read in the debris from that environment. Any aggraded area is to the land as the negative is to a photographic print. The alteration of material by weathering before transportation, the selective action of the water before deposition, the alteration of material as it lies below the surface of either stagnant or moving water, the extraction or addition of material by the waters, all these and many more confuse the record.

The physical condition of the sediments presents many confusing problems. The author has submitted sand and sandstone samples to experts to determine their origin, whether aerial or subaquatic, only to be told in several cases that it was windblown sand that had finally been blown into the water. The question remained whether the fossils were to be interpreted in correlation with the sand as a terrestrial or as a subaqueous sediment. It is interesting to note that most of the vertebrates of the Upper Triassic in the western part of the United States are found in river, delta or pool deposits; every implication of these deposits is that they were derived from an arid land. For the Stegocephalia and the Phytosaurs, which latter are so crocodile-like in structure as to leave little doubt of their habitat, the deposits and the animals are well correlated but it is a little difficult to picture the adjacent lands, because the remains of terrestrial animals and plants are so limited.

The occasional pool or water course in the desert of today is crowded with hydrophytic plants. Spalding long ago cited the presence of Willow and Arrowleaves in stream courses whose banks were sparsely dotted with Xerophytes, Greasewood, Chapparal, Cactus and so forth. The author has seen a large pool caused by the overflow of an irrigating ditch in extreme southwestern Wyoming crowded with wading and swimming birds and circled by gulls. A small exposure of either environment within a quarter of a mile of each other would lead to curious conclusions.

The author asks leave to quote an instance reported many years since.

"The author again calls to notice his experience on an area of wind-blown sand in a desert portion of Arizona, where he found ripple-marks, stalks of thin-leaved vegetation, obscure insect tracks, and a series of sinuous convolute markings where some insect burrowing beneath the burning sand had thrown up a

long trail indistinguishable from worm tracks at the bottom of a
shallow body of water. He went over much of the area most care-
fully, certainly over far more than is normally exposed in a geo-
logical, outcrop, and utterly failed to find a single criterion
that would have prevented him from pronouncing the exposure an old
sea-bottom or flood-plain if it had been found fossil, and yet the
formation was going on before his very eyes on a sun-stricken bit
of desert. The insect burrows would have unhesitatingly been called
worm tracks; the insect tracks might have been made by any one of
many aquatic forms instead of beetles or grasshoppers; the vegeta-
tion once fallen and recorded only as an imprint could not be told
from a bit of aquatic vegetation. The wind ripples upon most care-
ful analysis might have revealed their origin, but again, in the
author's experience, sand collected in a delta deposit has been pro-
nounced dunesand which had drifted into the water." (1)

In the Museum of Paleontology of the University of Michigan there is
a collection of many Stegocephalian skulls and other closely intermingled
bones recovered from Triassic deposits in western Texas. The skulls and
the clavicles and interclavicles showing peculiarly sharp and intricate
sculpture, the needle-like teeth, are perfect and the paper thin edges of
certain bones are intact; they are as perfectly preserved as any fossil ma-
terial the author has seen. These bones were recovered from a coarse sand-
stone with some bits ranging up to 18 to 20 millimeters in diameter and with
some, but slight, evidence of current sorting. How the fragile bones and
teeth and the sculpture could have been preserved in such material is dif-
ficult to imagine. Perhaps a quicksand, but a hydrostatic pressure that
could have given such coarse material the qualities of a quicksand would
have prevented the sinking of the flat bodies. No motion of the material
seems possible, the bones would otherwise have been worn or destroyed as in
a mill.

An abundance of instances could be cited by every worker, drawn from
his own experience, illustrating the direction of inquiry and observation
and the multitude of pitfalls that await the worker in paleoecology. It is
certainly apparent that only an approximation to the correct appreciation of
any environment can be realized by methods now at the command of any worker.
The most wholesome advice that can be given is that the inevitable separa-
tion of the two schools of paleontology be recognized and provided for by
adequate training of the workers to come.

The stratigrapher and areal geologist is concerned with the fossils
only as recognition symbols and time markers. The paleobiologist is con-
cerned with them as records of a life that has passed. No matter how clear-
ly the stratigrapher recognizes the biologic principles involved his work is
on other lines and the biologic factors are remote from his consciousness in
solving any problem. The paleobiologist is equally unready with the factors
that are of prime importance to the stratigrapher.

The condition is already well recognized in Europe where chairs of
paleobiology, divisions of paleobiology, and even large buildings are devoted
to the interpretation of past life and the location of the beds in time is

(1) Case, E.C., The Environment of Vertebrate Life in the Late Paleozoic in
North America. Carnegie Instit. of Washington, Publ. no.283 (1919), pp.
42-43.

but one of many necessary tools.

As written above, the fission is inevitable, the two schools must be prepared to afford mutual criticism and aid, the paleontologist in training must be prepared to know the elements of both phases of the work, but choose one for intensive training - and provision must be made for such intensive training.

- 22 -

PALEOECOLOGY OF THE ARTHROPODA

By

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Any account of the ecology of the extinct arthropods must of necessity be a tentative one. Relatively little has been written on the subject. Knowledge of fossil arthropods is so incomplete that most students of the phylum are still preoccupied by taxonomic work. Until the species are described, paleontologists will have little time to devote to the study of the relationship of the various animals to each other and to their environment. Such paleoecological information as is available at the present time relates chiefly to the habits, and secondarily to the habitats, of various arthropods. Inferences are drawn from the morphology of the fossils, and from the lithological characteristics of the strata in which they are found. In most instances our knowledge of the morphological characteristics is incomplete, and there is considerable difference of opinion about the environment of deposition of certain sediments.

In this first report, the writer may perhaps be pardoned if he refers more fully to problems which require solution, than to actual accomplishments.

Trilobites

Most students are agreed that the Trilobita are the most primitive of the Crustacea. They have been extinct since the end of the Paleozoic, and have no near relatives among existing animals. More than 99 per cent of them are incompletely known, for it is but rarely that specimens retaining the appendages are found. Until more actual facts have been accumulated, present ideas as to habits and habitats must be regarded as speculations rather than deductions. Such speculations, as had been printed up to 1918 have been reviewed by the writer. A series of papers by Rudolph Richter appeared too late to be incorporated in my paper. These are critically reviewed in the manuscript article by William E. Schevill, appended to this report.

The broad, depressed, flattened shell of the trilobite suggests that almost all members of this group were primarily dwellers in the zone at or near the sea floor. The shape of the test suggests that most were equally efficient as crawlers or swimmers. This suggestion is borne out by the shape of the appendages of such forms as retain them. All appendages, other than those whose function was tactile, are biramous, the lower, (inner) ones suitable for use in crawling or burrowing, the outer for respiration, or possibly for swimming. Only by means of detailed study of the appendages is it possible to infer habits. For example, the flattened segments of the posterior endopodites of Triarthrus suggest that it was a more successful swimmer than crawler, whereas the stout limbs of Neolenus indicate that

it was able to walk about on its "toes," i.e., the terminal spines of each endopodite. Trails on Upper Cambrian sandstones (Proticnites) were probably made by similar trilobites.

The blind or nearly sightless trinucleids probably sought their food in the superficial layers of the bottom ooze, ploughing along just beneath the surface of the mud, as does Limulus. The broad head-shield and bowed endopodites are very similar to those of the modern horse-shoe crab. Other trilobites, particularly those which are more or less shovel-faced and high-eyed, probably prowled about in the mud seeking food. That any trilobites were strictly burrowing animals, in the sense that they excavated and lived in burrows, is doubtful. Walcott described certain Cambrian fossils as trilobitan burrows, but none has ever been found with a trilobite still within it, or with any markings which could have been produced by no other animals than trilobites. Most burrows and trails are more or less permanent puzzles. However ingenious the explanations of their origin, absolute proof is always lacking.

It should perhaps be emphasized that the trilobites were no more specialized in their habits than they were in their structure. When one says that Cryptolithus was a burrowing animal, one does not mean that it could not crawl or swim. It means merely that Cryptolithus seems to have been somewhat better adapted for burrowing that most of the other trilobites. To cite another instance, the writer has argued that the broad axial lobe and large pygidium of Isotelus indicate that this animal was capable of propelling itself forward and backward in lobster-like fashion, using the pygidium as a swimming telson. But I have also described trails on sandstone which I interpreted as having been made by an Isotelus crawling on its gnathobases. No trilobite yet known is so specialized as to suggest that it was confined to a single environment. Nor does the history of any genus or family indicate any progressive adaptation to a particular sort of environment. Possibly a case in exception to this sweeping statement might be made for the Homalonotinæ, for the Devonian Dipleura certainly has a very much wider axial lobe than was (probably) possessed by its as yet unknown Cambrian Calymene-like ancestors. But the Ordovician members of the sub-family had axial lobes proportionally as wide as those of Dipleura. The Calymeniæ and the Homalonotinæ from earliest Ordovician times appear to have had different habits. As the writer interprets their structure, the former were crawlers, the latter dominantly swimmers. But there is nothing to suggest that with the passage of time the one group produced better crawlers, or the other better swimmers. As a matter of fact, the coarse silty and sandy nature of the strata in which Devonian Homalonotinæ are most common, both in Eastern North America and Germany, suggest that the later members of the group were chiefly crawlers.

It is an as yet unsolved problem as to how much weight is to be given to the nature of the sediment in which fossils are found, in judging the habits and actual habitats of the animals when alive. It is true that some genera and species are found only in sandstone, in shale, or in limestone. On the other hand, there are many that are found in all kinds of sedimentary rocks. Calymene and Isotelus, for instance, are just as common in Ordovician sandstones and shales as in limestones, but since Ordovician carbonate rocks

- 24 -

are more widespread than argillaceous ones, most of the specimens one sees
are in limestone.

As a matter of fact, the sandstone, shale, and limestone environ-
ments are probably not so different as the names of the rocks suggest. It
is probably true that most limestone was deposited in relatively warm water,
but it is just as true that sandstone and shale were formed under the same
conditions. Most sandstones were deposited in shallow water, but so were
many shales and most limestones. In judging the nature of the environment
from the sediments, texture is much more important than chemical composition.

Even if this be kept in mind, it may be difficult to infer the orig-
inal conditions from the consolidated sediments. Many a coarse-grained
limestone may have been deposited as grains of almost colloidal proportions.
Two argillaceous shales, equally fine-grained, may contain very different
sorts of fossils, for one may have been deposited under such conditions as
to maintain a relatively firm sea-floor, whereas another may have presented
a fluffy, soft, bottom on which no benthonic life was possible. It is well
known that some modern "sandy" (argillaceous or calcareous) sea-floors teem
with crawling and burrowing animals, whereas others on which the sand is
constantly shifting, are devoid of life.

In some instances, fossil animals do show definitely the effects of
"bottom-control." Perhaps the most striking example is in the Oriskany
fauna. It is well known that the same genera, perhaps the same species of
brachiopods occur in the Oriskany of New York and the Oriskany of Gaspé.
Yet in most instances the species from the thin coarse-grained sandstone
of New York have approximately four times the volume of those found in the
limestone of Canada. The Oriskany of New York and Maryland is noted for
the large and thick shells of its brachiopods. It has been suggested that
the animals "needed" them, to withstand the vigorous wave action near shore.
It is more probable that the animals grew larger because of the greater
supply of food near shore.

As has been intimated, most trilobites could live under a variety
of conditions. Only rarely is the nature of the rock in which they are
found of any significance, at present known, in regard to their habits and
habitat. In support of the first statement it is interesting to compare
the geographic range of Tropidoleptus and Phacops. They are the most abun-
dant fossils of the sandy and shaly Mid-Devonian strata of New York and the
Allegheny plateau, but although Phacops occurs in considerable abundance in
the calcareous Hamilton equivalents in the Mississippi basin, Tropidoleptus
seems to be rare or absent west of New York.

The one instance in which there seems to be a definite correlation
between the type of trilobite and the nature of the sediment is in the fine-
grained black shale and fine-grained black limestone of the Ordovician. The
muds, argillaceous or calcareous, which produced these strata seem to have
been too soft to support any ordinary benthonic fauna; their fossils are,
for the most part, remains of holo- or epiplanktonic, or nectonic creatures,
although there are a few which probably lived on the bottom. The trilobite

- 25 -

fauna is not a large one, but it is interesting in that it contains blind forms such as agnostids, trinucleids, raphiophorids, and dionideids, animals with very large eyes, such as Remopleurides and Robergia, and a very few with normal, medium-sized eyes, chiefly species of Triarthrus.

The natural assumption is that the blind trilobites were either inhabitants of deep seas or dwellers in the mud. This may not be true of all the agnostids, for their remains are not confined to fine-grained shales, but are found in strata of all sorts. It is not to be supposed that all members of so large a group would have the same habits. Each species must be judged by itself. The facial sutures indicate that the ancestors of the raphiophorids had eyes. One judges that they lost their sight through adaptation to life in the aphotic zone, probably in rather deep water. The long glabella and genal spines, coupled with a short and rather feeble body, suggest that this sort of animal would not be very successful in shallow waters, where it would be constantly in danger of getting tangled up with sea-weeds. Probably they puttered about, swimming feebly, in rather deep water. As for Remopleurides and Robergia, their forms and their tests would suggest a floating existence. However, their very large eyes give one the impression that, like certain modern crustaceans mentioned by Dollo, their natural habitat was deep water, but that they were nocturnal visitors near the surface. Very likely they fed on graptolites, and were rather efficient swimmers. The extraordinarily long hypostoma awaits explanation in terms of function.

Triarthrus was rather a generalized trilobite, at home everywhere, equally good at swimming and crawling. Its constant association with graptolites suggests that they were its favorite food.

The implications of the association of these trilobites with the particular sort of sediments in which their remains are found are perhaps of some interest. After the publication of the "Challenger" reports, geologists became interested in deep-sea deposits, and all such fine-grained sediments as contained Foraminifera or Radiolaria were for a time thought to have been formed at considerable depths. All chalks and fine-grained limestones and shales were generally accepted as deep-sea deposits. Then the pendulum swung back. Geologists found ripple-marks and shrinkage cracks in these so-called oceanic strata, and rather suddenly, about twenty years ago, opinion reached the other extreme; almost all Paleozoic strata, at any rate, were supposed to be of shallow-water origin. Did not the pendulum swing too far? The evidence obtained from lithology and fauna seems to indicate that certain shales and limestones were formed in rather deep water; certainly so deep as to be beyond the depth to which sunlight can penetrate.

Other Arthropods

This report has been devoted particularly to a discussion of trilobites, since they are the arthropods in which the writer has been most interested. Other groups within the phylum present problems even more important. Probably of greatest general interest is the discussion as to whether the merostomes inhabited fresh or salt waters during the Ordovician and Silurian parts of their history. A detailed discussion of the evidence will be reserved till a

later date. As is well known, T. C. Chamberlin, Marjorie O'Connell, and
A. W. Grabau have maintained that the eurypterids were, from the beginning
of their history, fresh-water animals, which implies, of course, that they
were the first fresh-water arthropods. If, as Chamberlin has suggested,
life originated in the soil and organisms first evolved in fresh water,
the eurypterids may have been the first and most primitive of arthropods.
The discussion becomes doubly important, if we accept Romer's ideas about
the influence of the eurypterids upon the armor of the ostracoderms, early
fish-like creatures. This group, like the merostomes, was according to
Chamberlin, of fresh-water origin.

The general form of the O'Connell-Grabau argument is well known.
Specimens of Ordovician eurypterids are found in marine sediments, but all
are very fragmentary, hence the animals lived in rivers, and pieces of their
skeletons were occasionally carried into the sea. Specimens found in late
Silurian strata are remarkably complete, which shows that the animals were
at home in fresh water, and were killed immediately if by any chance they
were carried by currents into salt water.

Many paleontologists still believe, despite the facts so ably mar-
shalled in support of this theory, that the eurypterids were originally
marine and did not become adapted to life in fresh water till late Silurian
or early Devonian times. The mere fact that their remains are found in
marine strata is, however, no proof of the theory that they were buried
where they lived. Since some new evidence on this question is just now
coming to light, further discussion is best postponed to a later report.

The question about the habitat of the eurypterids is largely academic,
for their only possible descendants, the scorpions, had become terrestrial
by Pennsylvanian times. Much more important, although almost nothing has
been written about it, is the history of those animals which for convenience
are termed the schizopods, late Paleozoic crustaceans which were presumably
ancestral to amphipods, isopods, anaspides, and malacostracans. We know
practically nothing of the history of this group till its sudden appearance
in the Carboniferous, at which time all its members appear to have been in-
habitants of fresh water. One of the lines, that of the anaspides, appears
to have remained in fresh water, being represented today by small and rare
animals in Australia and Tasmania. The other groups are, and have been,
so far as the geological record tells us, chiefly marine since Triassic
times. Some isopods and some malacostraceans now living are fresh water or
terrestrial, but such forms are rare as compared with their marine relations.
How are we to interpret this record? Were the ancestors of the modern crus-
taceans marine animals which shifted their habitat to the fresh waters in
late Paleozoic times, only to return to the seas during the Triassic? If
so, do the modern fresh water and air breathing members represent a second
migration to the land? These groups are so poorly represented as fossils
that we may never know the full history. If the modern Crustacea originated
in fresh water, then the Arthropoda must be polyphyletic, for the oldest
trilobites and branchipods are certainly marine.

One history, which is fairly well documented, and which may parallel
that of the recent Crustacea, is that of the Xiphosura. If our ideas about
relationships are correct, these animals were marine from Mid-Cambrian till
late Silurian times, fresh water during the Carboniferous and Permian, and

marine again from the Triassic to the present. Of course it may be that
there were marine as well as non-marine representatives of the group in
existence in Carboniferous times, but if so, why have their remains not
been found? We know thousands of marine for every fresh-water Carbonifer-
ous fossil.

This report touches upon but a few of the subjects which are involved
in the study of the paleoecology of the Arthropoda.

An attempt has been made to show that something can be inferred as
to the possible habits and habitats of the trilobites, and attention has
been called to the need for further investigation of some other groups. A
brief bibliography is appended.

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(Appendix to "Paleoecology
of the Arthropoda")

HABITS OF TRILOBITES

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Alimentary Apparatus and Diet

In 1919 A. Born described the cephalic musculature of trilobites as
his studies of Chasmops odini Eichwald led him to see it (6)*. Aside from
his discussion of the muscles of the cephalic appendages, he maintained that
the entire space between the hypostoma and the glabella was empty of ali-
mentary tract, being occupied to its exclusion by a web of muscles operat-
ing the hypostoma. This is his interpretation of the interior pustulation
of the frontal lobe, and of the hypostoma.

Schmidt's figures (32*, pl. II, figs. 2, 3, 10, 16 and pl. V, figs.
1, 7, 9) of this and allied species show two rows of scars diverging from
the center of the frontal lobe and extending towards the anterior edge. He
does not illustrate their meeting after a sharp inward turn near this border,
or the group of three or four dots, also made known by Born, a little to the
rear. Born correlated this pattern with scars on the interior of the hypo-
stoma which lie directly beneath, and suggested the existence of a web of
muscles stretched between them, which would have restricted the alimentary
tract to the space above and behind the mouth (6, fig. 4, p. 166, or 30,
fig. 15, p. 87), which he places at the distal end of the hypostoma**.

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* See bibliography, pp. 41-43.

** So do Walcott (37, pl. IV, fig. 6), Beecher (4, pl. V, fig. 11), and Raymond
(23, p. 69, and fig. 24, p. 81). Its situation in the Apodidae (the speci-
mens examined were of Lepidurus productus (Kröyer)), and in cirriped nauplii
(10, pl. V, fig. 7), is within the hypostoma, which in the Apodidae, for
example, covers also the large mandibles. As Beecher says (4, p. 96) the
appendages of Triarthrus were doubtless displaced backwards with the col-
lapse of the ventral membrane against the dorsal shell, -- why not, there-
fore, the metastoma as well? (For evidence that the mouth could well have
been in the lee of the hypostoma, v. Raymond (23, pp. 94-95, fig. 30). By
allowing for this one might restore the mouth, still in front of the meta-
stoma, but also in front of the distal tip of the hypostoma. Something
of this sort is shown in Jaekel's restorations (18, fig. 28, p. 168; cf. also
pl. VI) and in Richter's (30, fig. 16, p. 86)

- 30 -

Richter (30), replying to Born's paper, begins by citing a number of genera, mostly Phacopidae, which show comparable markings: Chasmops, Pterygometopus, Phacops, Trimerocephalus, Dianops, Phacopidella, Acaste, Asteropyge, Dalmanites, Dalmanitina, Cheirurus, Ceraurus, Cryptolithus, Solenopleura, and Scutellum. The last three are mentioned as not being strikingly comparable. He also restricts the discussion to the frontal lobe of the glabella, and the hypostoma, ruling out any other of Barrande's "impressions auxiliaires," but recognizing the possibility that any other glabellar impressions of this nature may be connected with the stomach (as a matter of fact some of his examples - e.g. Ceraurus milleranus Miller and Gurley (24, pl. I, fig. 7) are of post-frontal markings). Great emphasis is laid on the "reversal of the impression." His figure 6, p. 80 (30) shows an internal cast of the head of Dianops anophthalmus (Frech) on which the glabellar furrows are raised ribs. The word "impression" is generally used by Richter to include both pustules and puncta, with their occasional linear extension as ribs (keels) or grooves.

In some forms there is but one median impression, which may, as in Dalmanitina socialis (Barrande), be a short groove instead of a circular depression; in others, as in Dalmanites cristata Barrande and D. hausmanni (Brongniart), there are three punctate impressions, outlining the angle as seen on, e.g., Chasmops. (These and others, up to five "fossettes," may be seen in Barrande's atlas (3, pl. 24-26)). Richter illustrates examples not only of more than five impressions, but also of more than two rows, as on Acaste hemi (Richter) and Crotalocephalus gibbus (Beyrich). The impressions need not be arranged in diverging rows, but may be scattered over the median sector of the frontal lobe, though in many cases, as in Acaste downingiae (Murchison), the impressions within the two main rows are not, as Richter admits, to be distinguished from the general surface granulation.

So far all Richter's examples have been from the Proparia (he suggests some closer congenetic relationship between the Cheiruridae and the Phacopidae on this account). However, he also cites Moberg's impressions i and k (21, p. 296, fig. 1) on Nileus armadillo Dalman, as well as the lines on the glabella of Cryptolithus tessellatus Green, which Ruedemann (31, fig. 46, p. 147, and pl. 35, fig. 7) calls part of the "facial sutures" (and which Raymond (23) ignores in his discussion of Ruedemann's interpretation and elsewhere). Richter mentions also the nuchal tubercle of "some species of Scutellum, Nileus, etc." but considers the frontal impressions of the Phacopidae as sufficient for the present discussion, possibly in view of the great inclusiveness of the "etc." He further notices that these aligned (or at least especially restricted) impressions are observable on animals with otherwise smooth tests and that as the surface of the glabella becomes roughened, the special impressions are lost. This might be construed to mean that he considered the general granulose sculpture of the shell to serve as attachment for a diffuse muscle web, whereas the distinctly localized impressions indicated a more localized musculature, though he does not expressly say so. However, he avoids this imputation by following Born, who distinguishes the muscle scars by their independence of the "Durchporung der sonstigen Schale;" this distinction is supported by the

Report of the Committee on Paleoecology, 1935-1936: Presented at the Annual Meeting of the Division of Geology and Geography, National Research Council, Ma

http://www.nap.edu/catalog.php?record_id=18676

- 31 -

nature of muscle insertions in the test of Recent macruran Decapoda.

Richter's customary appeal to living forms leads him to a much more grateful interpretation of these controversial markings, that of muscles radiating from the alimentary tract not only to the dorsal test, but also to the hypostoma. These, in Recent crustacea, assist in peristalsis by opposing the action of annular (contracting muscles surrounding the canal (e.g., 10, p. 90, and pl. VI, fig. 6; this and other samples from Chun's "Atlantis" are of lepadid nauplii). Richter's fig. 9 (30, p. 83) is a sketch, after Chun (10, pl. V, fig. 7), showing that the only direct muscular (or ligamentous) connection between the dorsal test and the hypostoma attaches to the latter very near its proximal edge. Corroboration is found in Bernard's figure 13, page 56 (5), a diagram of the cephalic musculature of Apus. Such an arrangement would be ample for the operation of the labrum, which after all functioned chiefly, no doubt, as an operculum - - any grasping or holding would be performed by the paired appendages; and yet consider, for example, the power our biceps can apply to the forearm, where it exerts about the same amount of leverage. Richter does not, however, go into this, and instead calls attention to another drawing of Chun's (10, fig. 10, pl. 6) depicting on the dorsal surface of another lepadid nauplius a group of muscle scars roughly similar in plan to the frontal pattern of Chasmops, etc. Since these fasten the flexors of the tail and caudal spine such slight weight as they may have as testimony is in favor of Born's interpretation.

Richter adequately explains the correspondence in ground plan of the frontal and hypostomal markings (as on Chasmops) by pointing out the similar dorsal and ventral silhouettes of the reflexed alimentary canal. That is, from the ventral mouth the slender oesophagus widens forward into the stomach, whereas dorsally the wide stomach narrows behind into the intestine, this constriction being controlled, as he puts it, by the mandibular muscles, as well as by the dorsal furrows, which may also have supported radial gastric muscles. Thus the similarity and correspondence of these impressions need not - could scarcely, under the circumstances - imply direct connection between them, but merely a mirroring of their distribution to the walls of the alimentary canal. Born noted considerable irregularity and occasional slight asymmetry in these scar patterns, even in a single species; Richter cites this as additional evidence that the muscles ran to a (relatively more variable) soft part rather than to a (more constant) member of the skeleton.

It would appear, however, that one might interpret some, at least, of these muscles as hypostomal; surely one need not, like Richter in his diagram (30, fig. 16, p. 87), restrict them all to the radials. Indeed, one could, without overdoing, appropriate several of the anterior of these scars to the levatores hypostomae, for, as may be seen in Friederich Schmidt's figures (32, plates II and V), the "divergierende Punktreihen" are to a great extent on the steep fore part of the frontal lobe. Contrary to Richter's statement, there is in many cases considerable frontal space unoccupied by stomach, even in some of those nauplii to which he refers (vide 10, pl. V-IX, XI-XIII). Bernard's sketch of Apus (5, fig. 13, p. 56) shows how hypostomal muscles may run to the dorsal test even though the stomach is far forward; they even seem to be somewhat deflected by the stomach. Moreover, would it not be reasonable to suggest that such prominent scars indicate the place of attachment of the

- 32 -

more vigorous muscles rather than the more delicate peristaltic ones? However, as Richter points out, Gerstaecker (15, p. 960) and Chun (10, p. 177) remark that not only may a muscle starting from one insertion spread into a more or less diffuse web and so reach to more than one attachment, but more than one muscle may be attached to one scar.

That the glabella had as its chief function the housing of the stomach and associated important organs, has long been the natural belief of most students, Born being very nearly alone in his conclusions and quite so in his reasons therefor. Richter mentions Brögger's observation (7, pp. 22 f.) that the glabella and hypostoma constituted an admirable capsule for the reception of such vital organs, and further calls attention to the gibbous inferior surface of such dorsally flat trilobites as Scutellum palifer (Barrande).*

Although he agrees with most in repudiating the idea that swollen glabellae were gas bladders (esp. Deiphon and other bulbous Cheirurids), Richter accepts the proposition that oil or lumps of fat may have been present (such being found often in Recent primitive Crustacea); since these are interpreted as being hydrostatically functional, the globules of oil or fat may have served to produce a buoyant effect. There is of course no basis for this speculation.

An interesting point is Richter's absolute reversal of our generally accepted conception of the diet of the trilobites as inferred from their glabellar volume. We customarily consider the forms with large glabellae to have been given to mixed or even wholly vegetarian diet (e.g., Raymond, 23, pp. 81 and 103), while less expanded types have been considered to have been of carnivorous habits. Richter once more refers to Gerstaecker (14, pp. 89 f.) to prove just the opposite; apparently Recent herbivorous Crustacea have a simple, elongate, undifferentiated alimentary canal (vegetarianism may, however, lead to a widening of the tract if there is no possibility of lengthening it), whereas the carnivorous show a regional differentiation into a gizzard-like proventriculum and stomach proper, which are greatly expanded. Richter believes, moreover, that pronounced frontal muscle scars indicate a double stomach (apparently connecting the vigorous activity of the "gastric mill" with the exceptional development of the muscle insertions), and that this further confirms the conception that the Phacopidae, along with their cousins the Cheiruridae, were the most powerful and active of trilobites.

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*By way of offering further evidence of the presence of the stomach in the glabella Richter gives an original interpretation of one of Walcott's slices of Ceraurus pleurexanthemus Green (United States National Museum No. 68386, 38, pl. 104, fig. 5 - cf. Richter, 30, figs. 13-14, p. 86) - an interpretation far more attractive than Walcott's own. Richter compares it with a similar section through the head of a Recent lepadid nauplius (Claus, 11, pl. III, fig. 11) which shows a strikingly similar T-section in the collapsed stomach, which might quite conceivably be preserved as a cast in a fossil.

- 33 -

Locomotion

The locomotion of the trilobite may be considered under three main heads: benthonic, including any form of progression in or on a substratum; nektonic; and planktonic.

Following Dollo (12) and von Staff and Reck (35), themselves over-enthusiastic followers of Dollo, some rather glittering generalities on trilobite locomotion have found their way into the literature. It was largely on this account that Richter wrote the first of a series of papers (27); in it he demonstrated some of the fallacies that had gained widespread acceptance, chiefly in relation to swimming; he touched upon some of the benthonic aspects in the second (28).

He complains that trilobites with pointed cephalic and pygidial shields have been grouped together as progressing by "Fortstacheln," i.e., by pushing themselves along with their spikes or points (forms with spinose pleura, etc., are also included). Thus Dalmanites limulurus (Green) has been described as progressing (cf. occurrences of Dalmanites hausmanni (Brongniart) in the Devonian of Dworetz - vide 3, pl. 24, fig. 1; - and a more graceful individual (No. 1816) on exhibition in the Museum of Comparative Zoology) by fixing its caudal spine in the substratum and pushing with its body. This theory is allegedly (28, p. 24, and 35, p. 146) derived from Lockwood (20), but not rightly, for that author merely described the auxiliary use by the horse-shoe crab of its telson (which, incidentally, is movably articulated, as contrasted with the fixed spine of trilobites) in digging, where it aids by supplying a helpful purchase. Limulus walks, or crawls, if you will, normally by means of the legs. It is possible that trilobites with pointed or spinose pleura in the thorax, with the ends directed downwards, could progress some-what after the fashion of the snake, which may be said to walk upon the ends of its ribs, but it does seem over-elaborate, to conjure up such modes of progression when there are known appendages fully equal to the task of transportation. There is no dearth of other functions to assign to spines, which, as Richter says, must have been useful both as passive protection and hydro-dynamically.

Richter rightly repudiates the interpretation of the greatly developed cephalic brims* on the Harpedidae and Trinucleidae as "mud-shoes" or "slime-skates." As he remarks, there could be no need for any such contrivance - he cites Leander, on its ten steeply inclined legs, walking easily on the softest ooze; the idea of a natatory animal bogging in the sea floor does not seem very reasonable. Richter's chief point is stronger: such an apparatus, used as a skid, would be more a hindrance than a help. In the first place the surface is decidedly non-skid, although the irregularities might readily pick up enough mud to make it slippery; moreover, it is only exceptionally of a form adapted for skiing. Consider especially Cryptolithus, whose brim slopes steeply downwards to the front as well as to the sides; it is true that the distal row of pores is on a more or less horizontal border, but this is narrow and is bounded by two abrupt carinae. This structure is comparable to the

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*This word seems better than the bodily transfer of Barrande's "limbe" which so easily makes for misunderstanding in English; cf. Bather.

carapace of Limulus. The situation in the case of Harpes is similar, though
there are species in which the under surface of the brim is approximately
flat or convex downwards. The carinae -- the Rand- and Kämpferleisten of
Richter (26 and 29) -- are much less obstructive than in Cryptolithus, and
in some instances even turned up in front. Richter's profiles (28, p. 26,
fig. 1, and 30, p. 208, fig. 3) are instructive, and suggest the parallel
situation in Cryptolithus; figure b is probably the nearest approach to a
natural position, even for swimming, when the narrower posterior part of the
body, furnished with smaller and weaker appendages, might well tend to droop,
though a is likely if the animal had ploughed into the mud. Many of the
specimens of this species (H. macrocephalus Goldfuss) in the Museum of Com-
parative Zoology are intermediate between a and b.

As to real out-and-out burrowing, like moles or annelids, Richter is
right in objecting that the trilobites were not particularly well adapted.
Among Recent crustacea the burrowers are distinguished by being cylindroid -
at least less depressed than the rest of their kind, e.g., the Isopoda.
He points out that real burrowers make tubular passages, whereas even the
most nearly cylindrical of trilobites, and particularly those generally
called fossorial, would make slit-like tunnels which would readily collapse,
so that even had any ever been made they would probably not have lasted
long enough to be filled with mud or sand and so preserved. The Phacopid-
Cheirurid type has the best cross section for burrowing, and Richter would
not deny it the honors here any more than in other matters, as he has named
it as the most powerful and versatile trilobite type. However, the append-
ages of the Phacops described by Broili (8) are certainly not of the limuloid
type of Cryptolithus.

In the matter of the reflection of fossorial life in the external form,
consider the burrowing crayfish of eastern North America (Cambarus sp.).
This creature looks just like any other non-burrowing crayfish; its tunnels
extend for yards and culminate in the controversial "chimneys" (v., among
others, 1, 2, 33, 34). Perhaps fossorial adaptation among the Crustacea is
largely a matter of psychology!

Thus Richter is undoubtedly justified in saying that such trilobite
burrowing as did occur was undoubtedly a sort of ploughing, like that of
Limulus. (cf. Studer's remark on the similar habit of Serolis, quoted by
Richardson, 25, p. viii.) Even at such shallow depths the Trinucleids with
their long genal spines would have been in some difficulties when it came
to turning (e.g., especially Cryptolithus goldfussi (Barrande)), for the
at best only slightly flexible spines would have tended to keep the animal
on its initial course. In any case really deep tunnelling is unlikely (cf.
also 23, p. 103). As Raymond (loc. cit.) and others have pointed out, it
is probable that many trilobites habitually covered themselves thinly with
loose sediment by way of concealment, as do shrimps and many other Recent
crustaceans; but how an animal so buried as were the Vogdesias at Elgin,
Iowa (13, and 23, p. 102) could spring from ambush is not clear.

In connection with this surficial ploughing one might notice some
of the apparent digging tools mentioned and figured by Richter (28, pp. 41 f.,
figs. 9-13); they include forward-directed points on the hypostoma,

- 35 -

Euproetus cuvieri (Steininger)), epistoma (Homalonotus hippocampus Schwarz),
and ploughshares and denticulate brimlets on the cephala of some Phacopidae.

There has been some controversy over the swimming attitude of tril-
obites - whether they swam with the back up or down. This undoubtedly varied
in different types and at different times. Richter (27, p. 224) says about
all that there is to say about this: such Recent Crustacea as exhibit this
ability (e.g., the Apodidae, the isopod Dynamene, etc.) are generally equal-
ly proficient in either position. It is probably largely a matter of what
the animal is doing at the moment; if in search of food near the surface it
may swim upside down (Raymond, 23, p. 99)

The most likely assumption about the swimming methods of a trilobite
is that they are not much unlike those in use by the most trilobitoid of
living animals. These are in general found among the Isopoda, and it ap-
pears, both from Richter (27) and other sources (I have not been able to
observe any personally) that these customarily swim by means of the legs,
with the body extended. Many, if not most, have broadened or setiferous
swimming feet, or both. The trilobite exopodites approach the various forms
of Recent crustacean pleopods most nearly, - much more so than any known form
of trilobite endopodite. For this reason nearly all authors, except Raymond
(23), interpret the exopodites as the trilobite's swimming feet. In support
of Raymond's branchial explanation may be mentioned these same Isopoda, among
which "the pleopoda are in some cases natatory, but their function is respir-
atory for the most part" (25, pp. 2 f.). Of the six orders of isopods only
one has the pleopods entirely natatory, whereas of the three in which they
are entirely branchial one has them fitted for air-breathing. A member of
this terrestrial group, Oniscus asellus Linné, is, however, mentioned by
Calman (9, p. 201) as using the endopodites in breathing.

Raymond has said, though unfortunately without supporting analogy in
living forms, that trilobites with wide axial lobes probably swam forward by
vertical undulation of the entire body (the fish's method rotated laterally
through ninety degrees), though in his memoir of 1920 (23, p. 99) he speaks
of this as an incident in backward swimming by means, primarily, of downward
strokes of the pygidium. Once Richter suggests such wriggling, but as an
incident to forward swimming primarily by means of the legs, in the case of
Harpes (29, p. 211). This same author (27, pp. 221 f.) implies that Dollo
(12) pictured Deiphon swimming in what Richter believed to be whale-fashion,
i.e., "by sculling or screwing with the pygidium" ("...durch Wricken oder
Schrauben des Schwanzschildes"). Dollo did emphasize the similarity in ap-
pearance between the pygidium of Deiphon and the cetacean tail, but did not
explicitly say that the trilobite swam in this manner. Neither, however,
does the whale. There is in the Cetacea no such caudal musculature as that
to which Richter refers (27, p. 222). In the four longitudinal reentrants
of the posterior part of the vertebral column lie four muscles, the upper
pair of which (cf. the trilobite's extensors) lifts the tail, and the lower
(cf. the flexors) pulls it down. A very gentle and measured movement of
the tail in this manner can propel the animal at a respectable speed*, as
many ocean travellers must have observed in porpoises. Deiphon seems to
have had room enough for a musculature adequate to flap his spare pygidium,
but it is unlikely that it would be a highly efficient propeller.

* Dr. G. M. Allen - verbal communication.

Richter's objections to habitual backward swimming by means of py-gidial slaps are for the most part well taken, particularly in view of such publications as v. Staff and Reck's (35). He doubts the suitability of the cephalic and pygidial shields for such swimming (in many trilobites, except those with long thorax and strong longitudinal muscles, the cephalon would of necessity perform a corresponding arc when the pygidium was abruptly flexed). It may be that these shields would not have been strong enough to stand the stress of such use; it is certain, though, that they would, as he says, be too stiff in recovery; and there is no way in which they could be feathered, like the telson of Recent macrurans. Thus, as their concavity is in many cases such (particularly would this be true in forms with a ra-chis so deeply arched as to admit of strong longitudinal muscles) that the inertia of the water they would catch and hold would brake their rearward impetus rather strongly. Richter recognizes the advantages of moderate spooning, as in oars. His contention that such forms as the Illaenidae and Phacops are scarcely suited, when enrolled, to any motion save that compelled by gravitation will readily be admitted, and the lack of any sort of a di-rective drag, such as is provided by the rigid cephalothorax and extended chelae of Homarus and its kind will readily be admitted.

Richter also doubts that trilobites had adequate musculature for such methods of swimming, even those with a prominent rachis. The alimen-tary canal and the muscles of the appendages occupy too much room, and the sub-pleural spaces are too thin. Furthermore, he denies the existence on the pygidium of such muscle scars as have been described, crediting only those on the cephalon, hypostoma, and thorax. By no means isolated examples of pygidial muscle insertions are given by Hall and Clarke (17, pls. VIII A, fig. 15, XXV, fig. 8, and pp. 103 f.) and Walcott (37, pl. IV, fig. 5, and p.222). (It is true that this example of Walcott's is of extensor muscles - vide 23, p. 92). Richter also remarks on the flattened tests of those tril-obites with the largest pygidia, citing Scutellum and the Asaphidae - saying that their musculature would be most inadequate. This does not by any means apply to all Asaphidae, and one might mention Scutellum campanifer (Beyrich) and S. brongniarti (Barrande) as counter-examples. It has been suggested by Raymond that width even without much height would insure sufficient space for longitudinal muscles. The volume of the rachis is doubtless more impor-tant than extension in any one dimension - either height or breadth - alone. Richter appears much too exacting about muscles; he credits the muscles of the appendages with usurping an extreme amount of space in the axial lobe.

Richter also lays great emphasis on the absence of a differentiated "Polsegment" in the thorax, i.e., the prominence of that segment which would form the cut-water in back-flipping. Few even of the Decapoda show such a feature. Some, as, for example, Palaemonetes, have a marked kink in the ab-domen, but the double imbrication referred to by Richter is a special, but not too uncommon, feature of the pleura and does not occur in the tergum of the segment in question. There is an apparent reverse imbrication in the rachis at the joint between the carapace and the first abdominal segment, but this is merely a deceptive appearance.

Richter's point is that all Recent aquatic arthropods at all like

the trilobites swim forward with the body extended, paddling with the legs. This sound rather inclusive, but is essentially true. His reasons, however, as shown above, are not all of the best. Among living Crustacea back-flipping appears to be known only in homaroid animals.

Von Staff and Reck mentioned among their criteria for a retrogressively swimming trilobite eyes stalked or otherwise adapted for rearward vision. Other explanations may, however, be offered. For example, Raymond has suggested (23, p. 102) that Vogdesia vigilans was equipped for alertness in ambush, and supported this with Finch's account of the animal's occurrence (13). A further development of this is to be noted in such forms as Asaphus kowaleskii Salter. The stalked eyes of some of the spinose trilobites, as in the Odontopleuridae and Lichadidae, may represent a convergent line of adaptation. As these floated among their miscellaneous planktonic associates bits of seaweed and the like would become attached to them, probably serving well as camouflage. Thus the produced eyes would be used as probably by Asaphus kowaleskii, but might also be a necessity to enable the animal to see out of its dress of drift. Richter has made a somewhat similar suggestion in one of his papers. He is undoubtedly right in declaring that stalked eyes are not a dysphotic adaptation - what good could they possibly do there? - but there is no necessity for calling them balancing organs (27, p. 233). An interesting feature of these eyes is their forward raking, as if to make it easier to see directly ahead; even such normal eyes as those of Asaphus expansus are directed very much down and to the front. Might not this be taken as evidence that the animals habitually moved forward? Trying to judge from the eyes alone, or from any other one or few features, is likely to lead astray. This is particularly well shown by Dollo's Paléontologie Ethologique (12). For example, Apus has dorsal eyes, and Richter says it likes to burrow, but is nevertheless no mean swimmer. Dollo does seem open to the accusation of having judged the arthropods by the fish. So also Richter when he fears that a bluff glabella might tend to counteract, by its resistance as a cutwater, the power indicated by the deep rachis; he himself has frequently called attention to the expert swimming of such seemingly inept forms as some of the Hydrachnidae.

As to the weight of the test keeping the trilobites most of the time on the bottom, it seems no more likely than in the case of Recent Crustacea. I do not see that any generalization can be made about this, except that some doubtless were more completely benthonic than others, depending on a variety of factors, such as, indeed, weight of shell, but more immediately on their positive adaptations for swimming, such as musculature and nature of the appendages, general shape, including such details as the disposition and nature of the eyes.*

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* I certainly see no point to the assumption (27, p. 231 - after Jaekel) that the Agnostidae, even if their shields do balance and are relatively very large, should have had to swim or float because the weight of their shell was too great for their "few" legs. Even if minimum values are taken, they would still have had from twenty to twenty-four endopodites, which should be sufficient for crawling (the Isopoda get along with fourteen). In any case, however, regardless of the number of legs, why should a shield consisting of fused segments weigh significantly more than the same number of free segments?

- 38 -

What Richter says about using the dorsal shell as an index of na-
tatorial ability is very much to the point: We <u>know</u> practically nothing
about the relative development of the appendages on trilobites in general.
Their size is surely more important in this matter than variations in the
design of the rest of the body, whose ill-adaptation they might mitigate
or overbalance.

Richter believes that the fimbriated exopodites were pleopods. On
this account he assigns to <u>Triarthrus</u> and <u>Cryptolithus</u>, which he would not
call nektonic from their shells, strong swimming ability. The chief point
has been stated: the index-value of the dorsal shell is modified by the de-
velopment of other parts of the body, chiefly the appendages and their mus-
culature; but accomodation for the viscera is of course also important.

However, when he comes to naming his choice of the most active swim-
mer he reaches practically the same conclusion as Raymond (23, p. 103), who
names <u>Isotelus</u> and <u>Dalmanites</u>, whereas Richter selects his "<u>Phacops</u>-type."

Almost the only point of coincidence of the conceptions of criteria
for swimming trilobites of Raymond and Richter is the agreement that large
subequal shields indicate such habits. Whereas the former considers the py-
gidium as a propeller, Richter thinks of the two shields as supporting
planes, balancing one another. He also appeals to spines in the horizontal
plane for the same purpose; thus the genal spines of the Trinucleids would
carry the weight of the head far back and so balance it properly. The
same applies to <u>Harpes</u>, which he considers almost exclusively nektonic, not
seeing how it could do anything on the bottom except rest – because of the
discrepancy in levels noticed above (and vide 28, fig. 1, p. 26, and 29, fig.
3, p. 208). Richter refers to Woltereck (39), but appears to have missed
his point, for Woltereck declares that the spines are primarily directive –
immediately mechanically and secondarily photostatically. Gurney (16, p.
462) mentions the great directive influence of the median spine of the
<u>Corystes</u> zoaea, adding that spines (median) seem to be important balancing
organs, which disappear as the "auditory" organs develop to efficiency.
Richter mentions the raphiophorids as one of the types in which the head
was supported in swimming by the long genal spines (vide above). The fron-
tal spine, as of <u>Ampyx</u>, would not do this in just the same way, but would
undoubtedly help keep the head up in forward swimming. Woltereck's work
(39) on various kinds of <u>Daphnia</u> (esp. <u>Hyalodaphnia</u>) indicates that such a
spine has great influence on both attitude and direction in swimming.

Richter may be right in saying that no trilobite was entirely plank-
tonic, i.e., could hang motionless in the water, without sinking, but some
of them probably made a fairly close approach to it. He speaks of Recent
spinose plankton with exceptionally complicated appendages which may equal
or surpass the ramifications of the test, and he would expect similar devel-
opments in the Odontopleuridae. Such appendages would, of course, be a
nuisance to a benthonic animal, but would be of advantage off the bottom.
By way of proof that trilobites were not genuine plankton he offers the
testimony that their enrolled shells show that they sought refuge "when in
trouble, i.e., frequently" by folding up and sinking to the bottom. Even if
they were not entirely planktonic, the Odontopleuridae approached that con-
dition very closely, and their locomotor apparatus may have been somewhat
modified.

With Richter's summary of trilobite locomotion we have very little
quarrel - much less than with some of the evidence on which this summary is
apparently based. He considers the trilobites as primarily benthonic, but
also able to swim by paddling with the legs. Enrollment he looks upon as a
reflex which was manifested in any emergency, no matter, naturally enough,
what the animal was doing. But he makes no mention of burrowing, even of
the ploughing kind, which must have been quite common. He compares trilo-
bites to Serolis, as crawling and swimming with equal ease; to this I would
add that they probably, in great measure, also burrowed to about as great
degree as that of isopod.*

Enrollment

Enrollment is almost the first thought when one is asked how a tril-
obite could defend itself against attack.** This is because of numerous
finds of the animals so disposed, as well as upon analogy with living isopods.
In nearly all instances enrolled trilobites have been found to belong to
forms with the ends of the pleura facetted so that they slide easily upon one
another and make a close-fitting series of imbricated joints when the animal
is flexed. Trilobites without such bevelling are not, as a rule, found en-
rolled, though Ceraurus, for example, has been so collected. In this country
it has been customary to speak of the facetted forms as capable of enrollment
whereas this ability was implicitly or even explicitly denied to the rest.
They have not been so restrictive abroad, however, and Richter (28) reflects
this when he asserts that all trilobites could enroll; he cites Pompeckj***
as his authority as he continues to the effect that the friction of the slight-
ly confined facetted pleura upon one another would keep the animal in enroll-
ment even after the relaxation of the flexors (i.e., even in death, after
the decay of the viscera), whereas the unfacetted forms would unroll as soon
as the flexors ceased straining. Pompeckj made a cardboard model of Para-
doxides and found that it would enroll quite well, though not so perfectly
as, for example Calymene or Asaphus. (M. Neumayr appears to have appealed to
natural selection, and maintained that the rise of predaceous foes, such as
fishes and cephalopods, induced an increase in the distribution of facetted
pleura by putting a premium on ability to remain a long time enrolled).

I have examined a number of Recent isopods (mostly Sphaeromidae) in
search of facetted pleura and information on enrollment. The majority were
enrolled, and very firmly, so that attempts to unroll them or to enroll ex-
tended individuals were abandoned for fear of injuring them (they were alco-
holic specimens); in none of these did I observe anything like pleural facets.

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* See above, and 25, p. viii.
** Some have gone rather to extremes in this. Jaekel, for example, supposed
   alarmed Agnostidae to enroll with such vigor that they drove themselves deep
   into mud - out of sight! To Richter this does not, apparently, seem particu-
   larly far fetched, though he objects that they were so light that they prob-
   ably merely stuck in the surface of the mud (28, p. 32).
     Further, Richter seems to look upon enrollment as one of the trilobite's
   most important acts. He even (28, pp.29-30) refuses to consider enrollable
   trilobites as burrowing, on the ground that they could not then enroll; he ap-
   parently did not believe that their need for enrollment was much diminished
   in such circumstances.
*** Jahreschefte Ver. vaterl. Naturk.Württ.,XLVIII (1892), pp. 93-101.

Thus, although facetted pleura may well have been of use in enroll-
ment, they were evidently by no means indispensable. Although the accepted
explanations appear to fit the facts very conveniently, they should undoubt-
edly be modified.

The general assumption has been that such passive defense as en-
rollment and spines afforded was about all that trilobites were capable
of; similarly they have been considered chiefly as scavengers, and portray-
als of predaceous habits in trilobites have been repudiated (e.g., 23, p.
103). Richter, however, mentions Apus as successfully attacking active
prey (28, p. 40, footnote; he mentions Branchipus, tadpoles, and annelids).
Even this testimony is scarcely necessary to allow of a trilobite catching
at least some living food, particularly if it be granted that the creature
could dart about suddenly.

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– 42 –

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THE ŒCOLOGY OF PORIFERA, AND POSSIBILITIES OF DEDUCTIONS AS TO THE PALEOECOLOGY OF SPONGES FROM THEIR FOSSILS

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At the present time sponges in their morphology and in their distribution show reactions to the effects of environment. Even with our present limited knowledge some things may be said as to the nature of the environmental effects in question. Consequently, knowing only the environmental effects, one may deduce a little about the environment that was the causative agent. Furthermore, by assuming that the procedure in bygone ages was much the same as that which prevails now, one may draw some conclusions from fossils regarding the environment which was formerly present.

Environment may be considered under the headings of physical, chemical, and biological.

Sponges grow only in the water. They may survive in spite of emergence, as for instance at low tide, but they cannot carry on out of water. When dead they may be washed up in the wrack. They may even conceivably be blown inland. Direct observations of such occurrences are quite rare, however. Occurrence of fossil sponges, therefore, constitutes almost perfect proof that during their life, the horizon in which they occur had been submerged.

Among the more important physical items in the environment of the sponge is the matter of currents of water, their presence, absence, or degree; and also the nature of that which is transported by them.

It is noted, for instance, among the collections made by the "Challenger" and other dredging operations, that the stations which yielded no sponges were consistently far from land, furthermore that no stations which were a great distance from the nearest island or continent yielded many sponges. One can only speculate as to what may be the nature of the material required, but certainly something or other must be brought by currents from land, otherwise sponges cannot exist. It may possibly be concluded from this that wherever fossil sponges occur there was probably a large island or continent within a few hundred kilometers.

Another matter bears on the question of whatever it may be that the currents bring to the sponge. We have numerous observations of sponges growing in aquaria but having no other nourishment than what they may obtain from the current of water that is being introduced into said aquaria. The fact that sponges regularly die when kept in stagnant water may indicate that in such the oxygen supply becomes exhausted and that they perish from suffocation, but the fact that they can live in aquaria where they are not fed otherwise than by that which is brought in by the current is significant of a nutritive as well as respiratory importance.

One of the most important effects of the current on the sponge is in connection with removal of waste products from it. In nearly every case where sponges are found growing in calm water, a high collar or "chimney" is found erected about the exhalent aperture or oscule. It is fairly evident that this has the value of separating the exhalent current from the inhalent, thus reducing the possibility that the material just ejected from the sponge might be at once re-admitted to its pores. The occurrence in a fossil sponge of such oscular chimneys indicates a high probability that during the life of the individual it was surrounded by relatively stagnant water. As noted below, the deposition of silt may also account for oscular chimneys. Since such deposition is frequently also associated with relatively calm waters something can be said as to the lack of current indicated by such morphology.

Sponges that live amid rapid currents always lack pronounced surface elevations. This is a relative matter. The stronger the current, the more nearly level will be the surface of the sponge. Where the currents are very violent indeed, the rule (to which there are very few exceptions) is that the sponges take what is called the encrusting form, extending laterally indefinitely but never protruding far above the substratum. If they do grow perpendicularly it is in a hemispherical or low, rounded manner that is very characteristic. Each of these simple architectures may also occur in calm water. It would appear quite justifiable, however, to argue from the appearance of anything other than encrusting or hemispherical form in a fossil sponge that there were no considerable currents about it during its lifetime.

The preceding paragraph refers chiefly to conditions wherein current frequently changes direction so that the sponge is affected from nearly all sides. Wherever the current is confined to a channel so that it affects the sponge principally from just one side, or from two opposite sides, it is the rule (although there are quite a few exceptions) that the sponge fauna exhibits significant shapes. Sponges that in calm water grow up in a bush-like form, when growing in a current tend to become flabellate or fan-shaped. Another shape common in currents is the lamellate form, frequently having all the oscules on just one side and the majority (though not quite all) of the pores on the opposite side. In this manner the current may be helpful in respect to the circulation of the sponge, the oscules or exhalent openings being on the downstream side and the inhalent openings on the upstream side. It is by no means certain that the role of environment in cases such as this is as simple as it seems to be at first. It may be mentioned here that specimens of sponge are found having this lamellate form and living in a current, but that it is seldom (if ever) found that similar specimens nearby, out of reach of the current, have another shape. Instead, in such adjacent localities, occur what seem to be clearly different species. The assumption may therefore be made that lamellate sponges succeed in living in a current of comparatively uniform direction, whereas sponges of some other shapes do not thrive there. The Hyalospongiae (or Hexactinellidae) afford an interesting field for speculation with reference to the possible effects of one-way currents upon the morphology of the sponge. Many varieties of this class grow in an erect, hollow, cylindrical form, with their pores distributed about the convex exterior while a large internal cloaca leads to an

- 46 -

apical exhalent aperture. The whole structure is so openwork that currents may sweep through it. Now it frequently occurs that upon collection such sponges (Euplectella is an example) are found to have a sharp bend in the cylindrical form. This is so clearly ingrown that it must have been long present. Spongelogists therefore conclude that as it grew the sponge leaned downstream with respect to a permanent or semi-permanent current which could thus pour in at the inhalent openings and sweep out at the exhalent, in this way reinforcing the sponge's inadequate hydraulic efficiency. It is impossible to verify this conclusion by means of diving apparatus because of the great depth at which such species grow, none the less, the theory is so plausible as to command respect. Such morphology in a fossil sponge very probably indicates that when still alive the animal in question was bathed with current of uniform direction, and at a depth to be measured at least in terms of hundreds of meters. Many calcareous sponges or Calcispongiae also have a cylindrical form with the inhalent openings on the outside and the exhalent openings apical. It may be noted in these which occur at such shallow depths that they can be observed directly, that they are so pivoted upon their bases that regardless of the direction of the current, the oscule is always downstream. This lends additional support to the credibility of the above mentioned theory. It is rather easy to discriminate between the morphology permitting such pivoting, and that which instead implies rigidly sessile fixation.

Another factor in connection with currents is that of the deposition of silt. To begin with, it may be stated that where very fine silt is settling, no sponges can live, apparently because their inhalent openings become clogged. This is necessarily a somewhat inexact statement because there is no sharp dividing line; the finer the particles in question, the fewer are the sponges that occur. An occasional member of this phylum is found living, however, even where the fineness is such that the conditions might appropriately be referred to as muddy.

The mere occurrence of a fossil sponge does not prove that there was no silt being deposited during its lifetime at the place where it grew, but one could say roughly that the more abundant the sponges are in any given geologic horizon, that the less likelihood therefore exists that said horizon was muddy at the time of growth of the sponges.

Where coarse sand is being deposited sponges frequently flourish, but invariably with a certain morphology that is quite distinctive. In them, as also in sponges that grow in very calm water, (but even more regularly) there are thrown up collars or "chimneys" from the oscules, frequently to a height of many centimeters. The pores are of course sometimes covered up by the sand, but where this is coarse enough, the currents may still enter the sponge through the interstices between the particles.

The ooze which forms very slowly on the bottom of the ocean affords a very different type of problem from the standpoint of the sponge. One may judge that there is little difficulty in the way of clogging the pores by rapid accumulation of this ooze, but that there is a problem of support lest the sponge sink into it. The rule is that sponges occurring in this

type of locality have what are known as "root tufts" of long spicules in dense masses which run out into and down among the surrounding masses of ooze, thereby holding the functional portion of the sponge on the surface of it. Wherever a fossil sponge shows clear cut evidence of such root tufts the assumption may be made with great confidence that it was growing on ooze, hence probably at a considerable depth, and not upon any rapidly forming silt or mud.

Another item that needs to be considered in connection with currents, although having only a slight paleontological connection, is the matter of larval distribution. There are indications that sponges spread from one place to another more slowly than members of most other phyla. In Puget Sound the conditions for sponge life are very good, which is proven by the fact that enormous numbers of individuals live there; on the other hand, the number of different species is very small. The species which do occur are confined largely to those which might be carried in on the backs of mollusks, hermit crabs, or on ship bottoms.

The indications are that during the interval which has elapsed since the region that is now Puget Sound sank below the sea level, only a score or so of exceptionally migratory species has had time to work in. It is tempting therefore to assume if in an horizon there are found numerous different sorts of fossil sponges, that the locality in question had been continuously favorable for the growth of sponges for many thousands of years at the time when those fossilized were still living. In further confirmation of this general idea one may note that the sponges at the Pacific side of the Isthmus of Panama, show a most remarkable resemblance to those occurring on the Atlantic or Caribbean side. Among the invertebrates in general such a resemblance does not exist, and indeed is not to be expected, because in that region there has probably been no connection between the two oceans for a very long time, even geologically speaking. The inference is that once sponges are established in a given locality they remain for many millennia.

There is another matter that has very little to do with currents, but has much to do with the shape of the sponge, and needs therefore to be kept in mind in deductions (as to presence or absence of currents) based on sponge morphology. When sponges are forced to grow on a small substratum they grow principally perpendicularly, at the expense of lateral growth. This may be because there is only a small area available that is stable, that is to say, not shifting, inasmuch as sponges require a relatively fixed point of attachment. Again this state may indicate that other sessile organisms (such as other sponges) grew abundantly in the vicinity, and crowded in upon the specimen in question. The fact that there are these two interpretations would make it difficult to come to conclusions as to environment, and an additional even greater difficulty is brought about by the fact that there are many species of sponges that assume the erect cylindrical form even when growing in completely uncrowded quarters. One may say just this much, that the appearance of fossil sponge showing a certain amount of point of attachment, proves that at least that much of its environment was fixed and stable.

The individual sponge is very sensitive as to temperature. It has,

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http://www.nap.edu/catalog.php?record_id=18676

- 48 -

one may say, no margin to spare in this regard. We find it capable of sur-
viving at the maximum and minimum temperatures of the place at which it is
found, but perishing at extremes colder or warmer than this range. This
delicacy does not extend to species as a rule, if ever. A striking case is
Aplysilla glacialis, which occurs in the Arctic, Antartic, in intermediate
regions on the Pacific coast of the United States, and also in Panama, near
the equator. There is little if any evidence of ecological modifications
evidenced by the specimens form these different localities. This partic-
ular species is especially noteworthy in this regard as it is a sponge hav-
ing no proper mineral skeleton whatever. It is frequently stated in the
earlier works on sponges that such species are characteristic of the trop-
ics or warmer waters, and not at all of the colder portions of the earth.
Further investigation indicates that a more nearly correct statement would
be as follows: in warm waters those sponges lacking mineral skeletons are
more numerous in comparison to the others, whereas in colder waters the
latter are more numerous in comparison to the former. Either sort may oc-
cur in either place and where so occurring shows apparently little if any
modification as a result of its environment. One may conclude that it is
impossible to decide from any single fossil whether or not the water in
which it grew was relatively cold or warm (regarding equatorial regions as
warmer and polar regions as colder). A fossil record might have just this
much value in connection with deductions as to temperature, that if very
numerous sponges be in evidence, and the majority appear to have been kera-
tose, there would be some cause for surmise that the waters in question
might have been tropical or sub-tropical. This is of very little help, how-
ever, in view of the fact that the sponges which lack proper spicules are
seldom fossilized because of their lack of hard parts.

The question of light as a factor affecting sponges is of some sig-
nificance from the standpoint of paleontology. We have, it is true, the
situation exemplified by Acarnus erithacus of the California coast. It oc-
curs normally where the illumination is very good, that is to say, in in-
tertidal waters. One specimen, however, has been dredged from a short
distance off shore where the depth was so great (700 meters) that it may be
assumed no light was present. The difference between the specimens from
the two localities were quite noticeable but involved only the matter of
color at the time of collection; this would not be evident in fossilized
specimens.

Whereas we may conclude that migration away from light does not
bring about morphological alteration, it nevertheless remains true that
some sorts of sponge are more likely than others so to migrate. Little
may be deduced as to light from the presence or absence of Porifera (such
as the above mentioned Acarnus) of the class Demospongiae. The class Cal-
cispongiae (or Calcaraea) occurs in relatively shallow water, however, that
is to say at depths of less than one hundred meters. It may be further-
more stated with confidence that nearly all of the members of this group
grow where there is illumination. The occurrence of a fossil Calcisponge
may be taken as a moderately good indication that the immediate surroundings
in which it grew were illuminated. In contrast to this, the entire class
Hyalospongiae (or Hexactinellida) grows exclusively in the darkness. Prac-
tically no specimens of this class are on record as having been collected

- 49 -

at less than one hundred meters, and in the very few cases where the depth
was shallower the conditions were such that one must conclude that little
or no light reached the sponge where it grew. Even if a few exceptions
should still turn up in regard to this matter one may nevertheless state
with considerable confidence that the occurrence of fossil hexactinellid
sponges indicates that their horizon had been characterized by darkness.

With regard to osmotic pressure or tonicity the individual sponge is
somewhat sensitive. An increase above that which is normally true of the
sponge's environment brings about immediate damage. The effect of a hy-
potonic solution is not so quickly evident, there is a lag, so that re-
duction in osmotic pressure does not immediately begin to show its ill
effects, but if it is carried to any considerable extent the sponge is
certainly damaged. The extent in question varies considerably with the
species studied. The net result of this is that a marine sponge is not ser-
iously injured (even though near the surface) if a severe spell of rain con-
siderably dilutes the surface of the ocean with fresh water for a short
period of time.

From the standpoint of geologists it is very noteworthy, however,
that an entirely different fauna of Porifera occurs in fresh water than in
the oceans. The occurrence as fossils of the type of sponge at present
known to occur in fresh water constitutes a fairly good proof that the im-
mediate surroundings at the time of fossilization were not marine, and vice
versa. There is some warning that needs to be given in this connection
however, in that marine species have been found in the very large fresh
water lake Baikal in eastern Siberia.

In brackish water no sponges seem to thrive and not many species of
any sort occur, but those which are found in such localities are divided a-
mong the marine and fresh water sponges, the two sorts occurring side by
side.

The relationship between bathymetric pressure and the occurrence or
absence of sponge types and any effect on the morphology of individual sponges
cannot be considered apart from the probably more important question of light.
As already noted there are distinct orders or classes of sponges which seem
to be found only in the light (Calcispongiae), or only in the darkness
(Hyalospongiae). This is correlated with the occurrence of the latter class
in relatively deep water. The class Demospongiae is well represented where
any sponges at all occur, in shallow or very deep water.

A second type of ecological reaction is to the chemical environment
instead of to the physical. This would concern substances perhaps to be
listed as poisons, which by their presence might be inimical to sponge growth,
and also other substances which are necessary as accretions or auxiliary sub-
stances if the sponge is to maintain its existence.

With respect to the first item; needless to say there are numerous
toxic substances which affect sponges adversely, but there does not seem to
be good evidence that any of the minerals commonly occurring in the sea or

- 50 -

in fresh water are seriously injurious to Porifera. Rare occurrences can scarcely be deduced from the evidence of fossil sponge morphology.

From the standpoint of substances required positively by the sponges, oxygen may be considered first. There is, as might be expected, rather good evidence as to the need for free oxygen in solution on the part of members of this phylum. In other words there is little or nothing to indicate that any of the members of this group are directly anaerobic. On the other hand it should be noticed that very numerous species of sponges commonly live in symbiosis with plant cells, and the latter possess appropriate pigment by means of which photosynthesis is carried on, carbon dioxide consumed, and oxygen released. It is therefore conceivable that during the day such sponges might live in the absence of free oxygen, were sufficient carbon dioxide present. This would not carry over into the night, and since there seems to be no method of storing up oxygen from the day's production, we may take for granted that the presence of sponge life indicates that at the time the specimens were growing oxygen was available.

There is much work bearing upon the requirement of sponges with respect to hydrogen ion concentration and the presence of metallic and nonmetallic ions in general. Aside from calcium carbonate and silicon dioxide, there is little of this material of interest for the geologist. Those salts most important to the existence of sponges are so widespread that one can do little reasoning from the occurrence in fossils to what salts were or were not present in their environment during life, other than to assume that they must have been present much as in the ocean and lakes and streams of today. Even the questions of silica and calcium carbonate are of little help from the ecological standpoint in connection with paleontology. Sponges can satisfy their needs for either in the presence of amazingly small quantities. Very few places in the world lack the minimum necessary to the Porifera that might live there if other factors permitted. It is, for instance, noteworthy that siliceous sponges thrive in the vicinity of coral reefs where there is a considerable lack of siliceous material on the bottom or in the surrounding vicinity, and conversely that calcareous sponges thrive especially well on granite shores where there is no limestone very near. Since (for other reasons noted above) it is sometimes significant to notice whether or not the fossil sponge considered was in its lifetime calcareous or siliceous, it must be kept in mind, as is well known, that these two substances occasionally replace each other during fossilization. Also it may be remarked that either of the two may be replaced during fossilization by pyrite.

In connection with fossil sponges and deductions that may or may not be made from them it should be noted that the skeletal material, as we find it in existing sponges, is usually in units called spicules, which (aside from perishable organic stuff) are entirely separate from each other. When such sponges die, the skeletal material usually soon breaks up completely. Needless to say they are not readily susceptible to fossilization. On the other hand in each of the three main classes of sponges we find special instances as follows: among the Calcispongiae we have the so-called Pharetrones; among the Hyalospongiae we have the so-called dictionine sponges; and among the Demospongiae we have those referred to as the

- 51 -

Lithistida. In each of these three special cases the spicules during the lifetime of the sponge become interlocking or even actually cemented together. These therefore are especially suitable for fossilization and loom up large in the paleontological record. This does not mean that they were formerly much more common than they are at present, but merely that the other kinds are less susceptible to preservation in strata. It has been very generally assumed, particularly in works on paleontology, that each of these three constituted a particular sub-division within the class in question. This is not at all to be taken for granted, and in fact the current opinion is tending more and more to the belief that the lithistid modification may happen to sponges in almost any family of the Demospongiae; the dictyonine modification to species in almost any of the orders of Hexactinellid sponges, and the Pharetrone modification to at least several sorts of the Calcarea.

One of the most interesting chemical ecological situations is that pertaining to food. The sponges can occur only where suitable materials are present and if we knew what sponges eat we might be able to carry on very interesting deductions from the occurrence of certain types in the fossil record. There is such widespread assumption that much is known about the nutrition of sponges that some remarks on this question may be in order at the present time.

Many, perhaps the most, of the experiments bearing on the so-called nutrition of sponges have involved introducing carmine powder, indigo, India ink, and other such readily observed minute particles of material into the organism in question. As a result of these experiments it is well known what occurs to such particles. They are taken in by certain cells, sometimes passed on to certain other cells, and eventually forced on out. It may at first appear to be rank heresy to criticize, but actually it is only fair to state that these experiments are nearly valueless and prove nothing as to the nutrition of the sponge. One might just as well blow bits of charcoal dust into the lungs of a human being and record the capturing of this dust by the mucous in the alveoli of the lungs, its passage in the ciliated epithelium upward to the nostrils, and its final discharge from the nose. Clearly the sponge could not go on being clogged up indefinitely with carmine particles and must push them on out someway or other, and equally clearly it is evident that neither carmine, indigo, nor India ink constitutes a natural diet for the Porifera.

But do we find sponges ingesting such things as diatoms, or protozoans, which might conceivably be natural items of food? There are many observations of the ingestion of flagellates, but also other observations that these may exist as still living symbionts after their entry into the sponge cell. There are a few authentic records of the ingestion of diatoms and bits of plant material in the same way that carmine particles are taken in, but these instances are so rare and involve so few of the millions of cells in an ordinary sponge colony that they should not be taken very seriously.

Another type of investigation as to possible diet of sponges has been to take specimens of this phylum and analyze the material for the presence or absence of certain enzymes which are known to act on certain types of food. Some enzymes, as a matter of fact, are thereby discovered to be present within the material studied, but it is very generally overlooked (as

- 52 -

should not be the case) that in the materials studied there are not only
sponge cells, but also numerous beneficial, neutral or antagonistic sym-
bionts (such as bacteria) and that the enzymes which are undoubtedly there
may have been provided by the other cells, and not by those of the sponge.

Whereas photosynthesis cannot possibly play any part in the nutri-
tion of the Hexactinellida (or Hyalospongiae) which live at great depths
in the ocean, it is very interesting to note that very many of the shallow
water sponges, as mentioned above, do have abundant symbionts. Included
in this category are many of the fresh water sponges. One may say that in
the majority of cases where the diet of any given sponge is really known,
that it is in connection with, or brought about by some Thallophyte.

Passing mention should be made of an hypothesis much considered but
not readily susceptible to proof (or disproof), that sponges live upon ma-
terial already in solution in sea water about them. To judge from the sta-
tion records of some of the extensive oceanographical explorations, sponge
individuals and species are slightly more common in waters opposite the
mouths of rivers than elsewhere. This might indicate that dissolved sub-
stances were brought from land to nourish the Porifera in question. On the
other hand it must be noticed that the amount of data bearing upon this
matter is utterly inadequate; the few items from literature here referred to
are susceptible to explanation on the grounds of mere coincidence and no ex-
tensive conclusions from them are warranted.

In summary of the above paragraphs it must be said that at the pres-
ent time our state of knowledge with respect to the food of sponges is so
utterly inadequate that no safe conclusions with respect to environment
may be drawn as to matters of this sort from any studies, morphological or
distributional, of fossil sponges.

The third item in consideration of the ecology of sponges, whether
fossil or recent, is the biological or living environment, which all may be
summed up under the general heading of symbiosis. Sponges come into rela-
tionship with animals from all the other major phyla and these relationships
may be considered as follows.

The chordata have very little to do with the sponges. Almost the
only ones to do so other than man himself are a few fish, and most fish as
a rule ignore all sorts of sponges. Some of the angel fish that browse a-
round the tropical coral reefs are frequently found to have bits of sponge
in their stomachs, but it is a matter of doubt as to whether they were tak-
en intentionally or not; they may have been accidently secured along with
bits of other sorts of food as (for instance) worms or shrimps that live in
the sponges.

There are exceedingly numerous instances of interrelationships be-
tween arthropods and sponges. Many kinds of insect larvae eat fresh water
sponges, or live in them, thereby securing shelter. Very numerous marine
arthropods live in the canals or other cavities within sponges. Further-
more there are crabs which deliberately place bits of sponge upon their
shells of which the growth may lend protection to the crustacean in ques-
tion.

- 53 -

Fairly numerous sponges of all the classes have sieves over their exhalent openings. These in some cases are reticulations of fibers. In many of the deep-sea species they are elaborate screens of siliceous strands. It is certainly known that the cavities beneath the screens in a considerable number of sponges contain symbionts, principally shrimps. In regard to the others, our lack of information as to conditions during the life of the sponge is noteworthy. In them also, shrimps may have once lived. Do the sponges profit by the animals they thus hold prisoner? Does the imprisoned commensal profit more by the protection he receives than he loses by his confinement? These questions are not easily answered. Nor can one be too sure of the significance of cloacal or oscular sieves in fossil sponges. They probably, but by no means certainly, kept symbiont animals within their cavities while still alive.

The matter of symbiosis with mollusks has been rather less studied, but is probably more important. There are fairly numerous individuals of the nudibranch gastropods which have as their regular diet the tissues of sponges. These often closely resemble the sponges on which they customarily feed. Furthermore, there are sponges which regularly grow on the shells of mollusks. In some instances they employ these merely as a basis of support, but even in this case they may smother the mollusk. Again we have the boring sponges for consideration; by their excavation of galleries within the calcareous material of the mollusk's shell they may do him irreparable damage. Their work is frequently evident in fossil shells.

Although sponges and echinoderms frequently live in very similar environments their relationships with each other appear to be in most cases of the most casual nature. Ophiuroids very commonly seek shelter in coarsely cavernous sponges.

More important matters concern various of the different phyla of worms. Nematodes are occasionally found in sponge colonies, and are probably living there at the expense of the surrounding flesh, but may be merely commensal. That the latter is the case with regard to the very numerous annelids found in the canals of sponges seems fairly evident. One cannot find upon dissecting such sponges that the annelid has been damaging the tender lining of the canals in which it occurred. One may even imagine that the sponge derives some benefit from chemicals given off by the worms in question. Some of the Platyhelminthes of the class Turbellaria are indirectly of great benefit to the sponges, in that they destroy the above mentioned nudibranchs which feed upon sponge tissues.

With the phylum Coelenterata the relationship is largely one of attachment. There are fairly numerous anthozoans which grow perched upon sponge tissues, as for instance those on the rooting tufts of the hexactinellid sponge Hyalonema, and the anemones of the genus Parazoanthus which may grow upon shallow water ramose sponges. Porifera, moreover, very frequently grow upon dead coral skeletons.

Symbioses between different species of sponge are usually of a nature similar to that mentioned above; one species may grow upon the framework of another that has died, or may even perhaps be still living. Mutual crowding

is of considerable importance. One species may be so overgrown by another as to be smothered. Some sponges invade the galleries of <u>Cliona</u>, either destroying the flesh of the burrowed sponge, or merely inhabiting passages from which the defunct <u>Cliona</u> had decayed. It must therefore be noted that the occurrence of a sponge in such burrows does not prove that it did the excavating.

Fossil sponges are often found associated with the fossils of other phyla, as for example, at Solenhofen (Jurassic). The nature of these other fossils affords clews as to the paleoecology of said sponges. Such instances are very little discussed in the treatises on fossil Porifera. All too often the animals of one group are discussed by one expert, those of another group by another expert, and each treats of almost nothing save his particular specimens.

What little evidence is available from references to polyphyletic fossil faunas bears out the theory that the ages have witnessed little change in the methods whereby sponges react to their environments. It appears that in the past Porifera occurred in much the same environments as at present, and lived similar lives.

PALEOZOIC PLANTS AND THEIR ENVIRONMENTAL RELATIONS

By

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I. Introduction

The fundamentals of the paleoecology of Paleozoic plants are essentially the same as those of any other era as far as they concern relation to environment. The reasons for recognizing a separate problem for the Paleozoic are that special consideration should be given to certain limiting factors, and that some things have to be dealt with from a standpoint based on an intimate knowledge of Paleozoic plants.

Any consideration of ecology of past ages must depend upon present day ecology for guidance. For example, nothing can be postulated about the temperature relations of extinct plants without first knowing something of the thermal requirements of living plants. In a like manner we decide whether a given fossil form was adapted to a terrestrial or aquatic existence by comparison with familiar living forms showing the same or similar adaptations. Comparison with living forms is, therefore, the starting point for paleoecology.

The problem of environmental adaptations of Paleozoic plants differs materially from that of Mesozoic and Tertiary plants in that all Paleozoic types are extinct and their nearest living relatives are so remote that ecological comparisons are difficult to make. Predominant among the Paleozoic plant types were the pteridosperms, or Cycadofilices, which before the discovery of their seeds, were assumed to be ferns. In the living flora ferns are most abundant in the tropics, and consequently a tropical steamy atmosphere was once postulated as the type of environment in which existed the forests of the Carboniferous coal swamps. But these pteridosperms have no close modern relatives and we cannot assume that their ecological requirements were similar to those of ferns. Ferns did exist in the Paleozoic in considerable diversity of form and habit but they were not closely related to the living ones, nor did they exist in sufficient numbers to establish the existence of tropical surroundings.

The culmination of a prominent Paleozoic gymnosperm line was realized in the Cordaitales. While these may resemble modern conifers to a slight extent their relationship to them is remote, and the predominance of cordaitean forms in a flora is not necessarily an indication of upland conditions without the support of evidence furnished by other forms. Some of the cordaitean forms have ecological significance in that they show structures suggestive of adaptations to certain conditions.

The Paleozoic Lycopodiales, which culminated in such genera as Lepidodendron and Sigillaria, have as modern representatives a few straggling and slow growing remnants as Lycopodium and Selaginella. These latter are widely distributed and exist in a variety of habitats, not being confined to situations such as must have prevailed in the coal swamps. The same thing is true

- 56 -

of the Paleozoic calamites and their modern remnant, the genus Equisetum.

This brief résumé of the predominating plant forms of the Paleozoic is sufficient to show conclusively that we can tell little or nothing about the ecology of that era by knowing what plants existed then. They are too remote from modern plants to permit ecological comparison. Also, the extent of relationship between these early and later plants is often poorly understood. Furthermore, members of the major groups as the Cycadofilices and the Cordaitales were so widely diversified and lived under such a variety of habitats that generalizations concerning their ecology are difficult to formulate.

Another item of major significance in securing ecological data from Paleozoic plants is that the entire plant can seldom be reconstructed. Because of the size and shape of the plant body, the mode of attachment of the organs, and the frequent and periodical shedding of leaves, bark, cones, seeds, etc., most paleobotanical information is secured from detached parts. These parts which make up the great bulk of Paleozoic plant material furnish valuable data on phylogeny and classification, but usually have limited ecological significance.

One of the lines of approach to the subject of Paleozoic plant ecology is through the study of structurally preserved remains which involves some knowledge of the relations between structure and environment. In living plants there is frequently a distinct correlation between foliar structures, and moisture and light requirements. The difficulty, however, in applying the same inferences to Paleozoic plants is that very pronounced structural adaptations are not common among plants growing under normal surroundings. It is only when plants are subject to extreme conditions, as aridity, salinity, etc., that they develop specialized structures which are conspicuous enough to be recognized in Paleozoic plants and a similar environment postulated for them. Moreover, certain specialized structures were developed in some Paleozoic plants that do not exist in living plants. This is shown by the extraordinary development of surface periderm in some species of Lepidodendron or the internal periderm in stems of Medullosa. In Lepidodendron this external periderm served for support of the trunk since the vascular cylinder was small, but the ecological significance of this has not been fully explained. Another difficulty is the different structural adaptations which different species show. If all species reacted the same toward their environment it would be much easier to determine anatomical adaptation in plants, extinct and living.

II. Paleozoic plants in relation to the sediments

Fossil plants are usually preserved in water deposited sediments and hence removed from the environment in which they grew. They might have been removed by streams, ocean currents, wind, or by any number of agencies. For this reason a fossiliferous deposit often contains plant débris from a variety of habitats, dry uplands as well as the more moist lowlands, and the remains occur together in inseparable confusion. It is usually to be expected, however, that the lowland species will predominate in deposits formed

- 57 -

under such conditions as probably existed in the Carboniferous coal swamps, and this fact has doubtless influenced attempts to determine climatic conditions of that period. Since a deposit of fossil plants is likely to contain a mixture of types the problem of elucidating the environment under which the plants grew is quite different from that relating to aquatic organisms which were fossilized in their natural surroundings. Land plants and land vertebrates present many paleoecological problems in common.

When the site of deposition is far removed from the locality in which the plants grew, little can be determined concerning the natural environment other than what can be gathered from the structure and morphology of the plants themselves. In a few important instances, however, plant remains have been found in place and still rooted in the original soil where they grew. Such fossil deposits often reveal much concerning the surroundings, not only at the moment of deposition of the enclosing sediments but also those under which the plants existed as living organisms. An example of such is the Rhynie chert deposit near Aberdeen, Scotland (11).* Here many stems are still standing erect and attached to horizontal underground rhizomes. The chert has every appearance of having been a peat bed which was saturated with water highly charged with silica of volcanic origin. The small plants, some of which were leafless, suggest vegetation growing in the vicinity of volcanic fumaroles and hot springs. Other examples of plants buried in place are the Lepidodendron trunks in the volcanic ash beds on the island of Arran (Seward, 15, Fig. 51) and those which are so admirably exposed in Victoria Park in the city of Glasgow. Here are suggestions that during Lower Carboniferous times conditions prevailed which were quite similar to those in the Great Basin and on the Columbia Plateau regions during Tertiary times. The well known Gilboa trees, of Hamilton age, in eastern New York afford an excellent example of a forest submerged by an encroaching sea. It is probable that here the forest covered a swampy lowland as is indicated by the layer of black shale in which the upright trunks are still rooted (8).

Instances such as those mentioned in which plants are preserved more or less in their natural environment are comparatively rare; usually the plant fossils are fragmentary remains of detached parts which had been transported for some distance. Remains of land plants may occur with marine invertebrates, which means no more than that the plant remains were derived from a nearby land source.

The difference between two fossil floras may be as much due to geographical, i.e., environmental, factors as to time differences.

During the process of transportation of plant remains from the place where they grew to the place of final deposition a kind of "sorting out" process may occur, and not all of the components of the flora of a given locality will always remain in recognizable form in the ultimate deposit. Such factors as distance from shore, direction of currents, presence of petrifying minerals, rate of deposition of sediments, and a number of other things usually exert a selective influence by setting up an environment of deposition suitable for the preservation of some plants but not for others of the same plant association.

* See bibliography, page 64.

- 58 -

An example of such a sorting out of species is shown by the occurrence of Archaeopteris and Callixylon in the Upper Devonian beds of New York and Pennsylvania. Archaeopteris is commonly cited as an index fossil of the Upper Devonian, and in eastern North America it is supposed to characterize the uppermost beds commonly designated as Catskill and Chemung. Since it has recently been shown, however, that the so-called "Catskill" represents an environment of deposition which extended from Hamilton to the end of Devonian time instead of representing a distinct time interval at the top, it follows that the occurrence of Archaeopteris in these deposits, or any other deposits for that matter, proves very little concerning their exact place in the Upper Devonian. Archaeopteris occurs in portions of the so-called "Catskill" which are now known to belong to the Hamilton, and it may occur at any level above. In the westward marine extensions of these beds, which in the east bear Archaeopteris, calcified remains of Callixylon occur (3). That these two genera were contemporaneous is most certain, but in no single instance have they been found together where the identification of both is beyond question. Archaeopteris, is known only from its leaves and sporangia, and such destructible material is seldom preserved in recognizable form at any great distance from its source. It usually occurs in shallow water deposits of mud and fine sand. The trunks and branches of Callixylon were preserved only when they fell in deeper water which carried them away to places where limey or siliceous muds were accumulating. In shallow waters favorable for the preservation of the delicate impressions of the leaves of Archaeopteris the stranded Callixylon trunks mostly decayed. Other possible instances of this selective tendency are known.

Because of the structure of certain organs partial decomposition of the plant may have a marked influence on the external appearance of the fossil. Failure to take this into account has been responsible for many superfluous generic names. The cases of Knorria, Aspidaria and Bergeria, being the different stages in decortication of Lepidodendron, or the Syringodendron condition of Sigillaria, are too familiar to require explanation. Seward (16), taking this state of affairs into account, recently described under a single specific name a considerable assemblage of sigillarian remains from Persia. All the material came from the same horizon and there was no convincing evidence for the presence of other types. In the Antrim, New Albany and Ohio shales are some rather spectacular jointed fossils resembling slender carbonized stems. These had been variously identified as Calamites, Pseudobornia and Callixylon, but a careful examination showed them to be indistinguishable from water soaked woody plant débris which had become cross-cracked as a result of frequent wetting and drying (5). Without this simple and rather obvious interpretation an indefinite number of attempts might be made to explain these curious structures.

The examples given in the foregoing paragraphs seem to indicate two points: First, that a so-called flora may represent a sequence of similar environmental conditions rather than a definitely fixed time interval; and second, that the environment of deposition may so alter an organism that it may present a deceptive appearance.

III. The problem of the relation of structural responses to environment

It is impossible to consider the entire realm of paleoecology without delving into the problem of Paleozoic climate. A full discussion of this subject will not be undertaken but certain features having a direct bearing on fossil plant structures will be treated briefly.

Before the study of fossils had developed into a science speculations were made concerning the climates under which the organisms existed, and in recent times much has been written about Paleozoic climates. In 1882 Seward (14) wrote a prize-winning essay entitled: "Fossil Plants as Tests of Climate." Even here an enormous amount of data is presented. Our knowledge of Paleozoic plants has probably doubled since Seward wrote his essay, but with respect to the climates that existed during this era most of the recent contributions have centered about arguments designed to show the fallacy of previous interpretations. The warm steamy atmosphere highly charged with carbon dioxide as postulated by earlier writers has given way to the conception of more temperate conditions with even an occasional glimpse of a glacier. Most investigators, it seems, have largely given up the notion of world wide tropical conditions during the Paleozoic, but there still exists much disagreement about the degree of seasonal fluctuations. Considerable assistance has been derived from a study of recent peat bogs which has dispelled the ideas that any era had but one set of climatic conditions throughout, or that if there were changes it was one uniform and continual change from the beginning until the end. Peat bogs have shown us that within the brief space of human occupation there have been marked variations in the climate of North America. When we once adopt that point of view for the Paleozoic some progress may follow.

The difficulty attending the problem of deciphering Paleozoic climates is that the objects upon which the most profound imprints were made - the plants - are extinct. Many of the earlier assumptions that the Paleozoic climate was tropical were based upon the supposed prominence of ferns, but the discovery of the pteridosperms induced certain authors to stress the fact that we know nothing of the temperature requirements of the prominent Paleozoic genera. It has also been pointed out that luxuriant vegetation is by no means proof of tropical conditions. The reduced and less ornate foliage of some of the plant types that survived the Permian glaciation has been referred to as an example of a response to a climatic change, but here the evidence furnished by the flora is largely substantiated by that of the sediments themselves. As with certain living species, of which the bracken fern is a stock example, it is quite possible that certain Paleozoic species were able to tolerate a considerable range of temperature, although specific examples cannot be cited.

The presence or absence of growth rings or "annual rings" in Paleozoic stems is often employed as evidence concerning climate. In modern woody plants of the temperate zones the seasonal fluctuations are often strongly recorded by marked difference in cell size. This reaction is so strong in some trees, as Pinus ponderosa and Sequoia gigantea, of the southwestern United States, that they reveal climatic cycles for centuries past (2; 10). Many

things may influence ring development, of which temperature and moisture
are most important. Fires, defoliation, late or early frosts, direction
of wind, shading, production of seed, etc., are factors known to be influ-
ential. The woody dicotyledons react in the same way as do conifers in the
temperate regions but the resulting rings are often less distinct because
of differences in structure of the wood. These differences are differences
in degree only.

Most north temperate zone species react to seasonal changes in the
same way, but in the tropics some are different. The Araucarian conifers,
for example, do not respond as markedly to seasonal fluctuations as do some
other species in the same habitat. Seasonal fluctuations of either moisture
or temperature have little effect on the development of the rings although
indistinct rings seem to form in these trees under most any natural outdoor
conditions. On the other hand, the common persimmon, Diospyros virginiana,
has been observed to develop absolutely uniform wood in an unchanging cli-
mate, but when the same species is subjected to seasonal fluctuations well
marked rings will form (1).

From such observations as these it becomes evident that in judging
climatic conditions from growth rings it is necessary to know how the par-
ticular species in question reacts to seasonal changes. The Sequoiae and
the pines of the southwestern states react to a decided degree but it is
known that other species in other places do so to a lesser extent. It is
quite possible that some species, when subjected to such extreme seasonal
changes of temperature as prevail in Arizona and the High Sierras, gradu-
ally become more responsive. But from observations on some tropical spe-
cies it is apparent that the presence or absence of rings in a tree is not
governed wholly by seasonal fluctuations. The physiological sensitivity
of the plant is as responsible for the obvious anatomical differences as the
vigor of the environmental change.

Growth rings occur in some Paleozoic woods. They appear frequently
in the Permian and to a somewhat lesser extent in the Pennsylvanian. They
are quite recognizable in several Devonian forms. It seems that a greater
proportion of Devonian woods show them than do the Pennsylvanian types.
Neither the Pennsylvanian nor the Devonian rings show the same prominence
of development as do those of our north temperate zone coniferous species
but they are more comparable to those of certain tropical trees. The rings
of the fossil woods are usually several millimeters wide and the summer
wood zone seldom exceeds three or four cells. In some cases, the rings ex-
tend only part way around the stem. Without making a careful examination
of the fossil wood it is sometimes difficult to distinguish a growth ring
from a zone of crushed cells, and it is quite probable that such appearances
have misled some investigators.

Probably the best example of a Devonian plant showing growth rings
is Callixylon. A stem of C. erianum from the Genesee shale and which has a
radius of 23 mm. shows five complete rings (3). Similar rings are shown in
C. Newberryi from the New Albany shale. Calamopitys eupunctata from the
Portage of New York also shows definite rings (13).

Rings have been observed in the Lower Carboniferous Pitys antiqua
from Scotland (9).

- 61 -

In rocks of Pennsylvanian age Cordaites michiganensis from the Saginaw formation (Pottsville) of Michigan shows no ring development in a wood cylinder 1 cm. thick (4). Dadoxylon romingerianum, probably of the Conemaugh group, from Coshocton, Ohio, shows absolute uniformity of growth in a radial extent of 5 cm. (4). From Kansas some interesting facts are available. A specimen as Cordaites materiarum (17) from the Des Moines series shows distinct layers which vary from 3.5 mm. to 6.5 mm. in width. From the Virgil series Dadoxylon douglasense is without growth rings, although to the unaided eye a transverse section of the wood shows indefinite zones which might be mistaken for such (17). At a higher level, at the base of the Big Blue series, a specimen identified as Cordaites recentium (7) shows rings varying in width from 3 to 8 mm.

In the Permo-Carboniferous growth rings are common, as is evident from even a casual examination of the literature.

The examples just noted of growth rings in Paleozoic woods are relatively recent discoveries and are not mentioned in the older literature from which most conclusions pertaining to Paleozoic climates have been drawn.

Most of the best known Coal Measures plants as Lepidodendron, Sigillaria, Mesoxylon, Lyginopteris and Medullosa are typically without any indications of growth responses, but other forms such as those just mentioned, which were nearly contemporaneous with them, show rings in unmistakable fashion. It is significant that the rings usually occur in forms which are believed to represent upland types, of which Callixylon, Pitys, and various specimens assigned to Cordaites and Dadoxylon are examples. Furthermore, it is believed that the Cordaitales were represented during the Carboniferous by both swamp inhabiting and upland species.

The apparent occurrence of growth rings in some Paleozoic woods and their absence in others might also have some correlation with long range climatic fluctuations within that era, and it is believed that many all inclusive statements about Carboniferous climates do not take into account this probability. It is inconceivable that a lapse of time as long as the Carboniferous should have a uniform climate throughout or that conditions during that time could have been uniform over the whole earth. Coleman (6) has warned against sweeping conclusions concerning Paleozoic climates from the limited amount of available data.

Although growth rings in Paleozoic woods cannot be interpreted as constituting evidence of marked seasonal fluctuations within that era, it is impossible to explain them on other grounds than that they reflect seasonal changes of some sort. Without seasonal variations of some kind it is impossible to account for the origin of regular growth rings in the first place. It is reasonable to assume that the most primitive plants with secondary growth developed uniform wood and year after year each successive addition of cells was indistinguishable from the previous one. Only when vascular plants had become more specialized both in structure and in their ability to respond to the environment did growth rings appear.

Considering all the information available it is believed that the following conclusions are justified: (1) that the occurrence of growth rings in some

- 62 -

of the Paleozoic woods is not a strong argument in favor of marked season-
al fluctuations during that era, nor do their absence in others prove uni-
formity of climate; and (2) that growth rings such as do occur are in all
likelihood responses to seasonal fluctuations of some sort, to which cer-
tain Paleozoic species were not sensitive.

Various attempts have been made to correlate other structures shown
by Paleozoic plants with the environment. Bilignea solida, from the cal-
ciferous sandstone (Lower Carboniferous) and Megaloxylon scottii from the
Lower Coal Measures show large cavities in the pith which have been inter-
preted as water storage structures. Whether they served this purpose or
not is entirely a matter of conjecture. Unless there was an inadequately
developed root system it is difficult to understand the utility value of
such structures except for plants subject to extreme aridity. However, if
the plants grew in situations where there was a marked seasonal lowering
of the water level the accompanying dryness might account for the presence
of such cavities.

Investigators have long hoped that an examination of structurally
preserved leaves would ultimately throw more light on the question sur-
rounding Paleozoic ecology, but the results obtained have not come up to
expectations. Such features as epidermal outgrowths, size and number of
intercellular spaces, arrangement and position of the stomata, cuticulari-
sation and enrolling of the margin are known definitely to have some corre-
lation with environment, but the degree of correlation is usually peculiar
to the species. Only under extreme aridity, salinity, exposure to high
winds or other strenuous conditions do any of these features show specializa-
tion to the extent of being conspicuous. The tolerance of structural var-
iations under normal conditions of temperature and moisture is large, and
different species in a similar habitat may show considerable variety of
structure with respect to the features mentioned. Most Paleozoic leaves
of which the structure is known could apparently survive very well under
north temperate zone conditions such as prevail in the eastern or southern
portions of the United States or along the Pacific coast as far north as
Alaska. They show no special adaptation to subdued light, high temperature,
or to excessive humidity. Seward's statement is appropriate: "Broadly
speaking we see no indication that these leaves were exposed to any condi-
tion of climate other than such as now obtain." (14, p. 72)

IV. Environment and the origin of floras characteristic of certain periods

The assumption that an assemblage of species, or a certain species
regarded as an "index species," furnishes definite proof of the age of a
deposit sometimes leads to erroneous conclusions. To accept a given species
or type as an absolute and undisputable time marker is frequently a con-
fession of ignorance concerning its ecological relations. A given species
exists in a given deposit largely because the environment was suitable for
its existence up to the time of deposition, and with the approach of less
favorable conditions it became less abundant or extinct. In this way fossils
may best be regarded as "environment markers" rather than strict time mark-
ers. The occurrence of Archaeopteris throughout the landward phase of the
Upper Devonian delta on the northern Appalachian region is a specific example.

Another instance bearing out the same idea is the recent discovery in eastern Kansas (12) of an assemblage of plants consisting of Walchia, Taeniopteris and other typical "Permian" forms in a deposit of undisputed upper middle Pennsylvanian age. A competent paleontologist, basing his assumption upon the floral assemblage alone, maintained that the deposit is unquestionably of Permian age. A study of its stratigraphic position, however, completely invalidates this view. The flora represented here is regarded as an upland one, and although contemporaneous or nearly so with the swamp floras of other parts of North America, developed along different lines. Then, with the approach of more favorable Permian conditions this upland flora survived and spread, and the descendants became the typical Permian types as they are now known. Here, as with Archaeopteris, what would otherwise be a stratigraphic anomaly can be satisfactorily explained when the environment and the adaptations to it are taken into consideration.

V. Summary and conclusions

Any treatment of the paleoecology of Paleozoic plants is largely a consideration of problems and appraisals of previously offered theories. While the fundamental principles are probably the same as those applying to recent plants they are difficult to apply because the environmental relations of most Paleozoic plants are unknown. The same adaptations shown by recent plants cannot always be applied to Paleozoic plants because of the remoteness of the relation between them, and also by the fact that there is a great difference in sensitivity to adjustment among different species. Sufficiently pronounced structural features in Paleozoic plants may indicate adaptations of a certain kind if comparable adaptations can be recognized in living forms.

Environmental conditions varied in time and place during the Paleozoic, and sweeping conclusions regarding temperature, seasonal fluctuations and humidity should not be drawn from plants within a limited area or restricted horizon. The old idea of a graduated climate from hot to cool within the Paleozoic has been gradually abandoned, but there still exists too great a tendency to regard the eras or periods as climatic units.

The visible differences between fossil floras may be due as much to the various agencies in operation at the time of deposition, or to geographical location, as to differences in time. Also, because of the complicated structure of the plant body, the appearance of the resulting fossil may present a deceptive appearance.

Lastly, fossils may be regarded as markers of environmental units as well as time units, and plant associations which developed within one period but within a restricted range may have survived to a later time in which they spread when favorable conditions developed.

- 64 -

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