ART. XXVIII.—*The History of Corals and the "Limeless" Oceans*; by PERCY E. RAYMOND.

One swallow may not make a summer, but in the realms of Paleontology one discovery may let a flood of light into provinces previously most obscure. Perhaps the most remarkable single "find" which ever rewarded the fossil hunter was that made by Dr. Walcott at Burgess Pass, British Columbia. No such aggregation of soft-bodied animals had ever been seen in the rocks before, not even at Solenhofen. The fossils are so unusual, and so different in their preservation from those usually studied, that even now, ten years after the first of them was described, their significance is not fully appreciated.

Among these fossils there is one which has given rise to certain suggestions which I wish to bring forward, as to a possible interpretation of the somewhat obscure history of the corals.

Mackenzia costalis Walcott¹ (fig. 3) was described as a holothurian, but H. L. Clark² in a review of the original paper, and after a study of the specimens, considered it an Actinian, in which determination Austin H. Clark has concurred.³ An extract from the article by the latter may be quoted:

"The type specimen of *Mackenzia costalis* shows a pleated structure which can only be interpreted as due to longitudinal mesenteries, probably eight in number; there appear to have been sixteen processes around the mouth, which probably indicate sixteen tentacles retracted before preservation; the distal portion of the body resembles closely the distal portion of the body in the genus *Edwardsia*. Thus, as *Mackenzia costalis* presents characters not found outside of the Zoantharia, and in that group peculiar to the family Edwardsiidae, it seems necessary to assign it to a position in the family Edwardsiidae, near the genus *Edwardsia*." (loc. cit. p. 507.)

This determination of the fossil is of peculiar interest, since the Edwardsiidae are considered the most primitive of the Zoantharia, and in their ontogeny, modern Hexacoralla pass through an *Edwardsia* stage. There is, fur-

¹ Smithsonian. Misc. Colls., vol. 57, p. 55, pl. 13, figs. 2, 3, 1911.

² Science, vol. 35, p. 275, Feb. 16, 1912.

³ Am. Naturalist, vol. 47, p. 503, 1913.

thermore, a possibility that Mackenzia is even more primitive than is suggested by Dr. Clark. Although his interpretation of the ring about the mouth as a series of contracted tentacles is a very probable one, still their small size suggests that they are simple "out-pushings," and that the actinian of the Middle Cambrian retained in the adult a structure like that of the larva of the modern actinian just before fixation (fig. 2). If further discoveries sustain this opinion, then Mackenzia can be added to the list of "ancestors" whose recognition has been brought about by the aid of the doctrine of "recapitulation."

FIGS. 1-3.

FIG. 1. *Edwardsia beauteupsi*. After de Quatrefages. Two-thirds natural size.

FIG. 2. *Urticina crassicornis*. Larva just before fixation. After Appelöf. Much enlarged.

FIG. 3. *Mackenzia costalis*. Somewhat restored. After Walcott. Two-thirds natural size.

The chief interest in Mackenzia lies, however, in the fact that it is a limeless Zoantharian which can be placed in a primitive position in relation to modern corals. Hexacoralla pass through a Mackenzia-Edwardsia stage, and it is very probable that the Tetracoralla did also.

One of the puzzles in the history of the corals has been the abrupt replacement of the Tetracoralla by the Hexa-

coralla in the early Mesozoic. No one of the former survived the Paleozoic; none of the latter is represented by a calcareous fossil in that system, Robinson having shown that the supposed Paleozoic hexacorals really do not belong to that group.⁴ What caused the extinction of the Tetracoralla, and whence did the Hexacoralla come? Arguments that the latter were derived from the former have been put forward repeatedly, but do not seem convincing. That they had a common ancestry seems practically demonstrated by studies in ontogeny.

It seems possible that the answer to these questions may be connected with physical changes at the end of the Paleozoic. The waters of the oceans were doubtless greatly chilled at the time of the Permian glaciation, and this may have caused the killing of the Tetracoralla. That these animals had, like modern reef-building corals, become adapted to life in warm seas is shown by the fact that they are almost confined to limestone, and that practically all are of reef-building or reef-inhabiting nature. Even the simple unbranched corals are found in great numbers when found at all, and there is every indication that before the end of the Paleozoic they had become fully adapted to life in clear, shallow, warm waters. Many tribes did not, of course, survive even to the end of the Paleozoic, and in eastern North America perished during the uplift which followed the deposition of the Middle Devonian limestones.

Tetracoralla appear first in the Middle Ordovician, and although the earliest representatives now known are simple, it is very probable that further collecting will reveal them in the Lower Ordovician and perhaps in somewhat older formations. Mackenzia is a form which could have been ancestral to either of the groups mentioned and it is possible that they diverged as early as the Upper Cambrian. Edwardsia, with which Mackenzia is comparable, is today an inhabitant of the sand, and does not secrete a skeleton. Members of the family occur in shallow, cool waters about the British Isles. It might seem that Mackenzia and its descendants remained, during the Paleozoic, in the cooler waters along sandy and rocky shores, and living thus in places where calcium carbonate remains readily in solution, they did not get the lime

⁴ Trans. Conn. Acad. Arts and Sci., vol. 21, p. 145, 1917.

habit. Being accustomed to cool water they survived the Permian glaciation, but due to geographic and climatic changes, were perhaps driven from their original homes, and, the temperature of ocean waters being universally lowered, attained a wide distribution. They found the geographical and ecological positions of the *Tetracoralla* uninhabited, and so began to thrive and to change.

Writers have repeatedly commented on the fact that corals are exceedingly rare in the older Triassic deposits, and reefs of *Hexacoralla* first appear after the middle of Triassic time. It may be inferred from this that the oceanic temperatures did not become favorable for corals for some time after the melting of the Permian ice, and by this time the limeless corals had become established in many regions previously unoccupied by them. With the warming of the waters there came a surplus of calcium, and the animals no longer being able to fully eliminate it, began to build skeletons. By this time the larval form had been sufficiently changed so that septa were deposited in cycles of six instead of four, and a new era in the history of corals was inaugurated.

It does not appear that the question of temperature, and inferentially of climate, has been given sufficient attention in connection with the discussion of the origin of the "lime habit" in animals. The first great development of calcareous skeletons was in the Ordovician, and was coincident with the first appearance of great masses of non-clastic limestone, and with the first relatively complete world-wide peneplanation. The almost universal Pre-Cambrian mountain building indicates that the Cambrian sedimentation began with differentiated but probably cool climates, and while small deposits of limestone formed during the Lower Cambrian testify to local, warm basins, the universal rise in temperature came later.

A second factor connected with the secretion of calcareous skeletons is that of the habits of the animal, whether active or sedentary. Although there are exceptions to the rule, active animals usually have less thick shells or bones, not because they have less need for them, but probably because they eliminate lime more readily. If one surveys the Cambrian fauna, he finds there few sedentary animals. Those which are present are sponges, a few cystids, some protrematous and a few atrematous

brachiopods, and the anomalous Archaeocyathinae. The sponges are all of the siliceous types, and only the Archaeocyathinae secrete calcium carbonate in any quantity; they are also, aside from the sponges, the only animals which are firmly fixed in one spot. Reproduction by budding in colonial fashion was also in its infancy in Cambrian times, showing incidentally that the sexual preceded the asexual method, and this indicates clearly that animals had but recently "discovered the ocean bottom." Colonial life really developed first in Ordovician times, when sedentary animals like the Hydrozoa, Bryozoa and Anthozoa first became abundant.

Throughout geological history the times of great expanse of shallow, warm seas have been the times of great development of animals with thick shells. Once the lime-secreting habit had been acquired, animals persisted in it. The chief factors in its origin, however, would appear to be excess of salts, due to warming of the waters, and decrease in power of elimination, due to sedentary habits.

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