

AMERICAN MUSEUM NOVITATES

Number 197

Published by
THE AMERICAN MUSEUM OF NATURAL HISTORY
New York City

Nov. 21, 1925

56.53,5P(112:74.7)

THE SUPPOSED PALEOZOIC BARNACLE *PROTOBALANUS* AND ITS BEARING ON THE ORIGIN AND PHYLOGENY OF THE BARNACLES

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Recent articles by Ruedemann (1924, Bull. N. Y. State Museum, No. 251, pp. 93-104, Pls. I, II; and Ann. Mag. Nat. Hist., (9) XIV, pp. 533-544) and Withers (1924, Ann. Mag. Nat. Hist., (9) XIV, pp. 318-324) have called renewed attention to the interesting questions of the origin and antiquity of the group Cirripedia as a whole and of the two chief divisions of that group, the Balanomorpha, the sessile or acorn barnacles, and the Lepadomorpha, the stalked or goose barnacles. While the strength of Withers' argument for a comparatively recent origin for the barnacles and especially for the Balanomorpha must be admitted, and while we may doubt the cirriped character of Ruedemann's *Eobalanus*, and some of the other supposed Paleozoic barnacles, we still have *Protobalanus hamiltonensis* from the Devonian (Marcellus Shales, Hamilton Group at Avon, New York) to account for, a form much more like a modern acorn barnacle than any of the other Paleozoic fossils. The first description of this form appeared in the 'Natural History of New York,' 1888, Paleont., VII, p. 209, Pl. xxxvi, fig. 23. Though the name and description are credited in this work to R. P. Whitfield of The American Museum of Natural History, New York, it seems doubtful whether they should not rather be credited to the authors of that volume, James Hall and John M. Clarke. Whitfield himself published a description and figure of the fossil the following year (1889, Bull. Amer. Mus. Nat. Hist., II, p. 66, Pl. XIII, fig. 22), stating in a footnote (p. 67) that, for the purpose of including this form in the volume of the New York Paleontology, the generic and specific name had been given to Prof. J. M. Clarke, and the specimen loaned for illustration.

Neither the two descriptions nor the two illustrations agree in all particulars. A re-examination of the type and only known specimen, which is in The American Museum of Natural History, New York, shows that the first description and illustration are open to the least criticism, the later one of Whitfield erring on the side of seeing more in the fossil

than seems to be warranted from the state of its preservation. The original (1888) description is here quoted.

"**PROTOBALANUS**, n. g. (R. P. Whitfield).

Protobalanus hamiltonensis, n. sp. (R. P. W.)

Plate XXXVI, Figure 23

Shell small, ovate in general outline, narrowing toward the carinal extremity; surface depressed-convex, most elevated at the apex of the carina; composed of twelve peripheral plates.

Carina sub-semicircular in peripheral outline, conspicuously elevated to an obtuse apex, which lies just within the proximal margin of the plate; regularly sloping on the anterior surface, but slightly incurving or concave upon the sides.

Rostrum short, posterior margin broadly curving, apex scarcely elevated.

The *lateralia*, which are regularly disposed in five pairs, are symmetrical, and of the same general elongate, triangular form and of nearly the same size, the anterior members being somewhat the larger. The apices of these plates, as far as preserved, are slightly elevated and elongated in a short ridge toward the axis of the shell. All these plates are marked by low, radiating ridges, which become obsolete before reaching the apex. Of these, twelve may be counted upon the *carina* and six or eight upon the *rostrum*; on the *lateralia* they vary in number from four to seven. The *radial areas* are conspicuous and, as far as can be discerned, smooth. A portion of the type specimen has been broken away, removing the summits of the posterior plates and covering the spot where the *scutum* and *tergum* would normally lie.

The specimen, which retains the replaced substance of the original shell, shows an expanded margin about a portion of the periphery, and this probably represents a portion of the edge of the valves which has been flattened and creased by compression.

Dimensions. Length 4.5 mm., greatest width, 3.5 mm."

A comparison with the photograph and the diagram (Fig. 2) here given, will disclose certain minor inaccuracies as to the number of furrows on the plates, etc., and the point of view from which it is written, that the specimen is a near ally of the modern *Balanidæ*, will of course be objected to. It is most unfortunate that the central or apical part of the specimen has been broken away. The broken area has been scaled off so as to leave a lower layer of the rock that fills the interior of the fossil exposed. On this broken surface several somewhat smoother areas are noticeable. How much significance these may have it is difficult to say; if they have any at all they are probably indistinct and incomplete impressions of the interior surface of the five parietal plates which extended into the broken area; that they are to be interpreted as indicating that there were three paired opercular plates as Whitfield (1889) claimed, seems entirely unwarranted.

It does not seem possible to discover anything in regard to the central or apical aperture from the fossil. It may have been entirely in the

broken area. On the median line between the apices of the second lateral plates from the "carina" there is a somewhat pyramidal nodule that may represent a small median plate, but that it lay within any central aperture or that it is in any sense of the word a true opercular plate as Whitfield called it cannot in my opinion be satisfactorily demonstrated. I can find no reliable indications of any such plates in the fossil. Proof that they did not exist is likewise wanting.



Fig. 1. Photograph of type of *Protobalanus hamiltonensis* enlarged nearly twelve diameters. The specimen was whitened with sublimed ammonium chloride to bring out the relief. The photograph has not been retouched or altered in any way.

The triangular "radial areas" between the parietal plates merge into the uneven central area. What was the character of these "radial areas," which are somewhat depressed below the surfaces of the parietal plates, it is difficult to decide. As the description says, they appear smooth, as if a somewhat flexible membrane connected the plates. That they may have been occupied by overlapping "alæ" and "radii" as in modern barnacles is not impossible, but after studying the specimen with various degrees of magnification and with light coming from different directions, I feel that such a conclusion would be based more on preconceived notions of what we should see, than on anything that can be

demonstrated in the fossil. Yet admitting the uncertainty on all these important points, the fossil looks strikingly like a barnacle.

One of the most peculiar features of the fossil has not yet been discussed; the radiating grooves extending out from the margin of the fossil around a part of its circumference, explained in the original description as representing a marginal

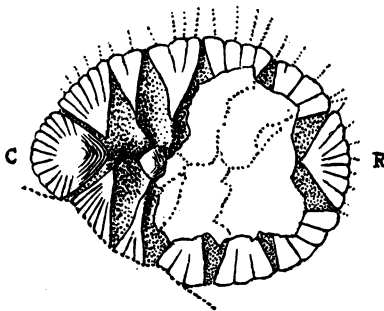


Fig. 2. Diagram representing the distinguishable features in the type and only known specimen of *Protobalanus hamiltonensis*. Enlargement about 10 diameters.

C, carinal plate; R, rostral plate.

portion of the plates "flattened and creased by compression." This does not seem to be a possible explanation. In the first place how could such a creasing happen? Even if it occurred, it could not explain the actual condition of the fossil, for these grooves are clearly on the surface of the matrix outside the fossil, and they are not (except in occasional apparently accidental cases) coincident and continuous with those on the plates, though corresponding with them more or less nearly in number and direction. Whitfield in

his later description refers to these grooves as a "narrow fringe," but gives no explanation of them. In his figure he incorrectly represents them as extending around most of the circumference of the fossil. I can distinguish them around less than half the circumference. These grooves in the matrix are very distinct in some places, but are of various degrees of obscurity in others, and it is often hard to distinguish between them and accidental depressions in the surface of the matrix.

Perhaps they may be explained by the supposition that the base of the fossil had radial grooves corresponding rather nearly to those of the parietal plates, and that these grooves left their impress on the mud where the specimen rested. Before an additional deposit of mud buried it, the specimen appears to have been shifted laterally, and rotated slightly, uncovering a little of the area on which it had been resting. This is borne out by the fact that the grooves in the matrix are best preserved where they lie in or nearly in the direction of such shifting, and that near the ends of the specimen, where they lie across that direction, they are short and more or less obliterated. Moreover the edge of the specimen seems to have been forced down into the matrix a little on the side opposite, as though by the same impulse that moved it so as to

make it expose the grooves in the mud. This is the most plausible explanation I can give of these grooves. It would not hold if they existed all around or nearly all around the fossil, as in Whitfield's (1889) figure, but I consider the figure entirely wrong in that respect. I cannot distinguish any reliable traces of them except as shown in the diagram (Fig. 2).

The small size of this specimen (it is little over 4 mm. in greatest diameter) and the large broken area make its interpretation difficult, yet, as already stated, a strong superficial resemblance to a modern barnacle is evident.

If it is not a barnacle, what is it? If it is one, we should expect to find fossils connecting it with the modern forms, and the total absence of connecting forms is hard to explain. But this remarkable specimen exists. That fact we cannot get away from; we cannot ignore it. If we deny it a place in the Cirripedia, apparently we must assume for it a separate class of animals, which, though evidently highly specialized and which developed a system of protective plating that should fossilize easily, has left no known remains except this one individual. Not the least extraordinary feature of the specimen is this uniqueness. Where are the ancestors it must have had? Where are the descendants it probably had? Why have no other individuals ever been found? If we deny that it is a barnacle we still have many of the same difficulties to explain away in the matter of the absence of paleontologic records that we have if we admit that it is one. In any event it furnishes us a most striking illustration of the incompleteness of the information that paleontology affords us.

While I feel that one should keep the question of the character and relationships of *Protobalanus*, and that of the antiquity of the barnacles in general, open, it seems to me that it is only by an unwarranted disregard of the evidence furnished by the structure of the internal parts and limbs and by the ontogeny of the existing cirripeds that separate origins of the modern Balanomorpha and Lepadomorpha from free-swimming Crustacea, as is considered probable by Ruedemann, can be regarded as a possibility. They agree in too many important characters of structure and development for us to doubt for a moment that they had a common ancestor that was already a true cirriped and which had tergal and scutal plates, although we can be pretty sure that this primitive form had neither the peduncle of *Lepas* nor the conical, broadly sessile form of *Balanus*.

Both these peculiarities are different specializations for a particular environment, that of strong waves and currents of water likely to tear the animal from its attachment and thus destroy it. The Balanomorpha

resist the force of the water by a low compact form and wide, strong base of attachment, the Lepadomorpha by a narrow flattened body attached by a flexible peduncle that yields to the currents and waves.

It is not likely that the barnacles originated in such an environment. The permanent attachment of free-swimming animals would be practically impossible under such conditions. My own view is that the barnacles originated from their bivalve crustacean ancestors, whether phyllopod, as most of us believe, or phyllocarid, as Ruedemann believes, while they lived partially or almost completely buried in the mud or fine sand of the bottom. These animals, as Ruedemann suggests (Bull. N. Y. State Mus. No. 251, p. 96) and as many of their modern allies do, probably swam on their backs, and when buried would be likely to assume

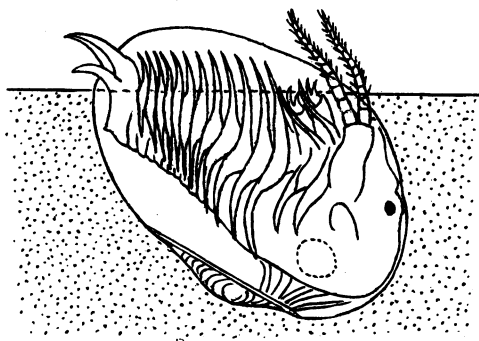


Fig. 3. Diagram representing the probable position, partially buried in the mud of the sea bottom, in which the phyllopod ancestors of the barnacles underwent the first stages of their evolution into barnacles.

a similar position with the head somewhat lower, and the rear ventral part exposed (Fig. 3) so that the valves, which were hinged along the mid-dorsal line, might open and admit water for respiration, a current within the carapace being doubtless maintained by motions of the appendages, as in modern Crustacea. Would not this furnish an ideal opportunity for the development of the shrimp-like form into a true cirriped, that would otherwise be a difficult transition, as Ruedemann admits (Ann. Mag. Nat. Hist., (9) XIV, p. 542)? Long periods, thousands of years probably, would be required in the transition, during which time its organization would be poorly adapted for existence or for obtaining food, either as a motile or a fixed animal. (In the ontogeny of individuals such transition takes place by a rapid metamorphosis and these difficulties

are not important.) When thus buried in the mud in favorable situations, the water currents drawn in for respiration would also bring in enough food, probably small organisms or mud loaded with organic matter, to suffice without the necessity of the animal moving.

The development of glands at the anterior end of the body to produce a byssus-like or adhesive secretion to help anchor the body would be an advantage and would be favored by natural selection. Calcareous protective plates would, however, be of minor advantage excepting perhaps plates corresponding in location to the scuta and terga of modern barnacles. When, from accident or lack of suitable soft bottom, individuals attached themselves in exposed places, they would not ordinarily survive, but if occasionally they did succeed in establishing themselves, the development of calcareous protective plates in their descendants would certainly be an advantage that natural selection would tend to perpetuate.

Even in the recent barnacles, though they form a fairly compact group, we find variations in the number and arrangement of the calcareous plates, notwithstanding great uniformity in the fundamental plan and also in many of the details of their structure. This condition would be well explained by the theory that these plates (with the possible exception of the scuta and terga as above suggested) were late developments formed only after the animals, having already acquired the important morphological characteristics of cirripeds while leading a more or less protected existence as burrowing forms, came to attach themselves in more exposed situations. Such a change in habits probably happened not once only but at many different times and in many places, and in members of different genera and families differing in the external form of the body and in the form of and degree of mobility of the carapace and other cuticular parts. Consequently we should expect to find important differences in the calcareous armor even in forms quite closely allied to each other.

Small size, lack of hard parts, and such a buried existence might explain the absence of fossils of the main stem of the barnacles during the Paleozoic. Only such aberrant side lines as developed hard plates would have much chance of preservation. It seems to the writer that such possibilities give additional reason for keeping an open mind on the subject of the antiquity of the Cirripedia. The extraordinary and fundamental modifications that have occurred in the Rhizocephala, evidently an offshoot of that group, furnish still another argument for their great antiquity.

In conclusion, I would like to call attention to certain interesting facts regarding the Cirripedia.

One is that though they have been sessile degenerate animals since the Triassic at least, and perhaps very much longer, they have never developed the power of budding and forming true colonies or compound animals. This lends some support to my contention, expressed elsewhere (1921, *Bull. American Mus. Nat. Hist.*, XLIV, pp. 275-282), that true budding and colony formation are functions that must be inherited from the earliest stages in the phylogeny of any group and elaborated along with its phylogenetic development, and that if once completely lost they are lost permanently.

Another point is the extraordinarily effective specialization of the Cirripedia for the particular environments in which they live. They are the most efficiently specialized of all permanently attached animals, as is well shown by their living in millions on rocks exposed not only to the strongest waves, but left uncovered for long periods every tide, so that practically no other permanently fixed organisms can survive there. So effectively are their limbs adapted for netting food that they can get what they need in an hour or two every tide, and remain closed up the rest of the time. Likewise they can grow on sea turtles, the fins of whales, ships' bottoms and other places where most organisms would be washed away, and when certain of them become modified for a parasitic life, where in the whole animal kingdom is there a more remarkable example of complete adaptation than that furnished by the Rhizocephala? They exemplify the greater faculty for perfect adaptation that the two highest phyla of the animal kingdom, the arthropods and chordates, possess.