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ON THE STRUCTURE OF THE CARAPACE IN THE DEVONIAN CRUSTACEAN RHINOCARIS; AND THE RELATION OF THE GENUS TO MESOTHYRA AND THE PHYLLOCARIDA.

By John M. Clarke.

In the original account of the peculiar fossil *Rhinocaris*,\(^1\) the carapace was described, from the best evidence then obtainable, as univalvular, with a rostrum projecting conspicuously and consolidated with the valve. The type of structure appeared to be a remarkable departure from that exemplified in the prevailing phyllocarid crustacea of the Devonian (*Echinocaris, Elymocaris, Tropidocaris*), and seemed to evince in the very structure mentioned, strong affinities with the Decapods.

The diagnosis of the genus was virtually based upon a single specimen in which the carapace had been laterally compressed in such a manner as to demonstrate the non-existence of a median suture or hinge, and to conceal any evidence of other longitudinal sutures; and in which, also, the rostrum was laterally flattened and apparently continuous with the carapace.

For several years I have been carefully searching for additional information concerning this peculiar crustacean. A considerable number of specimens from the shales of the Hamilton group of Ontario County, New York, have come into my hands, but the test of the animal is so very tenuous that it seems well nigh impossible to secure examples which have not been subjected to some distortion, and that is usually the greatest at structural points of critical importance. Several excellent specimens, however, have been obtained, some of them kindly furnished by Mr. F. B. Loomis, of Spencerport, N. Y.

The carapace of *Rhinocaris columbina* Clarke, (the typical

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\(^1\) Paleontology of New York, vol. vii, pp. lviii, 195, pl. xxxi, figs. 16–21, 1888.
species) consists of four distinct and separate parts; two broad lateral plates or valves, a narrow median or axial plate, and an anterior median plate or rostrum.

The valves have an elongate, somewhat semi-oval marginal outline, narrower posteriorly than anteriorly, with a truncate or concave posterior extremity. They come into contact at only a single point, and that is in the axial line at about one-fourth of the median length from the anterior margin. At this point a projecting angle is formed on each by the attenuation and termination of the rostrum and median plate, and the projecting points appear to come into simple apposition, though it is possible that they slightly overlap; there is, however, no satisfactory evidence of the clasping of the valves at this point, such as that occurring in the great species *Mesothyra Oceani*.

![Diagramatic figures showing the carapace structure in *Rhinocaris*.](image)

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of a low pustule with a single central depression or pit. From the base of this node radiates a series of linear, sparsely branching sinuses which extend laterally and posteriorly toward the marginal regions, the longest traversing nearly one-third the length of the valves. There is a very faint ridge or carina which lies just outside the middle of each valve and extends subparallel to the outer margin, for nearly the length of the valve, though reaching neither its anterior nor posterior margin.

In addition to these characters, the valves, over the marginal regions, bear the fine anastomosing elevated lines which characterize all the phyllocarid crustacea.

*The rostrum* is an elongate plate having, when flattened horizontally, somewhat the form of a willow leaf. Its broader end is inserted into the anterior gap between the valves and its posterior extremity is acute. As the plate begins to project beyond the anterior edge of the valves of the carapace, it narrows, its lateral expansions become deflected, the median portion tapering rapidly and becoming slightly incurved toward the tip.

The plane of the anterior half of the plate stands at nearly right angles to that of the posterior half, as shown in the accompanying figures. That this organ is in symphysis with

**Fig. 2.** Dorsal view and outline profile of the rostrum of *Rhinocaris columbina*.

the valves is evident from the fact that it is rarely found in its normal position. The surface is peculiarly ornamented by a series of elevated lines forming a sort of midrib; over the lateral posterior expansions the lines become much finer, diverge
radially from the center after the manner of leaf veins, anastomosing to some degree, frequently terminating in oblique punctæ, and in parts where the lines disappear the punctæ remain.

*The median plate.* This is a very narrow body, its width exceeding at no point the greatest diameter of the rostrum. It begins at the union of the valves, in an acute angle, but its lateral margins soon become subparallel or convex outwardly. In relative proportions its length is about eight times its width.

Along the median axis it bears an elevated ridge-like line, from which there is a gentle slope on each side, and it was essentially from this evidence of continuity of the test on the axial line and from the concealment of the sutures between this plate and the valves, that the carapace was originally described as univalvular. The fine incised lines of the surface diverge anteriorly from this ridge.

In discussing, in Volume VII of the Paleontology of New York,\(^3\) the structure of the great carapaces from the lower Chemung beds at Ithaca, N. Y., which had theretofore been known as *Dithyrocaries neptuni*, it was shown that these carapaces (now termed *Mesothyra oceani*) must have had a composition similar to that we now find to have actually existed in

\(^3\) *Op. cit.* p. 184, pl. xxxi, figs. 8–10.
Rhinocaris. This presumptive structure was exhibited in a diagrammatic figure upon Plate xxxii, of which a reduced copy is here given. Though neither the rostrum nor the median plate in *Mesothyra* has yet been seen, all doubt of their existence is removed, and it affords a personal gratification to find this reconstruction of *Mesothyra* so fully substantiated by our present knowledge of the carapace in *Rhinocaris*.

The structure of the visual organ affords a further correspondence in the two genera, and one of some morphological significance.

In regard to the number of abdominal segments, present evidence indicates a difference in the two, *Rhinocaris columbina* having at least three, and *Mesothyra* having shown but two.

In the genus *Tropidocaris* Beecher, it has been shown that the type species, *T. bicarinata*, possesses a rostrum, and its anterior extension is not unlike that of *Rhinocaris*, but there is now no satisfactory evidence of a free median plate in any of these species. Unfortunately the accessible specimens of the species are not very satisfactorily preserved, and the originals described by Mr. Beecher in Report PP of the Second Geological Survey of Pennsylvania, are understood to be beyond the reach of further investigation for the present. In plaster casts of the originals, the median suture on the hinge appears to be invariably in the longitudinal axis of the test. The original specimens of *Rhinocaris scaphoptera* and *Tropidocaris hamiltoniae*, which were collected by me in the Hamilton shales of Ontario County, N. Y., both show some evidence of a quite narrow median plate, and the former possesses a stout rostrum, while in the *Mesothyra (Dithyrocariis ?) veneris*, from the Marcellus shales, both median plate and rostrum are distinctly seen.

It may be questioned if the multcarinate carapaces composing the genus *Tropidocaris* should be placed in close asso-

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5 *Op. cit.* pl. xxxiii, fig. 3.
ciation with the unicarinate carapaces such as are possessed by *Rhinocaris columbina*, *R. scaphoptera*, *Mesothyra oceani*, *M. (Dithyrocaris?)* *veneris*, *Tropidocaris hamiltoniæ*, etc. All the latter appear to have possessed the carapace structure of *Rhinocaris columbina*, and if they are to be considered as representing different modifications of this type, sufficient to entitle them to distinct generic appellations, the following division of them may be preferable to that now standing: under *Rhinocaris*; *R. columbina*, *Mesothyra veneris*; under *Mesothyra*; *M. oceani*, *Tropidocaris hamiltoniæ*, *Rhinocaris scaphoptera*.

In regard to the unicarinate genus *Argas*, or *Dithyrocaris*, it may be stated that as described and illustrated by European writers, it has not been shown to exist in the Paleozoic faunas of North America. When the structure of the carapace in the type species shall become more precisely known, we shall have a better basis for the comparison of these fossils with those under consideration, but at present we are not justified in assuming that they possessed the same structure as the unicarinate Rhinocarids.

Leaving these points of systematics, we find in *Rhinocaris* and its allies a remarkable carapace structure, an explanation of which it is difficult to find among fossil or recent crustaceans. We may conceive the double suture to have been a temporary modification of the Ceratiocarid type, induced by a necessity for movement of the lateral parts of the carapace after anchylosis has become established along the original median hinge. The evidence favors the belief that the valves were capable of motion along the double hinge, and nearly every specimen demonstrates the fact that the parts were separable along these lines after but slight maceration of the tissues.

No satisfactory elucidation of the origin and morphological significance of this structure appears from a study of the embryological phases of *Nebalia* as given by Metschnikoff, Claus and Packard, nor in the development of the Decapods as shown by Sars, S. I. Smith, Brooks, Bumpus and others. It is, nevertheless, in the development history of *Nebalia* and the
Decapods that the key to the taxonomic value of these features must be sought.

The existence of such a structure among the fossils usually classed as Phyllocarida, suggests a question as to the latitude of this ordinal term, proposed by Packard in 1879, for the living Nebalia and its fossil allies. The hinging, or median division by suture, of the carapace in many of these creatures, has been regarded here as among the Phyllopods, as of minor importance by most authors who have agreed to associate with Nebalia such fossil forms as Ceratiocaris, Echinocaris, etc. Claus used the term Leptostraca (also founded upon the structure of Nebalia) with a somewhat more restricted meaning. In a recent work on the Ceratiocaridæ of Great Britain, the authors, Professor T. Rupert Jones and Dr. Henry Woodward, have divided the Phyllocarida into two groups (1) those with univalved, and (2) those with bivalved carapaces. The greater number of the genera included in the first of these divisions are imperfectly known and quite obscure in their structural relations. Such are Discinocaris, Spathiocaris, Aptychopsis, Ellipsocaris, Dipterocaris, etc., etc. As the living Nebalia is univalved and without hinge, it is in this division that one would expect to find the closest approach to its structure, and it is, in fact, the case that none of the so-called Phyllocarida approaches Nebalia so closely in the structure of the test as the early paleozoic (Cambrian) genus Hymenocaris. In both, the telson is represented by a modification of three pairs of caudal spines or setæ, and both have about the same degree of abdominal segmentation, though Nebalia possess a rostrum, while Hymenocaris, as far as we now know, is devoid of one.

Another very early univalved species, not unlike Nebalia, but wonderfully similar to the living Phyllopod Apus, is the Protocaris marshii Walcott, from the Olenellus-zone of the Cambrian. The figures here introduced, taken from the works of Walcott and Packard, will serve to show this similarity. The
single example of Protocaris known, has probably been subjected to some horizontal distortion in the shale, giving the carapace a disproportionate size with reference to Apus, possibly also serving to obliterate any external evidence of ocular nodes which may have existed, but the remarkable closeness in the form of the abdominal segments, the degree of segmentation and the single strong pair of caudal processes, renders it highly probable that in Protocaris, we have to do with an apudiform phyllopod rather than with a nebaliioid phyllocarid.

Among the bivalved genera, not including Estheria and Leaia which Messrs. Jones and Woodward have placed with the Phyllocarids, there is throughout a general resemblance to
Nebalia except in this division of the carapace; a rostrum was present in most, though in some, as Echinocaris, a large amount of material has as yet failed to establish its existence. Nebalia possesses stalked compound eyes, which make no node or other configuration upon the exterior of the carapace. In Echinocaris, one of the numerous nodes in the cephalic region is undoubtedly ocular, and sometimes shows a slight depression at its summit; the other nodes are probably of muscular origin.

In Ceratiocaris there is no external evidence of eyes, while Emmmelezoe; Tropidocaris and Elymocaris all possess nodes which may be definitely referred to the ocular organ.

Figures of Emmmelezoe given by Jones and Woodward indicate that its structure is similar to that of Rhinocaris, and it is evident that differences of structure in this respect between all of these genera and Mesothyra as represented in the accompanying figures, is simply one of degree. It is, therefore, a pertinent query whether such a fixed external ocular body as this, with a single central depression, is in any way indicative of stalked compound eye. We are strongly of the opinion that it is not, but, rather, indicates that these ancient representatives of nebalid structures were sessile eyed.

Among the crustaceans we have been considering there appear to be at least four types of test-structure which are well distinguished.

1. That of Apus (Protocaris; a synthetic type, not necessarily a Phyllopod because Apus is one.
2. That of Nebalia, in a restricted sense (Hymenocaris).
3. That of Ceratiocaris (Echinocaris, Elymocaris, etc.).
4. That of Rhinocaris (Mesothyra, Dithyrocaris ??).

It was proposed, when Rhinocaris was believed to represent a univalved, rostrate carapace, to distinguish it not only as a genus, but as a separate family, Rhinocaridae, from other Phyllocarids; and it was at the same time proposed to place Mesothyra, with a supposed structure which we have now shown to exist in Rhinocaris, in a distinct family, the Pinnicaridae. It is now evident that the two fossils are very closely related and it will not do to separate them by more than a generic difference; we may therefore retain the family term Rhinocaridae and discard the other.