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THE MORPHOLOGY OF TRIARTHRUS.

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ART. XXIX.—*The Morphology of Triarthrus*; by C. E. BEECHER. (With Plate VIII.)

MOST of the recent advances in the knowledge of trilobite structure have come from the study of *Triarthrus*. Since Valiant's discovery of the antennæ, and its announcement by Matthew in 1893, the writer has published a series of papers on the detailed structure of this trilobite. Much time has also been spent in carefully working out the numerous specimens from the abundant material in the Yale Museum. Altogether upwards of five hundred individuals with appendages more or less complete have been investigated; and at the present time, it may safely be said that the important exoskeletal features have been seen and described.*

Notwithstanding the amount of information regarding the details of the various organs, very little has been shown illustrating the general appearance of the animal with the appendages in a natural and lifelike position, and it is one object of the present article to supply this deficiency.

Several specimens have been lately developed which preserve not only the appendages in great perfection, but also show them extended and disposed in a very lifelike manner. No new structural points are here brought out, yet the representation of the complete animal serves as a summary of present knowledge, and also gives a definite picture of great assistance in forming a conception of general trilobite morphology.

* The more important literature relating to the structure of the genus *Triarthrus* is given at the end of the present article; numbers in the text refer to this.

The dorsal view represented on Plate VIII is from a camera drawing based upon three specimens of about the same size. One gives the entire series of legs down to the ninth free segment, with the exception of the exopodites of the head, which are supplied from a second individual. In the third specimen, the anterior appendages are bent and irregularly arranged, while from the ninth backward to the end of the pygidium they are complete and uniformly extended. The figure is, therefore, a restoration only in so far as representing the best portions of three individuals.

The ventral view, Plate VIII, is based mainly upon two very excellent specimens. One was figured on Plate IV, vol. xv, of the *American Geologist*, and another, since found, nearly completes the ventral aspect. The under side of the head and pygidium was carefully compared with all the available material, and no attempt was made to supply any characters except as to the exact number of joints in the endopodial cephalic elements and the precise form of the cephalic exopodites, which from every character observed, and from analogy with similar structures elsewhere, were as represented.

So many specimens preserve the appendages in the position shown in the figures, that this must be recognized as natural and one likely to have been assumed by the living animal when extended. Few, however, show the details of the limbs with sufficient clearness to enable one to make out all their joints, and more minute characters.

In comparison with what is now known of the appendages of several other genera of trilobites, especially *Trinucleus*,* those of *Triarthrus* seem to have been exceptionally long. On this point Bernard, in a letter to the writer, suggests that "*Triarthrus* must have been a sort of 'Daddy longlegs' among the Trilobites, as *Scutigera* is among the Myriapoda." The entire length of a thoracic leg, including the coxal joint, is nearly equal to the width of the body at that point, and about half the length projects beyond the pleura.

The limbs of the head diminish in length forwards until the anterior pair scarcely extends beyond the border of the cephalon. The anterior thoracic legs are the longest, and there is a gradual shortening backward in the series, especially noticeable after passing the fifth, those at the extremity of the pygidium being about one-ninth the length of the first thoracic leg. Their position is also of interest. At the posterior extremity they point almost directly backwards, while those on the head are directed more or less forwards. Between these two extremes, all the intermediate positions occur in regular order.

*Structure and Appendages of Trinucleus, C. E. Beecher. This Journal, vol. xlix, April, 1895.

The gnathobases, or coxopodites, become more and more specialized anteriorly, growing broader and having their inner edge denticulate, until on the head they function as true manducatory organs. The second pair, however, corresponding to the mandibles of higher crustacea, has not become clearly differentiated from the rest of the series, and apparently has not lost the exo- and endopodial branches.

Few changes of importance can be traced in the exopodites, though the latter are considerably reduced in size on the cephalon. Over the anterior half of the thorax, they functioned as vigorous paddles, and on the pygidium their length and compact arrangement made them overlap each other, thus producing two broad flaps, or fin-like organs. The conclusion cannot be avoided that *Triarthrus* must have been an active creature, and with its rows of endopodites and exopodites it was as fully equipped as the bireme in classic navigation. The form of the animal and the multiplicity of locomotor organs were well adapted for rapid motion either along the sea-bottom or through the water.

The youngest and most immature limbs are on the pygidium, and in a young trilobite they are very much like those in the larval *Apus*[4] and are typically phyllopodiform. According to the law of morphogenesis, these limbs may be taken as of phylogenetic value and indicative of the primitive type of limb structure.

The whole series of endopodites anterior to the last two or three show modifications from the phyllopodous type, the change involving progressively from one to all of the endites. The endopodites of the pygidium have a true phyllopodiform structure, and are composed of broad leaf-like joints, wider than long. This character is gradually lost in passing anteriorly, the distal endites being the ones first affected. By the time the anterior pygidial limb is reached, the three distal joints are longitudinally cylindrical. The ninth thoracic endopodite shows a fourth endite becoming cylindrical, and on the first and second thoracic legs even the proximal ones are thus modified, making all the endites of these limbs slender in form.

This gradual modification of a phyllopodiform swimming member into a long, jointed, cylindrical, crawling leg deserves more than passing notice, for here, probably, better than in any known recent form can the process and its significance be studied. No living type of crustacean more nearly conforms to the theoretical archetype of the class than do the trilobites, and as *Triarthrus* belongs to an ancient Cambrian family, it may be expected to retain very primitive characters.

In this genus several causes evidently influenced the modification of the appendages. First may be mentioned the specialization into oral organs of the gnathobases of the head, which would tend toward a reduction of the other portions of the limbs. Next, the assumption of a walking habit would gradually lead to a corresponding adaptation of the anterior thoracic endopodites, this region of the body being naturally the place where they would be most operative. Lastly, any tendency to change the form of the anterior limbs would be accelerated through the greater number of moults they undergo as compared with the abdominal appendages.

Since the anal segment of crustacea contains the formative elements out of which all the trunk segments are successively developed, it may be considered as the same segment in all crustacea, no matter how many nor what kinds of segments may intervene between it and the head. The youngest segment, therefore, is always in the budding zone, just in front of the telson, or terminal somite, and those further anterior and more differentiated are older. This sequential order in the age of the segments and appendages may be greatly obscured in higher forms, so that, as in the Thoracostraca, the last pair of pleopods, forming with the telson the caudal fin, appears at an early stage of the ontogeny. In such cases, as Lang says, "the grade of development and physiological importance of a section of the body or of a pair of limbs in the adult animal may be recognized by the earlier or later appearance of their rudiments."*

In *Triarthrus*, these disturbing factors are hardly to be recognized, for no pair of limbs had an excessive physiological importance over any other pair or series of pairs, and increase progressed regularly by the addition of new members in front of the anal segment. The pygidium being formed of fused segments accommodated itself to this kind of growth by pushing forward the series of limbs and by the formation of a new free segment at the posterior end of the thorax. This process of metameric growth continued from the protaspis stage with no free thoracic segments, and successively added segment after segment with corresponding moults, until the full complement was reached, after which the moulting resulted mainly in increase in size. The repetition of moults afforded the chief means by which modifications in the appendages could be brought about.

The earliest protaspis stage shows, from the segmentation of the axis, that there were present five pairs of appendages on the head and two on the pygidium.[6] The adult animal has thirteen or fourteen free thoracic segments and six pygidial.†

* Text-Book of Comparative Anatomy, English edition (Bernard), p. 410.

† A few individuals of this species (*T. Becki*) have been observed with one or two additional thoracic segments. Walcott.[11]

Now, so far as is known of trilobite ontogeny, there was never more than one segment added at a single moult, though there is no evidence that there may not have been more moults than segments between the protaspis stage and the finished segmentation. In *Triarthrus*, the average full number of segments was attained by the time the animal reached a length of about 7^{mm}. So that the limbs of the anterior thoracic segment in an individual 7^{mm} in length, and containing the full complement of fourteen free and six pygidial segments, must have undergone at least seventeen moults. The second thoracic segment, therefore, at this stage of growth would have been moulted sixteen times, the fifth thirteen times, the tenth eight times, and the fourteenth four times. The length of full-grown individuals is from 25 to 40^{mm}, and to have reached this size a considerable number of additional moults must have occurred, in which all the segments participated alike.

Some mention should be made of the probable method of respiration of *Triarthrus*. No traces of any special organs for this purpose have been found in this genus, and their former existence is very doubtful, especially in view of the perfection of details preserved in various parts of the animal.

The delicacy of the appendages and ventral membrane of trilobites and their rarity of preservation are sufficient demonstration that these portions of the outer integument were of extreme thinness, and therefore perfectly capable of performing the function of respiration. Similar conditions occur in most of the Ostracoda and Copepoda, and also in many of the Cladocera and Cirrepedia, where no special respiratory organs are developed.

The fringes on the exopodites in *Triarthrus* and *Trinucleus* are made up of narrow, oblique, lamellar elements becoming filiform at the ends. Thus, they presented a large surface to the external medium, and partook of the nature of gills. But, as Gegenbaur says, "the functions of respiration and of locomotion are often so closely united that it is difficult to say whether certain forms of these appendages should be regarded as gills, or feet, or both combined."* For purposes of locomotion, the limbs of the cephalon and pygidium were of feeble assistance compared with those on the thorax, and in the higher crustacea, these two regions are the ones where the greatest branchial specialization takes place.

Yale Museum, New Haven, Ct., February 24th, 1896.

* Elements of Comparative Anatomy, English edition (Bell and Lankester), p. 241.

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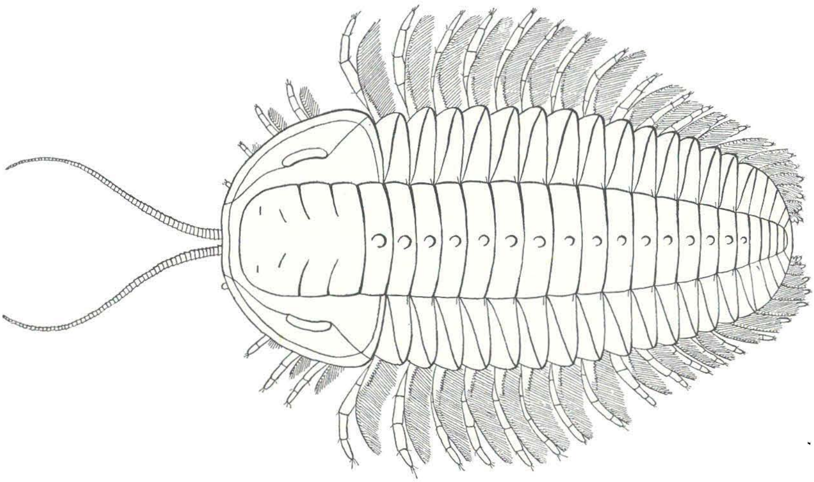
EXPLANATION OF PLATE.

FIGURE 1.—*Triarthrus Becki* Green; dorsal view; showing character and extent of antennules and limbs beyond the carapace. × 2½.

FIGURE 2.—*Triarthrus Becki* Green; ventral view; showing entire series of appendages, together with hypostoma, metastoma, and anal opening. × 2½.

Utica Slate, Ordovician, near Rome, New York.

1.



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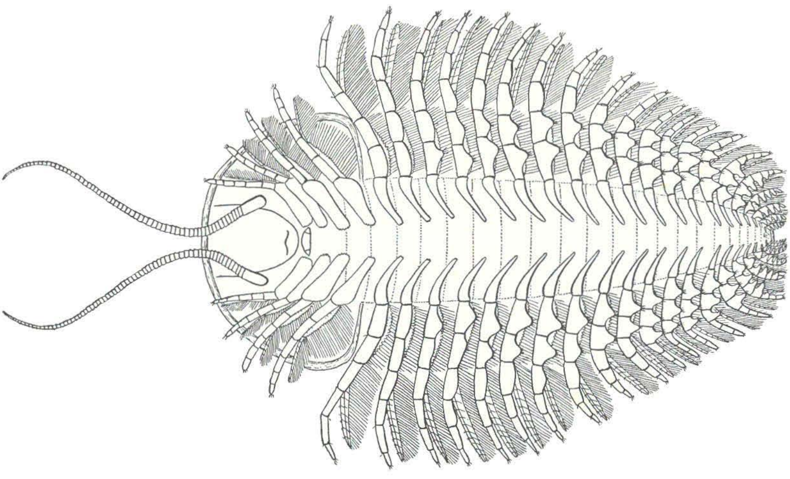

TRIARTHRUS BECKI Green. × 2½. (Beecher.)