VOL. IX, PP. 89-97, PL. I

MARCH 30, 1894

## PROCEEDINGS

OF THE

# **BIOLOGICAL SOCIETY OF WASHINGTON**

## NOTE ON SOME APPENDAGES OF THE TRILOBITES,

### BY CHAS. D. WALCOTT.

The results of Mr. W. S. Valiant's long search for the appendages of trilobites have recently been made known by Mr. W. B. Matthew, who described the material sold to the Columbia College of New York by Mr. Valiant.\* Mr. Valiant informs me that he discovered traces of what he considered to be antennæ, and that for several years he continued collecting until he found a locality where the specimens were well preserved and show, not only the antennæ, but legs and what he supposed to be the swimming appendages. Not having confidence that he could properly describe the specimens he sold part of his material, and in this way it came to be first described by Mr. Matthew, a student at Columbia College. His step-brother, Mr. Mitchell, continued to collect; and in August, 1893, through the courtesy of Mr. Valiant, I visited the locality with Mr. Mitchell and obtained a few specimens for the National Government.

The most important part of the discovery, announced by Mr. Matthew's paper, is that the trilobita have true antennæ. The discovery of the legs and plumose appendages is also of great interest, as it adds to our information respecting the appendages of the trilobite some of the details of another genus.

A collection was made for the Yale College Museum by Dr.

Read March 24, 1894.

<sup>\*</sup>Am. Jour. Sci., Vol. 46, 1893, p. 121.

C. E. Beecher, and in some notes on the thoracic legs of Triarthrus\* he describes and illustrates a dorsal view of the legs of the second and third free thoracic segments. These show that the endopodite of the leg is essentially the same as in Calymene and Asaphus, and that the exopodite is unlike that of Calymene or Ceraurus.

Through the courtesy of Prof. J. F. Kemp of Columbia College, I have examined the material studied by Mr. Matthew; and Prof. A. H. Chester, of Rutgers College, kindly loaned me for study five specimens that he purchased from Mr. Valiant. From these and the specimens in the National Museum a few notes have been taken that permit of some comparisons with the extremities found in Ceraurus, Calymene and Asaphus.<sup>†</sup> The limbs of Triarthrus differ in the details of the joints of the inner branch of the limb (endopodite) and still more in the character of the exopodite.

Cephalic limbs.—The antennæ are uniramose, and, judging from the position in which they are found, were attached to the body near the postero-lateral angle of the hypostoma (Fig. 1, e, Plate 1). In one specimen a cephalic limb somewhat detached from its true position shows a large basal joint and six slender joints (Fig. 1, f). The basal joint does not show conclusive evidence of the presence of a masticatory ridge. On another specimen, however, the form of the basal joint strongly suggests that it subserves the purpose of mastication. This is illustrated at g in Fig. 1.

A slender jointed appendage like that attached to the basal joint of g occurs between it and the antennæ and is probably a portion of another one of the cephalic limbs. No other cephalic appendages have been observed in the material at hand.

Since the publication of my articles on The Trilobite<sup>†</sup> I found in a section of the head of *Calymene senaria* a slender jointed limb that appears to have been an antennule. It is unlike any limb found beneath the head and thorax, and, if not an antennule, it may represent a fifth pair of cephalic limbs. This is

<sup>\*</sup>Am. Jour. Sci., Vol. 46, 1893, pp. 467-470.

<sup>&</sup>lt;sup>†</sup>The Trilobite; New and Old Evidence Relating to its Organization. Bull. Mus. Comp. Zool., Vol. 8, 1881, p. 6.

<sup>‡</sup>Bull. Mus. Comp. Zool., Vol. 8, 1881, p. 191-224. Science, Vol. 3, 1883, p, 279.

also suggested by a section of the limbs within the head of Calymene, illustrated on Plate 1, Fig. 9, Bull. Mus. Comp. Zool., Vol. 8, 1881. In this, a fifth limb is indicated close to the hypostoma. The trilobite was enrolled so as to include the antennule entirely within the border of the head. A sketch, taken from a photograph of the thin section by transmitted light, is shown by Fig. 8, Pl. 1.

The hypostoma of Ceraurus\* shows a rounded indentation of the antero-lateral sides, where an antennule probably passed by it. This character is strongly marked in *Sao hirsuta*, *Proetus bohemicus*, *Amphion fischeri*, etc., as illustrated by Barande.

The character and position of the remaining cephalic limbs of Triarthrus are not shown in any specimens that I have examined, but, from the relations of Calymene, Ceraurus and Triarthrus, especially the two latter, it is probable that their arrangement is essentially the same.

Thoracic limbs.—Many specimens show the thoracic limbs extending out from beneath the carapace of Triarthrus. It was not until by a fortunate dissection that I obtained the material illustrating the limbs in position beneath the thorax. The anterior limbs are formed of a protopodite and a somewhat complex exopodite. The protopodite consists of a short basal and a long joint, (Fig. 2, d, e,) to which the endopodite and exopodite are attached. This appears to be direct in the posterior limbs of the thorax (Fig. 3, a), but as yet the point of attachment of the basal joint of the exopodite has not been seen in the anterior limbs.

The endopodite of the anterior portion of the thoracic limbs varies in the number of joints and in their relative length (Fig. 1, a, a). Two show four long proximal and three shorter distal joints. Other limbs show two smaller distal, and three or four proximal, while in several there is a more or less uniform gradation from the protopodite to the distal joint. In Fig. 1, some of these variations are indicated. In Fig. 2, eleven limbs are shown, as seen from the under side. The basal (coxal) joint is seen at b, d, e, and nine show the long second joint of the protopodite. At e and f a new phase is indicated by the enlargement of the proximal joints. This is marked in a, b, c, d, and in Fig. 3, the details are more fully shown. These joints occur

<sup>\*</sup>Luc. cit., Pl. iv., Fig. 5.

on the seven posterior thoracic limbs of Fig. 2; and in the specimen from which Fig. 3 was drawn the limb opposite the tenth segment from the pygidium shows a slightly triangular second (meropodite) and third (carpodite) joint. In Fig. 2, the limb *a* is opposite the second free segment of the thorax anterior to the pygidum. The limbs *a* and *b*, Fig. 3, clearly show that the four proximal joints are broad and subtriangler in outline. A glance at the abdominal swimming legs of the Phyllocarida (Paranebalia), Schizopoda and Cumacea, suggests that the functions of these legs were both natatory and ambulatory.

The expododite illustrated by Beecher shows the dorsal surface (Fig. 6). A number, presenting the ventral surface, are shown on the right side of Fig. 2. They occur on the same specimen as the endopodities, on the left side, but have been pushed out of place. The most perfect is represented by m. The proximal portion is formed of a rather large basal joint and a number of short joints, 7 or 8. The distal end is formed of an inner and outer segmented portion. The inner side is divided into numerous segments by oblique divisions that give the impression of a closely coiled spiral. The outer side is a cylindrical, jointed, stem-like rim that is attached to the inner side, a narrow, distinctly impressed line separating the two, except at the somewhat flattened tip where they merge into each other. On the outer or upper surface of the outer side numerous crenulations occur that extend into long setæ, n, Fig. 2; b, b, Fig. 1. Dr. Beecher considers the expodite as a swimming organ; but from the manifest branchial character of the exopodite and attached epipodite in Calymene (Fig. 7), it seems probable that this exopodite of Triarthrus served largely as a gill, and that the animal used the broad proximal joints of the posterior limbs of the thorax as its principal propulsion in swimming. The exopodite of Triarthrus looks like a consolidated exopodite and epipodite, very much as though these two organs as they occur in Calymene were merged into one.

Several specimens illustrate appendages beneath the pygidium. Some have the broad proximal joints, d, Fig. 1, while others show the outer rim of the exopodite c, Fig. 1. The material I have seen indicates very little difference between the appendages of the posterior half of the thorax and the pygidium, except

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that those of the latter are less developed in size and details.

Mr. Matthew suspected the presence of a flap, formed by the anchylosing of the appendages beneath the pygidium. From the appearance of a similar structure, where the limbs are matted together along the side of the thorax. this tentative view is received with doubt. More perfect material may show distinctions not recognizable at present.

If future investigations prove, as it now seems probable, that the modified swimming joints of the endopodite are attached to ten or more of the thoracic segments, the anterior eight segments can be grouped together as the typical thorax, and the remaining segments of the body as the abdomen.

Mr. Matthew suggests that the homology between Triarthrus and Limulus may not be as close as between Limulus, Calymene and Ceraurus. This is true from what we now know of Triarthrus, but, if a sixth pair of cephalic limbs should be discovered in 'Triarthrus the resemblance would be strengthened. Triarthrus does not differ from Ceraurus and Calymene more than would be anticipated in such unlike genera. Triarthrus is essentially a "Primordial" type that has continued until upper Ordovician time. It represents a large group of Cambrian trilobites, while Calymene and Asaphus represent the more highly developed Ordovician and Silurian forms.

Dr. Lang held the view that if a fifth pair of cephalic limbs were found, comparable to the anterior antennæ "Trilobites might then be regarded as original *Entomostraca*, to be derived from the same racial form as the Phyllopoda." He says further, "Xiphosura, Hemiaspidæ, and Gigantostraca are themselves again perhaps racially connected with the *Trilobites*. In any case, however, in the present state of science, it seems probable that all these groups are only connected at their roots with the Crustacea.\*"

From the paleontological record I am essentially in accord with this view, but I am not yet prepared to abandon the position taken in 1881, that all these groups should be arranged under one class and not as an appendage to the Crustacea, as proposed by Dr. Lang.

Text Book of Comparative Anatomy, Eng. Ed., 1891, p. 415.

<sup>\*</sup>Loc. cit., p. 421.

I would go still further and form a class of the *Trilobita* and one of the Merostomata.

Two general facts lead me to think that the modern crustacean is descendant from the Phyllopod branch and the Trilobita from a distinct branch.\* 1st. The Trilobita branch exhausted its initial vital energy in Paleozoic time and disappeared. 2nd. The Phyllopod branch developed slowly until after the Trilobita passed its maximum and then began its great differentiation that approaches culmination in recent times.

When the trilobite and phyllopod diverged from their common ancestral crustacean the trilobite began at once to differentiate and to use its initial vital energy in developing new species, genera and families. Probably two thousand species and one hundred or more genera are known from the Paleozoic strata. With this great differentiation the initial vital energy was impaired and the Trilobita died out at the close of Paleozoic time.

The Phyllopod branch continued with little variation until after the trilobite passed its maximum, and then began to differentiate until to-day its descendents form the class Crustacea, that corresponds to the class Trilobita in Paleozoic time. Springing from a common crustacean base the two groups have many features in common, and in carrying out of details of structure in the limbs and gills many striking resemblances occur. It does not impress me that trilobites were true Entomostracans or Malacostracans; they have certain characteristics in common, but these are not necessarily the result of lineal descent one from the other but are the result of descent from a common ancestral crustacean type of pre-Cambrian time that lived in the pelagic fauna in which all the earlier types of life were probably developed<sup>†</sup> and from which, as time passed on, additions must have been made to the paleontologic record of geologic time. The Phyllopods, Ostracods and Trilobita are clearly differentiated in the lower Cambrian fauna. Bernard is

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<sup>\*</sup>This view is only confirmatory of the result of the profound study of the Apodidæ by Bernard (The Apodidæ Nature Series, 1892).

<sup>&</sup>lt;sup>†</sup>See Brooks' beautiful memoir on Salpa, with its suggestive theory of the origin of the bottom faunas of the ocean and the early geologic faunas. The Genus Salpa, Memoirs from the Biological Laboratory of the Johns Hopkins University, II, 1893, pp. 140–177.

confidant that the Trilobites may take a firm place at the root of the Crustacean system, with the existing Apus as their nearest ally.\*

There is yet much to be learned from the study of Triarthrus. A great amount of material can be readily collected at the locality near Rome, N. Y. It is also of interest to note that the locality at Trenton Falls, N. Y., from which the specimens of Calymene and Ceraurus were obtained, is only seventeen miles from the Rome locality; that both occur within the Ordovician; and that the stratigraphic position of the bed at Rome is between six and seven hundred feet above that at Trenton Falls.†

<sup>\*</sup>Nature, Vol. 48, 1893, p. 582.

<sup>†</sup>The appendages of Triarthrus are replaced by iron pyrites and are usually well preserved. The specimens of Calymene and Ceraurus from the Trenton limestone of Trenton Falls, N. Y., were replaced by calcite and in them there were preserved even more delicate parts than I have yet observed in Triarthrus. Thin sections were made of the latter and photographs obtained by transmitted light, that were used in illustrating the paper in the Bulletin of the Museum of Comparative Zoology, Vol. 8, 1881.

#### Description of Plate.

- Fig. 1.—*Triarthrus becki* (X3). Outline of carapace, with appendages represented as they occur on several specimens, their relative position being retained.
  - a, a, a, a. Endopodites of limbs showing variation in joints.
  - b, b. Plumose portion of exopodite.
  - c, c. The outer or supporting portion of the set e or fimbrize of b, b.
  - d. Limbs extending from beneath the pygidium, showing large proximal joints. Those of the left side are imperfectly preserved.
  - e. Antenna extending back nearly to the postero-lateral margin of the hypostoma.
  - f. One of the cephalic limbs. The basal joint may be broken away on the inner side.
  - g. Cephalic limb.
- Fig. 2 (X7). Limbs attached to the under surface of an individual preserving 13 thoracic segments and the pygidium. The limbs (a to k) on the left side are mainly in place. A fracture cuts out one limb between g and h.
  - a to g. Limbs preserving traces of the enlarged proximal joints.
  - b, d. Limbs preserving the two joints of the protopodite and two of the large proximal joints.
  - l, m, o. Exopodites, showing under or side views.
  - n. Enlargement of fimbriæ of m.
  - r, s. Distal joints of endopodites of right side.
  - y. Portion of an exopodite showing its inner support.
- Fig. 3. Limbs occurring on the under side of an individual of 14 thoracic segments.
  - a, b, c, d. Limbs with flattened, enlarged proximal joints and slender distal joints.
  - a. Limb preserving large joint of protopodite, four enlarged proximal joints and three slender distal joints. At x the point of attachment of an exopodite is shown, and in the specimen it looks as though f had been broken away from x.
- Fig. 4. Restoration of the thoracic limbs of the fifth segment anterior to the pygidium.
  - en. endopodite. p. protopodite. a. four proximal swimming joints. b. three distal joints.
  - ex. exopodite, attached to same joint of the protopodite as the endopodite.

Fig. 5. Restoration of the thoracic limbs of the fourth thoracic segment posterior to the head.

en. endopodite. ex. exopodite.

- Fig. 6. Diagramatic restoration of the second thoracic limb. (After Beecher.)
- Fig. 7. Restoration of thoracic limb of Calymene senaria. en. endopodite. ex. exopodite. ep. epipodite. (Bull. Mus. Comp. Zool. Vol. 8, 1881.)
- Fig. 8. Cephalic limb of Calymene X 3; supposed antennule.
- Fig. 9. Cephalic limb figured by Dr. Henry Woodward. (Quart. Jour. Geol. Soc. London. Vol. 26, 1870, p. 487. a. side of hypostoma.
- Fig. 10. Slender jointed legs associated in same beds with Calymene at Cincinnati, Ohio.

PLATE I.

