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IV

No. 4.—APPENDAGES OF TRILOBITES

(With Plates 14 to 42)

BY
CHARLES D. WALCOTT

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INTRODUCTION

In September, 1873, I said to Professor Louis Agassiz that if opportunity offered I would undertake as one bit of future research work to determine the structure of the trilobite. This promise has kept me at the problem for the past forty-five years, and except for the demands of administrative duties the investigations would have been advanced much more rapidly.

Since 1873 I have examined and studied all the trilobites that were available for evidence bearing on their structure and organization. The first summary of results was published in 1881 [1] and a restoration and cross-sections given of the ventral surface of *Calymene senaria* (*loc. cit.*, pl. VI) based on sections cut through the test, ventral cavity and appendages. These proved that the trilobite had a pair of biramous appendages for each segment of the thorax and abdomen and four pairs of cephalic appendages, the enlarged proximal joints of which served as organs of manducation. The restorations have since been shown to be essentially correct with the possible exception of the enlargement of the terminal joints of the posterior cephalic

[1] The Trilobite: New and Old Evidence Relating to its Organization. Bull. Mus. Comp. Zool., Cambridge, Mass., Vol. VIII, No. 10, 1881, pp. 191-224, pls. I-VI.

legs and the too short, proximal joints (protopodites). The placing of the Trilobita under the Class Pœcilopoda in 1881 was changed in 1894[1] when it was suggested that the Trilobita, Entomostraca, and Malacostraca were descendent from a common ancestor of pre-Cambrian time. In 1912[2] the Trilobita were represented as descendent from the Branchiopoda and on the line of descent of the Merostomata. The presence of antennules was not known positively until Valiant discovered antennules on *Triarthrus*[3] in 1892, and caudal rami until Walcott found them on *Neolenus* twenty years later.[4]

During the field seasons of 1910 to 1913 and 1917 I collected from the Burgess shale member of the Middle Cambrian Stephen formation of British Columbia with the aid of assistants a large fauna including specimens of the highly organized trilobite *Neolenus serratus,* some of which have beautifully preserved ventral appendages. *Neolenus* has a large head and tail, a short compact thorax, and is far advanced in the development of the Trilobita. Always hoping for more perfect specimens, a detailed description with illustrations was deferred, and only a few of the best specimens photographed and incidentally used in illustrations.[5] More data are desired, but I have decided to now record the evidence at hand as the Burgess shale quarry on the ridge connecting Mounts Wapta and Field is about exhausted and only a new locality or a chance specimen in the debris from the quarry will give further material from there for study.

For a description of the Burgess shale and the mode of occurrence of fossils the reader is referred to notes published in 1912.[6] In this paper I stated that [p. 192]

> In the near future I wish to review the conclusions published in my paper of 1881,[7] and those that have been entertained regarding *Triarthrus becki* and the new material from the Burgess shale.

As it is not probable that I shall again write on the structure of the trilobite I am now assembling in this paper notes and illustrations on the material studied from time to time since 1894. This includes the

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[1] Proc. Biol. Soc. Washington, Vol. IX, p. 94.

[2] Smithsonian Misc. Coll., Vol. 57, p. 164.

[3] The Mineral Collector, New York, Vol. 8, No. 7, 1901, pp. 105-112.

[4] Smithsonian Misc. Coll., Vol. 57, 1912, p. 208, pl. 24, figs. 1, 1*a*.

[5] Idem, 1911, pl. 6, figs. 1, 2; 1912, pl. 24, figs. 1, 1*a;* pl. 45, figs. 1, 2, 3, 4.
Text-book Pal. (Zittel), Eastman 2d ed., 1913, Vol. I, p. 701, fig. 1343, p. 716, figs. 1376, 1377.

[6] Smithsonian Misc. Coll., Vol. 57, pp. 149-153.

[7] The Trilobite, New and Old Evidence relating to its Organization. Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, 1881, pp. 208-211.

specimens of the Cambrian genera *Neolenus, Kootenia,* and *Ptychoparia* and the Ordovician genera *Calymene, Ceraurus,*[1] *Isotelus,* and *Triarthrus.*[2] Of these, *Neolenus* has given the best and most instructive material of a trilobite in advanced development, and *Triarthrus* of a more primitive form.

The discussion of the appendages found in the several genera follows the description of the material known to me of each of the genera mentioned.

In a memoir soon to go to press by Dr. Percy E. Raymond I understand there will be a very complete statement of Beecher's work and a full review of what is known of the trilobite.

ACKNOWLEDGMENTS

I am indebted to the Museum of Comparative Zoology, Harvard University, for the opportunity of studying the Walcott collection of *Calymene senaria* and *Ceraurus pleurexanthemus* showing appendages. To the Peabody Museum, Yale University, for the loan of a portion of the Beecher collection of *Triarthrus becki.* To several assistants in the field collecting at Burgess Pass, notably Dr. Lancaster D. Burling, now of the Geological Survey, Canada. Mr. R. D. Mesler, of the U. S. National Museum, and to the members of my family who worked with me during several field seasons. In the office, Mr. Clarence R. Shoemaker, of the U. S. National Museum, made the final drawings of the restorations of the ventral surface of *Neolenus, Calymene,* and *Triarthrus,* using his knowledge of the crustacea to give a less diagrammatic appearance to my outline sketches. Mrs. Mary V. Walcott retouched the photographs used in illustration on plates 14, 18, 19, 20, 22, and 23. Miss G. R. Brigham, Ph. D., lettered the plates and read the text-proofs.

CORRECTION

In 1911 I referred figures 2 and 3, plate 2, also text figure 10, p. 206 (1912), of *Emeraldella brocki* to *Sidneyia inexpectans* in the paper on the latter species.[3] At the time I had not thoroughly studied *E. brocki,* and assumed that the specimens before me belonged to *Sidneyia.* In both cases the reference should be to *Emeraldella.* I expect in the near future to revise my preliminary work on the crustaceans from the Burgess shale.

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[1] Through the courtesy of the Museum of Comparative Zoology, Harvard College.

[2] Through the courtesy of the Peabody Museum, Yale University, and the U. S. National Museum.

[3] Smithsonian Misc. Coll., Vol. 57, 1911.

SECTION 1

NOTES ON SPECIES WITH APPENDAGES

Mode of Occurrence [1]

The two species of Ordovician Trilobites, *Calymene senaria* and *Ceraurus pleurexanthemus,* from which nine-tenths of the sections illustrating appendages were obtained, are the two most abundant forms in the Trenton limestone of Central and Northern New York. Their remains, or those of representative species, occur, usually in a fragmentary condition, in nearly every layer of the Trenton limestone, and range, above, into the Cincinnatian and, below, into the Black River limestone. Their geographic distribution is also great, as they occur in the Eastern Canadas and at nearly all the exposures of the Trenton series in the Northern United States, as far west as the Mississippi River. *Calymene* is much more abundant in Ohio, but at the locality from which the specimens of *Ceraurus* preserving appendages were obtained, the latter far exceeded it in numbers. The special interest attached to the occurrence of both species near Trenton Falls, Oneida County, New York, as well as of several other species, is their very perfect state of preservation in a thin layer of limestone outcropping in a small ravine half a mile east of the Trenton Falls canyon or gorge in the Township of Russia, Herkimer County, New York. An examination of the same horizon that this bed occupies, for several miles along the canyon, which is but half a mile away at one point, failed to give a single entire trilobite, and the fragmentary remains are rare. They are found both above and below the prolific layer of limestone, but not with any more of the animal preserved other than the dorsal shell and hypostoma. This indicates that in the vicinity of the outcrop in the small ravine there is a limited area, which was surrounded by conditions in Ordovician time that did not prevail elsewhere in the region, as the topography of the adjacent country permits of a close examination of the strata, and outcrops at about the same horizon were examined in all directions in the vicinity for the purpose of finding appendage-bearing trilobites.

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[1] Walcott, C. D.: The Trilobite: New and Old Evidence relating to its Organization. Bull. Museum Comp. Zool., Harvard Coll., Vol. VIII, 1881, No. 10, pp. 211-214.

The layer of limestone on which the prolific layer rests is about ten inches thick, and formed of the comminuted remains of crinoids, trilobites, etc., indicating the action of shore waves and a distributing current. A change supervened, and this surface was depressed beneath deeper water, or a barrier reef was formed, affording a quiet habitat in which flourished bryozoans, echinoderms, brachiopods, pteropods, entomostracans, and trilobites. The remains of all these are now found in a fine state of preservation attached to the lower surface of the superjacent layer of limestone which appears to have been a fine calcareous mud or ooze, deposited rapidly on the surface of the subjacent stratum, so as to form when solidified a layer from one-half to two inches in thickness. It did not destroy all the forms of life that existed on the surface prior to its deposition, but many species are not known to occur above it. The trilobites, however, flourished on the new upper surface as the beautifully preserved interiors of the dorsal shell testify, an illustration of which is given on plate 28.

Where the layer is over one inch in thickness, and there is no intermingled argillaceous shaly matter, as sometimes occurs, the best preserved specimens for cutting sections are found. They are usually with the dorsal surface downward, and partially enrolled. It was frequently noticed in polishing the sections that the imbedding rock showed dark laminations curving beneath the trilobite, as though the soft mud had been compressed by its sinking down into it. Similar traces proved that the mud flowed over into the half-enrolled shell, but buried the appendages, or such as were left of them, as often the laminations of the inflowing mud have not been disturbed since covering the viscera and fragments of the branchiæ and limbs.

In a former paper[1] it is stated that 1,110 trilobites out of a total of 1,160 had been found resting on their backs, and it was argued from this that that was their normal position when living, as Burmeister had shown for *Branchipus* and theoretically for the trilobite. In subsequent work the proportion was found to remain nearly the same, but with the discovery of ambulatory thoracic legs the view of their living in that position was necessarily abandoned. Mr. Henry Hicks writes that he had observed the same position in the Primordial Trilobites of Wales, the shell of the great *Paradoxides,* eighteen inches in length, occurring with its dorsal surface downward. He attributes it, and I think correctly, to the accumulation of gases in

[1] Ann. Lyc. Nat. History, Vol. XI, p. 159, 1875.

the viscera, which, with the boat-shaped shell, would cause the animal to turn over on the slightest motion in the water, and it would there remain to be buried beneath the next deposit of sediment.

Beecher calls attention to his finding nearly all of the specimens of *Triarthrus becki* with the back down. His explanation of the occurrence is as follows: [1]

> It seems most probable that trilobites could both swim freely and crawl along the bottom, and that, on dying, they coiled themselves up in the same manner as the recent isopods. Then upon unrolling they would necessarily lie on their backs. Even if they did not coil up, any swimming animal having a boat-shaped form would settle downward through the water with the concave side up.

The specimens of *Neolenus* from the Burgess shale were obtained from blocks of shale after they had been blasted from the quarry, and there is no record of their position. In one case illustrated on plate 15, one specimen was ventral side up and the other showed the dorsal side. The appendages are about equally well preserved and do not show the bending under the edge of the dorsal shield, as suggested by Beecher in event of a trilobite being turned over after settling to the surface of the mud on the bottom of the body of water in which it was living.[1]

From the great abundance of trilobite tracks on shales and sandstones, and from the nature of their food, it is quite probable that they usually moved about with their dorsal shield uppermost, and turned over after death.

Conditions of Preservation

Trilobites preserving ventral appendages have been found in limestones and both argillaceous and siliceous shale. The specimen of *Isotelus* from the Trenton limestone at Ottawa, Canada, was found about 1860 in a thin slab of typical dark bluish-gray compact limestone. The animal had evidently settled in the calcareous mud without any considerable disturbance of its legs (endopodites) as the protopodites of the anterior three pairs of thoracic legs are now at nearly right angles to the median axis; the posterior legs are sloping backward as in the Ohio *Isotelus* (pls. 24, 25). From the fact that the legs occur near the under surface of the dorsal shield it is probable that the animal settled in the mud with the ventral surface up and that the accumulating sediment crowded the legs down into the concave shield and displaced them more or less, but did not tear them

[1] American Geologist, Vol. XIII, 1894, p. 40.

from their fastenings to the ventral surface. The appendages are preserved as limestone replacements of the original parts.

The Ohio *Isotelus* (pl. 24, fig. 3; pl. 25, fig. 1) also occurs in a fine-grained, compact limestone, and it shows the effect of compression in the sediment by the backward slope of the proximal joints (protopodites) of the legs. In both specimens mentioned the embedding mud was relatively soft and the animal must have been quickly covered over. The limbs are preserved as a limestone replacement of the original limbs, the integument having disappeared.

The specimens of *Isotelus* from the Trenton limestone, near Trenton Falls, New York, preserving traces of the thoracic limbs, occur in a compact, hard, bluish-gray limestone that was formed from a relatively soft, calcareous mud into which the animal readily sank and became embedded.

The specimens of *Calymene* and *Ceraurus* with ventral appendages preserved are from a thin layer of compact, fine-grained, bluish-gray limestone which was originally a relatively soft calcareous sediment that quickly covered the trilobites on the bottom or in some instances they sank into the mud and were buried without material disturbance of the appendages. The integument of the limbs and all parts have often been replaced by calcite, which makes it possible to obtain sections showing the outlines of the appendages in the dark limestone matrix.

Triarthrus with appendages occurs in a black, compact thin band of argillaceous shale and the appendages and often the dorsal shield are preserved by being replaced by iron pyrite. I have found hundreds of specimens of *T. becki* in other localities than that near Rome, New York, but none showed traces of appendages. Local conditions were favorable for their preservation in the thin band of shale near Rome just as they were favorable for those found in the Middle Cambrian Burgess shale.

The Burgess shale trilobites *Neolenus, Kootenia,* and *Ptychoparia* occur in a band of fine siliceous shale about one meter in thickness in which the appendages are preserved as a black, almost glistening, carbonaceous appearing substance that is not readily attacked by acids. The siliceous shale of the layers containing the trilobites with appendages is remarkably uniform throughout and it was evidently a fine, rapidly deposited silt. "That carbonic acid gas was present in the mud and immediately adjoining water is suggested by the very perfect state of preservation of the numerous and varied forms of life. These latter certainly would have been destroyed by the worms and predatory crustaceans that were associated with them, if the animals that dropped to the bottom on the mud or that crawled or were drifted onto it were not at once killed and preserved with little or no decomposition or mechanical destruction. This conclusion applies to nearly all parts of a limited deposit about six feet in thickness, and especially to the lower two feet of it."[1] The fact that there are few trilobites found in the deposit and that their fragmentary remains are unusually abundant in the rocks beneath indicates that those found with appendages were individuals that strayed in from more favorable surrounding areas.

Manner of Life[2]

Burmeister gives us, as his view of the manner of life the trilobites led, "that they most probably did not inhabit the open sea, but the vicinity of coasts, in shallow water, and that they here lived gregariously in vast numbers, chiefly of one species; that they moved only by swimming in an inverted position, and did not creep about on the bottom; that they lived on smaller water animals, and, in the absence of such, on the spawn of allied species."

Barrande supposed that they lived in deep water and swam on the surface of the sea.

Dr. Dohrn considers that they lived at the bottom of the sea, and with extremities like those of *Limulus* crawled about. This view was necessarily taken by all authors who considered the trilobite as related by its zoölogical affinities to *Limulus*.

Dr. Packard states[3] that Mr. Alexander Agassiz had captured the larva of *Limulus* swimming free on the surface of the ocean, three miles from the shore. From the comparisons made by Dr. Packard between the young *Limulus* and the young trilobites as described by M. Barrande, there is no reason to doubt that the young trilobite may have had the same power of distributing itself and its species over extended areas in the wide-spread paleozoic seas. As in *Limulus* its later growth changed its manner of life, and its movements were finally largely restricted to crawling about the sea bottom in search of food.

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[1] Smithsonian Misc. Coll., Vol. 57, 1911, No. 3, p. 42.

[2] Walcott, C. D.: The Trilobite: New and Old Evidence relating to its Organization. Bull. Museum Comp. Zool., Harvard Coll., Vol. VIII, 1881, No. 10, pp. 214-215.

[3] Development *Limulus polyphemus*, Memoirs Boston Soc. Nat. Hist., p. 155, 1872.

We have seen from the views of Burmeister, Barrande, and others, that it has been thought to be both an inhabitant of shallow waters along the coasts and also of the deeper seas. It is found in both littoral and deep-water formations. Muddy or sandy, fine or coarse, hard or soft, argillaceous or calcareous deposits, it occurs in all. With these facts in view, it is probable that it ranged along the shore in quiet bays, and also in the habitat of the brachiopods and other deeper water invertebrates. In conclusion we may say that the trilobite in its younger stages of growth was active and a free swimmer, thus distributing itself over broad areas; that on reaching a larger growth it became more limited in its natatory powers and crawled about the bottom in search of soft-bodied organisms for food and during the spawning season for a place to deposit its eggs.[1] From the presence of broad setiferous exopodites on the limbs of *Neolenus* and *Triarthrus,* and endopodites (legs) with flattened joints on other species it is highly probable that the trilobite as we now know it may have had limited natatory powers, during its adult life, but it probably swam about in its local habitat, and rarely moved far away after once finding a favorable environment.

Method of progression.—The strong, long legs of trilobites enable them to crawl rapidly over the surface of hard or moderately compact sediments either under water or over the wet surface of the beach between tides. When searching for worms, their principal source of food, they evidently worked down into the mud very much as the horseshoe crab (*Limulus*) does and by means of their strong protopodites and legs pushed the dorsal shield along, thus forming deep trails and half burrows, which when made in moderately stiff clay or arenaceous mud retained the form of the trail and burrows until the next tide or current filled them up and a natural cast was formed; these trails and casts occur in great abundance as fossils, and thus preserved the record of the method of movement of the trilobite when crawling about and when feeding. Often the deeper trails appear as though the animal had settled in the mud and then lifted itself up on the ends of its legs, moved ahead a little, and then settled down again, repeating the movement for considerable distances.

Swimming was the method of more rapid progress by some species when the animal moved any considerable distance, or was avoiding immediate danger which it could not escape by burrowing or clinging

[1] See Dr. Packard's description of the spawning of *Limulus* and its probable occurrence in the same manner with the trilobite. *Ibid.*, p. 186.

to the bottom. Of the species of which we know something of their limbs, all had a limited development of swimming power either by using the flat, jointed legs or the exopodites or epipodites. It is not probable, however, that they were great swimmers with possibly the exception of *Triarthrus*.

Food.—The gnathobases of the cephalic limbs of trilobites clearly indicate that their food was largely worms and such soft bodied and small, minute life as came in their way, also rotting algæ and any decomposed animal matter.

The habitat of *Neolenus* abounded in worms, soft invertebrates, and fine, delicate algæ, and in all rocks where I have known entire trilobites to occur there has been strong evidence that worms and usually algæ were abundant. There is not any evidence that the trilobite possessed strong manducatory jaws similar to those of the Eurypterida or the more insignificant branchiopod *Apus*.

Defense and offence.—The known limbs of the trilobite were without offensive or defensive power. For defense many of them could enroll, and all could settle down closely on the bottom or burrow in the mud and thus present only a smooth, hard surface or a spiny shell to attack. *Calymene* is frequently found enrolled, the head and pygidium fitting closely together, so that no opening is left at any point, the legs being all drawn within the shell and entirely protected from injury from without. With *Ceraurus pleurexanthemus*, a perfect closing of the shell by enrolment is impossible, and the space formed by the partial enclosure of the spinous extension of the pleuræ affords but an incomplete protection to the numerous legs and branchiæ.[1] *Neolenus* and *Triarthrus* could not have rolled up effectively as compared with *Calymene*.

Without offensive or special defensive parts they were evidently peace-loving and depended on great reproductive power and favorable environment for continued existence. In Cambrian time they were the largest element in the fauna and had only two known species of Eurypterida to interfere with them. After this, enemies gradually increased and the number of species and of individuals decreased until the race became extinct in early Carboniferous time. Bacteria undoubtedly existed, but as yet we have no record of their presence in the trilobite.

[1] Walcott, C. D.: The Trilobite: New and Old Evidence relating to its Organization. Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, No. 10, 1881, p. 203.

DESCRIPTION OF SPECIES WITH APPENDAGES

Order OPISTHOPARIA Beecher

Family ORYCTOCEPHALIDÆ Beecher

Genus NEOLENUS Matthew

NEOLENUS SERRATUS (Rominger)

PLATES 14-23

Ogygia serrata ROMINGER, 1887, Proc. Acad. Nat. Sci. Philadelphia, p. 13, pl. 1, figs. 2, 2*a*. (Description and illustration.)

Neolenus serratus MATTHEW, 1899, Trans. Royal Soc. Canada, 2d ser., Vol. 5, sec. 4, p. 53. (Mentioned in proposing genus *Neolenus*.)

Neolenus serratus WALCOTT, 1908, Canadian Alpine Jour., Vol. 1, No. 2, pl. 4, fig. 3. (Figure of dorsal test.)

Neolenus serratus GRABAU and SHIMER, 1910, North Am. Index Fos., Vol. 2, p. 271, fig. 1566. (Reproduces Walcott figure.)

Neolenus serratus WALCOTT, 1912, Smithsonian Misc. Coll., Vol. 57, p. 190, pl. 24, figs. 1, 1*a*. (Figures specimens showing appendages.)

Neolenus serratus EASTMAN, 1913, Text-book Pal. Zittel, 2d ed. by Eastman, Vol. 1, fig. 1343, p. 701, figs. 1376, 1377, p. 716. (Illustration of appendages from photographs furnished by Walcott.)

Neolenus serratus WALCOTT, 1916, Ann. Rept. Smithsonian Inst. for 1915, 1916, pl. 9. (Figured with appendages.)

The dorsal surface of the test or carapace is illustrated by figure 1, plate 14. The cephalon is formed of seven fused segments or somites, the thorax of seven free segments, and the pygidium of five fused segments, a total of 19 segments. The large cephalon and pygidium and thorax with only seven thoracic segments indicate an advanced form of trilobite as compared with *Ptychoparia, Triarthrus, Calymene,* and *Ceraurus*. *Neolenus* more nearly approaches *Isotelus* of the Cincinnati formation in form of its dorsal shield, but unfortunately only the protopodite and endopodite (leg) are known of the ventral appendages of *Isotelus* (pl. 25).

Cephalon of Neolenus.—The cephalon is formed of seven combined or fused segments. These include:

(*a*) The ocular or eye-bearing segment represented by the free cheeks;

(*b*) The palpebral or palpebral ridge-bearing segment which at the center is merged into the anterior lobe of the glabella.[1]

(*c*) The four segments fused in the glabella.

(*d*) The occipital or posterior (neck) segment.

The four posterior segments fused in the glabella are usually clearly indicated by the glabellar furrows, but owing to compression of the test in the shale the short, faint anterior pair of lateral furrows

[1] Smithsonian Misc. Coll., Vol. 53, 1910, p. 237, last paragraph.

indicating the division in the anterior lobe of the glabella are to be seen only in rare specimens that preserve the natural convexity of the test. The fusing of the segments of the cephalon of the trilobite is finely shown in the young of the Mesonacidæ.[1]

Cephalic Appendages

These consist of the antennules and four pairs of cephalic limbs. The first pair may represent the antennæ; the second pair the mandibles; the third pair the maxillulæ, and the fourth pair the maxillæ of the theoretical crustacean head.

Antennules.—The antennules are long, slender, and formed of short joints for the first half or more of their length and of longer segments in the distal portion. A flattened antennule projecting from beneath a dorsal shield 65 mm. in length has a width of 2 mm. at base and 13 segments in the first 12 mm. of its length; at 0.75 mm. in width the segments are 1 mm. in length. The exact point of attachment of the antennule is unknown, but from the contour of the sides of the hypostoma it probably was attached to the ventral surface near the posterior third of the side of the hypostoma as shown on plate 31. Its length and flexibility are well shown on plate 15. Short, fine acicular spines occur at the distal end of the joints.

Endopodites.—Several specimens show one or more well-preserved cephalic limbs. The limb is essentially the same as the thoracic limb with the large elongate basal joint (protopodite[2]) modified slightly for the purpose of aiding in manducation. In two examples this joint is seen to be narrowed at the proximal end, but owing to the flattening of the leg by compression its exact form is not preserved (fig. 1, pl. 16). The protopodite as flattened in the shale expands slightly midway and the inner margin is slightly rounded so that if the leg extends obliquely forward its proximal margin may be more or less parallel to the longitudinal axis of the dorsal shield. On one specimen rather strong, short spines occur on the inner margin of the protopodite of the third cephalic leg (pl. 16, fig. 1). The four following joints are strong, compact, and very gradually decreasing in size; the sixth and seventh are more slender and proportionally more elongate; the distal extremity is formed of a small, strong, curved

[1] Smithsonian Misc. Coll., Vol. 53, 1910, pl. 25, figs. 9-13, 19-22, and pl. 36, figs. 10-15.

[2] The protopodite is considered to be in all trilobites preserving their limbs to be formed by the fusion of the coxopodite and basopodite.

claw and two small spines, which give when they are spread out a tripartite termination to the leg.[1] Two or more short, fine spines occur on the margin of the distal end of each joint of the leg.

The four cephalic legs extend well out from beneath the dorsal shield in several specimens and appear to be essentially similar. As yet no " precoxal " joint has been observed connecting the large, long protopodite to the ventral surface and it is doubtful if one existed distinct from the latter. The protopodite appears to have been strongly attached to the ventral integument of the head, probably by a narrow connection that extended from the dorsal side of the joint directly to a transversely elongate opening in the ventral integument through which the muscles of the limb passed.

Exopodite.—A long, flat, membranaceous lobe with a terminal joint is fringed on its posterior margin by fine, long, slender, flattened setæ out to the distal joint which has fine, short setæ on its posterior and outer margins; it appears to be attached to the protopodite at its distal end and extends outward into the space beneath the lateral extension of the cephalon and above the cephalic legs (pl. 16, fig. 1; pl. 20, fig. 2; pl. 22, fig. 1; pl. 34, fig. 3). This lobe appears to be similar to that attached to the protopodite of the thoracic and abdominal legs. Nothing has been seen of any epipodites such as are attached to the thoracic and abdominal limbs.

Thoracic Appendages

Each of the seven thoracic segments has a pair of limbs formed of a simple walking or crawling leg (endopodite), a lobe-like jointed exopodite, and a jointed epipodite. In addition there is a small, simple epipodite that was probably present on each one of the legs and a short, broad lobe with fine, short setæ along the margin that may be an exite such as occurs in *Anaspides* and *Koonunga*[2] (pl. 35).

Endopodite.—Each thoracic leg (endopodite) is formed of a large elongate proximal joint (protopodite); four strong joints each about 1.5 times as long as wide (basopodite, ischiopodite, meropodite and carpopodite); two slender elongate joints (propodite and dactylopodite) and a claw-like, more or less tripartite termination (pls. 17-20).

The protopodite is about 2.5 times as long as wide when flattened by compression (pl. 18); it expands between its distal and proximal extremities so that the posterior margin (as flattened) has a gentle

[1] Smithsonian Misc. Coll., Vol. 67, No. 5.

[2] See figs. 1, 2, p. 171, this paper.

curvature from end to end; the proximal and posterior margins are lined with short, fine spines similar to those on the second joint and at the distal end of each joint of the leg. The exact method of attachment of the protopodite to the ventral surface is unknown, but from its form it necessarily was strongly attached to the ventral integument of the body at a point on its dorsal surface somewhat as the limb of the living *Apus* or *Limulus* is attached. The form of the protopodite and the presence of a series of sharp, short spines clearly indicate that it is to be compared with the gnathobase of the branchiopod limb. The second joint of the leg is flattened and slightly expanded on the dorsal and narrowed on the ventral side, as are the third, fourth, and fifth joints; a marked feature is the sudden contraction in size of the sixth (propodite) joint which is about one-half the diameter of the preceding joints; both it and the seventh joint (dactylopodite) expand slightly from their base to the distal extremity. The terminal claw is strong, slightly incurved, and with two spines nearly as long as the claw inserted beside and a little back of it. A side view of the claw is shown by figure 1, plate 18, and a view of the claw and spines spread out by figure 3, plate 16.

The protopodite in its natural condition was probably narrow on its ventral face, a little broader on its dorsal side and deep on its anterior and posterior sides. A beaded longitudinal line that is preserved on several specimens (pl. 17, fig. 3; pl. 18, fig. 1) clearly indicates the edge of the dorsal face, the other edge being the line along which the joint folded when flattened out by compression.

Exopodite.—Of this there are a number of fairly well-preserved specimens. It is a broad, long, flat plate or lobe of two joints with many fine, long, flattened setæ on its posterior margin so closely arranged that they are often in the fossil slightly overlapping (pl. 21, fig. 6) except on the distal joint where the setæ are fine and short. The exopodite appears to have been attached to the protopodite at its distal end and to have extended outward nearly as far as the jointed leg (endopodite). The close joint towards its distal end is similar to that of the large epipodite. The position of the exopodite is illustrated by figure 3, plate 19; figure 6, plate 21, and figures 1, 2, plate 23, and in all relatively undistorted specimens it extends obliquely forward from the side of the axial lobe. Its relation to the jointed legs (endopodites) is shown by figure 6, plate 21, where the leg is beneath the exopodite. Figure 1, plate 22, indicates that the jointed epipodite was between the endopodite and exopodite when they were pressed down upon each other. From their position and form it is probable that the exopodites were used for (*a*) swimming; (*b*) for directing a flow of water over the gills; and (*c*) possibly for directing minute food particles towards the mouth; they may also have functioned as gills.

Epipodites.—The presence of a jointed epipodite was not suspected prior to the present study, although a few traces of a thin, structureless lobe were met with in attempts to uncover a complete lobe-like exopodite. A fortunate splitting of a small fragment of shale opened up a crushed trilobite on the left side of which jointed legs were exposed and above them four finely preserved epipodites. These were attached to the protopodite toward its distal portion, judging from their present position in relation to the endopodite (pl. 20, figs. 3, 4). The epipodite is formed of a long, proximal lobe or joint and a short distal lobe separated from the proximal by a well-defined, close joint. The test of the epipodite was very tenuous; it has left only a film on the surface of the shale, but this retains the outline of the joints, the transverse line of the joint, and the large interior. There are traces of fine spines or setæ on the posterior margins of the lobe-like joints. The epipodite is beneath the exopodite and above the endopodite in the specimens where their relations are clearly shown (pl. 20, figs. 3, 4; pl. 22, fig. 1). The function of the epipodite was probably that of a gill or branchia. It has not been possible with the material available for study to determine if there is a small basal joint uniting the long, flattened joint and the protopodite as in *Anaspides*[1] (pl. 35, figs. 1, 2).

A small, oval, plate-like lobe is definitely shown on one specimen (fig. 1, pl. 18, right side), which indicates that there is a second and smaller epipodite that was probably attached to the protopodite; its proximal end rests on a protopodite, but owing to the crushing down and flattening of both, it is impossible to detect where the point of attachment may have been.

Exites.—There is still another series of plate-like lobes that it is difficult to locate. They are broadly oval in outline with fine, short setæ or spines all around the margin except on the inner side. They are best shown by figures 3 and 4, plate 20, where the endopodite or leg appears to be *above* them. The separate lobes overlap so that the anterior margin of each passes beneath the lobe in front. They were probably attached to the inner side of the protopodite somewhat as the lobes of the protopodite of the first thoracic limb of *Anaspides*[1] (pl. 35, fig. 2). My first thought was that the lobes were attached

[1] On the genus *Anaspides.* W. T. Calman. Trans. Royal Soc. Edinburgh, Vol. 38, pt. 4 (No. 23), 1896, p. 791, pl. 2, fig. 12.

to the ventral integument just beneath the proximal joint owing to their position along the side of the axis, as shown by figure 3, plate 20, but this is highly improbable.

Abdominal appendages.—These consist of five pairs of limbs similar to those of the thorax except that they diminish gradually in length and size. There are also two caudal rami.

Caudal rami.—The caudal rami are very long, slender, jointed and with numerous fine spines on the proximal portion and very fine spines or setæ on the distal segments; the segments are numerous and slightly longer than the diameter of the rami except toward the distal portion where they are more elongate. The rami are strongly attached (probably articulated) to the posterior margin of the ventral membrane (pl. 17, fig. 3) and suggest a sixth pair of abdominal appendages corresponding to the posterior or anal segment of the pygidium. This segment is fused so closely with the fifth segment of the pygidium that it is rarely that a slight transverse depression outlines it.

Anal aperture.—The anal aperture is probably beneath the posterior margin and between the caudal rami (pl. 17, fig. 3). This view is sustained by the fact that in *Ceraurus pleurexanthemus* the intestine has been traced to the posterior margin of the ventral integument of the pygidium.[1]

Further reference to the appendages of *Neolenus* will be found under the discussion of the appendages of the trilobite.

Formation and locality.—Middle Cambrian: (35k) Burgess shale member of the Stephen formation; on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

KOOTENIA DAWSONI (Walcott)

Plate 14, figs. 2, 3

Bathyuriscus (*Kootenia*) *dawsoni* WALCOTT, 1888, Proc. U. S. Nat. Museum, Vol. XI (issued 1889), p. 446. (Describes species.)

Dorypyge Dawsoni MATTHEW, 1899, Trans. Royal Soc. Canada, 2d ser., Vol. V, sec. IV, p. 56, pl. 3, fig. 1. (Describes and illustrates, referring species to *Dorypyge*.)

Dorypyge (*Kootenia*) *dawsoni* WALCOTT, 1908, Canadian Alpine Journ., Vol. 1, No. 2, pl. 3, fig. 9. (Illustrates a dorsal shield.)

This species combines characters of *Dorypyge, Olenoides,* and *Neolenus.* It has the slightly expanded subquadrilateral glabella of *Olenoides* and *Neolenus* with the unfurrowed, fused, pygidial seg-

[1] Bull. Mus. Comp. Zool., Vol. VIII, 1881, pl. 4, fig. 6.

ments of *Dorypyge*. The fringing spines of the pygidium are similar to those of the two former genera and quite unlike those of *Dorypyge*. The glabella of *Kootenia* differs from that of *Dorypyge* in form.[1]

These characters serve to distinguish the genus *Kootenia* from *Dorypyge*.

Appendages.—Many specimens of *K. dawsoni* were collected from the Burgess shale, but only one preserved any of the ventral appendages and these were only on one side beneath the pleura (pl. 14, fig. 2).

The distal joints of several endopodites of the thoracic limbs appear from beneath the long exopodites which seem to be similar to those of *Neolenus serratus*. The proximal section of the endopodite is long, flat and fringed with strong setæ; the distal joint has fine, short setæ along the lower margin and is closely united to the proximal section. From what there is available for comparison it appears that *Kootenia* and *Neolenus* had essentially the same type of thoracic limb.

Formation and locality.—Middle Cambrian: (35k) Burgess shale member of the Stephen formation; on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

Family ASAPHIDÆ Burmeister

Subfamily Asaphinæ Raymond

There is little to add to published data on the appendages of *Isotelus,* the one genus of the Asaphinæ preserving remains of jointed appendages, except in relation to the form of the endopodites. The specimen described by Billings[2] proved that *Isotelus* had a series of strong, jointed legs, but without the Ohio specimen[3] of *Isotelus maximus* it would have been difficult to interpret the structure of the legs of the Canadian specimen.

[1] Compare fig. 2, pl. 14, with the cranidia of *Dorypyge richthofeni* Dames (Research in China, Carnegie Institution, Vol. III, 1913, pl. 8, figs. 1, 1*a*).

[2] Quart. Jour. Geol. Soc. London, 1870, Vol. 26, pp. 479-486, pls. 31, 32.

[3] Science, Vol. 3, 1884, pp. 279-281, figs. 1-3.

ISOTELUS MAXIMUS Locke

Plate 24, figs. 3, *3a;* plate 25, fig. 1

Asaphus megistos MICKLEBOROUGH, 1883, Cincinnati Jour. Nat. Hist., Vol. 6, p. 200, figs. 1-3. (Describes and illustrates specimen with appendages.)
Asaphus megistos WALCOTT, 1884, Science, Vol. 3, p. 279, fig. 1. (Illustrates some specimens used by Mickleborough and gives notes on same.)
Isotelus maximus ULRICH, MSS.[1]

The large cephalon of the dorsal shield of *Isotelus* is made up of fused segments, traces of which are indicated on the exterior surface, especially of the young. The number of segments is unknown, but it is probably the same as for *Neolenus,* where seven segments are indicated. The thorax has eight free segments and a large pygidium (fig. 2, pl. 24) clearly shows fourteen fused segments. If this interpretation is correct there are twenty-nine segments included in the dorsal shield of *Isotelus,* and there may have been one or two more not now discernible in the end of the median lobe of the pygidium.

The unique Ohio specimen shows the protopodites of twenty-six pairs of limbs (pls. 24, 25). Of these nine are situated directly beneath the eight segments of the thorax; one beneath the posterior margin of the cephalon, and sixteen beneath the pygidium. That this was their natural position is not probable as they must have been more or less displaced when the animal was pressed down by or in the mud. That the displacement was not destructive is indicated by the regularity of arrangement of the legs and the approximation of the inner ends of the protopodites of the limbs. It is also probable that the protopodites sloped obliquely forward towards the median line instead of backward as in the specimen. This is spoken of under the subheading *Position of the Limbs,* page 162.

The proximal joint (protopodite) (pl. 25) of each leg is large, elongate, flattened vertically and extends well in towards the median line as in *Neolenus* (pl. 31) and *Triarthrus* (pl. 32). The second and following five joints appear to be slender and much like those found in *Calymene senaria,* but the first four were probably flattened and the distal ones rounded as in *Neolenus* (pl. 31) and *Triarthrus* (pl. 32). The drawing, plate 25, shows all that is preserved of the appendages on both the cast and matrix of the specimen (figs. 3, 3*a,* pl. 24).

[1] Dr. E. O. Ulrich has done much work on the genus and species of *Isotelus* and he very kindly permits me to use his illustrations of this and a second species, *I. walcotti,* a form from the trilobite quarry near Trenton Falls, New York, that I discovered about 1870.

The few traces of setæ such as might occur on exopodites of the type of those of *Neolenus* are not satisfactory proof that such exopodites existed in *Isotelus,* but they strongly suggest that such was the case.

Formation and locality.—Ordovician: Cincinnatian (Richmond); Oxford, Ohio.

ISOTELUS COVINGTONENSIS Ulrich ? MSS.

Asaphus platycephalus BILLINGS, 1870, Quart. Jour. Geol. Soc. London, Vol. XXVI, pp. 479-486, pls. XXXI, XXXII. (Describes and illustrates specimen with fragments of thoracic limbs.)

Isotelus latus RAYMOND, 1913, Bull. Victoria Mem. Museum, Vol. I, 1913, p. 45, pl. V. (Species described and figured.)

Isotelus covingtonensis ULRICH MSS., 1918. Dr. E. O. Ulrich identifies the specimen described by Billings, which was found at Ottawa, Canada, with his *Isotelus covingtonensis,* which occurs at Covington, Kentucky, also at Montreal, Canada, in the upper portion of the Trenton limestone.

Billings described the legs as follows:[1]

> The legs are arranged in eight pairs, the bases of each pair being situated exactly under one of the eight segments of the thorax, and at the sides of the sternal groove.
>
> The legs of the first pair are better-preserved than the others. They curve forwards and can be traced to a point nearly under the outer edge of the eye, or, rather, between the eye and the outside of the head. The other seven pairs follow at the average distance of two and a half lines from each other. The eight pairs thus occupy about twenty lines of the length of the ventral surface. This is exactly the length of the thorax, measured on the upperside. This trilobite has always eight segments in the thorax; and there is thus on the underside one pair of appendages to each segment. Although some of them are very imperfect, and the portions that remain are somewhat displaced, with a little study of the specimen it can be seen that they all curve forwards, and are thus, most probably, ambulatory rather than natatory legs.
>
> There appear to be several joints in each of these appendages; but the exact number cannot be made out. On the left side, the first four legs show very clearly that there are at least two, one at five lines from the side of the groove, and another about three lines further out. The position of each of these is indicated by a small protuberance. On the right side the preserved portions of the legs are longer, and thus indicate a greater number of articulations, although they cannot be distinctly seen. I think that each leg consisted of at least four or five articulations.

Through the courtesy of Dr. R. G. McConnell, Director of the Canadian Geological Survey and Deputy Minister of Mines, I have recently had the opportunity of examining the specimen studied by Billings. The protopodites of the anterior thoracic limbs have a length of 11.5 mm.; they are separated along the median line of the

[1] Quart. Jour. Geol. Soc. London, Vol. XXVI, 1870, p. 480.

ventral surface of the thorax by a space of 4 mm. in width, which with the length of the two protopodites gives a transverse distance of 27 mm. or nearly the width of the axial lobe of the dorsal shield; this indicates that the protopodites were attached to the ventral surface near their distal end and extended well in over the mesosternites of the ventral integument. The original form of the protopodites and following joints of the endopodite has been largely lost through pressure and the deposition of calcareous matter upon them; the distal end of the protopodite is enlarged and all the joints of the endopodite preserved appear to have been filled with sediment before the matrix about them was consolidated. There is nothing to indicate that they differed materially from the limbs of *Isotelus maximus* (pl. 25). Dr. Billings' illustrations give a very fair idea of the appearance of the appendages, although a little diagrammatic.

Formation and locality.—Ordovician: Trenton limestone; Ottawa, Canada.

Family OLENIDÆ Burmeister

Genus TRIARTHRUS Green

TRIARTHRUS BECKI Green

Plate 29, figs. 1-11, Plate 30, figs. 1-20

Triarthrus becki[1] GREEN, 1832, Monogr. Trilobites North America, p. 87, pl. 1, fig. 6. (Original description and illustration.)

Triarthrus becki MATTHEW, 1893, American Jour. Sci., 3d ser., Vol. XLVI, p. 121, pl. 1, figs. 1-7. (Describes and illustrates antennæ, cephalic and thoracic limbs including endopodite and exopodite of limbs.)

Triarthrus becki BEECHER, 1893, American Jour. Sci., Vol. XLVI, p. 361, text fig. 1. (Describes mode of occurrence of trilobites with appendages.) Idem, p. 467, text figs. 1-3. (Describes and illustrates thoracic legs.) Idem, 1894, American Geol., Vol. XIII, pp. 38-43, pl. III, figs. 1-9. (Describes and illustrates antennæ and thoracic limbs, and discusses mode of occurrence.) Idem, 1894, American Jour. Sci., Vol. XLVII, pp. 298-300, text fig. 1, pl. VII, figs. 1-3. (Describes and illustrates appendages found beneath the pygidium.)

Triarthrus becki WALCOTT, 1894, Proc. Biol. Soc. Washington, Vol. IX, pp. 89-97, pl. I, figs. 1-6. (Notes and illustrations of appendages based on new material.) Idem, 1894, Geol. Mag. London, n. ser., Dec. IV, Vol. I, pp. 246-251, pl. VIII. (Reprint of preceding paper.)

Triarthrus becki BERNARD, 1894, Quart. Jour. Geol. Soc. London, Vol. 50, pp. 425, 426, text figs. 11, 12. Idem, 1895, Vol. 51, pp. 352-358. (Reproduces two of Beecher's figures and discusses the structure of the appendages of *Triarthrus becki.*)

[1] In this synonymy the references are only to the original description, and to other papers containing original description or illustration of the interior of the dorsal shield or of the ventral appendages.

Triarthrus becki Beecher, 1895, American Geol., Vol. XV, pp. 93-98, pl. IV. (Describes and illustrates a unique specimen showing antennæ, cephalic and thoracic limbs.) Idem, 1895, Vol. XVI, p. 172, pl. 8, figs. 12-14, pl. 10, fig. 1. (Describes theoretical larval stage of *Triarthrus becki*.) Idem, 1896, Amer. Jour. Sci., 4th ser., Vol. I, pp. 251-256, pl. VIII, figs. 1, 2. (Describes and illustrates restoration of appendages of *Triarthrus becki* and discusses its morphology.) Also printed in Geol. Mag., London, Dec. IV, Vol. III, 1896, pp. 193-197, pl. IX, figs. 1, 2.

Triarthrus becki Oehlert, 1896, Bull. Soc. Geol. France, 3d ser., Vol. XXIV, pp. 97-116. Text figs. 1-17, 34. (Summarizes and discusses published data to date on appendages and development.)

Triarthrus becki Beecher, 1900, Text-book of Pal., Zittel, pp. 615-616, text figs. 1267-1269, 1300, on p. 629. (Resumé of previous papers on appendages.) Idem, The preceding paper of 1900 was again printed in the 1913 edition of Zittel's Paleontology with same illustrations and slight modifications of the text (pp. 700-701, 715, text figs. 1343, 1344, 1345 and 1375). Idem, 1902, American Jour. Sci., 4th ser., Vol. XIII, pp. 167-174, pl. 2, figs. 1-5, pl. 3, fig. 1, pl. 4, fig. 1, pl. 5, figs. 2-4. (Describes and illustrates ventral appendages and integument.) Idem, 1902, Geol. Mag., London, Dec. X, Vol. IX, pp. 152-162, text figs. 1-3, pls. 9, 10, 11. (Reprint of preceding paper.)

Triarthrus becki Jaekel, 1901, Zeits. deut. geol. Gesellsch., Vol. LIII, p. 161, text fig. 24, p. 162. (Discusses Beecher's conclusions, proposes new interpretation of appendages, and illustrates fragments of an antenna.)

Triarthrus becki Valiant, 1901, The Mineral Collector, Vol. VIII, pp. 105-112. (Account of discovery of appendages and general remarks.)

Triarthrus becki Moberg, 1907, Geol. Fören. Forhandl., Bd. 29, Haft 5, pp. 265-272, pl. 4, fig. 2, pl. 5, fig. 1. (Discusses and illustrates appendages in connection with supposed appendages of *Eurycare angustatum*.)

I have long had a sentimental interest in this species largely because my early home was on a knoll formed of the Utica shale in which *Triarthrus becki* occurs, and I collected many specimens of it as a school-boy in and about the city of Utica. In 1879 I published an illustrated paper that described the development of the dorsal shield from the young with one segment to the fully developed individual with sixteen segments.[1] Later Beecher described a younger stage and in several papers discussed and illustrated the ventral surface and appendages. It is unfortunate that he did not live to prepare an extended memoir that he had planned for on its structure. I agree with his interpretations of the appendages of *T. becki* except in some details. His conclusion that the minute elongate lobes beneath the pygidium were endites of a limb similar to that of *Apus*,[2] is not satisfactory in view of the appendages found beneath the pygidium of specimens in the National Museum collections. These are illustrated

[1] Trans. Albany Inst., Vol. X, 1879, pp. 23-33, pl. II, figs. 1-14.

[2] American Jour. Sci., Vol. XLVII, 1894, pl. VII, figs. 1-3.

by figures 4-8, plate 29. Figures 4 and 5 show slender jointed legs (endopodites) similar to those of the thoracic legs, down to the extreme end of the body, a structure similar to that found in *Neolenus* and *Calymene*. The setiferous exopodites are also present to the end of the pygidium. The absence of four expanded subtriangular joints on each leg in figure 4 may be owing to their absence or to the dorsal side of the leg being uppermost and the expanded ventral side of the joints concealed in the rock. This condition of preservation is often met with in the legs of *Marrella*[1] which have expanded joints somewhat similar to those of *T. becki.* The specimen represented by figures 4 and 5 indicates the presence of jointed legs to the end of the pygidium. With this in view, Beecher's conclusion that the limbs beneath the pygidium are similar to those of the young of *Apus* requires further consideration. His diagrammatic sketch (*loc. cit.*, fig. 3) is very much like that of his figure 4 of *Apus,* but his figures 1 and 2 indicate elongate narrow lobes of nearly equal width throughout and similar to those seen in our specimen represented by figures 5, 8, 11. That the legs beneath the pygidium in figures 4 and 5 are typical slender thoracic legs and those beneath the pygidium in figures 8 and 11 are typical branchiopod (*Apus*) limbs is not probable and I am giving in the description of the exopodites a different interpretation to the series of lobes shown in our figures 4, 7, 8 and Beecher's figures 1, 2, 3.

The illustrations of the exterior of the dorsal shield are reproduced on plate 30, but it is unnecessary to reprint the descriptions of the specimens as the figures are sufficient to serve for comparison of the dorsal shield with that of other species which have their ventral appendages described in this paper.

Limbs

We owe to Beecher the working out of the epistoma and cephalic limbs of *T. becki,* although the antennæ found by Valiant had been described by W. D. Matthew.[2] Before considering the true limbs, mention should be made of the metastoma or lower lip discovered and described by Beecher[3] as follows:

> The metastoma is generally clearly shown as a convex arcuate plate just posterior to the extremity of the hypostoma. On each side, at the angles, are two small elevations, or lappets, which suggest similar structures in many

[1] Smithsonian Misc. Coll., Vol. 67, No. 5.
[2] American Jour. Sci., 3d ser., Vol. XLVI, 1893, pl. 1, figs. 1-7.
[3] American Geol., Vol. XV, 1895, p. 97, pl. V, figs. 8-11.

higher Crustacea, and apparently represent the entire metastoma in *Apus* and some other forms. (Pl. 32, fig. 1.)

Beecher worked out the thoracic limbs and found them to be biramous with a strong long proximal joint (protopodite) to which a jointed leg (endopodite) and a jointed setiferous exopodite were attached. Unfortunately most of his illustrations are diagrammatic and give only an approximate idea of the limb. Even the reproduced photographs[1] given an inadequate conception of the true form of the limb, especially of the structure of the exopodite.

Cephalic limbs.—Antennules.—The anterior antennules or antennæ are uniramose, the exopodite of the primitive limb having disappeared. Each one is composed of a strong basal joint (protopodite) attached to the ventral side of the head at the side of the hypostoma about midway of its length. The numerous short joints composing it (pl. 29, fig. 9) each expand slightly at the distal end, giving it a striking appearance quite unlike the smooth, slender antennules of *Neolenus* (pl. 15, fig. 1).

Beecher describes the remaining cephalic appendages as follows:[2]

First pair of biramous appendages, or posterior antennæ.—The second pair of appendages, corresponding to the posterior antennæ, are attached to the head at each side of the glabella, on a line with the extremity of the hypostoma. They are apparently biramous, and thus agree with the second pair of nauplian limbs and with the typical posterior antennæ of many Entomostraca and Malacostraca. They may be compared with the posterior antennæ in *Euphausia pellucida,* one of the schizopods, especially with the *Furcilia* and *Cyrtopia* stages. The details of the endopodite and exopodite are not clearly shown. The former is more commonly preserved, and its distal joint extends just beyond the edge of the carapace. The coxopodite is developed into a triangular plate, the inner angle carrying a masticatory ridge, the whole extending about three-fourths the distance from the side of the glabella to the median line, just below the hypostoma, and directly obliquely backwards (pl. V, figs. 8-11).

Second pair of biramous appendages, or mandibles.—The appendages here correlated with the mandibles are immediately behind the first pair of biramous limbs. The proximal portion, or coxopodite, is similar in form to the preceding, though somewhat smaller, and overlapping its basal part. The palps, or endopodial and exopodial branches, have not been distinctly traced, though their presence is indicated on plate IV, figure 1, where, on the left side, there are endopodites and exopodites in sufficient number for each appendage of the head. That these should be referred to the cephalic limbs is further indicated by their being in advance of the endopodite, which manifestly pertains to the first thoracic segment. The inner edge of the mandibles as well as that of the

[1] The Ventral Integument of Trilobites, American Jour. Sci., 4th ser., Vol. XIII, 1902, pls. II-V.

[2] American Geol., Vol. XV, 1895, pp. 94-95, pls. IV and V.

other gnathobases of the head is apparently finely denticulate, as shown on plate IV, figure 1, and plate V, figure 2.

Third and fourth biramous appendages, or maxillæ.—Following the appendages referred to the mandibles are two pairs of strong limbs, with broad plate-like basal portions, or coxopodites, serving as gnathites (pl. V, figs. 8-11). They resemble each other, and are similar in form to the two preceding limbs, though somewhat larger. They are usually fairly well preserved and their form and structure can be approximately made out. The endopodites are composed of stout joints, and could be extended but a short distance beyond the margin of the head. The exopodites are more slender and carry an abundance of stiff setæ, which often diverge in a fan-like manner from their line of attachment. These brushes of setæ occupying the cavities of the cheeks are often preserved in specimens where the other details of the limbs are obscure or obliterated. In *Triarthrus* they are evidently homologous with similar brushes observed by Walcott in *Calymene*.[1]

This completes the number of paired appendages which can be definitely referred to the head. It is evident they do not differ conspicuously from each other, and, as will be presently shown, they closely resemble the thoracic legs in all essential structural characters [*Loc. cit.*, pp. 94-95].

Beecher describes the protopodite of the limbs as follows:

First it has a slender cylindrical form in the posterior half of the series, then becomes flattened and denticulate, and finally widens, until on the head it forms the triangular plate-like coxopodite, with masticatory ridge and functioning as a gnathite [*Loc. cit.*, p. 96].

The study of the material available of the protopodite of *Neolenus* and other trilobites and of the Branchiopoda (*Apus*) leads me to conclude that it is flattened and plate-like on all the appendages from the head to the end of the series beneath the pygidium. It may be more rounded beneath the pygidium, but the tendency to flat sides is still shown. The positions and form of the appendages in the fossil state is no guarantee that they were the same on the living animal. (See *Restoration of ventral appendages*, p. 165.)

Thoracic limbs.—These consist of an elongate protopodite to which the endopodite (leg) is attached and apparently the exopodite.

The protopodite is described by Beecher[2] as having a slender, cylindrical form in the posterior half of the series, then becoming flattened and denticulate, and finally widened, until on the head it forms the triangular, plate-like protopodite (coxopodite) with masticatory ridge and functioning as a gnathite.

I have not obtained any additional information about the protopodite but from its form in *Isotelus* and *Neolenus* I am inclined to consider that it may have been flattened on all of the limbs and that

[1] Bull. Mus. Comp. Zool., Vol. VIII, No. 10, 1881.

[2] American Geol., Vol. XV, 1895, p. 96.

its position was, as shown by Beecher in 1895,[1] vertical to the plane of the body and not flattened out as shown in his classical restorations of the ventral side of *Triarthrus* in 1896.[2] In this restoration the protopodite and the flat joints of the endopodite are on the same plane which is probably the position they would assume when gradually forced by compression into one plane, but in a natural position the protopodite would arch beneath the ventral surface of the mesosternites (axial lobe) and the flat joints would project downward in the opposite direction as in Beecher's transverse sections of the thorax published in 1895 and referred to above.

Endopodite.—This is formed in the anterior portion of the thorax of four rather long, flattened joints and two relatively short, rounded distal joints. From the distal end of the last joint a strong spine or claw with a short spine on each side gives a trifid termination similar in appearance to that of the leg of *Neolenus* (pl. 16, fig. 3).

Beecher describes the "endites" as follows:[3]

> 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.

During my study of the specimens in the National Museum collections I found that flattening out and enlargement of the joints (endites) was not always as regular as described by Beecher. Typical anterior endopodites are illustrated by figure 1, plate 29, and typical posterior endopodites by figure 20, plate 30. In two instances I found endopodites that occurred beneath the pygidium with the two distal endites round and slender (figs. 4, 5, pl. 29) and in one example the last three distal joints were cylindrical (fig. 7, pl. 29). The joints (endites) of the endopodite of *Marrella splendens* are similarly enlarged by flattening, and extend downward, but as in *Triarthrus* they are apparently not constant in size in all specimens.[4]

Exopodite.—The exopodite is nearly as long as the endopodite and usually much more in evidence in the fossils. It is formed of a

[1] American Geol., Vol. XV, 1895, pl. V, figs. 1-4.

[2] American Jour. Sci., 4th ser., Vol. I, pl. VIII, fig. 2.

[3] Idem, p. 253.

[4] Smithsonian Misc. Coll., Vol. 67. This paper will be No. 5 of this volume.

strong, many jointed arm (pl. 29, figs. 2, 11) to which is attached a diagonally arranged series of bases or supports for strong setæ, which may be jointed near their base and which are extended into long more or less flattened setæ forming a fringe. The jointed arm appears to be attached to the end of the protopodite beside the proximal joint of the endopodite. Beecher describes and illustrates a long proximal joint with a denticulated lower edge to which setæ are attached and beyond that a many jointed support; the proximal joint is represented to be as long as the first and second proximal joints of the endopodite. In the specimens now available for study I find that the diagonal crenulations extend up to the point of attachment of the arm to the protopodite and that there does not appear to be room for the very long proximal joint illustrated by Beecher (I have not seen the specimens). The structure of the exopodite is fairly well shown by figures 2, 3, 8, 10, 11, plate 29. In figures 2 and 3 the diagonal crenulations outlining the bases of the setæ are shown just beneath the closely jointed supporting arm, also portions of two of the larger endopodites. Figure 10 has the crenulated structure over the entire supporting arm in such a position that it appears that it is the upper and posterior side of the arm to which the crenulations and setæ are attached. In figure 11 the anterior and lower side of the exopodite is shown: it consists of a strong, closely jointed arm with about twenty segments and a flat, slender, lobe-like terminal segment or joint; the distal end of the crenulated margin begins at the proximal end of the terminal section and extends up along the arm past some twenty segments; the setiferous portion or fringe is attached to the crenulated portion. The elongate distal segment of the arm is beautifully shown in figure 8, where numerous minute exopodites are crowded from beneath the pygidium and the transversely lobed joints of the arm of the exopodite appear to rest one on the other. This structure is finely shown on the exopodites of figures 4 and 5.

The flat, narrow terminal joint of the exopodite is a marked character (fig. 11) and when a number are grouped beneath the pygidium (fig. 8, pl. 29) they have the appearance of a series of lobes somewhat similar to the limb of *Apus* as suggested by Beecher,[1] particularly when the minute exopodites beneath the pygidium have their joints flattened and drawn out on the posterior side until they appear like a row of minute, lobe-like exites arranged side by side so as to give the appearance seen in figures 4 and 5.

[1] American Jour. Sci., 3d ser., Vol. XLVII, 1894, p. 300, pl. VII, figs. 1, 2, 3.

Beecher, in describing the appendages of *Trinucleus concentricus,* said:[1]

The endopodites on the pygidium offer no conspicuous differences from those just described, except that a gradual change in form is manifest as the terminal limbs are reached. The separate endites become more and more transversely cylindrical, until the whole limb appears to be made up of cylindrical segments transverse to its length. A similar condition was observed in the young of *Triarthrus.*[2]

As I interpret the specimens of *T. becki* illustrated on plate 29, figures 4, 5, 8, of this paper, it is the exopodites and not the endopodites that have the transversely elongated endites. This is probably a phyllopod character but not as interpreted by Beecher.

Epipodite.—The presence of a flat epipodite attached to the protopodite of the leg near its proximal end cannot be absolutely proven by the material I have for study but it is quite probable that it existed as there is on three specimens a flat, elongate oval angular disk or lobe that is wider than the joint of the limb; it has a distinct margin on the sides and distal end and in two instances clearly lies above the limb and resting on it. The anterior margin is slightly arched or angular and merges into the distal end and the posterior margin has a slightly angular projection about midway of its length; usually this lobe is so mashed down on either the proximal joint of the endopodite or exopodite that it cannot be clearly separated from the limb. On one specimen preserving several of the probable epipodites (pl. 30, fig. 19) the distal end is bluntly pointed and the margins have very fine, short setæ projecting from them.

Not one specimen in fifty of *Triarthrus becki* shows traces of limbs, and among a hundred or more specimens preserving more or less of the limbs, only four or five specimens show the long protopodite, hence it is not strange that small epipodites, if they existed, have not heretofore been found. In the case of the large epipodites of *Neolenus* it was only by a fortunate splitting of three fragments of shale that they were found at all.

Summary.—The appendages of *Triarthrus becki* are outlined in the restoration of its ventral side (pl. 32) and the cross-sections on plate 34. Comparisons between them and the known appendages of other genera of trilobites may be found under *Observations on the Structure of the Trilobite* (pp. 159-161).

Formation and locality.—Ordovician: Utica shale; three miles (4.8 km.) north of Rome, Oneida County, New York.

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[1] American Jour. Sci., 3d ser., Vol. XLIX, 1895, p. 310.

[2] Idem, Vol. XLVII, pl. VII, fig. 3, April, 1894.

DEVELOPMENT OF *TRIARTHRUS BECKI*[1]

Plate 30, figs. 1-15, 18

"The larval *Triarthrus*[1] in its first known stage is ovate in outline, widest behind, where it also attains its greatest convexity. The frontal margin is marked by a convex fold of the test. The axis is annulated. The anterior six annulations apparently belong to the cephalon, the sixth one being considerably stronger than the others and probably representing the occipital ring. The pygidial portion is defined by a narrow, shallow, transverse furrow; and the axis has two annulations.

"Near the lateral anterior margins are two slight elevations which may represent the palpebral lobes of the eyes, and from them extend two furrows curving inward to the axis and dividing the cephalic region into two portions. The occipital pleura are indicated by slight depressions extending from the occipital ring. The specimen illustrated by figure 15 has a length of .63 mm. and a width of .46 mm."

The second known stage has one thoracic segment; the glabella has broadened in front and the transverse furrows have retreated to its lateral margins; the occipital segment is strong and carries the median node that is characteristic on all later stages of growth; fixed cheeks, narrow and without traces of the palpebral ridge and eye lobe; a node occurs on the thoracic segment and the pygidium is elongate with five fused segments in the axial lobe.

There is a gradual increase in size after the first segment is liberated in the thorax, but not of sufficient importance to indicate distinct periods of development. If any change is to be noted, it is, that, after the development of the twelfth segment, individuals having the same number of thoracic segments vary very much in size, some even being smaller than those having a lesser number of segments; this period of development is a marked one in the history of this trilobite, as an individual of thirteen thoracic segments is larger than one having sixteen. Again we find that an individual of thirteen thoracic segments is more than three times as large as one with fourteen, one being twenty-four and the other seven millimeters in length; that the largest with fourteen segments, thirty millimeters in length, is nearly double the smallest with sixteen segments, and that the adult individual of sixteen thoracic segments is fifty-three millimeters in length. Minor variations have been noticed in individuals having less than thirteen thoracic segments, but in no case has the

[1] Beecher, C. E.: A Larval Form of Trilobite. American Jour. Sci., Vol. XLVI, 1893, pp. 361-362.

size of the one having the lesser number of segments exceeded the next in the series of development. It is not until the twelfth degree of development is passed that this strange anomaly occurs.[1]

The pygidium gradually becomes proportionally shorter after the first stage with one segment and the eye lobe is indicated on individuals with two segments by a minute groove on the outer border of the fixed cheek. When the sixth thoracic segment is developed all parts have attained most of the characters of the adult.[2]

PTYCHOPARIA CORDILLERÆ (Rominger)

Plate 21, figs. 3-5

Conocephalites cordilleræ Rominger, 1887, Proc. Acad. Nat. Sci. Phil., p. 17, pl. 1, fig. 7. (Describes and illustrates species.)

Ptychoparia Cordilleræ Walcott, 1888, Amer. Jour. Sci., 3d ser., Vol. XXXVI, p. 165. (Refers species to the genus *Ptychoparia*.)

Ptychoparia cordilleræ Matthew, 1899, Trans. Royal Soc. Canada, 2d ser., Vol. V, sec. IV, p. 44, pl. 1, fig. 7. (Describes, comments upon, and gives diagrammatic illustration of portion of a specimen.)

Ptychoparia Cordilleræ Woodward, 1902, Geol. Mag., new ser., Dec. IV, Vol. IX, p. 536, text fig. 4. (Notes on species with outline figure of a dorsal shield.)

Ptychoparia cordilleræ Walcott, 1908, Canadian Alpine Jour., Vol. I, No. 2, pl. 3, fig. 5. (Illustrates nearly entire specimen from Mt. Stephen.) Idem, 1912, Smithsonian Misc. Coll., Vol. 57, p. 190, pl. 24, fig. 2. (Illustrates specimen showing branchiæ (exopodites).)

This species differs from the associated *Ptychoparia palliseri* in having a proportionally shorter frontal limb, narrower fixed cheeks, a less number of thoracic segments, eighteen or nineteen, and absence of a median node on the anterior thoracic segments. From the associated *Ptychoparia permulta* it varies in its broader fixed cheeks and frontal limb, rounded instead of spinous genal angles on the cephalon, more numerous thoracic segments, and in having a nearly smooth surface. *Ptychoparia cordilleræ* is quite abundant on Mount Stephen, and *P. permulta* is abundant at locality 35k, three miles (4.8 km.) to the north-northeast.

The dorsal shield of this species is well illustrated by figure 4, plate 21. The average number of thoracic segments is eighteen, but one example 23 mm. long has nineteen segments.

Ventral appendages.—Only one specimen has been found showing the thoracic limbs. This indicates very clearly the general character

[1] Walcott, C. D.: Fossils of the Utica Slate. Trans. Albany Inst., Vol. X, 1879, p. 29 (Advance print).

[2] Idem, pp. 26-29.

of the exopodite and that it is situated above the endopodite, although there are only imperfect traces of the latter projecting from beneath the exopodites as shown in figure 5, plate 21.

The exopodites are unlike those of any trilobite now known. They are long, rather broad lobes extending from the line of the union of the mesosternites and the pleurosternites. At the proximal end they appear to be as wide as the axial lobe of each segment, and to increase in width and slightly overlap each other nearly out to the distal extremity. They appear to have extended beyond the dorsal shield, but not as far out as the extremity of the leg (endopodite). They are finely crenulated along both the anterior and dorsal margins which indicates the presence of fine setæ.

Formation and locality.—Middle Cambrian: (14s) *Ogygopsis* zone of the Stephen formation; about 2,300 feet (701 m.) above the Lower Cambrian and 3,540 feet (1,089 m.) below the Upper Cambrian, at the great " fossil bed " on the northwest slope of Mount Stephen, above Field on the Canadian Pacific Railroad; (35k) Burgess shale member of the Stephen formation; on the west slope of the ridge between Mount Field and Wapta Peak, one mile (1.6 km.) northeast of Burgess Pass, above Field; (61j) yellow weathering band of calcareo-argillaceous shale, west slope of Mount Field, near Burgess Pass ridge, about 3,000 feet above Field, and (58r) about 2,200 feet (676.9 m.) above the Lower Cambrian, and 3,725 feet (1,146 m.) below the Upper Cambrian, in the limestones forming 2 of the Stephen formation, in the amphitheater between Mounts Stephen and Dennis, above Field, British Columbia, Canada.

PTYCHOPARIA PERMULTA, new species

Plate 21, figs. 1, 2

Dorsal shield.—Dorsal shield rather small and delicate, elongate ovate in outlines, probably quite sharply flexed at the geniculation before being flattened in the shale; its greatest width approximately two-thirds its length.

Cephalon.—Cephalon a little more than one-third as long as the entire shield, semielliptical in outline. Glabella long and slender, moderately elevated along an obtuse medial ridge which is highest a little behind the anterior extremity; dorsal furrows rather broad, not very sharply incised, slightly converging; anterior extremity of the glabella about two-thirds as wide as the base, broadly rounded; anterior furrow much more shallow than the dorsal; glabellar furrows very distinct in the younger forms, the medial and anterior pairs usually obscure in the older; posterior pair strongly oblique, persistent to the occipital ring which they intercept a little to the side of the median line; medial and anterior pairs linear, the medial pair very slightly oblique, the anterior nearly at right angles to the axis; occipital furrow rather broad, uniform in depth; occipital ring rather narrow, not nodulated, similar in character to the anterior segments of the thorax. Fixed cheeks low and wide, the distance from the palpebral lobe to the dorsal furrows about two-thirds the width of the medial portion of the glabella; posterolateral lobe short and broad, obtuse at the distal extremity; posterior groove deep, smoothly concave, in line with the occipital furrow. Palpebral lobe very short, contained more than three times in the length of the glabella, rather narrow and nearly parallel to the dorsal furrow, placed opposite the medial glabellar furrows. Palpebral ridge usually obscure, intercepting the dorsal furrows directly behind the anterior extremities. Frontal limb very narrow in the young, wide and broadly inflated in the adult. Frontal border narrow, upturned, cut off from the limb by a smoothly concave depression. Facial sutures with the posterior and anterior sections oblique and converging toward the short palpebral lobe. Free cheeks usually attached, of approximately the same width as the fixed cheeks. Peripheral border, like the frontal border, elevated and upturned and, like it, cut off from the inner portion by a smoothly rounded groove which intercepts the occipital groove at nearly a right angle; genal angles produced into short but acute spines which terminate opposite the second thoracic segment.

Thorax.—Thoracic segments normally fourteen in number. Axial lobe not very strongly convex, of about the same width as the proximal portion of the pleura; axial annulations narrow and sharply defined, but not nodose. Pleural segments narrow, very compactly arranged, the fourth to the ninth the most produced; pleural furrows almost as wide as the including segment, smoothly rounded; extremities petaloid; posterior inclination very slight.

Pygidium.—Pygidium short, a little more than twice as broad as it is long. Axial lobe relatively broad, truncate at the extremity which falls a little in front of the posterior margin; axial annulations, with the exception of the anterior, obscure, indicating three component segments and a terminal section. Pleural lobes small; pleural furrows distinct anteriorly, obsolete posteriorly, parallel to the anterior margin. Posterior margin an arc of a little less than 180°.

Surface.—Entire external surface finely and closely tuberculated; tubercles most crowded upon the cephalon; venation upon the frontal limb well developed.

Dimensions.—Length of dorsal shield, 25.5 mm.; greatest width of dorsal shield, 17.2 mm.; length of cranidium, 11.0 mm.; length of glabella, 7.0 mm.

Type locality.—(35k) One mile northeast of Burgess Pass, British Columbia.

Observations.—This fine species is associated with *Ptychoparia cordilleræ* and *P. palliseri* in the large Burgess shale fauna. It differs from the former in having a tuberculated surface, narrower fixed cheeks, longer frontal limb, spines on genal angles of free cheeks, fewer thoracic segments (four to five less in number), and from *P. palliseri* in the same characters except that the latter has six to seven more thoracic segments, and a somewhat narrower fixed cheek but broader than that of *P. permulta.*

One specimen has two antennules attached, which is the reason for noticing the species in this paper. The antennæ are so flattened in the shale that all traces of the joints are lost. As far as known to me it is the only specimen of the genus *Ptychoparia* preserving even the outline of the anterior antennæ (antennules).

Formation and locality.—Middle Cambrian: (35k) Burgess shale member of the Stephen formation; on the west slope of the ridge between Mount Field and Wapta Peak, one mile (1.6 km.) northeast of Burgess Pass; and (14s) *Ogygopsis* zone of the Stephen formation; about 2,300 feet (701 m.) above the Lower Cambrian and 3,540 feet (1,089 m.) below the Upper Cambrian, at the great " fossil bed " on the northwest slope of Mount Stephen, both above Field on the Canadian Pacific Railroad, British Columbia, Canada.

Order PROPARIA Beecher

Family CALYMENIDÆ Milne-Edwards

Genus CALYMENE Brongniart

CALYMENE SENARIA Conrad, 1841

Plates 26, 27, 28, 33

Calymene senaria CONRAD, 1841, Fifth Ann. Rept., New York Geol. Surv., pp. 38, 49. (Name proposed with brief description.)

Calymene senaria[1] WALCOTT, 1876, Twenty-eighth Ann. Rept., New York State Mus. Nat. Hist., pp. 89-92. (Notes discovery of natatory and branchial appendages of trilobites in Trenton limestone.) Idem, 1879, Thirty-first Ann. Rept. New York State Mus. Nat. Hist., p. 61, pl. 1,

[1] In the synonymy the references are to the original description and to papers containing description or illustration of the interior of the dorsal shield or of the appendages. No attempt is made to give all references to the species.

figs. 1, 2, 5. (Notes and illustrations of cephalic and thoracic appendages.) Idem, 1881, Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, pp. 198-216, pls. 1-6. (Description and illustrations of cephalic, thoracic and pygidial limbs with restoration of ventral surface of body with legs (endopodites) and a transverse section of the thorax with limbs attached.) Idem, 1884, Science, Vol. III, p. 279, figs. 2, 3. (Refers to *Calymene* in note on appendages of the trilobite.) Idem, 1894, Proceed. Biol. Soc. Washington, Vol. IX, p. 90, pl. 1, fig. 7. (Refers to discovery of an antennule-like appendage in *Calymene senaria.*) Also printed in Geol. Mag., London, n. ser., Dec. IV, Vol. I, p. 246.

As the sections of the appendages of *Calymene senaria* and *Ceraurus pleurexanthemus* have many similar characters the notes on them will be combined under the latter species.

Family CHEIRURIDÆ Salter

Genus CERAURUS Green

CERAURUS PLEUREXANTHEMUS Green

Plates 26, 27, 28

Ceraurus pleurexanthemus GREEN, 1832, Monogr. Trilobites North America, p. 84, text fig. 10. (Original figure.)

Ceraurus pleurexanthemus WALCOTT, 1875, Ann. Lyc. Nat. Hist., New York, Vol. XI, pp. 155-162, pl. XI. (Describes and illustrates interior of dorsal shield.) Idem, 1876, Twenty-eighth Ann. Rept. New York State Mus. Nat. Hist., pp. 89-92. (Notes discovery of natatory and branchial appendages of Trilobites in Trenton limestone.) Idem, 1879, Thirty-first Ann. Rept. New York State Mus. Nat. Hist., p. 61, pl. I, fig. 3. (Describes and illustrates thoracic leg of *Ceraurus.*) Idem, 1881, Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, pp. 191-216, pls. 1-4, 6. (Describes and illustrates sections of this species, showing appendages and gives a restoration of thoracic legs.) Idem, 1884, Science, Vol. III, p. 279. (Refers to *Ceraurus* in note on appendages of trilobites.)

The investigation made by me from 1875 to 1880 by cutting thin sections of specimens preserved in a limestone matrix resulted in determining the general character of the appendages of *Calymene senaria* and *Ceraurus pleurexanthemus.*[1] The restorations of 1881 failed, however, to show the presence of antennæ, the form and size of the protopodite or proximal joint of the thoracic and abdominal limbs, and there may have been an error in the restoration of the large distal joints of the fourth or posterior pair of cephalic legs. The antennules and the evidence indicating the larger, more elongate character of the protopodite (proximal joint) of the thoracic and abdominal limbs were not discovered and interpreted until after the publication of my paper of 1881.

[1] Walcott, Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, No. 10, 1881, pp. 198-224, pls. 1-6.

Cephalic Limbs

Antennules.—The occurrence of what might be the longitudinal section or part of an antenna or antennule was known to me in 1882, but it was not until 1894 that reference to[1] it was made as indicating an antennule. The section showing it cut through the head of an enrolled specimen of *Calymene senaria,* and near the cross-section of the hypostoma showed a longitudinal section of a slender jointed antenna-like rod sloping upward while the limbs sloped diagonally outward and downward. With our present information of the antennules of *Triarthrus* and *Neolenus* there is little doubt but that an antennule of *Calymene* is cut across by the section. Attempts to photograph it have been unsatisfactory owing to the density of the section.

Endopodite.—The protopodite of the first, second and third pair of cephalic limbs is smaller and the following joints are more slender than those of the fourth (figs. 6, 9, 11, pl. 26) pair and the limbs of the thorax. Traces of fine spines were seen on the inner end of the protopodite in some of the sections, which indicates that the protopodite functioned more or less as a gnathite. My conception of the relative position and form of the limbs is indicated by the restoration on plate 33.

In the restoration of 1881 of *Calymene* the enlarged distal joints of the posterior pair of cephalic legs (endopodites) were based upon evidence afforded by several slides, four of which are illustrated by figures 9, 10, 12, and 13, plate 26. If such broad joints were present, sections like those in the figures mentioned must result if the section cut through the broader axis of the joint. If it cut through the narrow axis, sections like those represented by figure 11, plate 26, would result. The sections mentioned appear to be best explained by assuming the presence of large, flat distal joints on the posterior cephalic legs, and I am now putting them in the restoration of *Calymene senaria* (pl. 33, fig. 1), although such expanded joints are unknown in *Neolenus* and *Triarthrus.* Probably the broad, flat joints were used in swimming, as the other known appendages are not very well adapted for the purpose.

Exopodite.—Sections cut through the heads of many specimens of both *Calymene* and *Ceraurus* showed more or less of the cephalic legs and the setiferous epipodites, but only rarely was a trace of the spiral exopodite met with. In fact, in only one instance was there

[1] Note on some Appendages of the Trilobites, Proc. Biol. Soc. Washington, Vol. IX, p. 90.

apparently evidence that the spiral belonged to a cephalic limb and in this there was no direct connection shown. There probably was a small exopodite attached to the large protopodite of the posterior cephalic limbs, and a more or less rudimentary one present on the three anterior pairs as short, slender, wire-like or flattened ribbons.

Epipodite.—The presence of flat setiferous lobes beneath the cephalic shield was known in 1881,[1] but the interpretation of their relations to the limbs was not then attempted. Comparing the lobes with those attached to the cephalic limbs of *Neolenus* (pl. 16, figs. 1, 2) we find that the setiferous lobes of *Calymene* and *Ceraurus* are relatively smaller, shorter, and bear stronger setæ. This is shown by figure 2, plate 26, and figure 14, plate 27 (*Ceraurus*), and possibly by figure 11 (*Calymene*). In figure 11, plate 27, the lobe is merged into the mass filling the central part of the space beneath the head, but in figure 12 the lobe is detached on the right side, although it is close to the large protopodite of the posterior cephalic limb to which it was probably attached very much as a similar lobe is attached to the protopodite of the thoracic limbs (pl. 27, fig. 14, left side, and pl. 26, fig. 2, left side).

Thoracic Limbs

The restoration of the thoracic limb of *Calymene* shows a large elongate protopodite, an endopodite, a curious, slender, bifid, spiral exopodite, and a lobe-like setiferous epipodite. The relative positions of the parts are indicated in the restoration, figure 6, plate 35.

Protopodite.—In the case of the proximal joint (protopodite) of the thoracic limbs there is every reason to change my restoration of 1881 and replace the relatively short joint with a long joint that extends inward on each side of the longitudinal axis of the ventral surface about one-third the distance across the axial lobe. This change is based on such sections as those illustrated by figures 1-8, plate 26, and such proximal joints are characteristic of the limbs of *Neolenus, Triarthrus,* and *Isotelus.* Each of these sections represented by figures 1-8 clearly indicates strong, elongate, proximal joints, and those represented by figures 4 and 15 had short, strong spines on the proximal end. It is surprising that such good results were obtained by cutting sections, but these illustrated (figs. 1-8) are selected from among hundreds that did not happen to cut through the limbs at the right angle to show definitely their size and form.

[1] Walcott, Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, No. 10, 1881. pl. 3, figs. 1 and 2.

The proximal joints shown in the restorations of 1881 were correct for transverse and closely associated sections, but not for the longitudinal section of the limb. The form now assumed to be nearly correct for the protopodite is shown by figures 1-8 of plate 26, and by the restoration, figure 1, plate 33.

Endopodite.—The endopodite is formed of six slender joints, the two and it may be three proximal ones being more or less flattened and the distal joints more cylindrical and terminating in a short curved hook or claw and two short spines as in *Neolenus.* The joints of the endopodite of *Ceraurus* appear to have been more expanded at the distal end than those of *Calymene.* This is indicated in the restoration of the cross-section of the dorsal shield and ventral appendages (pl. 34, fig. 1).

Exopodite.—The exopodite is apparently situated between the endopodite and epipodite, but the exact point at which it was attached to the protopodite is unknown, but from comparisons with *Neolenus* and the Anaspids (Malacostraca) the attachment was presumably at the distal end of the protopodite.

The first or proximal portion or base was slender and elongate and from it a bifid, slender, wire-like spiral curved outward and downward so as to be above and free from the leg (endopodite) (pl. 27, figs, 2, 4, and 5). The sections apparently cut across strong, closely coiled spirals that had sufficient rigidity to usually retain their form even when they were crowded together (pl. 27, figs. 4, 6, 8, 9). Occasionally there is a partially drawn-out spiral (fig. 7) or it may have been pulled out into a straight wire or a ribbon (pl. 26, fig. 14).

I was greatly puzzled by the spirals when I began cutting sections of *Calymene* and *Ceraurus* in 1875 and endeavored to find something indicating a long linear support, but in no instance has a trace of such been found or an indication of attached setæ. The latter abound in some sections of *Calymene* and *Ceraurus,* but they belong with the epipodites. When the exopodite of *Triarthrus* was found to have obliquely arranged setæ supported by a jointed arm it seemed as though the problem was solved, but it was soon found (1894) that these were attached to a strong jointed exopodite and did not have a spiral structure. I have more recently worked out and studied several exopodites of *Triarthrus* and have confirmed my former opinion that no sections of them could give the spiral structure shown by the spiral exopodites of both *Calymene* and *Ceraurus.*

Longitudinal and oblique sections of closely coiled spirals of wire set in plaster and cut across are identical in form with the spirals in the trilobite sections (pl. 27, figs. 10, 10*a*). In fact practically every section of the fossil spirals illustrated on plate 27 may be duplicated by making close coils of wire of various sizes and bending them to secure the right longitudinal curvature before embedding in plaster. Elongated or drawn out spirals such as shown in figures 6 and 7 are also easily produced.

Epipodite.—Sections of a setiferous lobe indicate the presence of an epipodite. It appears to have been flat with a fringe of long, strong, simple setæ as shown by figures 12 and 14, plate 27; figure 2, plate 26. In the latter figure and in figure 13, plate 27, the setæ of several epipodites appear to have been cut across so as to give the effect of long rows of setæ. The same condition occurs in specimens of *Marrella* when the setæ of several exopodites are matted against each other.[1]

Two sections show an epipodite near their point of attachment to the protopodite. In figure 12, plate 27, this is shown on both sides not far from the cephalon, and in figure 2, plate 26, on the left side and well back in the thorax.

From these sections I infer that the epipodite was attached to the protopodite well out towards its distal end.

Other sections show the base of the spiral exopodite in the same position, a fact not at all surprising as the exopodite and epipodite may be either accidentally or actually nearly on the same line with relation to the leg (endopodite).

There are two sections (pl. 27, fig. 4) of an enrolled *Calymene* that suggest a small, slender appendage with two long joints, the distal one having a few minute setæ along its outer side. Whether this is a flattened leg (endopodite) cut across on its narrow section or a part of an appendage with which we are not acquainted is difficult to decide with only one indefinite specimen available for study.

Of the appendages beneath the pygidium I wrote in 1881:

> The character of the appendages beneath the pygidium is one of unusual interest, and for a long time was highly problematical, and at present the evidence is not all that could be desired. Four sections, two transverse and two longitudinal, show their presence in *Ceraurus*. That they are jointed is shown by plate II, figure 8, and also in a similar section not illustrated. A transverse section, plate II, figure 4, of the extreme posterior segment of the pygidium also shows the base of the leg and sections of the succeeding anterior legs. The position of the base is the same as that of the posterior leg, plate II, figure 8. That these legs were not foliaceous and branchial is evident, but what their terminal joints were like is yet an unsettled problem of the investigation.[2]

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[1] Plate 25, figs. 3, 6, Smithsonian Misc. Coll., Vol. 57.

[2] Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, No. 10, 1881, p. 204.

We have no further information except that from the character of the appendages beneath the pygidium of *Triarthrus* and *Neolenus* it is probable almost to a certainty that the limbs were similar to those of the thoracic region.

Further description and discussion of the appendages and structure of *Calymene* and *Ceraurus* is given in the general discussion, also in the description of illustrations and the restorations.

Formation and locality.—The specimens preserving appendages and illustrated are from the Ordovician: Trenton limestone (upper section): One mile (1.6 km.) east of the middle fall of Trenton Falls, on the West Canada Creek, in the town of Russia, Herkimer County, New York.

ODONTOPLEURA TRENTONENSIS (Hall)

Acidaspis trentonensis HALL, 1847, Nat. Hist. Surv. New York, Pal., Vol. I, p. 240, pl. 64, figs. 4*a-f*. (Describes and illustrates species.)

Acidaspis Trentonensis WALCOTT, 1881, Bull. Mus. Comp. Zool., Harvard College, Vol. VIII, p. 206. (Refers to appendages of.)

Odontopleura trentonensis CLARKE, 1892, Forty-fourth Rept. New York State Mus., p. 101. (Changes generic references.)

In this species fragments of both cephalic and thoracic limbs have been observed with the endopodite and exopodite apparently of the same character as those of *Calymene* and *Ceraurus* with which they were associated.

Formation and locality.—The specimens preserving appendages are from the Ordovician: Trenton limestone (upper portion): One mile (1.6 km.) east of the middle fall of Trenton Falls, on the West Canada Creek, in the town of Russia, Herkimer County, New York.

Order HYPOPARIA Beecher

Family TRINUCLEIDÆ Emmrich

Genus TRINUCLEUS Murch

TRINUCLEUS CONCENTRICUS Eaton

Dr. C. E. Beecher found traces of the thoracic limbs of this species, which indicate that they were essentially of the same type of those of *Triarthrus becki* with which the specimens of *T. concentricus* were associated[1] at the locality near Rome, New York.

[1] Structure and Appendages of *Trinucleus*. American Jour. Sci., 3d ser., Vol. XLIX, 1895, pp. 307-311, pl. III.

ORDOVICIAN CRUSTACEAN LEG

Plate 36, figs. 1, 2, *2a-d*

A crustacean leg, represented by several specimens, occurs on the surface of a fragment of calcareous shale of Ordovician age from Ohio. It is quite unlike the leg of *Neolenus, Triarthrus,* or *Isotelus.* The proximal joints, coxopodite and basopodite are very short and provided with two sharp processes on the ventral side; the third joint is somewhat similar to the second but is longer; the next four are of nearly equal length and might be compared with second, third, and fourth joints of the leg of *Neolenus;* the distal joint is long, slender, and without a terminal claw. The ventral side of the joints has a fine crenulation indicating the bases of setæ. The unusually fine drawing of a leg made by Mr. Clarence R. Shoemaker shows that the joints were united by a thin membrane that did not resist destruction so well as the thin integument forming the covering of the joints.

The legs are associated with fragments of *Calymene meeki,* but it is not probable they belong to that species; if they did, they are unlike any trilobite leg known to me. The very short coxopodite and basopodite are unknown in the trilobites of which we have the legs, as they are fused into one joint forming the long protopodite in the trilobite. The distal joint is also unlike that of the trilobite legs known to us. The leg (pl. 36, fig. 1) is more like one that we might expect in an Isopod. The legs average about 10 mm. in length. One was illustrated by me in 1881.[1]

Formation and locality.—Ordovician: Cincinnatian, *Cynthiana* limestone. Bank of Ohio River below Covington, Kenton County, Kentucky.

SECTION 2

STRUCTURE OF THE TRILOBITE

Dorsal shield.—The structure of the dorsal shield and hypostoma of the trilobite is so well known that it is unnecessary to discuss it further than to state that the known range of variation in form and segmentation is so great that it undoubtedly has affected the details of the ventral appendages but not their fundamental arrangement and structure.

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[1] Bull. Museum Comp. Zool., Harvard College, Vol. VIII, pp. 204, 224, pl. VI, fig. 5*a*.

The structure of the ventral surface, intestinal canal, and appendages will be considered and incidental reference made to the possible position of the organs within the visceral cavity.

Ventral integument.—Beecher has reviewed the evidence bearing on the structure of the ventral integument[1] briefly and concisely and summed it up as follows:

The ventral integument in trilobites is a thin uncalcified membrane, which may be divided into pleurosternites and mesosternites, corresponding to the mesotergites and pleurotergites of the dorsal test, and like them connected segmentally by an inarticular membrane.

The mesosternites are usually marked by five longitudinal ridges, or buttresses, representing thickenings of the membrane, which may be homologized with apodemal structures in other crustacea, and not with the appendicular system.

These buttresses, or apodemes, include a single median one for each mesosternite, with two others on each side extending forward and obliquely inward, and enclosing subtriangular or rhombic spaces.

The presence and disposition of these buttresses apparently afford information regarding the ventral musculature of the trilobites. A pair of flexors is indicated, together with the lateral strands attached to each mesosternite and extending forward and inward to their union with the main bundles within the cavity of the next anterior somite.[2]

My present review has not led to the discovery of additional evidence, and I agree with Beecher that Jaekel was greatly misled in his interpretation of the cast of the ventral membrane of *Ptychoparia striata*,[3] and that he was led on the evidence furnished by this one specimen of *Ptychoparia* "to reconsider on a false premise the entire question of the anatomy, ontogeny, phylogeny, and affinities of the trilobite."[4]

In connection with my investigation of the structure of ventral integument and appendages of *Calymene* and *Ceraurus* I found[5] that in those longitudinal sections in which the ventral integument is most perfectly preserved it had been a thin, delicate pellicle or membrane, strengthened in each segment by a transverse arch. These arches appear as flat bands separated by a thin connecting membrane, somewhat as the arches in the ventral surface of some of the Macrouran Decapods. The finest illustrations of this structure have been found

[1] American Jour. Sci., 4th ser., Vol. XIII, 1902, pp. 165-174.

[2] Idem, p. 172.

[3] Jaekel, Otto.—Beiträge zur Beurtheilung der Trilobiten. Theil I. Zeits. deut. Geol. Gesells., Bd. LIII, Heft 1, 1901, pp. 133-171, figs. 1-31, pls. IV-VI.

[4] Beecher, C. E., American Jour. Sci., 4th ser., Vol. XIII, 1902, p. 166.

[5] Walcott, C. D.: The Trilobite: New and Old Evidence relating to its Organization. Bull. Mus. Comp. Zool., 1881, Harvard Coll., Vol. VIII, No. 10. pp. 199-200.

in *Calymene,* but several sections of *Ceraurus* show it very well defined. The section represented on plate 28, figure 8, gives a very fine view of the membrane and arches in a longitudinal section. The specimen illustrated on plate 28, figure 7, shows a portion of the dorsal shell of the median lobe broken away so as to exhibit the openings in the ventral surface that gave passage to the muscles, etc., of the legs, the partitions separating the segments of the ventral surface, and the central ridge to which they are attached. This ridge, with the partitions and arches in the membrane beneath, would give the necessary strength and firmness to form the base of attachment of the limbs. The membrane uniting the margins of the dorsal shell and the median lobe of the ventral surface curves upward close to the pleural lobes of the dorsal shell, and leaves but a narrow space between it and the dorsal shell.

In by far the greater number of sections, both transverse and longitudinal, the evidence of the former presence of an exterior membrane protecting the contents of the visceral cavity, rests on the fact that the sections show a definite boundary line between the white calcspar, filling the space formerly occupied by the viscera, and the dark limestone matrix. Even the thickened arches are rarely seen. This is almost universally the case with the legs and attached appendages, as their external membrane is not to be distinguished as such. It would appear that in the process of mineralization the calcspar that replaced the viscera and contents of the appendages also replaced the substance of the membrane, thus forming one continuous mass and effacing all traces of the delicate external test. The nature of this covering is also shown by the present imperfect condition of the appendages. Only in a few rare instances are they found in an approximately perfect state, and the many bizarre forms prove that it was semielastic, and forced into many irregular forms.

On the same small block of limestone with the two jointed legs illustrated on plate 36, figures 2, *2a-d,* occur the remains of the dorsal shell of both *Calymene senaria* and *Trinucleus concentricus.* The contrast in the test of the joints forming the legs and that of the dorsal shell is very striking. The latter is firm, thick, and of a yellow or opalescent color, while the former is of a bronze color, thin and indented with numerous imprints as though it had contracted or shrunk after the decomposition of the muscles of the leg.

The intestinal canal.[1]—Attention was first called to the existence of

[1] Walcott, C. D.: The Trilobite: New and Old Evidence relating to its Organization. Bull. Mus. Comp. Zool., 1881, Harvard Coll., Vol. VIII, No. 10, pp. 200-201.

the intestinal canal in the trilobite by Prof. Beyrich, who discovered it in a specimen of *Trinucleus ornatus*.[1] M. Barrande subsequently gave numerous illustrations of its preservation in *Trinucleus goldfussi,* where, he says, it extended from the middle of the glabella along the interior of the median lobe to the extremity of the pygidium. In some examples it is filled with very fine, soft clay. This substance has, perhaps, largely contributed to preserve the form of the canal, which, once filled and buried in incompressible sand, has undergone no other deformation. There must have been some peculiarity of conformation that preserved the intestinal canal in this species, as in other trilobites from the same quartzites no traces of it are to be seen.[2] M. Barrande mentions that Dr. A. de Volborth discovered in an *Illænus* a lengthened and articulate organ which originated in the glabella and became attenuated toward the pygidium.[3] A cast of the interior, as shown in plate 28, figure 7, might have such an appearance. This, however, is conjectural, as I have not seen an illustration of Dr. Volborth's specimen.

In my cutting of sections of trilobites it was a very rare occurrence to find traces of the intestinal canal. One specimen out of one hundred was a large proportion. The visceral cavity was usually filled with calcspar, and all vestiges of the canal or any other organ obliterated.

In a note taken while cutting sections in December, 1876, it is stated that when grinding down a section from the anterior towards the posterior extremity of the head the cephalic cavity which was filled with calcspar, had a dark, round spot midway between the hypostoma and median lobe of the head. A sketch taken after the grinding had carried the section a short distance back shows the dark spot with the same outline as the opening seen in plate 28, figure 4, that leads into the intestinal canal from the cephalic cavity as exposed in the specimen. That this was the normal form of the intestinal canal is doubtful, but the transverse section, plate 28, figure 5, shows the opening in figure 4 divided into two openings caused in all probability by the ventral integument with its central ridge, having been pressed up against it. In several transverse sections a round, dark spot is seen in the spar a little distance beneath the thoracic segments. This was filled with sediment or food, and thus distinctly outlined.

[1] Ueb. Trilob., II. Stück, p. 30, pl. IV, fig. 1*c*, 1846.
[2] Sys. Sil. Boh., I., p. 229, 1852.
[3] Idem, II, p. 182, 1872.

The position of the opening of the canal in the specimen represented by figure 4, plate 28, and in the section ground away, would indicate that it passed beneath the cephalic shield into the cephalic cavity, and then recurved to the opening of the mouth. Posteriorly it extended to the extremity of the pygidium, as described by M. Barrande.

The space occupied by the canal and other internal organs is not large, as it is contained mostly between the arched median lobe of the dorsal shell and the ventral membrane, as shown in the restorations of the cross-sections of the thorax (plate 34).

Appendages

limbs

The hypostoma, metastoma, and caudal rami are not treated as true limbs.

The limbs are essentially the same for all of the trilobites of which we now know them (pl. 35, figs. 4-7). They have with the exception of the antennæ a protopodite bearing two rami, the endopodite and the exopodite. The coxopodite and basopodite of the theoretical primitive crustacean limb is fused into one large joint which in this paper will be designated as the proximal joint or protopodite. To this stem or base there is attached a strong jointed endopodite or walking leg and an exopodite varying greatly in form and structure, but always present in those trilobites of which we have the limbs well preserved, except possibly on some of the cephalic limbs. The protopodite may also bear one or more appendages known as the epipodite and possibly another lobe or exite. In the antennæ the exopodite has disappeared, leaving only the simple jointed endopodite. The various joints of the limb were probably connected by a thin flexible membrane protecting the muscles as with recent crustaceans. Some of the details of the limbs will be found in the description of the appendages of the several species.

Antennules.—The antennule of the trilobite is formed of a simple, jointed endopodite, the exopodite of the primitive limb having disappeared. In *Triarthrus* the long, slender antennules are composed of a strong, elongate basal joint (protopodite) attached to the ventral side of the head beside the hypostoma; the remaining joints are short and expand slightly at the distal end (pl. 32, fig. 1). In *Neolenus* (pl. 31) the joints of the antennules are much like those of *Triarthrus,* but there is less expansion at the distal end of each joint which results in a smoother, more cylindrical surface. The antennules of *Ptychoparia* are too imperfect to obtain details, but they appear to be similar to those of *Neolenus.*

Protopodite.—The protopodite is now fairly well known for the limb of the Ordovician species, *Calymene senaria, Ceraurus pleurexanthemus, Triarthrus becki, Isotelus maximus,* and particularly well for the Cambrian species *Neolenus serratus.* In all, it is large, elongate, and presumably formed of two fused joints, the coxopodite and basopodite. No traces have been seen of a precoxal joint. In all but *Triarthrus* the point of attachment to the ventral surface of the body appears to have been about midway and in *Triarthrus* nearer the distal end. The exact form of attachment to the ventral integument is unknown, but as stated under *Neolenus* it was probably narrow and long and connected the dorsal side of the protopodite with the ventral integument and interior supports somewhat as the limbs of *Apus* and *Limulus* are attached to the body. The original form of the protopodite is not fully preserved in any specimen known to me, but from Beecher's specimens a fairly accurate idea may be obtained for *Triarthrus* and from the flattened specimens found in *Neolenus* it appears that the cross-section is much like that of the protopodite of *Apus* (pl. 36, fig. 4), and another suggestion is obtained by comparing it with the leg of *Limulus.* In *Apus* and *Limulus* the protopodite is flat with the nearly vertical sides, and the proximal margin thin with rows of fine spines that continue more or less along the ventral margin towards its distal end. A longitudinal outline of the protopodite of *Neolenus* as restored is shown by figure 4, plate 35, and this may have been the section of the protopodite of nearly all trilobite limbs as they appear to have had the same function in all the genera in which they are now known.

Endopodite.—The endopodite or leg extends outward from the distal end of the protopodite. It is composed of six joints and a short curved terminal claw with two short spines projecting from near the base of the claw. The joints vary in length and relative size in the several species now known. They appear to be essentially the same in form for *Calymene* and *Triarthrus,* but in *Triarthrus* they extend further beyond the edge of the dorsal shield as the pleural lobes of the latter are proportionally narrower. In *Neolenus* the legs extend beyond the dorsal shield very much as in *Triarthrus,* but not quite as far. *Calymene, Ceraurus,* and *Isotelus* are often found enrolled, which indicates that the legs could be drawn within the margin of the shield.

Exopodite.—The exopodite appears to spring from or near the distal end of the protopodite. It varies from the bifid spiral of *Calymene* and *Ceraurus* to the simple, two-jointed, broad, flat, setiferous lobe of *Neolenus* and the many jointed, complicated, setiferous exopodite of *Triarthrus.* A setiferous exopodite is indicated for *Ptychoparia, Isotelus,* and *Trinucleus,* but the structure is unknown.

Epipodite.—The large epipodite of *Neolenus* (pl. 20, figs. 3, 4) is a flat, two-jointed elongate lobe attached to the protopodite and reaching out to the edge of the carapace. A second and much smaller elongate lobe is indicated on one specimen that was attached near the larger lobe (pl. 18, fig. 2). A small setiferous epipodite is attached to the protopodite of *Calymene* (pl. 35, fig. 6) and *Triarthrus* seems to have a small, flat, oval, finely setiferous lobe in about the same place (pl. 30, fig. 19).

Exite.—What may be an exite on the protopodite of *Neolenus* is shown on figures 3 and 4, plate 20. Its assumed position is indicated on the restoration of this species (pl. 18, fig. 2, and pl. 31).

Cephalic limbs.—The cephalic limbs of *Calymene* except the antennules were determined in 1881,[1] and those of *Triarthrus* in 1895,[2] and *Neolenus* including antennules in 1918 (pl. 31). In the three genera the protopodites of four pairs of limbs form gnathobases to which are attached the endopodite or jointed leg as the main stem of the limb and an exopodite that is fairly well known for *Triarthrus* and *Neolenus* and less so for *Calymene.* The character of the limbs and their position indicate that the trilobite lived on soft food that was pushed along to the mouth by the protopodites. No evidence has been discovered of the existence of specialized gnathobases capable of crushing or triturating hard food.

Thoracic limbs.—The thoracic limbs of the species of trilobite with which they have been found have a large protopodite and a strong, relatively large and long endopodite that formed a powerful walking leg of six joints and a short terminal claw; the legs vary somewhat in size in the several species, but all were adapted to the needs of the animal both when walking and when forcing its way through soft mud and sand in search of food. In addition to the endopodite an exopodite is known to have been present in the thoracic limbs of *Calymene, Ceraurus, Neolenus, Kootenia, Triarthrus, Trinucleus,* and *Odontopleura.* The spiral exopodites are found in *Calymene,*

[1] Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, 1881, pl. VI, fig. 1.

[2] American Geol., Vol. XV, 1895 (February), pl. V, figs. 8-11.

Ceraurus, and *Odontopleura;* the flabelliform types in *Neolenus* and *Kootenia:* the setiferous plumes of *Triarthrus* appear to have been capable of service as swimming organs, also of functioning as branchiæ.

It is probable that flat, more or less setiferous epipodites occurred on the protopodites of the limbs of most if not all trilobites, but we know them with certainty only on *Neolenus, Calymene,* and *Ceraurus,* and somewhat doubtfully in *Triarthrus.* They attain their greatest development in *Neolenus,* and the same is true of the small, flat lobes tentatively referred to as exites. The several types of thoracic limbs as now known are illustrated by diagrammatic drawings which are reproduced by figures 4-7, plate 35.

Pygidial limbs.—The limbs beneath the pygidium appear to be essentially the same as those of the thoracic region as far as the endopodite is concerned and usually the same is true of the exopodite, the known exception being in *Triarthrus* where the many jointed setiferous arm of the exopodite appears to resolve itself into a series of minute lobes that are transverse to the axis of the limb and look like the exites of a phyllopod limb.

Summary.—The appendages may be summarized as follows:

Cephalic:

1. *Antennules.*—Uniramose, slender, many jointed, and attached to the ventral integument of the cephalon about midway of the glabella.
2. *Antennæ.*—Represented by the anterior pair of cephalic limbs which are posterior to the opening of the mouth.
3. *Mandibles.*—Represented by the second pair of cephalic limbs.
4. *Maxillula.*—Represented by the third pair of cephalic limbs.
5. *Maxilla.*—Represented by the fourth pair of cephalic limbs.

Thoracic: A pair of biramous limbs to each segment or somite of the thorax, each limb consisting of a fused coxopodite and basopodite forming a protopodite; an attached, six-jointed endopodite or leg with a terminal spine or spines, one of which is usually in the form of a slightly curved claw; an exopodite that may or may not be jointed and which is attached to the distal end of the protopodite; one or more flabelliform epipodites attached to the distal part of the endopodite and in one instance (*Neolenus*) one or more exites (attached to the anterior side of the protopodite?).

Abdominal: No abdominal appendages are differentiated from those of the thorax by their structure. Those referred to as such are the limbs beneath the pygidium which are similar in structure to those beneath the thorax. A pair of pygidial limbs occur for each segment of the pygidium and the posterior ones may show traces of a more primitive structure.

Caudal rami: Known only for *Neolenus*. Long, slender, many jointed, uniramous and attached to the ventral integument at the posterior end of the pygidium. The caudal rami are not considered to represent true limbs, although in *Neolenus* they are quite similar in appearance to the antennules and are attached to the ventral integument. They may represent the appendages of the anal segment.

Position of the Limbs

When I took up the question of the restoration of the ventral appendages of *Neolenus* I decided to study first the form and arrangement of the appendages of the Branchiopoda, and following that the Malacostraca, as I considered the trilobite to be a form intermediate in its development between the Branchiopoda and the lower Malacostraca, as represented by the Phyllocarida, Syncarida, and Mysidacea. The appendages of the trilobite genera *Triarthrus, Calymene, Ceraurus,* and *Isotelus* were then examined with a view of ascertaining if possible their form and arrangement when the animal was living. These studies and comparisons led me to the conclusion that the limbs of the trilobites had essentially a similar arrangement as those of the Branchiopoda, that the cephalic appendages were less specialized, and that the form of the protopodite was that of a flattened joint projecting inward and forward toward the median line and providing at its distal end support for the endopodite or jointed leg and a varying form of exopodite, and epipodites if present.

I then examined some large specimens of *Apus lucasanus* Packard in which, looking on the ventral surface, the protopodites of the thoracic limbs extend obliquely forward from each side towards the median line at an average angle of 30°, and present the narrow ventral surface of the protopodite and its anteriorly sloping surface which almost passes beneath the next anterior limb when viewed from above as the animal is lying on its back. This gives the effect of broad, closely arranged thoracic limbs when actually they are narrow and deep. I next gradually pressed a specimen out flat between strong glass plates, so that it was possible to see just what happened to it from the beginning of the application of the flattening process until it was completely flattened out. The result was that the protopodite and connecting joints of the limbs were seen to change from pointing forward with the narrow ventral edge uppermost to a position where they were directly transverse or pointing backward and with the flat side of the joints pushed over so as to lie on the plane of the dorsal shield, a position usually found in the limbs of the fossil trilobite.

This experiment was repeated many times with the same result. If we now consider that the larger number of trilobites which have been found with the appendages attached were lying on their backs and that the silt settled down directly on the appendages and as the weight increased the appendages were pressed down on the dorsal shield and flattened out very much in the same manner as *Apus* with the glass plates, it is extremely probable that the limbs were pressed out of position and often pushed out beyond the edges of the dorsal shield. I also submitted a number of small specimens of *Limulus polyphemus* to pressure between glass plates and found that the flat proximal joints of their cephalic legs assumed nearly the same position as the legs of the fossil trilobite and pointed more or less backward.

The position of the limbs in the fossil specimens is clearly indicated for *Neolenus* on plates 15, 17-19, where the protopodite and endopodite (leg) extend outward and backward from the median axis of the dorsal shield; the exopodites extend outward and forward, plates 21-23; the cephalic limbs extend outward and forward as in plate 16. Although pressed flat on the shale and more or less forced away from their original position in relation to their points of attachment to the ventral integument, the limbs are probably in a more natural position than those of *Isotelus* and *Triarthrus*.

The limbs of *Isotelus* (pl. 25) slope forward in such a manner as to indicate that the protopodites have all been forced over and swung around so as to point backward towards the central axis and forward and outward or almost the reverse of their position when living; the endopodites are nearer their probable normal position, but still slope too much forward.

The limbs of *Triarthrus* have the axis of their protopodites sloping inward and backward as in *Isotelus,* with the endopodite and exopodite extending forward in a natural position.

The conclusion drawn from the study of the limbs of the fossils and recent crustaceans is that the normal position of the protopodites of the trilobite was that indicated in the restorations of *Neolenus* (pl. 31), *Triarthrus* (pl. 32), *Calymene* (pl. 33), also that the flat protopodites and adjoining joints of the endopodite (leg) were vertical or nearly so to the plane of the ventral surface and dorsal shield, and when viewed from directly above when the animal was lying on its dorsal surface would show only the thin edge of the joints as shown in the restorations, plates 31-33. The deep or broad side of the limbs is seen only on a side view as shown by the transverse sections on plate 34. It is probable that Beecher was misled by the appearance of the appendages of *Triarthrus* in the fossil state in making his restoration of the ventral surface and appendages of *T. becki* as he represents the limbs from the proximal end of the protopodite to the distal joint of the endopodite as lying on their side, and also has the protopodite pointing obliquely backward.

Respiration of the trilobite.—Walcott assumed that the function of respiration in *Calymene* and *Ceraurus* was performed by the spiral exopodites and setiferous epipodites.[1] Beecher wrote of the probable respiratory apparatus of *Triarthrus* and *Trinucleus:*[2]

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 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.

Beecher quotes Gegenbaur as follows:[3]

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

If the flat, epipodite-like lobes illustrated in figure 19, plate 30, are what they appear to be they would have served as gills.

Neolenus has an elaborate respiratory system if we consider the exopodite and the epipodites (pl. 35, fig. 4) as gills. In this species the protopodite and endopodite of the limbs were so strong that it is not probable that the test covering them functioned in respiration.

There is no doubt of the presence in the trilobite of well-developed and specialized organs of respiration comparable with those of the Malacostraca, such as the Nebaliacea, Anaspidacea, and Mysidacea.

[1] Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, 1881, pp. 207, 208.

[2] American Jour. Sci., 4th ser., Vol. I, 1896, p. 255.

[3] Idem.

Restoration of ventral appendages.—The restorations of the ventral surface and appendages of *Neolenus, Triarthrus,* and *Calymene* are undertaken in order to present in graphic form these crustaceans as I conceive they appeared when living. It was with great hesitancy that the broad, short protopodite as I drew it in 1881 [1] was abandoned and the narrow, deep, elongate protopodite substituted. The limbs of *Neolenus,* however, clearly had a deep, narrow protopodite and a similar form evidently prevailed in the first three joints of the endopodite. A study of specimens of the limbs of *Triarthrus* led to the same result and with these two in mind the sections of the limbs of *Calymene* and *Ceraurus* were found to be capable of a similar interpretation as far as the protopodites and to a limited extent the proximal joints of the endopodite were concerned. Another line of supporting evidence is given by the tracks, trails, and burrows made by trilobites on and in the muds and sands of Cambrian time. The sharp, deep, clearly lined imprints (pls. 38-40) could only have been made by a strong limb with a narrow and deep protopodite and endopodite. With this form of limb in mind the restorations are made as though looking directly down on the ventral surface, so as to show the narrow side of the limbs and a little of their sides for *Neolenus,* plate 31, *Triarthrus,* plate 32, and *Calymene,* plate 33. The exopodites of the three species were quite unlike and they have been represented so as to give some conception of their form by turning them partially over on their side. Their position in the transverse sections (pl. 34) is more nearly natural than as they are represented on plates 31-33.

I have planned for twenty years to redraw my restoration of *Calymene* of 1881,[2] but it was not until the material representing *Neolenus* was studied that I felt that the restoration could be undertaken with a prospect of improving on the first attempt. After working out *Neolenus* and *Calymene* I studied Beecher's restoration of *Triarthrus* and a number of original specimens and made a sketch from which the restoration on plate 32 was drawn. Sketches of the transverse sections were also made with a view of obtaining side views of the limbs; a third sketch is a diagrammatic outline of the limb of each species with all known appendages attached to the protopodite so as to clearly distinguish them.

[1] Bull. Museum Comp. Zool., Harvard Coll., Vol. VIII, 1881, pl. VI, fig. 1.

[2] Idem, pl. VI, fig. 1. Smithsonian Misc. Coll., Vol. 57, 1912, p. 192.

The sketches were turned over to Mr. Clarence R. Shoemaker, of the U. S. National Museum, as the base for the drawings reproduced on plates 31-34, with the request that he would, from his knowledge of the appendages of the Crustacea, give the restorations as natural an appearance as possible.

The restorations may be of service to the student of recent and fossil crustacea and also serve as a stimulus to further research in order that with new material and a different point of view more satisfactory results may be obtained by the future student. The restorations of the thoracic limbs are so fundamental I will mention them more fully.

Restoration of thoracic limbs.—As far as known the thoracic limb of *Neolenus, Isotelus, Triarthrus, Ceraurus,* and *Calymene* has a large protopodite to which the leg (endopodite), exopodite, and when present the epipodite or epipodites are attached. This large protopodite is presumably formed of a basopodite and coxopodite so closely fused that the line of jointing has disappeared.

Neolenus.—Represented by *Neolenus serratus* (Rominger), from the Middle Cambrian. This is the most complex limb thus far known among the trilobites. It has (pl. 35, fig. 4) a true ambulatory leg (endopodite) attached to a large protopodite that served also as a gnathobase and as the base for a large setiferous exopodite and large and small lobe-shaped epipodites, and on the anterior series of limbs at least one or two small, flat endites. This limb is much like the anterior thoracic limb of *Anaspides tasmaniæ* (pl. 35, fig. 1) and has the same elements in it as the first thoracic limb of *Paranaspides* (pl. 35, fig. 3). The exopodite in the first thoracic limb of *Anaspides* is a simple unjointed rod, but on the second limb it is jointed, somewhat setiferous, and antennæ-like in the outer portion. The endites on the inner side of the coxopodite of the first thoracic limb serve as gnathobases, but they are not present on the posterior limbs. The flat, lobe-like epipodites are essentially similar in all the genera of the Anaspidacea. Their position is shown on plate 35.

Calymene (pl. 35, fig. 6).—Represented by *C. senaria* Conrad of the Trenton formation of the Ordovician. This limb is nearly as complex as that of *Neolenus* as it has an endopodite, exopodite, and an epipodite, but in its simple bispiral exopodite and small epipodite it does not appear to be as highly developed a limb.

Ceraurus (pl. 35, fig. 7).—Represented by *Ceraurus pleurexanthemus* Green of the Ordovician. As far as known the limb of this species is essentially similar to that of *Calymene*.

Triarthrus (pl. 35, fig. 5).—Represented by *Triarthrus becki* Green of the Utica shale of the Ordovician. The anterior thoracic limbs of *Triarthrus* have the elements of the limb of *Neolenus, Calymene,* and *Ceraurus,* and may be compared with them except as to the details of the exopodite and epipodite. The more posterior limbs show flattened and transversely elongate joints (pl. 34, figs. 6 and 7) which Beecher compares with the large endites of the phyllopodan limb. In the restorations, plate 32, I have given the limb from beneath the pygidium nearly the same form as the thoracic limb, basing it on the specimens available for study in the collections of the National Museum. The transverse phyllopodan-like joints of the exopodite of the limbs of the posterior portions of the animal beneath the pygidium are not represented in the diagrammatic sections (See pl. 29, figs. 4, 5, 8, 11).

The longitudinal restorations of the thoracic limbs (pl. 35) were drawn in order to clearly indicate the various elements entering into the structure of the limb. These should be compared with the side views of the limbs in the transverse sections (pl. 34) and those of the restorations of the ventral side of *Neolenus, Triarthrus,* and *Calymene* (pls. 31-33).

Comparison with crustaceans.—Early authors (1750-1843) compared the dorsal shield of the trilobite with various crustaceans, especially *Apus* and *Limulus,*[1] and when traces of appendages began to be discovered these comparisons were continued[2] (1870-1881). Bernard, as the result of a very comprehensive study, felt confident that the trilobites may take a firm place at the root of the crustacean system with the existing *Apus* as their nearest ally.[3]

He concluded[4] that—

> *Apus,* on account of its richer segmentation, the absence of pleurae on the trunk-segments, and its more membraneoüs parapodia-like limbs, must be assumed to lie in the direct line upwards from the original annelidian ancestor toward the modern crustacea. The trilobites then must have branched off laterally from this line either once or more than once, in times anterior to the primitive *Apus,* as forms specialized for creeping under the protection of a hard imbricated carapace.

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[1] See Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, 1881, pp. 193-195.

[2] Idem, pp. 195-197.

[3] Nature, Vol. 48, 1893, p. 582. Quart. Jour. Geol. Soc. London, Vol. 50, 1894, pp. 411-432, and Vol. 51, 1895, pp. 352-359.

[4] The Systematic Position of the Trilobites, Idem, 1894, Pt. I, pp. 429-430.

In 1895, with the new evidence afforded by the trilobite *Triarthrus becki,* he concluded[1] that—

> The trilobites, therefore (as exemplified by *Triarthrus*), in spite of their extremely primitive mouth-formula, do not stand in the direct line of descent of the Crustacea, but are lateral offshoots, specialized for a creeping manner of life.

The discovery of the limbs of *Triarthrus* led Walcott to abandon the view (held in 1881) that the trilobite was closely allied to *Limulus*[2] in favor of its being a crustacean that was neither a "true Entomostracan or Malacostracan nor was it a lineal descendant from either, but was probably a descendant from a common ancestral type"[3] of all three.

Two general facts led me in 1894 to think that the modern crustacean is descendant from the Phyllopod branch of the Branchiopoda and the Trilobita from a distinct branch.[4] 1st. The Trilobita branch exhausted its vital energy in Paleozoic time and disappeared. 2d. The Phyllopod branch developed slowly until after the Trilobita passed its maximum and then began its great differentiation that in its descendants approaches culmination in recent times.

When the trilobite and phyllopod diverged from their common crustacean ancestor, the trilobite began 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 Paleozoic strata. With this great differentiation the initial vital energy was exhausted and the Trilobita disappeared at the close of Paleozoic time without leaving direct descendants.

The Branchiopoda, including the Ostracoda, Copepoda, and Cirripedia developed steadily during Paleozoic and subsequent geologic time until to-day their descendants form the subclasses Branchiopoda and Malacostraca, each of which is equivalent to the subclass Trilobita of Paleozoic time. Springing from a common crustacean base the three groups have many features in common, and in details of structure of the limbs many striking resemblances occur. It does not impress me that trilobites were true Branchiopodans 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

[1] Quart. Jour. Geol. Soc. London, Vol. 51, 1895, Pt. 2, p. 356.

[2] Bull. Mus. Comp. Zool., Harvard Coll., Vol. VIII, 1881, pp. 209-211.

[3] Proc. Biol. Soc. Washington, Vol. IX, 1894, p. 94.

[4] This view is only confirmatory of the result of the profound study of the Apodidæ by Bernard (The Apodidæ, Nature Series, 1892).

pre-Cambrian time that lived in the pelagic fauna in which all the earlier types of life were probably developed[1] and from which, as time passed on, additions were made to the paleontologic record of the geologic series of formations. We know that Phyllopods, Ostracods and Trilobites were clearly differentiated in lower Cambrian time.

Beecher compared the trilobite with the phyllopods and concludes that points of likeness may be established with almost every order of Crustacea, showing chiefly the relationship between the trilobite and the ancestors of modern Crustacea.[2] He has well summed up the evidence in favor of the trilobites being considered true crustaceans rather than allied with the Arachnids.[3] Also in his classical memoir on the " Natural Classification of the Trilobites " he states the claim of the trilobite to a position as a subclass of the Crustacea equivalent to the subclass Entomostraca and the third subclass Malacostraca. He concludes:[4]

> In nearly every particular the trilobite is very primitive, and closely agrees with the theoretical crustacean ancestor. Its affinities are with both the other subclasses, especially their lower orders, but its position is not intermediate.

I have neither the time nor space in which to review further the literature on the trilobites. It is too voluminous; the student will find the list of works given in the Zittel-Eastman Text-book of Paleontology, 1913, Vol. I, pp. 692-694, to be very helpful, and there is also there a valuable discussion of the trilobite by Beecher as revised by Raymond.

In connection with the study of *Neolenus* I have had occasion to compare the general arrangement of trilobite limbs with those of the order Notostraca (*Apus,* etc.) and to compare its limbs with those of the Malacostracan order Anaspidacea.

Apus.—The trilobite is clearly not a Branchiopod. Beecher considered that the supposed phyllopod-like legs (endopodites) beneath the pygidium of *Triarthrus* brought the trilobites close to *Apus,* but if my view is correct, that the endopodites are normal beneath the pygidium and that it is the exopodite that has the primitive lobe-like

[1] 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.

[2] American Geol., Vol. XV, 1895, p. 99.

[3] Text-Book of Palaeontology, Zittel-Eastman, 1900, p. 622.

[4] American Jour. Sci., 4th ser., Vol. III, 1897, p. 93.

joints, the relation to *Apus* is weakened as the exopodite is very much more variable in the trilobite than the endopodite.

The more simple oral appendages of the trilobite compared with those of *Apus* (Branchiopoda), which has reduced and considerably specialized mouth parts, indicates that they are more primitive than those of *Apus,* but the highly developed thoracic limbs of the trilobite and its dorsal shield point to *Apus* as somewhat nearer the primitive crustacean type.

The typical trunk limb of the branchiopod includes the primary elements of the limb of the trilobite, but while the trilobite limb undoubtedly passed through the branchiopod stage it was long before Cambrian time and before the life of the oldest trilobite we now know. Beecher thought that he had found evidence of a branchiopod limb in the limbs beneath the pygidium in *Triarthrus,* but as mentioned above the evidence for this view may be otherwise interpreted. The series of setiferous lobes on the proximal joint (protopodite) of the limbs of *Apus,* extending inward toward the median line of the ventral surface of the body and which function as gnathobases, is represented in the trilobite by the long protopodite of the limbs with its setiferous proximal end and ventral margin.

Marrella.—With the Middle Cambrian *Marrella splendens* Walcott[1] the trilobite has several characters in common. These include (*a*) sessile eyes, (*b*) a large hypostoma with the proximal joints of the cephalic limbs assembled at its posterior end or beneath it, (*c*) a pair of biramose limbs for each trunk segment, and (*d*) expansion of the joints of the posterior thoracic legs (endopodites).

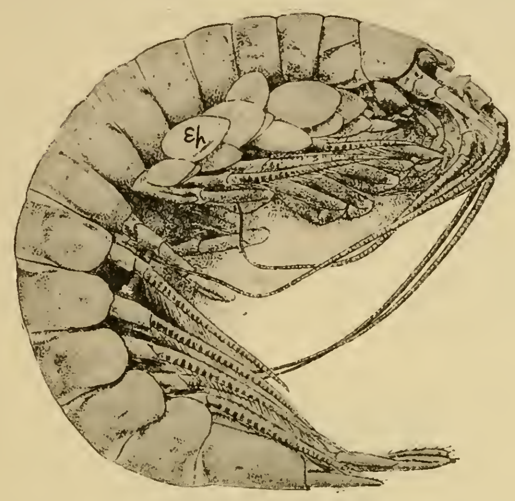
Its more specialized mouth parts, and absence of gnathobases on the thoracic limbs, indicate less primitive characters, while its carapace and an almost total absence of an abdominal section or pygidium points to it as a primitive form possibly ranking in development between *Apus* and the trilobite.

Anaspidacea.—The most striking instance of similarity of the thoracic limbs of a trilobite and those of a recent crustacean is that of the thoracic limbs of *Neolenus* which strongly suggest those of the Malacostracan genus *Anaspides,*[1] a crustacean of the order Syncarida, found in a fresh-water pool in Tasmania, New Zealand. The resemblance is shown by the presence in both of a strong ambulatory jointed leg (endopodite), a jointed setiferous exopodite, and two

[1] Smithsonian Misc. Coll., Vol. 57, 1910, p. 193, pls. 25, 26.

[1] On the genus *Anaspides,* W. T. Calman, Trans. Royal Soc. Edinburgh, Vol. 38, Pt. 4, 1896, p. 791, pl. 2, fig. 12.

jointed flabelliform epipodites attached to the proximal joints (coxopodite and basopodite) of the limb. Whether or not the plate-like lobes shown beside the median lobe of the dorsal shield in figures 3 and 4, plate 20, of *Neolenus* can be compared with the internal lobes



ANASPIDES TASMANIÆ G. M. Thomson

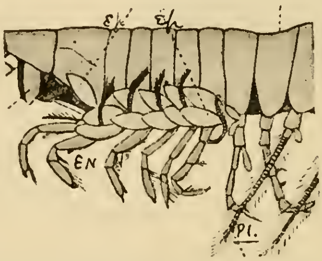
FIG. 1 (× 3.5).—Side view of male illustrated here to show thoracic legs with exopodites and epipodial lamellæ. This species is without dorsal shield. (After Calman, Trans. Royal Soc. Edinburgh, Vol. XXXVIII, pt. iv, 1896, pl. 1, fig. 1.)

KOONUNGA CURSOR Sayce

FIG. 2 (× 37).—Anterior part of the animal, showing character of first thoracic limb with its leg (endopodite), exopodite (*ex*), and epipodites (*ep*). (After Sayce, Trans. Linnean Soc. London, 2d ser., Zool., Vol. XI, pt. 1, 1908, pl. 1. fig. 3.)

of the coxa of the maxilliped of *Anaspides*[1] is not readily determined, but it is very suggestive and not improbable (pl. 35, figs. 1-3). The exopodite of the thoracic limb of *Anaspides* (text fig. 1) recalls in its jointed structure the exopodite of *Triarthrus,* but the exopodite of *Koonunga* (text fig. 2), although jointed is quite unlike it, and the exopodite of *Paranaspides* (text fig. 3) is slender, closely jointed and setiferous, and much like that of *Anaspides.*

Another form closely allied to *Anaspides* is *Koonunga* Sayce.[2] It differs from *Anaspides* in having a sessile eye as in all trilobites with eyes, in details of several of the appendages, the mouth parts, and in having the anterior thoracic segment fused to the cephalon. The thoracic leg is essentially the same as that of *Anaspides* (pl. 35, fig. 2). Mr. Sayce considers *Koonunga* the most primitive Edriophthalmatan known.



PARANASPIDES LACUSTRIS Smith
FIG. 3 (× 4).—Thoracic limbs with leg, epipodites and exopodite. (After Smith.)

The first thoracic limb of *Paranaspides* Smith[3] has a jointed leg (endopodite), a simple unjointed exopodite, two epipodites, and two simple flat lobes (exites) attached to the coxopodite (See pl. 35, fig. 3). The latter are of interest to us as they correspond in form and probably position to the flat, plate-like lobes (exites) found in connection with the thoracic limb of *Neolenus.* A feature to be considered is that these flat lobes occur only on the anterior or first thoracic pair of legs in the *Anaspides* while they are known to be

[1] On the genus *Anaspides,* W. T. Calman, Trans. Royal Soc. Edinburgh, Vol. 38, Pt. 4, 1896, p. 791, pl. 2, fig. 12.

[2] Trans. Linnean Soc. London, 2d ser., Zool., Vol. 11, Pt. 1, 1908, pp. 1-16, pls. 1, 2.

[3] Proc. Royal Soc. London, Ser. B, Vol. 80, 1908, p. 470, text fig. No. 6, p. 171.

present in a position to indicate that they were associated with several of the anterior thoracic legs of *Neolenus*.

The thoracic limbs of the trilobite differ from those of the Anaspidacea by having the coxopodite and basopodite of the latter fused in a strong protopodite, but it is quite evident that the latter have characters in their thoracic limbs that were present in the trilobite. In other respects the species of the Anaspidacea are quite unlike the trilobite as now known to us.

Nebaliacea.—The thoracic limb of *Nebalia* with its jointed leg-like endopodite, lobe-like exopodite and epipodite is much like that of *Neolenus* except in the development of the basopodite. In its more specialized cephalic limbs and separation of the thoracic limbs into two distinct tagmata of eight pairs of thoracic limbs and the abdominal section of seven somites, *Nebalia* is less primitive than the trilobite.

Cyamus.—An examination of the spiral branchiæ of the parasitic crustacean *Cyamus scammoni* Dall shows them to be formed of a slender, strong, tapering tube that may be a complete spiral as shown by figure 9, plate 28, or it may be straightened out near the base and irregularly coiled towards the distal end. If the spiral of an alcoholic specimen is bent over or pulled out of shape without breaking, it at once springs back to its original form when released. The spirals of *Cyamus* are apparently attached to the ventral surface directly, but not on the same segment with the jointed leg. As *Cyamus* is a highly modified parasitic crustacean it is probable (as suggested by Mr. C. R. Shoemaker) that the coxopodite of the leg that has been lost in the changes incident to a parasitic life has become fused with the segment and thus the spiral branchiæ have become apparently attached to the ventral surface of the segment. They are attached at the same point of the pleural part of the segment as the legs on the adjoining segments. The spiral branchiæ are introduced as they serve to explain the spirals of the exopodites of *Calymene* and *Ceraurus,* also as an illustration of the survival of an unusual character of the trilobite or a recurrence of the same form in a modern crustacean.

Conclusion.—Many further comparisons of parts might be made with other modern crustaceans (*e. g.,* the Mysidacea, Euphausiacea, some of the " Schizopods "), but they would only go to prove that the trilobite is a primitive crustacean far back on the line of descent from the original crustacean type which existed in pre-Cambrian or Lipalian time.[1]

Tracks of Trilobites

When writing of the tracks occurring on the Upper Cambrian Potsdam sandstone of Canada and New York in 1912, I said:[2]

> If we picture in our imagination a trilobite with a series of twelve pairs of legs posterior to the cephalon (figs. 1 and 2), and five pairs of cephalic legs, walking on the smooth or rippled surface of fine wet sand exposed at low tide, I think we can readily explain the *Protichnites* tracks on the Potsdam sandstone. Such a series of feet would make varied and complex series of tracks that would differ in depth, definition and details of grouping with the varying degree of consistency and hardness of the surface over which the animal was traveling and its method of moving. I have fine trilobite trails made on the surface of sandy mud that show the imprint of a considerable portion of the legs. On a hard surface the animal touched only the extremities of the legs, but on a muddy surface the terminal joint would sink in and other joints would leave an impression.
>
> The trifid imprint resulted from the impress of the end of the terminal joint of the trilobite's leg with its three movable spines.[2]

Some of the tracks referred to above are illustrated on plate 42, and on plates 37, 38, 41, a series of trilobite tracks and trails from the Middle Cambrian sandstones of the Grand Canyon of the Colorado River. The latter show the impression of the distal joints and some the entire length of the leg as the surface in places was less resistant and the leg sank deeper into it. The series of tracks and burrows also clearly indicate that the trilobite was the animal that made the trails, burrows, and wallows that gave rise to the casts that have been largely described by authors under the generic term *Cruziana* d'Orbigny.[3]

The size and depth of the trails left by the trilobite prove that their legs were long, strong, and attached to a large protopodite. When the animal was pushing its way through a soft surface of sand or fine muddy sediment in search of food (Annelids, etc.), the legs appear to have bunched together in groups of two, three or more, and slowly crowded the animal forward (pl. 38, figs. 3, 4; pl. 39, pl. 40). That it was annelids the trilobite was seeking is indicated by the presence in the sandstone or shale of large numbers of annelid borings and casts of trails, some of which follow along the furrow made by the

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[1] Smithsonian Misc. Coll., Vol. 57, 1910, p. 14 (footnote).

[2] Idem, 1912, No. 9, p. 278.

[3] See Delgado for description and illustrations. Estudo Sobre os Bilobites de Portugal, Acad. Sci. Lisbon, 4to, 1886.

trilobite (pl. 37, fig. 3), while others are beneath it or cross at various angles. One of the small slabs of annelid trails and casts of borings is illustrated on plate 42, and there is a large series of them in the collections of the United States National Museum.

I will not give a detailed description of the tracks and trails as the illustrations tell the story of the almost endless variation caused by the varying conditions under which they were made. We know something now of the variation in size, form, and length of trilobites' limbs, and it is evident from the tracks and trails that there were many other variations of which nothing is known. When experimenting with the common rock crab of the New England coast, I found that by causing the same crab to creep, run, or wallow on and in sediments of varying material, hardness, and consistency, many kinds of tracks and trails could be produced, and the same was true with the common "Horse Shoe" crab (*Limulus*) of the Florida shore. If we had a living crustacean with the same type of protopodite, endopodite and exopodites, and dorsal shield that the trilobite has, it would be quite possible to largely reproduce the trails and tracks illustrated on plates 37-42.

Just how the trilobite used its numerous limbs when pushing through the mud or sand it is difficult to imagine. The motion must have been very slow and probably there was a general irregularity of movement of the limbs when the more complicated trails were made. This is indicated by figure 6, plate 37; figure 3, plate 38; figures 1-4, plate 39; figures 1-5, plate 40. Such trails as that of figure 2, plate 41, are less complicated than the trail represented by figure 1, plate 39. There is no animal known from the rocks on which the tracks and trails occur but the trilobite that could have made them.

The trilobites that may have made the trails on the sands and muds of Middle Cambrian time include species of the genera *Agnostus, Eodiscus, Ptychoparia, Dolichometopus, Bathyuriscus, Asaphiscus, Neolenus,* etc. These give a wide variation in size, and undoubtedly in ventral appendages and the same is true of the trilobites of the Lower and Upper Cambrian, Ordovician, Silurian, and Devonian time. Some future student of the trails and tracks found on Paleozoic rocks should make great collections and also conduct many experiments with recent crustaceans in the making of trails and tracks under all possible conditions. Most interesting results will be secured by a careful, patient, thorough worker.

General Summary

At the risk of repetition of statements made in this paper and by authors I will give a brief summary of the structure of the trilobite that may possibly be of service to the teacher, and student, of recent and fossil crustacea.

Dorsal shield.—All known trilobites had a more or less chitinous shield or carapace which was thick and strong in the Illænidæ, etc., or thin and delicate in the Mesonacidæ, *Olenellus,* etc. As yet no forms have been found that were without a complete dorsal shield, but it is probable that such existed in pre-Cambrian time when the trilobite was diverging from its primitive crustacean ancestor. Naked phyllopod crustaceans lived in Middle Cambrian time and left their record on the Burgess shale,[1] so it is possible that such can be preserved. One trilobitic-like form, *Nathorstia,*[2] had a very delicate dorsal shield, and possibly others existed in earlier Cambrian time that will add to the story of the evolution of the carapace and structure of the ventral surface and appendages.

The subclass Trilobita may be defined, after Raymond in Zittel's Text-book,[3] modified to meet data afforded by *Neolenus,* as follows:

Marine Crustacea, with a variable number of metameres (segments); body covered with a hard dorsal shield or crust, longitudinally trilobate into the defined axis and pleura; cephalon, thorax and abdomen distinct. Cephalon covered with a shield composed of a primitively pentamerous middle piece, the cranidium, and two side pieces, or free cheeks, which may be separate or united in front, and carry the compound sessile eyes when present; cephalic appendages pediform, consisting of five pairs of limbs, all biramous, and functioning as ambulatory and oral organs, except the simple antennules, which are purely sensory. Upper lip forming a well-developed hypostoma; under lip (epistoma) present. Segments of the thorax movable upon one another, varying in number from two to twenty-nine. Abdominal segments variable in number, and fused to form a caudal shield. Ventral integument a thin uncalcified membrane, divided into pleurosternites and mesosternites connected segmentally by an interarticulate membrane. Mesosternites usually with five longitudinal ridges, a median one with two oblique extending obliquely forward on each side (the spaces thus formed indicate attachment of ventral muscles). All segments, thoracic and abdominal, carry a pair of jointed biramous limbs. All limbs have their proximal elements forming gnathobases, which become organs of manducation on the head. Respiration integumental and by bran-

[1] Smithsonian Misc. Coll., Vol. 57, 1912, pp. 157-170, pl. 27, fig. 6; pl. 28, fig. 1. *Opabinia.*

[2] Idem, pp. 194-195, pl. 28, fig. 2.

[3] Zittel-Eastman, Paleontology, 1913, Revised by Raymond, pp. 692-694.

chial fringes on the exopodites, epipodites, and exites. Development proceeding from a protonauplius form, the protaspis, by the progressive addition of segments at successive moults.

Intestinal canal.—Of the internal organs only the intestinal canal is known. This, starting at the mouth, curves upward, and extends beneath the median lobe of the dorsal shield the entire length of the body, terminating at the anal opening beneath the last segment of the pygidium. There were probably hepatic cæca opening into the anterior end, but as yet none have been seen, although they are present in the Branchiopod genus *Burgessia,* which is associated with *Neolenus* in the Burgess shale.[1]

The appendages may be summarized as follows:

Cephalic:

1. *Antennules.*—Uniramose, slender, many jointed, and attached to the ventral integument of the cephalon about midway of the glabella.
2. *Antennæ.*—Represented by the anterior pair of cephalic limbs which are posterior to the opening of the mouth.
3. *Mandibles.*—Represented by the second pair of cephalic limbs.
4. *Maxillula.*—Represented by the third pair of cephalic limbs.
5. *Maxilla.*—Represented by the fourth pair of cephalic limbs.

Thoracic: A pair of biramous limbs to each segment or somite of the thorax, each limb consisting of a fused coxopodite and basopodite forming a protopodite; an attached six-jointed endopodite or leg with terminal spines, one of which is usually in the form of a slightly curved claw; an exopodite that may or may not be jointed and which is attached to the distal end of the protopodite; one or more flabelliform epipodites attached to the distal part of the endopodite and in one instance (*Neolenus*) one or more exites (attached to the anterior side of the endopodite?).

Abdominal: No abdominal appendages are differentiated from those of the thorax by their structure. Those referred to as such are the limbs beneath the pygidium which are similar in structure to those beneath the thorax. A pair of pygidial limbs occur for each segment of the pygidium and the posterior ones may show traces of a more primitive structure.

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[1] Smithsonian Misc. Coll., Vol. 57, 1912, pp. 177-180, pl. 27, figs. 1-3; pl. 30, figs. 3, 4.

Caudal rami: Known only for *Neolenus.* Long, slender, many jointed, uniramous and attached to the ventral integument at the posterior end of the pygidium. The caudal rami are not considered to represent true limbs, although in *Neolenus* they are quite similar in appearance and seem to be attached to the ventral integument as though they represented the appendages of the anal segment.

Manner of life.—The trilobite was a marine crustacean that lived in shallow seas, bays, sounds and inlets, and sometimes deeper waters. In its younger stages of growth a free moving and swimming animal, it later became a half-burrowing, crawling, and sometimes swimming animal and moving at times with the flow of the tides and prevailing currents. Much of its life must have been spent searching for food in the mud and silt after its younger free swimming days had passed.

Its spawning habit was presumably much like that of *Limulus.* Eggs have been found both within and free from the body, and a younger stage of growth (protonauplius) occurs in the fossil state. It was at home on many kinds of sea-bottom and was able to accommodate itself to muddy as well as clear water.

It was intensely gregarious in some localities and widely scattered in others, depending upon local conditions, and habits of the various species.

Respiration.—Trilobites had an ample system of respiration by setiferous exopodites, epipodites, and exites attached to the cephalic, thoracic, and abdominal limbs. These may be seen in the restoration of the limbs on plates 34 and 35.

Food.—The structure of the gnathobases of the cephalic limbs indicates soft food such as worms, minute animal life, and decomposed algæ.

Persistence in time.—Without means of offence, and of defense only by covering itself closely by its dorsal shield or hiding in the mud, the trilobite persisted from far back in pre-Cambrian time to the close of Carboniferous time. This was owing largely to its being able to adapt itself to a varied and changing environment, and to its great reproductive powers. Its eggs must have been brought forth in immense numbers and in favorable localities for development.

Extinction.—The trilobite slowly developed in pre-Cambrian time, reached its maximum in the Cambrian period, and continued on in full tide until well into Ordovician time when the sea bottoms became crowded with a large and varied fauna, and numerous enemies, some small and insidious, parasitic in nature, others large and powerful, appeared, together with various types which, while not physically antagonistic, were economically so in being better adapted to live in the same manner under the same conditions. It kept up the struggle but, already an ancient type, it had lost its juvenile race plasticity and ability to modify itself to meet the new conditions, and it was therefore unable to adapt itself to its new environment. Never having penetrated into fresh or other non-marine waters, or into the deep sea, those havens of refuge where the relics of many ancient types may still be found, the trilobite, unable to cope with the new world in which it found itself, was consumed as food by its new enemies, both internal and external, and at the same time subjected to overwhelming competition, so that the individuals died off more rapidly than they could reproduce, and the race disappeared with the close of Paleozoic time. It persisted for many million years and left its remains more or less abundantly through about 75,000 feet of stratified rocks.

DESCRIPTION OF PLATE 14

PAGE

Neolenus serratus (Rominger) 126

FIG. 1. (× 1.5.) A nearly perfect dorsal shield flattened in the shale. It has one antennule, two caudal rami and a few legs (endopodites) extending out from beneath it. The glabella of the cephalon is crushed in as it is in all but one specimen of the species I have seen. The median spine on each segment of the thorax and pygidium is broken off close to its base, and usually the base and a piece of the test are broken off with it. U. S. National Museum, Catalogue No. 65510.

The specimens illustrating *Neolenus serratus* (pls. 14-23) are from locality **35k**, Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

Kootenia dawsoni Walcott 131

FIG. 2. (× 2.) A somewhat broken and crushed dorsal shield that illustrates the general character of the species. U. S. National Museum, Catalogue No. 65511.

3. (× 2.) Right side of a crushed and exfoliated dorsal shield with portions of the thoracic legs (endopodites) and exopodites fringed with long setæ. U. S. National Museum, Catalogue No. 65512.

This is the only specimen known to me of this species that shows remains of the ventral appendages.

The specimens represented by figs. 2 and 3 are from locality **35k**, as given above.

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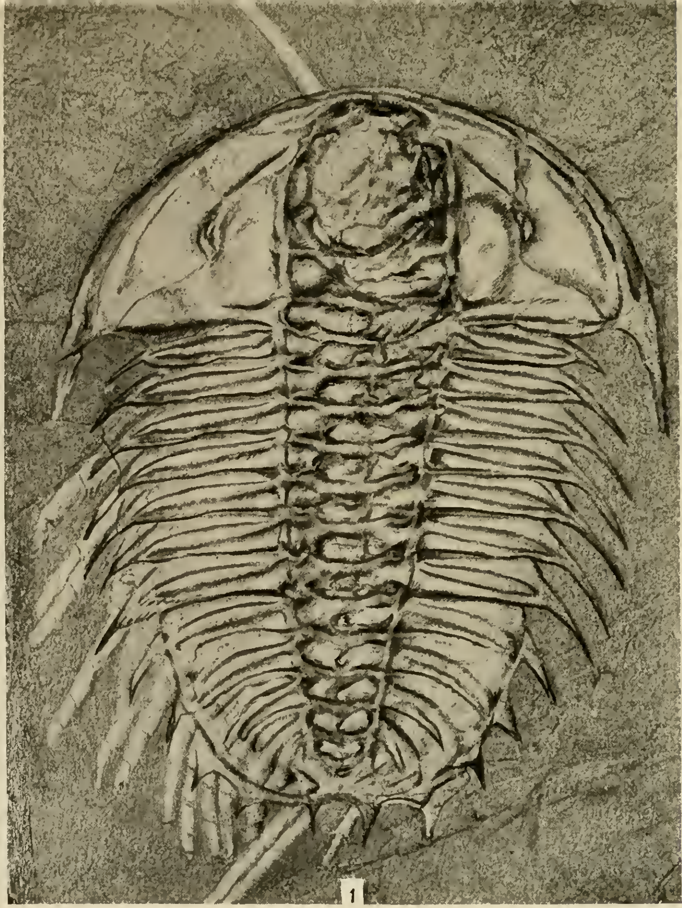

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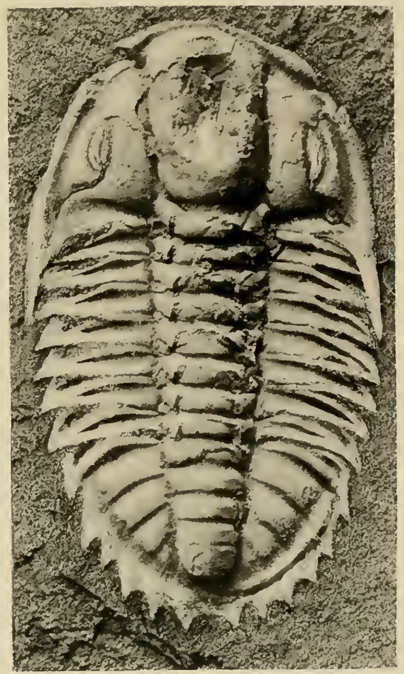

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NEOLENUS AND KOOTENIA

NEOLENUS SERRATUS (Rominger)

DESCRIPTION OF PLATE 15

PAGE

Neolenus serratus (Rominger) 126

FIG. 1. (Natural size.) Photograph of a large, partially exfoliated dorsal shield with the antennules projecting from beneath the cephalon, the caudal rami slightly pushed backward from their normal position, and a fine series of the thoracic and abdominal legs (endopodites). Some of the legs preserve the large proximal joint (protopodite). The posterior portion of this specimen is illustrated by an enlarged figure on pl. 17, fig. 3.

The matrix at the top of the plate preserves the impression of 15 endopodites of the same character as those with the dorsal shield. The photograph of this was reproduced by me in 1912 (Smithsonian Misc. Coll., Vol. 57, pl. 45, fig. 1).

U. S. National Museum, Catalogue No. 58588.

The specimens illustrating *Neolenus serratus* are from locality **35k**, Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

DESCRIPTION OF PLATE 16

PAGE

Neolenus serratus (Rominger).. 126

Fig. 1. (× 2.) Cephalic legs (endopodites) with one plate-like exopodite that probably was attached to the protopodite of the fourth cephalic leg. The protopodite of the third leg has numerous short spines on its inner margin that indicate that it served as a gnathobase. U. S. National Museum, Catalogue No. 65513.

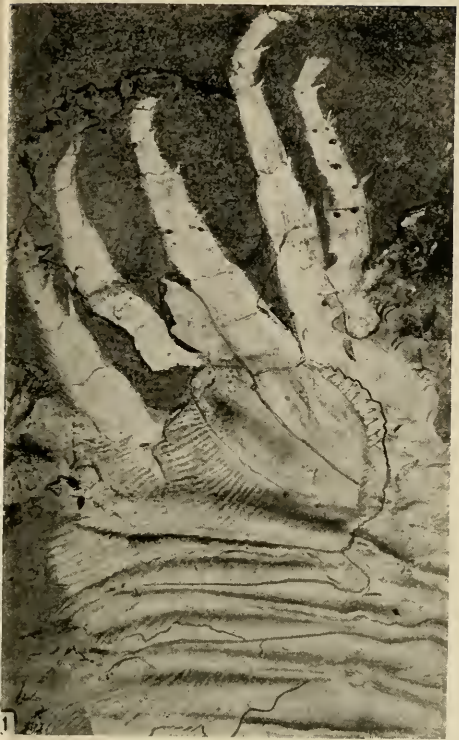
2. (× 2.) The matrix of the specimen represented by fig. 1. Fragments of the legs, etc., have exfoliated, so that the details of the specimen and the matrix differ, and a portion of the test of the dorsal shield is also shown on the right, lower side. The exopodite of fig. 2 is not shown at all on fig. 1, as its impression was removed in clearing the film of shale over the protopodite of the third cephalic leg. U. S. National Museum, Catalogue No. 58590.

This specimen was illustrated in 1912 (Smithsonian Misc. Coll., Vol. 57, pl. 45, fig. 3).

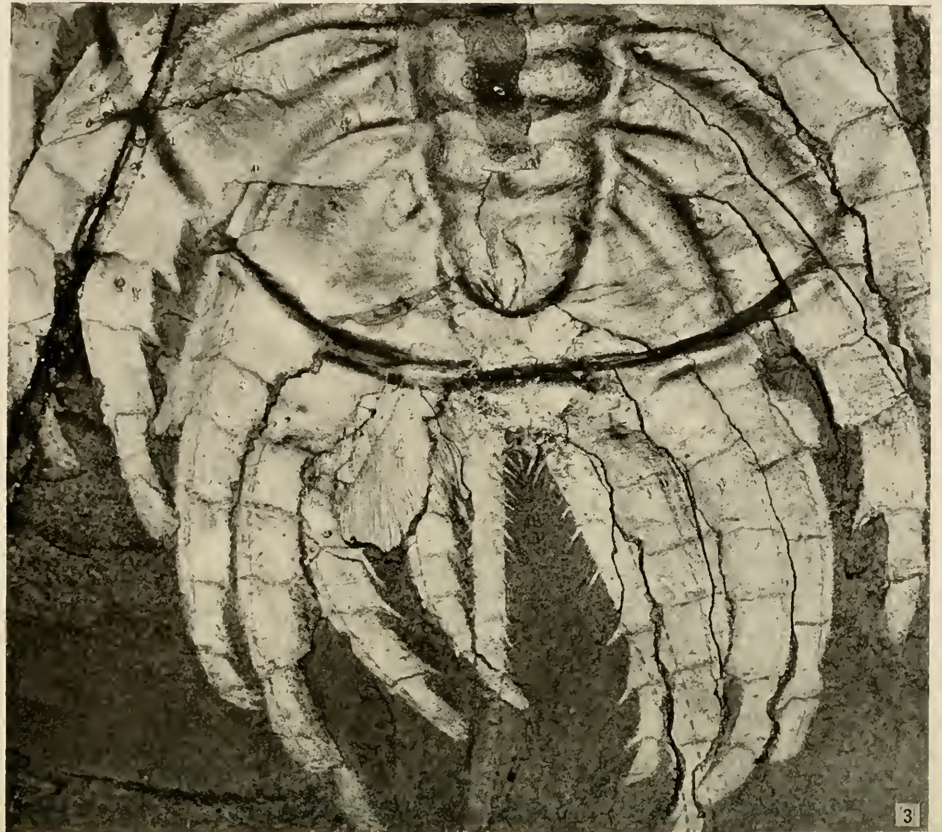
3. (× 2.) Anterior portion of a dorsal shield with an antennule and cephalic legs (endopodites). The distal joints of the legs show the terminal claw and two strong, short spines. Faint traces of the long setæ attached to an exopodite are shown near the right eye and also beside the right pleuræ of the thorax. U. S. National Museum, Catalogue No. 58591.

The right side of this figure was published in 1912 (Smithsonian Misc. Coll., Vol. 57, pl. 45, fig. 4).

The specimens illustrating *Neolenus serratus* are from locality **35k**, Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.



Cephalic appendages of
NEOLENUS SERRATUS (Rominger)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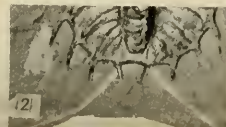
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DESCRIPTION OF PLATE 17

PAGE

Neolenus serratus (Rominger) 126

FIG. 1. (Natural size.) A partly exfoliated specimen, showing (*a*) an antennule, numerous thoracic legs (*thl*), and jointed caudal rami (*cr*). The caudal rami have been dragged backward, pulling with them a portion of the under edge of the ventral lining of the body cavity. U. S. National Museum, Catalogue No. 57656.

2. (Natural size.) Pygidium with the caudal rami extending out from beneath it in their probable natural position. U. S. National Museum, Catalogue No. 57657.

The above described figures were published in 1912 (Smithsonian Misc. Coll., Vol. 57, pl. 24, figs. 1, 1*a*).

3. (× 3.) Enlargement of the posterior portion of the dorsal shield and appendages illustrated by fig. 1, pl. 15. U. S. National Museum, Catalogue No. 58588.

The basal joints (protopodites) of the limbs are not well defined as they have been so flattened and crushed against the inside of the dorsal shield that they have the relief of the fused segments of the pygidium. Between the caudal rami there are two elongate oval spots that probably represent the anal opening which was forced out of shape and divided by pressure when the animal was buried in the fine sediment. It looks as though the limbs and caudal rami had been forced out from beneath the pygidium.

This figure was first published in 1913 (Text-book of Pal., Eastman ed. of Zittel, Vol. I, fig. 1376, p. 716).

The specimens illustrating *Neolenus serratus* are from locality **35k**, Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

DESCRIPTION OF PLATE 18

PAGE

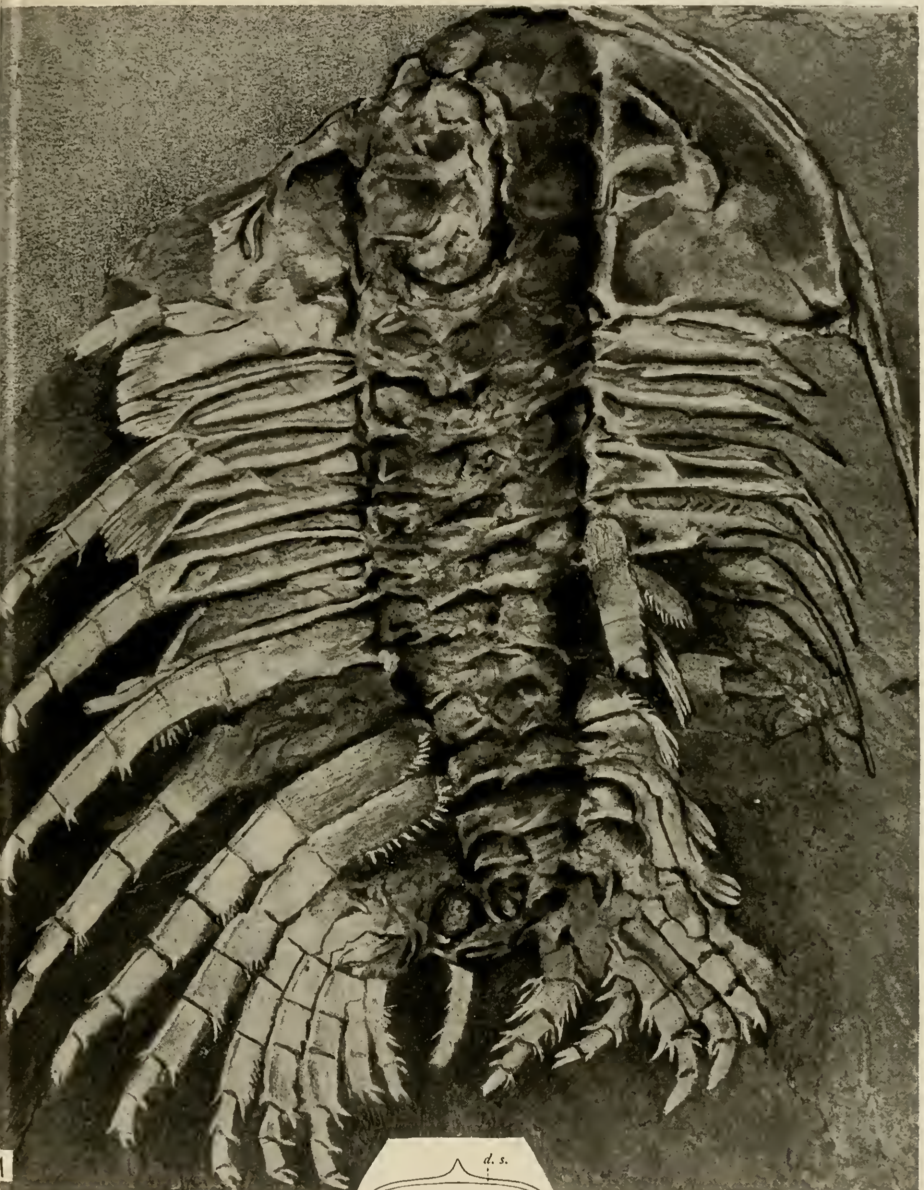
Neolenus serratus (Rominger) (See pl. 20, fig. 1) 126

FIG. 1. (× 2.) Enlargement of the specimen illustrated by fig. 1, pl. 20. The two anterior legs on the left side and details of the legs showing the protopodite were worked out of the shale after the photograph reproduced on plate 20 was taken. On the right side back of the fourth thoracic segment, a small lobe (epipodite) is seen with its proximal portion resting against the protopodite of a thoracic leg. On the left side long setæ of the exopodites appear from beneath the lateral margin of the thoracic pleura. A portion of the caudal rami projects from beneath the pygidium. The joint lines of the legs have been darkened and the spines on the protopodites lightened so as to bring them out in stronger relief. See description of this specimen on pl. 20, fig. 1, for catalogue number.

The specimens illustrating *Neolenus serratus* are from locality **35k**, Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

2. Diagrammatic transverse section at about the fourth thoracic segment. This is based on the restoration illustrated on plate 31. The lettering is as follows:

d. s. = dorsal shield.	exi. = exite.
en. = endopodite.	int. = intestinal canal.
ep. = epipodite.	pr. = protopodite.
ex. = exopodite.	v. i. = ventral integument.



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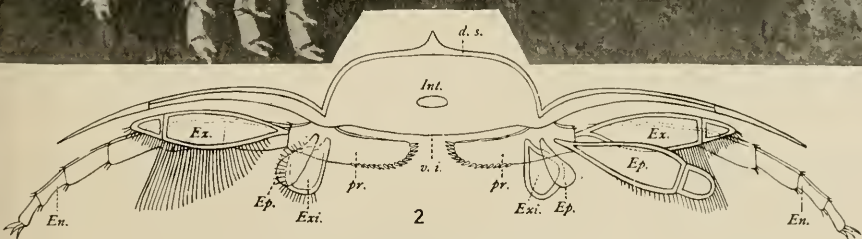

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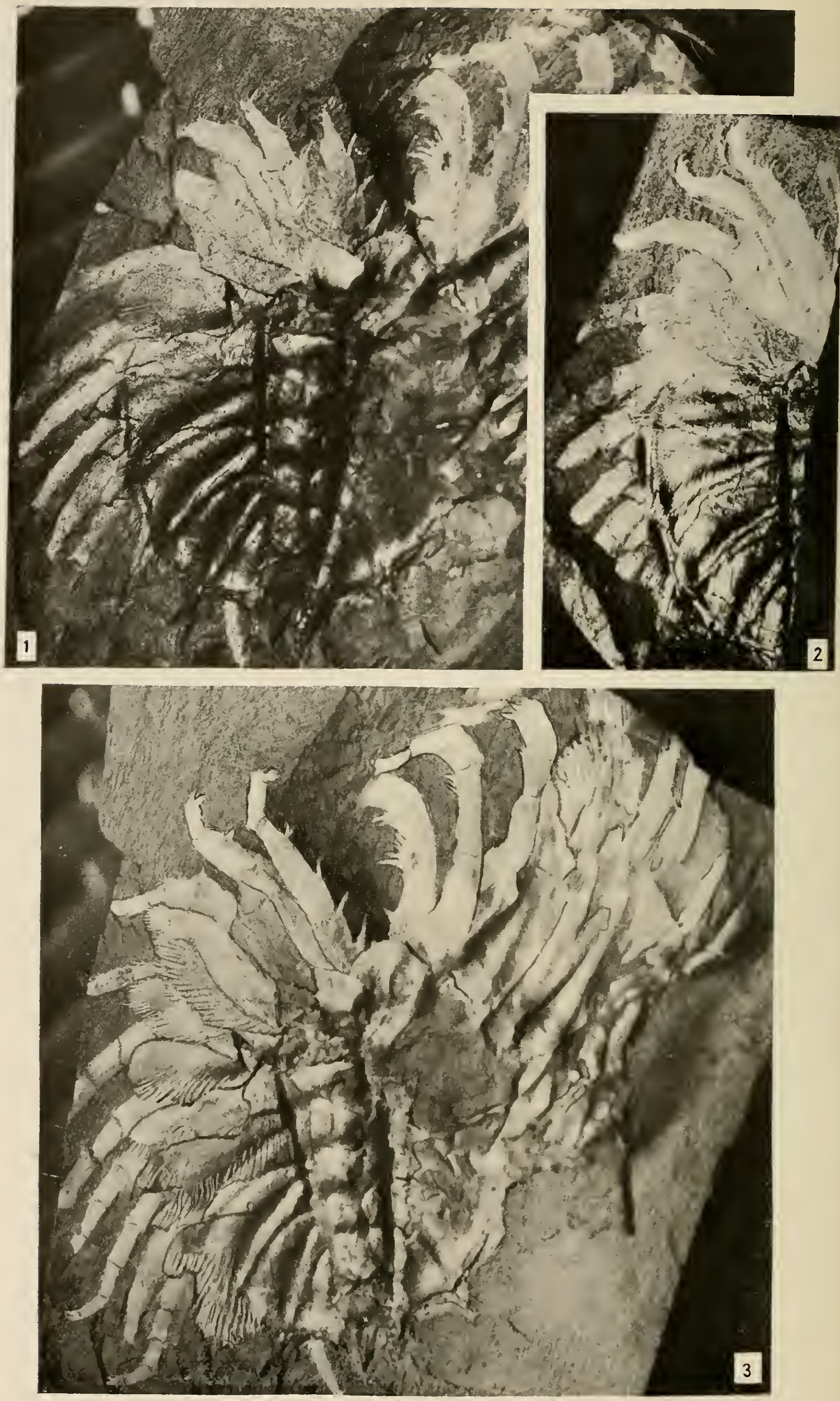
NEOLENUS SERRATUS (Rominger)



NEOLENUS SERRATUS (Rominger)

DESCRIPTION OF PLATE 19

FIG. 1. (× 2.) The specimen illustrated by this reproduction of an untouched photograph shows a pygidium to which the ventral surface and appendages adhered when the thorax and cephalon were broken up and pushed to the right side, dragging the legs out in a fan-shaped manner. A further description is given under fig. 3. U. S. National Museum, Catalogue No. 65514.

2. (× 2.) Photograph of the matrix of the left side of figs. 1 and 3, reversed so as to show the appendages adhering to it in a natural position. These have been drawn in on fig. 3 in order to restore some of the finer parts that were lost by exfoliation when the shale was split open at the quarry.

3. (× 2.) This distorted and crushed specimen has 17 legs (endopodites), several exopodites, and the ends of two of the large epipodites projecting from beneath the exopodites. The most important evidence given by it is that the exopodite and large epipodite are the same for the abdominal limbs as for those of the thorax. The epipodites occur between the leg (endopodite) and the exopodite. The characters seen on the specimen illustrated by fig. 1 and by the matrix, fig. 2, are combined in fig. 3.

The specimens illustrating *Neolenus serratus* are from locality **35k,** Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

DESCRIPTION OF PLATE 20

PAGE

Neolenus serratus (Rominger) (See pl. 18) 126

FIG. 1. (Natural size.) A partially exfoliated dorsal shield with finely preserved thoracic and abdominal legs (endopodites); three of these have the proximal joint (protopodite) one of which has spines on its proximal end, and another has fine spines along its posterior margin as well as on its proximal end. U. S. National Museum, Catalogue No. 58589.

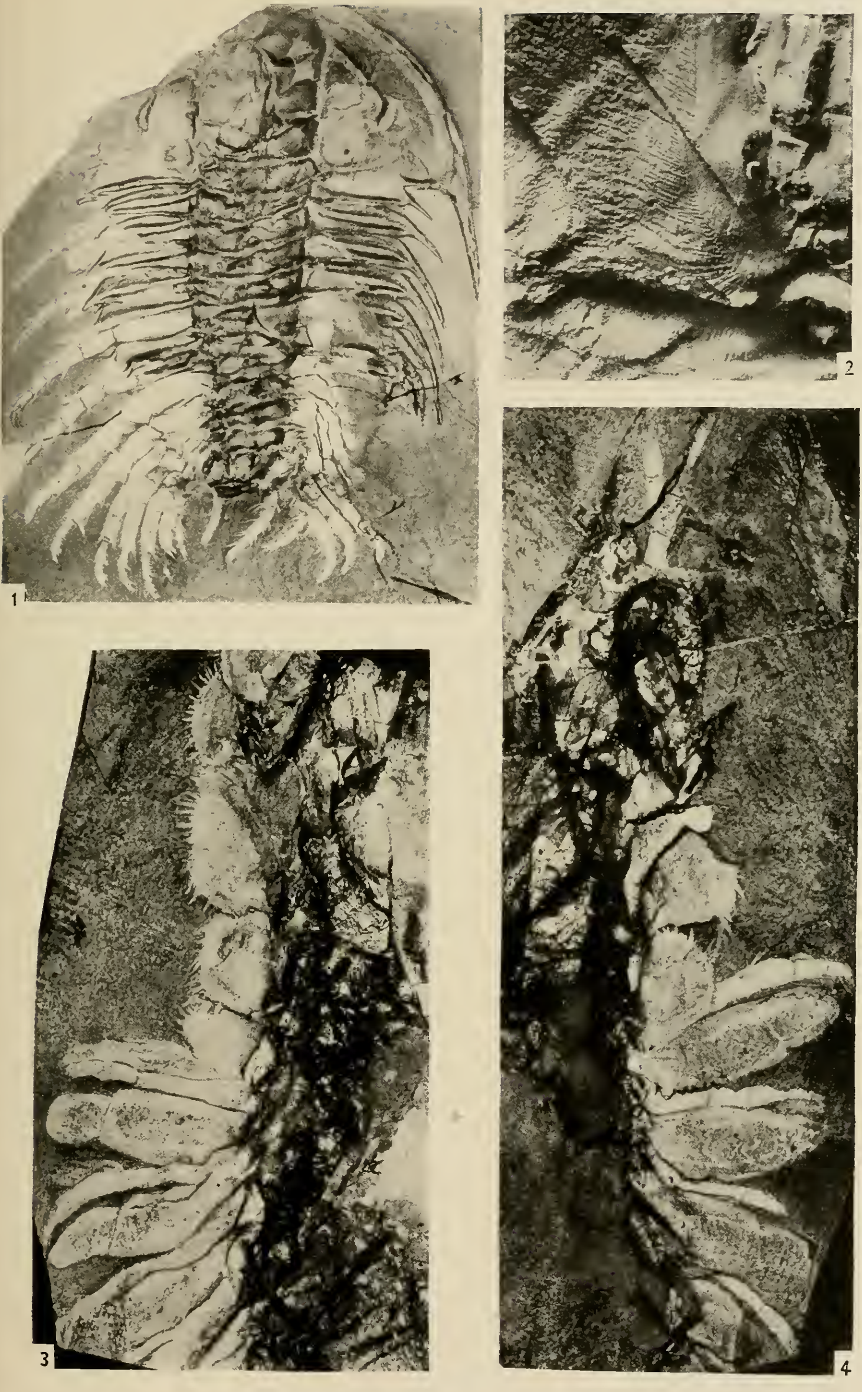
This figure has been published but at the time the proximal joints of the endopodites had not been uncovered. (See Smithsonian Misc. Coll., Vol. 57, 1912, pl. 45, fig. 2.) It was used again in 1913 (Text-book Pal., Eastman ed. of Zittel, Vol. 1, fig. 1377, p. 716).

2. (× 2.) An exopodite of one of the cephalic appendages with its long slender setæ. The thin, plate-like lobe was pushed up into the eye and molded by it. U. S. National Museum, Catalogue No. 65520.

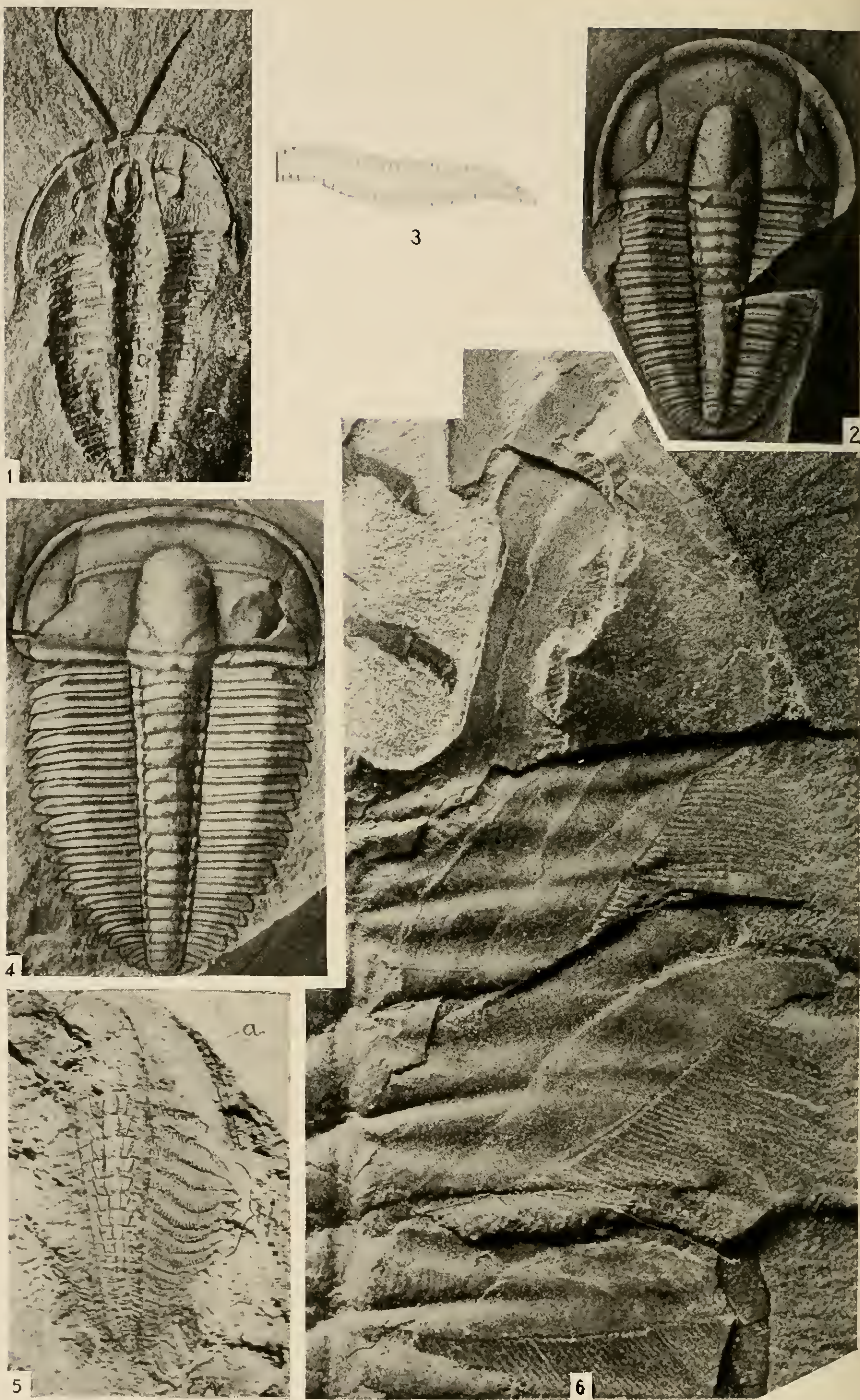
3. (× 2.) Jointed epipodites flattened on the surface of the shale. The legs (endopodites) are beneath the epipodites. Thin, flat lobes occur beside the axial lobe toward the upper end of the figure, that were probably attached to the inner side of the protopodite of the cephalic legs as an endite or epipodite. They have fine, short spines along the outer margin that are somewhat stronger than those of the epipodites of the thoracic appendages. It is barely possible that these plates were attached to the ventral integument just under the protopodite joint of the leg. U. S. National Museum, Catalogue No. 65515.

4. (× 2.) Matrix of the specimen represented by fig. 3.

The specimens illustrating *Neolenus serratus* are from locality **35k**, Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.



Branchiæ—NEOLENUS SERRATUS (Rominger)



PTYCHOPARIA AND NEOLENUS

DESCRIPTION OF PLATE 21

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Ptychoparia permulta Walcott 145

Fig. 1. (×2.) A laterally compressed and partially exfoliated dorsal shield with two flattened antennules projecting from beneath the cephalon in front of the glabella. U. S. National Museum Catalogue No. 65516.

2. (×2.) A broken dorsal shield preserving surface granulation and form except as changed by flattening in the shale. This is the type specimen of the species. U. S. National Museum, Catalogue No. 65517.

Ptychoparia cordilleræ (Rominger) 144

Fig. 3. Outline of one of the exopodites shown on the right side of fig. 5. The broad proximal end and crenulate margins are two prominent features. The general outline suggests the exopodite of *Neolenus,* fig. 6.

4. (×3.) A nearly entire dorsal shield with 18 thoracic segments. U. S. National Museum, Catalogue No. 65518. The specimen represented by fig. 4 is from locality **14s**, Middle Cambrian: Stephen formation; *Ogygopsis* shale on Mount Stephen, British Columbia, Canada.

5. (×6.) A small specimen with the dorsal shield exfoliated so as to expose the ventral integument of the axial lobe with the thickened ridges crossing the mesosternites; also obscure endopodites of the thoracic limbs and clearly defined crenulated exopodites. U. S. National Museum, Catalogue No. 57658. This specimen was poorly illustrated by Walcott, 1912, Smithsonian Misc. Coll., Vol. 57, pl. 24, fig. 2.

Neolenus serratus (Rominger) 126

Fig. 6. (×3.) Exopodites fringed with flattened setæ, exposed by the removal of the dorsal test. The position of the endopodite or leg beneath the exopodite is shown on the right lower part of the figure. U. S. National Museum, Catalogue No. 65519.

A drawing of a portion of this specimen was published in 1913 (Text-book Pal., Eastman ed. of Zittel, Vol. 1, fig. 1343, p. 701).

The specimens illustrated by figs. 1, 2, 5, and 6 are from locality **35k**, Middle Cambrian: Burgess shale member of the Stephen formation; on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

DESCRIPTION OF PLATE 22

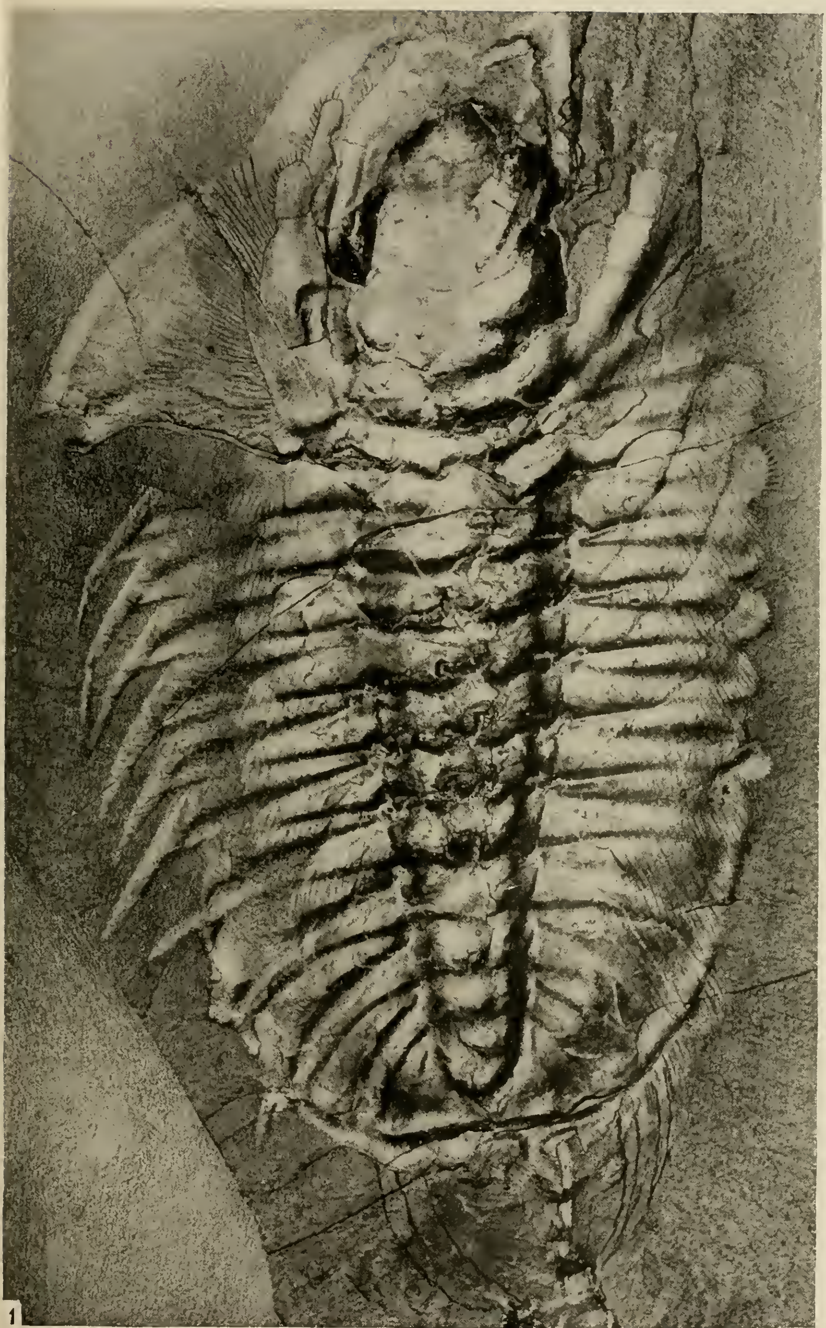
PAGE

Neolenus serratus (Rominger) 126

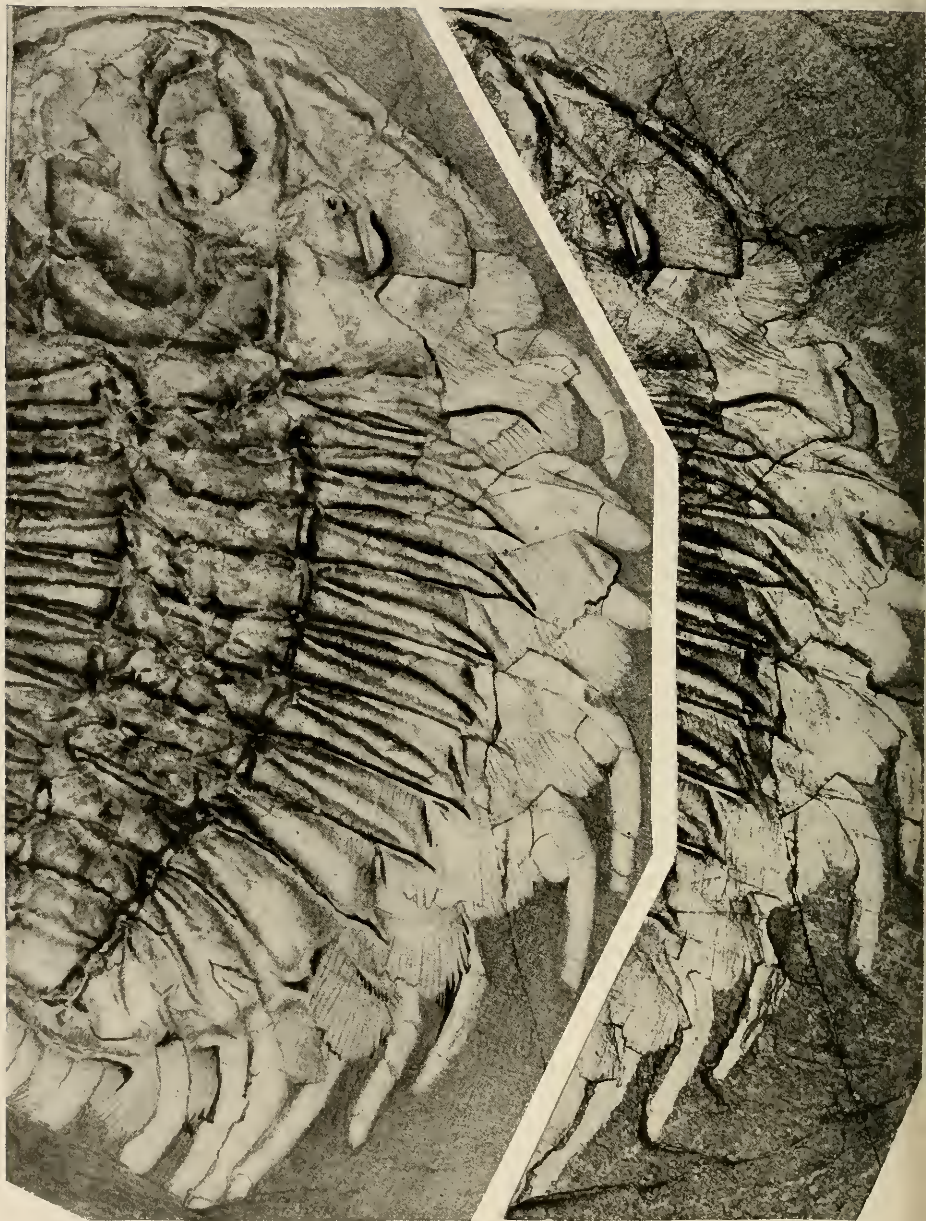
FIG. 1. (×2.) In the specimen represented by this figure the large, flattened exopodites (*ex*) have been bent forward and also pushed more or less to the right of their original position. The distal end of three of the epipodites (*ep*) projects slightly from beneath the thin fringed exopodites on the right side. The caudal rami and some of the posterior legs (endopodites) project backward from beneath the pygidium. Fig. 3, pl. 20, shows the epipodites more distinctly, also that their position is above that of the endopodite. U. S. National Museum, Catalogue No. 65520.

The exopodites of *Ptychoparia* (pl. 21, fig. 5) are similar in general form to those of *Neolenus*, and the same is true of the exopodites of *Kootenia dawsoni* (pl. 14, fig. 3).

The specimens illustrating *Neolenus serratus* are from locality **35k**, Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.



NEOLENUS SERRATUS (Rominger)
Illustrating exopodites



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NEOLENUS SERRATUS (Rominger)

DESCRIPTION OF PLATE 23

PAGE

Neolenus serratus (Rominger) 126

FIG. 1. (× 2.) Partially exfoliated interior of a specimen where the appendages on the right side have to a considerable extent clung to the specimen. These show the leg (endopodite), the end of the larger epipodite, also the outer portions of the large setiferous exopodite. U. S. National Museum, Catalogue No. 65521.

2. (× 2.) Untouched photograph of the right side of the specimen represented by fig. 1. Inserted here in order to show to what extent fig. 1 has been retouched. It is impossible in photographing specimens of this character to so reflect the light that it records all the details.

The specimens illustrating *Neolenus serratus* are from locality **35k,** Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

DESCRIPTION OF PLATE 24

PAGE

Isotelus walcotti Ulrich 134

Fig. 1. (× 3.5.) A very perfect dorsal shield retaining traces of the fused segments of the cephalon and pygidium and the points of attachment of the muscles of the median lobe of the cephalon and thorax. This illustration should be carefully studied in connection with pl. 25. U. S. National Museum, Catalogue No. 61261.

The specimen illustrated is from the Ordovician: Trenton limestone; 1 mile (1.6 km.) east of the Trenton Falls, in town of Russia, Herkimer County, New York.

Isotelus gigas var. *insignis* Ulrich 134

Fig. 2. (Natural size.) Natural cast of the interior surface of the test of a pygidium on which 14 fused segments are clearly outlined. U. S. National Museum, Catalogue No. 61255.

The specimen illustrated is from the Ordovician: Trenton limestone; Covington, Kentucky.

Isotelus maximus Locke (See pl. 25, fig. 1) 133

Fig. 3. (About one-half natural size.) Matrix of the specimen represented by fig. 3*a*, showing the impression made by the thoracic legs, and traces of the legs to the extremity of the pygidium. U. S. National Museum, Catalogue No. 33458.

3*a*. (About one-half natural size.) Ventral surface of a specimen preserving more or less of the thoracic legs. The matrix of this specimen is shown by fig. 3.

These two figures are from untouched photographs, and are inserted for the purpose of showing the data upon which the appendages shown by fig. 1, pl. 25, are based.

The specimen illustrated by figs. 3, 3*a*, is from the Ordovician: Cincinnatian (Richmond); Oxford, Ohio. U. S. National Museum, Catalogue No. 33458.

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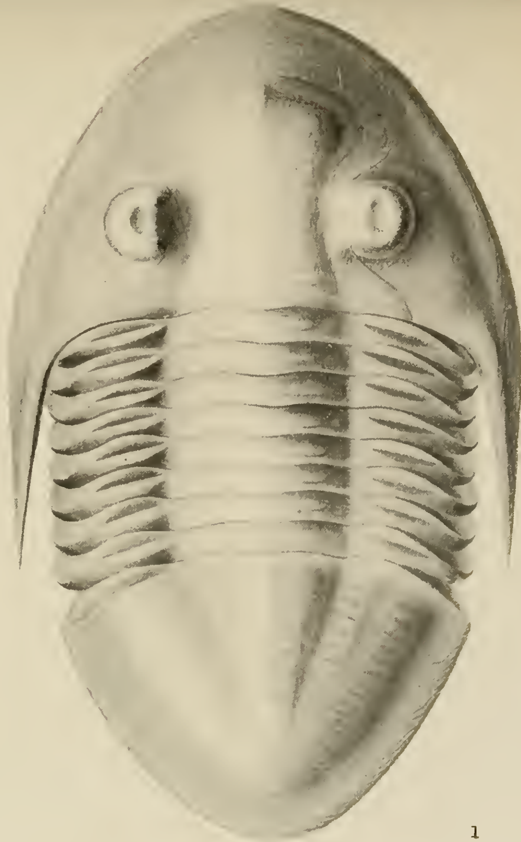

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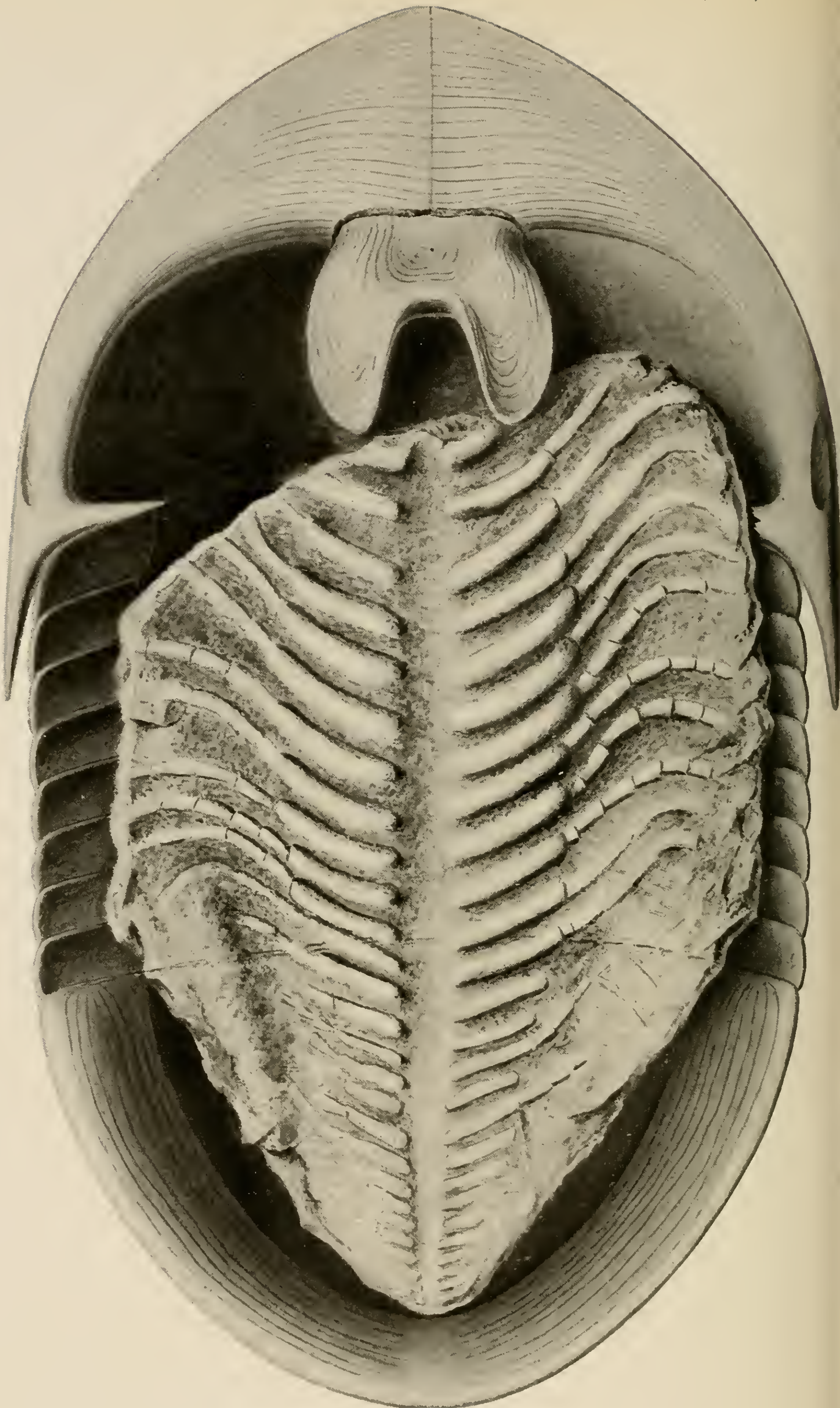
ISOTELUS



ISOTELUS MAXIMUS Locke

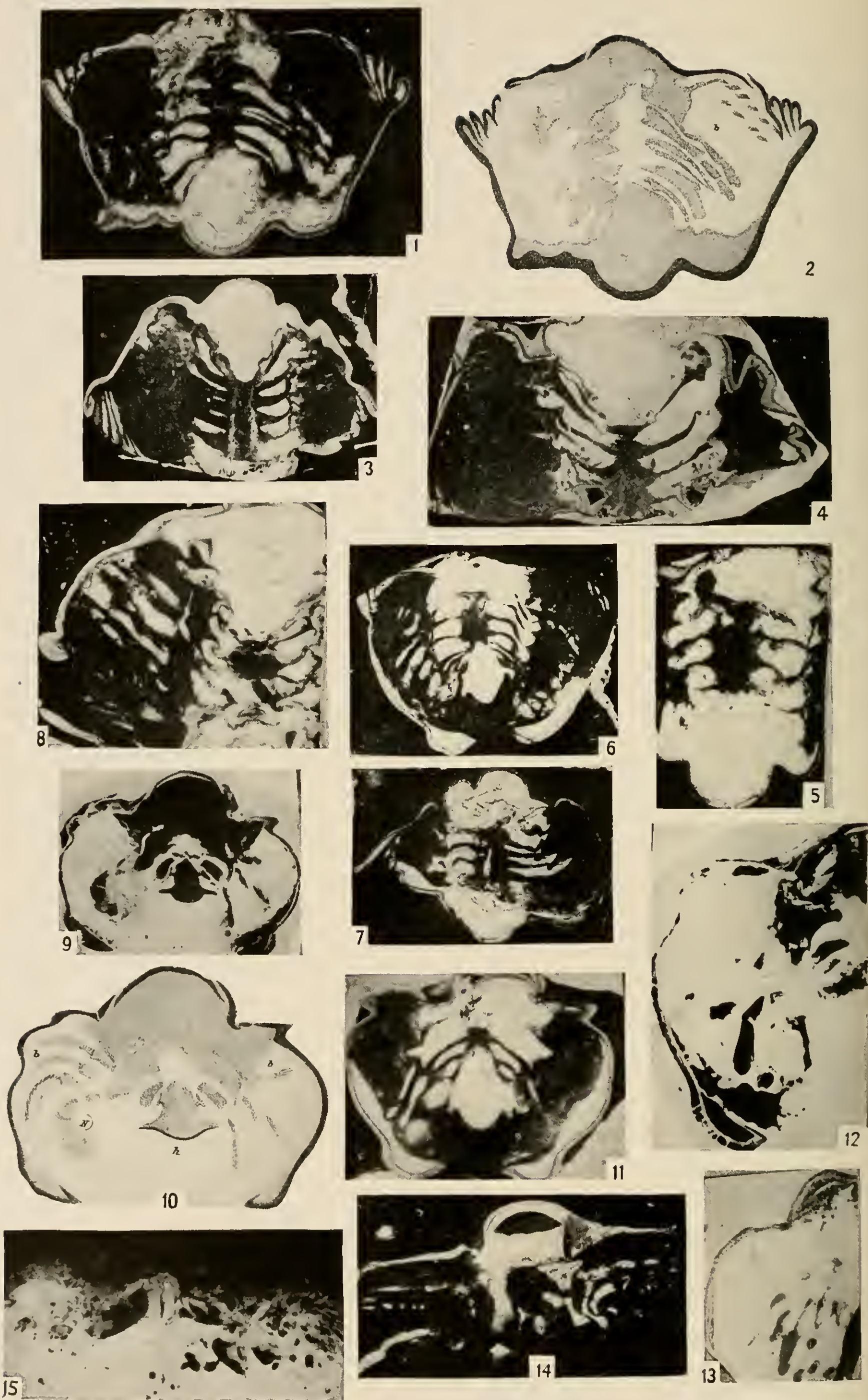
DESCRIPTION OF PLATE 25

PAGE

Isotelus maximus Locke (See pl. 24, figs. 3, 3*a*) 133

FIG. 1. (Natural size.) Illustration of the under side of the original specimen with the shaded outlines of an entire interior of a dorsal shield projecting beyond the broken specimen on all sides. The 26 pairs of appendages preserved include the legs (endopodites) and traces of the setæ of an exopodite on the right side. The joints of the legs represent all that is shown in the matrix and relief. The most prominent character is the very large proximal joints (protopodites) of the legs, which correspond to the large protopodites of *Neolenus* (pl. 18) and *Triarthrus* (pl. 32). U. S. National Museum, Catalogue No. 33458.

The specimen illustrated is from the Ordovician: Cincinnatian (Richmond); Oxford, Ohio.



SECTIONS OF TRILOBITES
CALYMENE AND CERAURUS

DETAILED DESCRIPTION OF PLATE 26

PAGE

Calymene senaria Conrad 147

FIG. 1. (× 3. Untouched photograph.) Transverse section through the head from the anterior side back to the lower posterior margins and thence across five segments of the thorax of an enrolled specimen. The large basal joints (protopodite) on five pairs of legs are shown. The four lower pairs on the right hand side of the figure are cut nearly on the longitudinal axis of the joint, while those on the left are cut across diagonally, which makes their sections much shorter. The two joints at the top which correspond to the fourth or fifth thoracic segment give the characteristic section where the joint is cut across obliquely (See also pl. 26, fig. 14; pl. 27, figs. 1, 2, 4).

Several joints of the leg are attached to the upper right hand basal joint, also a short section of the coiled portion of an exopodite. On the left side a section is shown of the epipodite with its attached setæ. Both the exopodite and epipodite are so delicate in the slide that the camera failed to reproduce them. They are restored in fig. 2.

The filling of the cephalic cavity is shown in the lower portion of the figure, also the outline of the eye on the left side, and the basal joint of one of the cephalic legs. The next pair of joints above presumably belonged to the cephalic region.

2. A drawing made from the section represented by fig. 1, and published by me in 1881 (Bull. Museum Comp. Zool., Harvard Coll., Vol. 8, pl. 3, fig. 3).

3. (× 3. Untouched photograph.) This section is essentially the same as that represented by fig. 1, but varies in details. It illustrates the tapering out of the proximal end of the basal joints (protopodites), a character that is also indicated in figs. 1 and 4.

4. (× 4. Untouched photograph.) Another section similar to that represented by figs. 1 and 3, in which the two pairs of large upper protopodites approach closely and they are also provided with minute spines on their proximal end.

Traces of the spiral portion of the exopodites are faintly shown on the left side. These are very clear in the section but do not photograph well. The same is true of the same appendage in the enclosed space on the left side of fig. 3.

5. (× 4. Untouched photograph.) Central portion of a section, showing the basal joints of the leg cut across obliquely, also the filling of the visceral cavity beneath the thorax.

6. (× 4. Untouched photograph.) Section cutting through the head in nearly the same direction as that represented by fig. 1. It shows, however, the hypostoma, the basal joints of the legs, and some of the following joints. One of the most interesting features is the presence of the basal joints of two of the anterior slender cephalic limbs that in the section are between the large joints and the hypostoma. This section also shows traces of the exopodites.

7. (× 3. Untouched photograph.) Section through the thoracic portion of an enrolled specimen, showing large protopodites.

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FIG. 8. (× 4. Untouched photograph.) Section approximately the same as fig. 1, showing the proximal joints of the legs and some of the distal joints, also traces of the spiral portion of the exopodites.

The enlarged basal joint shown on the left side near the outer edge may have been one of the enlarged joints of the posterior cephalic leg.

Figs. 1 to 8 are given for the purpose of illustrating the large elongate proximal joints (protopodites) and to show that their inner ends are drawn in toward the median line of the longitudinal axis of the ventral surface and that from their form and position they undoubtedly were closely allied both in shape and function to the proximal joints of the limbs of *Neolenus* and *Triarthrus*.

Calymene senaria Conrad.. 147

FIG. 9. (× 3. Untouched photograph.) Transverse section through the head, which cuts across the proximal joints of some of the cephalic legs, the hypostoma, and the enlarged basal joints of the posterior pair of cephalic legs. Other portions of various legs are cut across, which are outlined in the drawing (fig. 10).

10. (× 4.) Drawing based on the section represented by fig. 9. This was published as fig. 1, pl. 6, in 1881 (Bull. Mus. Comp. Zool., Harvard College, Vol. 8).

11. (× 3. Untouched photograph.) One of the best sections illustrating the cephalic legs. This shows the large proximal joints of the posterior pair and the relatively small joints of the second and third pair of legs.

This section was used as the base for a drawing published in 1881 (Bull. Museum Comp. Zool., Harvard Coll., Vol. 8, pl. 1, fig. 6).

12. (× 5. Untouched photograph.) This section is nearly on the same line as that of fig. 11. It is given to show the supposedly enlarged distal joints of the posterior pair of the cephalic legs.

13. (× 3. Untouched photograph.) Another section showing the enlarged joint similar to that of figs. 9 and 12.

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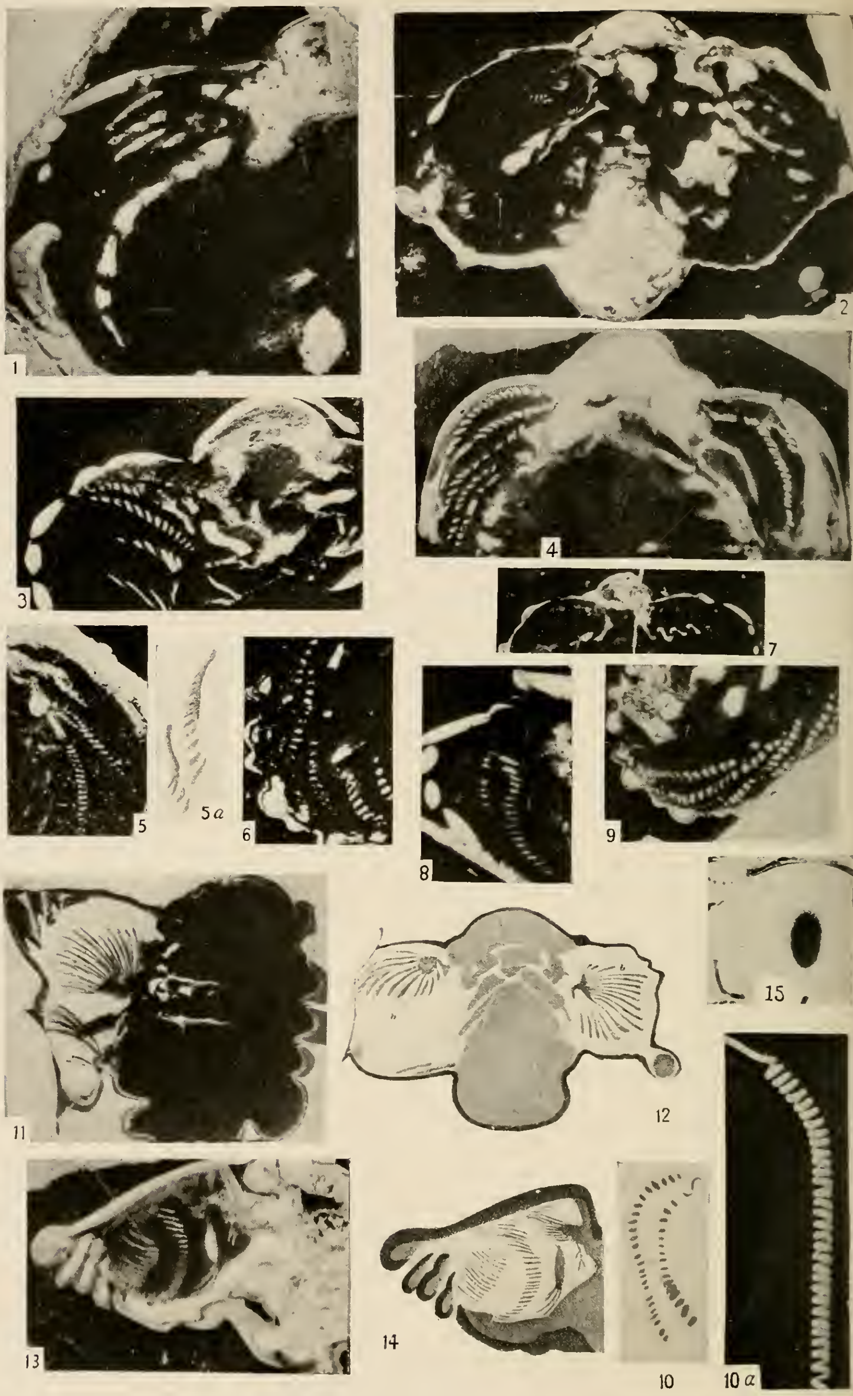
FIG. 14. (× 3. Untouched photograph.) Transverse section of the thorax of a specimen showing on the right side an oblique section of the proximal joint of the limb, sections of a crushed and broken leg on the left side, and sections of the support and the drawn-out, ribbon-like, more or less coiled exopodites.

This section was illustrated by a drawing in 1881 (pl. 2, fig. 3, Bull. Museum Comp. Zool., Harvard Coll., Vol. 8).

15. (× 3.) Photograph of a thin section cutting across on the left side a protopodite which has some of the fine spines attached to its ventral and inner margins.

All of the sections illustrated on this plate were made by me and are now in the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts.

The specimens illustrated are from the Ordovician: upper portion of the Trenton limestone; 1 mile (1.6 km.) east of the middle fall of Trenton Falls, on the West Canada Creek, in the town of Russia, Herkimer County, New York.



SECTIONS OF TRILOBITES
CERAURUS, CALYMENE, WIRE SPIRALS

DETAILED DESCRIPTION OF PLATE 27

PAGE

Ceraurus pleurexanthemus Green.. 148

FIG. 1. (× 5. Untouched photograph.) Section of an enrolled specimen, showing one-half of a transverse section through the thorax. The jointed limb is broken across the proximal joint and slightly pulled to the left. It shows six joints in addition to the protopodite and above the latter traces of the exopodites. This is the best example of a leg obtained in sectioning several hundred trilobites. A drawing based on this section was illustrated by me in 1881 (pl. 2, fig. 2, Bull. Museum Comp. Zool., Harvard College, Vol. 8).

2. (× 3. Untouched photograph.) Transverse section of an enrolled specimen which cuts through several joints of a pair of thoracic limbs. These corroborate the form of the joints shown in fig. 1. A drawing based on this section was illustrated by me in 1881 (pl. 2, fig. 1, Bull. Museum Comp. Zool., Harvard College, Vol. 8).

3. (× 4. Untouched photograph.) Transverse section through the thoracic portion of an enrolled specimen, showing traces of the proximal joints, thoracic legs, and particularly the spiral structure of the exopodites.

6. (× 4. Untouched photograph.) Longitudinal section of the thorax, cutting across displaced branches of the exopodite. One of these shows the spiral character very clearly.

7. (× 3. Untouched photograph.) Transverse section of the thorax of a small specimen in which the section is cut across a pulled out spiral of the exopodite.

8. (× 5. Untouched photograph.) Portion of a section in which the section of an unusually long, curved, and somewhat distorted spiral is preserved.

9. (× 4. Untouched photograph.) A section somewhat similar to that represented by fig. 6 where the spiral exopodites were closely coiled to form a relatively stronger structure. In figs. 6, 8, and 9 it appears as though the ventral appendages had been displaced and pushed against the interior of the dorsal shield. These sections are instructive in showing the strength of the spirals and also of the vicissitude to which the appendages were subjected antecedent to their mineralization.

15. (× 4.) Portion of a section cutting through the head and showing five segments of a slender appendage that may have been an antennule.

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FIG. 4. (× 4. Untouched photograph.) Transverse section of the thorax of an enrolled specimen, in which the proximal joints of the legs are preserved, also the bifurcating spiral exopodites. This section is one of the best illustrating the exopodites of this species. Another section cut through the same trilobite a short distance from this one shows the bifid exopodite more clearly. In a drawing made from this section and published by me in 1881 (pl. 3, fig. 9, Bull. Museum Comp. Zool., Harvard College, Vol. 8) the narrow arm extending down from the protopodite on the right hand side was considered to represent the epipodite as it was thought that there were traces of setæ on the lower portion. I now doubt the correctness of this interpretation, as it is more probably a cross-section of a flattened leg (endopodite). At the time of writing I do not have available for

Calymene senaria Conrad—Continued. PAGE

examination either of the sections cut through this trilobite, therefore cannot give as conclusive an interpretation of the section as otherwise would be possible.

A drawing based on this section was illustrated by me in 1881 (fig. 9, pl. 3, Bull. Museum Comp. Zool., Harvard College, Vol. 8).

Fig. 5. (× 4. Untouched photograph.) Section of an exopodite, showing its bifid character and the short, arm-like support. A drawing based on this section was illustrated by me in 1881 (pl. 4, fig. 3, Bull. Museum Comp. Zool., Harvard College, Vol. 8).

5*a*. (× 4.) Exopodites from *Ceraurus* showing the attachment of the spiral to the supporting basal joint or arm. The sections used in these drawings are in the Museum of Comparative Zoology, Harvard College. The drawings were first used in 1881, on pl. 4, fig. 4 (Bull. Museum Comp. Zool., Harvard College, Vol. 8).

11. (× 5. Untouched photograph.) Transverse section cutting across the upper posterior margin of the head and the anterior upper side of the thorax in such a manner as to show the filled-in visceral cavity and the basal portion of several setiferous, presumably thoracic appendages, which are interpreted as epipodites (See fig. 2, pl. 26; fig. 12, pl. 27).

A drawing based on this section was published by me in 1881 in which the right side was restored (fig. 1, pl. 3, Bull. Museum Comp. Zool., Harvard Coll., Vol. 8).

12. (× 4. Untouched photograph.) A drawing based upon a section which is now not available for making a photograph. This shows an epipodite on each side, also the proximal joint of some of the cephalic legs. The presence of a metastoma is suggested by the small triangular section which occurs between the proximal ends of the two large protopodites.

This figure was reproduced in 1881 (pl. 3, fig. 2, Bull. Museum Comp. Zool., Harvard Coll., Vol. 8).

13. (× 5. Untouched photograph.) Oblique transverse section of several epipodites, displaced and more or less crowded together. A drawing (fig. 14) based on this section was published in 1881 (fig. 8, pl. 3, Bull. Museum Comp. Zool., Harvard College, Vol. 8).

14. A drawing based on the section represented by fig. 13.

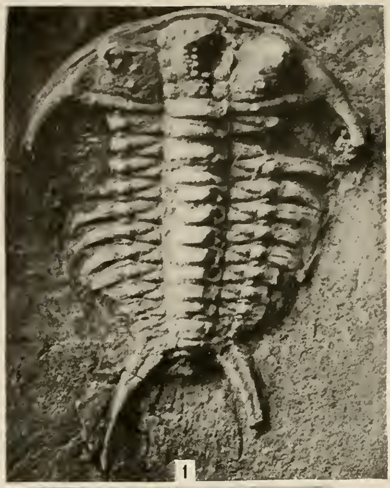
The specimens illustrated by figs. 1-14 are now in the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts.

They are from the upper portion of the Trenton limestone, Ordovician; 1 mile (1.6 km.) east of the middle fall of Trenton Falls, on the West Canada Creek, in the town of Russia, Herkimer County, New York.

Wire spirals 152

Fig. 10. Untouched photograph of wire spirals which have been set in plaster and filed across so as to obtain sections corresponding to those found in enrolled specimens of *Calymene* and *Ceraurus*.

10*a*. Photograph of a white wire spiral against a dark background, illustrating a closely coiled spiral such as those cut across in the sections represented by figs. 3-6 and 9.



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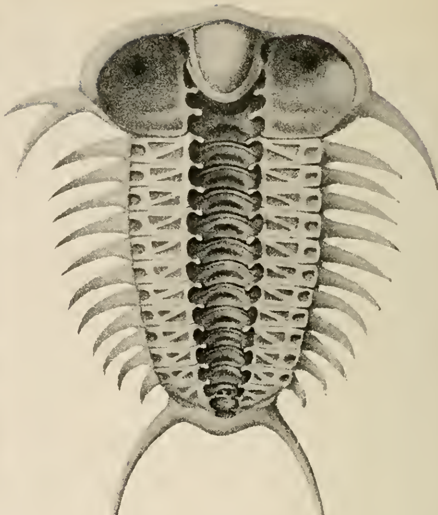

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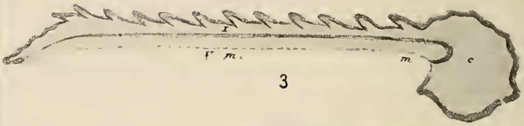

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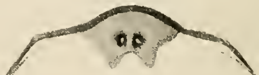

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9

10

ORDOVICIAN TRILOBITES

DESCRIPTION OF PLATE 28

PAGE

Ceraurus pleurexanthemus Green.................................... 148

FIG. 1. (× 2.) Untouched photograph of the dorsal shield of a specimen from the thin layer of limestone from which all of the specimens showing appendages of this species and *Ceraurus pleurexanthemus* were obtained. U. S. National Museum, Catalogue No. 18038.

2. Restoration of the interior of the dorsal shield drawn from specimens associated with that represented by fig. 1. (After Walcott, Ann. Lyceum Nat. Hist., Albany, N. Y., Vol. XI. 1875, pl. XI. Idem, Bull. Museum Comp. Zool., Harvard Coll., Vol. VIII, 1881, pl. IV, fig. 5.)

3. Diagrammatic median longitudinal section showing dorsal shield, hypostoma, and outline of ventral membrane (*vm*), and position of intestinal canal, based on data obtained from thin sections and the specimen represented by fig. 4. (After Walcott, 1881, pl. IV, fig. 6, Bull. Museum Comp. Zool., Vol. VIII.)

4. (× 2.) Cephalon with the dorsal test broken away over the cephalic cavity so as to show the inner side of the hypostoma and the enlarged opening of the intestinal canal. Museum Comparative Zoology, Harvard College.

5. (× 2.) A transverse section of fig. 4 across the third thoracic segment. The section of visceral cavity and intestinal canal are the only traces of parts other than the dorsal shell. The light spot in the center of each dark spot represents the light shining through from the front. The division of the intestinal canal into two parts is undoubtedly of accidental occurrence.

(Figs. 4 and 5 are after Walcott, 1881, pl. IV, figs. 1 and 2, Bull. Museum Comp. Zool., Vol. VIII.)

Calymene meeki Foerste 197

FIG. 6. (× 1.5.) Exterior of dorsal shield of the Cincinnati variety of *Calymene senaria,* introduced to illustrate the dorsal shield of *Calymene.* U. S. National Museum, Catalogue No. 65522.

Locality: Ordovician: Maysville formation; Cincinnati, Ohio.

Calymene senaria Conrad.. 147

FIG. 7. (× 1.5.) Enrolled specimen showing the cast of a portion of the ventral integument. This appears to show the cast of the mesosternites, and the openings that led into the base of the limbs. A median ventral ridge is also indicated.

Calymene senaria Conrad—Continued. PAGE

Fig. 8. (× 3.) Section cutting longitudinally through the axial lobe of a partially enrolled specimen. This shows a section of the dorsal shield for its entire length, the hypostoma and filling of the cephalic cavity, portion of a distorted cephalic leg and the ventral integument with its thickened, transverse mesosternites—of the latter only seven of the twenty present are clearly shown in the figure. (After Walcott, fig. 2, pl. V, Bull. Museum Comp. Zool., Harvard Coll., Vol. VIII, 1881.)

Cyamus scammoni Dall.. 173

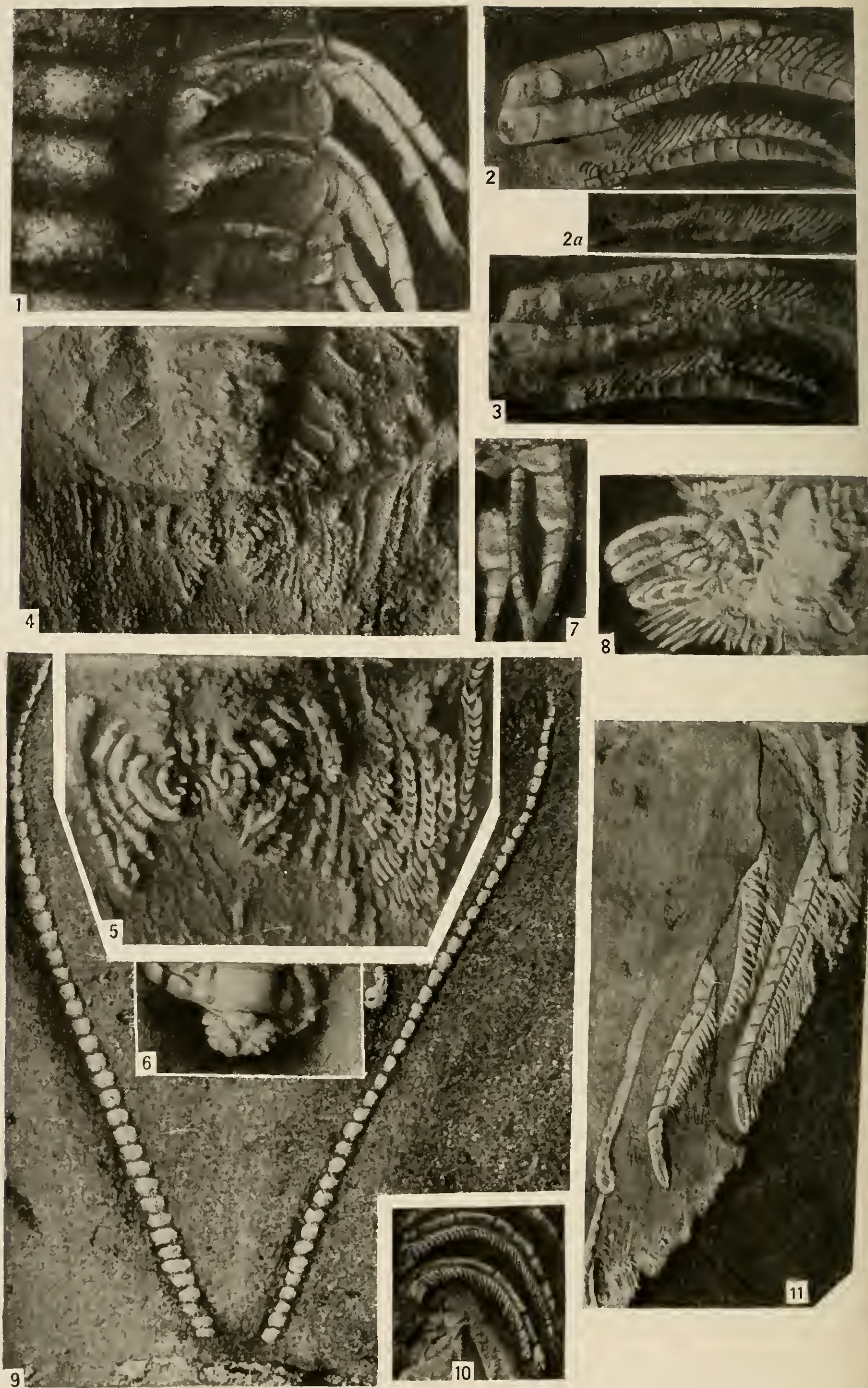
Fig. 9. (About × 8.) Spiral branchia attached to the third and fourth thoracic segments. (After Dall.)

Cyamus diffusus Dall.. 173

Fig. 10. (About × 8.) Ribbon-like branchiæ attached to thoracic segments. (After Dall.)

The two species of *Cyamus* are described by Dr. W. H. Dall (Proc. California Acad. Sci., Vol. IV, 1872, pp. 281-283) and illustrated (Marine Animals and the American Whale Fishing, Chas. C. Scammon, 1874). Of the branchiæ of *Cyamus scammoni* (fig. 9) Dr. Dall wrote, "The third and fourth segments each have a branchia attached on each side. This, near the base, divides into two cylindrical filaments spirally coiled from right to left." The branchiæ of *Cyamus diffusus* Dall, fig. 10, are described as "single, cylindrical, slender, with a very short papilliform appendage before and behind each branchia." They are attached to the segments as shown in fig. 10.

Figs. 9 and 10 are reproduced from Walcott, 1881, pl. IV, figs. 9, 10, Bull. Museum Comp. Zool., Harvard Coll., Vol. VIII. The specimens on which figs. 4 and 7 are based are in the Museum of Comparative Zoology, Cambridge, Massachusetts.



APPENDAGES OF TRIARTHRUS BECKI Green

DESCRIPTION OF PLATE 29

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Fig. 1. (× 6. Untouched photograph.) Two thoracic limbs, showing the endopodite and the setiferous exopodite. (Collection, Peabody Museum, Yale University.)

2 and 3. (× 8. Fig. 3, untouched photograph. Fig. 2, endopodites and exopodites outlined.) The setæ of the upper exopodite are jointed as indicated in fig. 2. U. S. National Museum, Catalogue No. 65523.

2a. (× 6.) An exopodite illustrating the crowding of the setæ on the jointed arm. This occurs on the same specimen as the parts represented by fig. 8.

4. (× 12.) Untouched photograph of endopodites and exopodites that were forced from beneath the pygidium. The endopodites are attached to the protopodites and appear to have the same structure as those beneath the thorax. The exopodites, however, show the joints of the supporting arm as overlapping lobes (See fig. 8). A further enlargement is made in fig. 5 (× 20).

5. (× 20.) Enlargement of the posterior portion of fig. 4 to bring out the minute, overlapping, lobe-like joints of the arm of the exopodite.

These photographs illustrate the appendages that have been crowded out posteriorly from beneath the pygidium, and show the strong proximal joints of the legs and the setiferous exopodites. U. S. National Museum, Catalogue No. 65524.

6. (× 8. Untouched photograph.) Another specimen showing the ventral membrane and the bases of the limbs that have been crowded out from beneath the pygidium. U. S. National Museum, Catalogue No. 65525.

7. (× 8.) Ends of legs (endopodites) from beneath a pygidium. U. S. National Museum, Catalogue No. 65526.

8. (× 18. Untouched photograph.) Minute exopodites crowded from beneath the pygidium. See text for discussion of these interesting appendages. U. S. National Museum, Catalogue No. 65527.

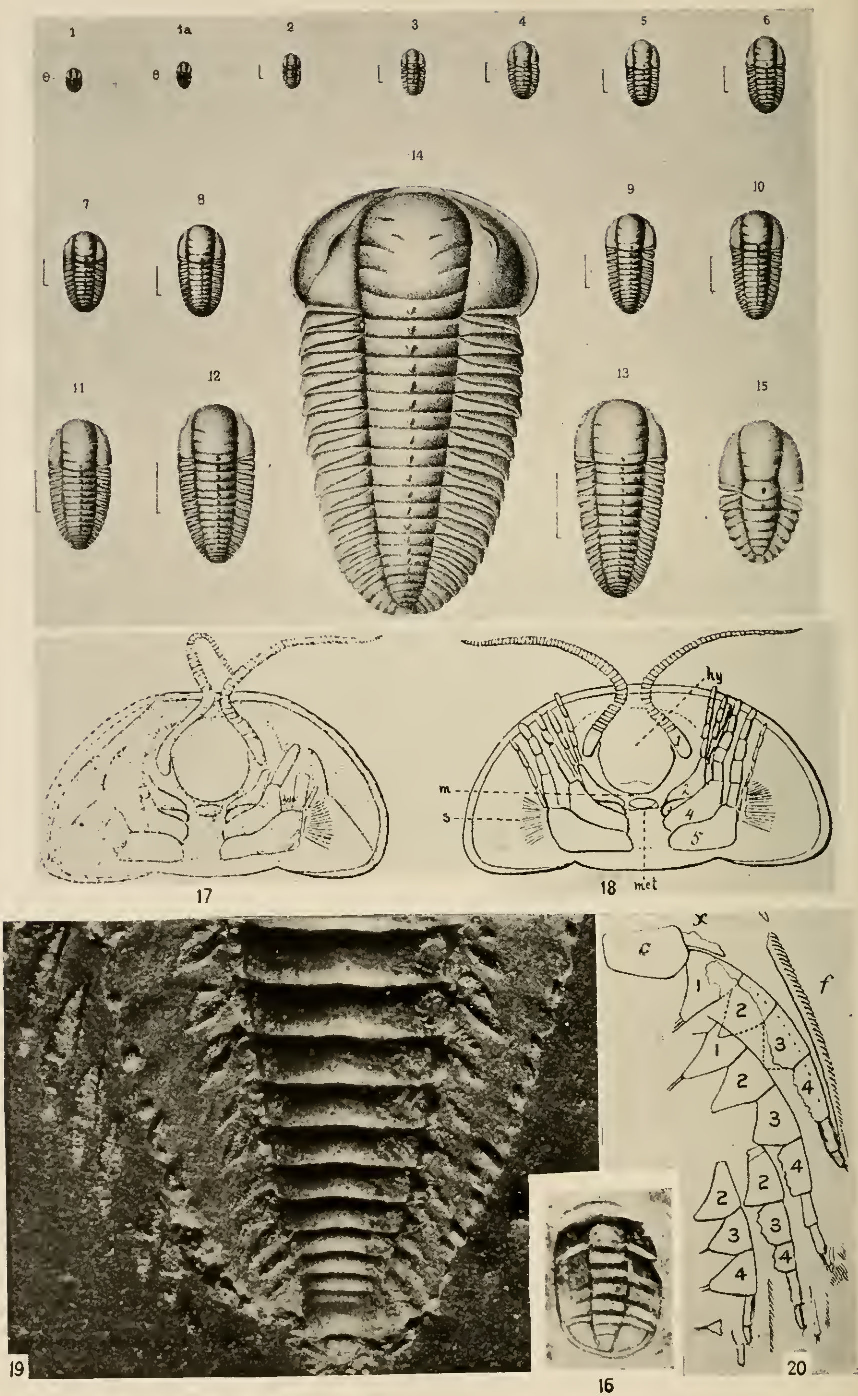
9. (× 6. Untouched photograph.) Illustration of a very fine pair of antennules, projecting from beneath the anterior margin of the head. (Specimen in the Collection of Peabody Museum, Yale University.)

10. (× 6.) Outer portion of thoracic limb of anterior portion of right side of thorax, showing the jointed endopodite and setiferous exopodite. The lower endopodite has a trifid spinous termination. The joints of the endopodite and the separation of the base of the setæ on the exopodite have been outlined on the photograph. U. S. National Museum, Catalogue No. 65528.

Triarthrus becki Green—Continued.

Fig. 11. (× 15.) This figure illustrates the structure of the exopodite of the thoracic limb more clearly than any other specimen I have seen. The supporting jointed portion terminates in a flattened elongate narrow lobe or section similar to that shown in fig. 8, where several of the terminal sections of exopodites projected from beneath the pygidium. U. S. National Museum, Catalogue No. 65529.

The specimens illustrated by figs. 1-11 are from locality **373**, Ordovician: Utica shale; 3 miles (4.8 km.) north of Rome, Oneida County, New York.



TRIARTHRUS BECKI Green

DESCRIPTION OF PLATE 30

PAGE

Triarthrus becki Green 135

FIG. 1. Natural size and enlargement of an individual having one thoracic segment.

1*a*. A narrow and more elongate individual having one segment in the thorax.

15. Natural size, and enlargement of 1*a*, to fifteen diameters to show the character of the head and pygidium and their relative proportions and size.

1-13. A series of individuals illustrating the gradual development of the head and thorax on the addition of each thoracic segment. The pygidium diminishing in size as compared with the other parts of the body. The numbers 1-13 also indicate the number of segments in the thorax of each individual to which they refer. All enlarged to three diameters.

13. Enlargement to three diameters of an individual having fourteen thoracic segments.

14. Fully developed individual of sixteen thoracic segments, natural size. All the larger specimens have been flattened by compression. The convexity in the figure is the same as in an individual of sixteen segments, 33 mm. in length.

The free cheeks are also pressed out so as to show their margins.

All of the specimens illustrated by figs. 1-14, 15, are from a locality northwest of Holland Patent, Oneida County, New York. They occur in the Utica shale of the Ordovician and are now in the collection of the Museum of Comparative Zoology, Harvard College.

Figs. 1-14, 15, are after Walcott, 1879, Trans. Albany Inst., Vol. X, pl. II, figs. 1-15.

16. (× 20.) Outline of an embryonic specimen that preceded fig. 1 in development. This shows the cephalon and pygidium well outlined, and the thorax undeveloped. U. S. National Museum, Catalogue No. 65530.

The two specimens that were used in sketching this figure are from locality **373**, Ordovician: Utica shale; 3 miles (4.8 km.) north of Rome, Oneida County, New York.

17. (× 4.) Diagrammatic sketch of a specimen preserving the hypostoma, epistoma, and cephalic appendages. After Beecher, American Geologist, Vol. XV, 1895, pl. 5, fig. 10.

The specimen is in the collection of the Peabody Museum, Yale University, from the same locality as that represented by fig. 16.

18. Diagrammatic restoration of the cephalic appendages: *hy* = hypostoma; *m* = metastoma; 1 = antennæ; 2 = first pair biramous appendages, or posterior antennæ; 3 = mandibles; 4, 5 = maxillæ. (After Beecher.)

Triarthrus becki Green—Continued.

FIG. 19. (× 15.) Photograph of a specimen that appears to indicate the presence of epipodites. The flat, rounded, diamond-shaped lobes originate along the line between the mesosternites and pleurosternites of the ventral integument, and extend obliquely backward in the direction in which the limbs are usually found. The dorsal shield was removed from over them, and in one example nearer the cephalon, the limb is clearly situated beneath the lobe. U. S. National Museum, Catalogue No. 65525.

The specimen is from the same locality as the specimen represented by fig. 16.

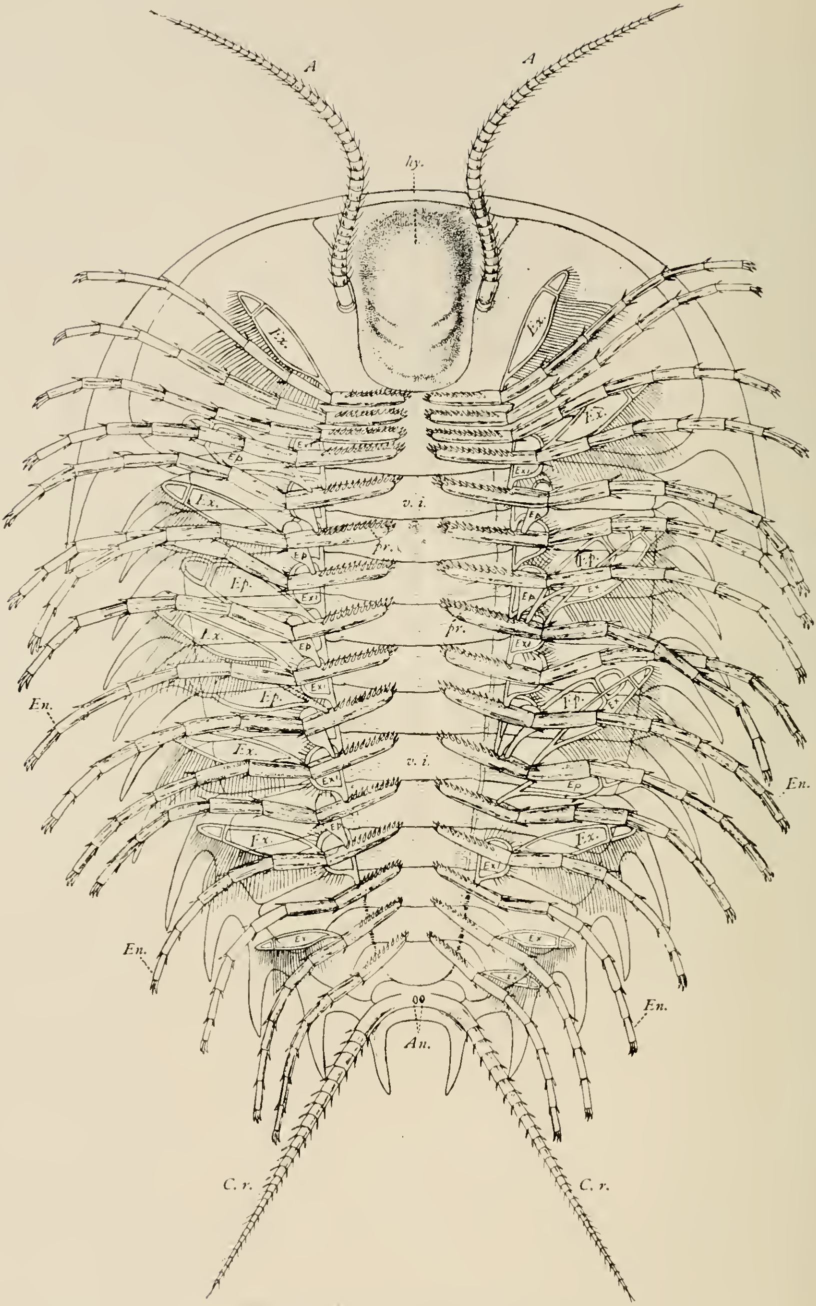
20. (× about 6.) Limbs occurring on the under side of an individual of 14 thoracic segments. Limbs with flattened, enlarged proximal joints and slender distal joints.

c. 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*.

The above appendages lie so irregularly on the inner side of the segments of the thorax and pygidium that it is not practicable to make a satisfactory photograph. U. S. National Museum, Catalogue No. 65531.

An outline drawing based on this specimen was published by me in 1894 (Proceed. Biol. Soc. Washington, Vol. IX, pl. 1, fig. 3).

The specimens illustrated by figs. 16-20 are from locality **373**, Ordovician: Utica shale; 3 miles (4.8 km.) north of Rome, Oneida County, New York.



Restoration of ventral surface of
NEOLENUS SERRATUS (Rominger)

DESCRIPTION OF PLATE 31

Legend

d. s. = dorsal shield.
hy. = hypostoma.
a. = antennules.
an. = anal aperture.
c. r. = caudal rami.
en. = endopodite.
ep. = epipodite.
ex. = exopodite.
exi. = exite.
pr. = protopodite.
v. i. = ventral integument.

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Neolenus serratus (Rominger) 126

Fig. 1. (About two times the average size of the species.) This restoration is based on study of all available specimens of the species that show any of the ventral appendages. Reference will be made to the specimens illustrated on plates 14-23 in describing the restoration as they show more or less of every appendage represented.

(1) Antennules (a). Shown by figs. 1, pl. 14, 1, pl. 15, 3, pl. 16.

(2) Cephalic limbs: Figs. 1, 2, 3, pl. 16, 2, pl. 20, 6, pl. 21, 1, pl. 22. The endopodites are best shown by figs. 1, 2, pl. 16, and the exopodites by fig. 1, pl. 16, and fig. 1, pl. 22. Whether the exites, figs. 3 and 4, pl. 20, are present beneath the cephalon, is not determined. No traces of epipodites were observed.

(3) Thoracic limbs: Figs. 1, pl. 14, 1, pl. 15, 1 and 3, pl. 17, 1, pl. 18 (the best one), 1, 2, 3, pl. 19, 1, 2, 4, pl. 20, 6, pl. 21, 1, pl. 22, 1, pl. 23. The endopodite is best shown by fig. 3, pl. 17, and fig. 1, pl. 18. The exopodite by figs. 3, pl. 19, 6, pl. 21, 1, pl. 22, 1, pl. 23. The large epipodite by figs. 3 and 4, pl. 20, and the small epipodite by fig. 1, pl. 18.

(4) The abdominal limbs or those beneath the pygidium are not differentiated from those of the thoracic region. They are well shown by figs. 1, pl. 15, 3, pl. 17, 1, pl. 18, 1, pl. 20.

(5) Caudal rami (c. r.). These are best shown by figs. 1, pl. 15, 1, 2, 3, pl. 17.

(6) Anal aperture or genital openings (an.): indicated only on fig. 3, pl. 17.

Observations.—In the restoration all the endopodites are essentially the same, decreasing only in length and size from the cephalon to the end of the body. The exopodites, epipodites, and exites are represented on only a few of the limbs as otherwise they would be so crowded together that it would be difficult to distinguish the various members of the limbs.

In looking at the restoration the observer must recall that the limbs are seen from their narrow lower side and that they are quite deep in the vertical section as shown in the transverse view, fig. 2, pl. 18. The latter view also shows the protopodites, endopodites, exopodites, epipodites, and exites in position.

This restoration should be compared with the restoration of *Triarthrus* on pl. 32 and of *Calymene*, pl. 33.

DESCRIPTION OF PLATE 32

Legend

d. s. = dorsal shield.	ep. = epipodite.
hy. = hypostoma.	ex. = exopodite.
a. = antennules.	pr. = protopodite.
en. = endopodite.	v. i. = ventral integument.

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Triarthrus becki Green 135

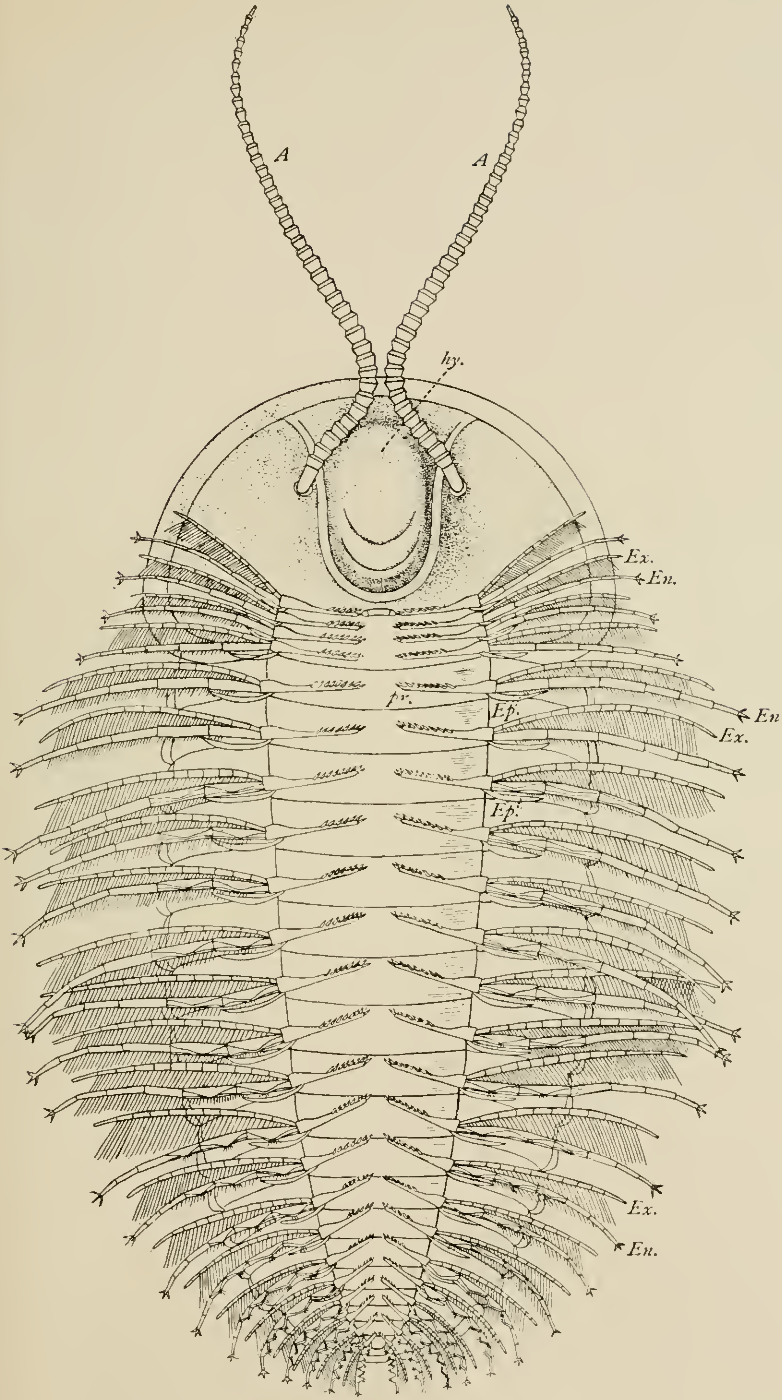
FIG. 1. (About 3 times the size of the average adult specimen of the species.) This restoration of the ventral surface and limbs is based on study of all specimens available at this time and old notes on some of those in the collection at Peabody Museum, Yale University, a few of which were illustrated by Beecher.

The specimens illustrated on plates 29 and 30 were studied with others when making the restorations of this species. From the one represented by fig. 19, pl. 30, I first gained the impression that there was a small epipodite attached to the proximal joint of the leg. From figs. 2-5, 8-11, pl. 29, the conception of the structure of the exopodite, especially the transverse, lamellated joints suggesting the endites of the limb of *Apus* was obtained. Fig. 4 led me to consider that the leg (endopodite) beneath the pygidium was similar to that of the thorax and that the phyllopod-like endites were part of the exopodite and not of the endopodite as tentatively interpreted by Beecher. Fig. 7, pl. 29, and fig. 20, pl. 30, illustrate the expanded joints of the endopodites.

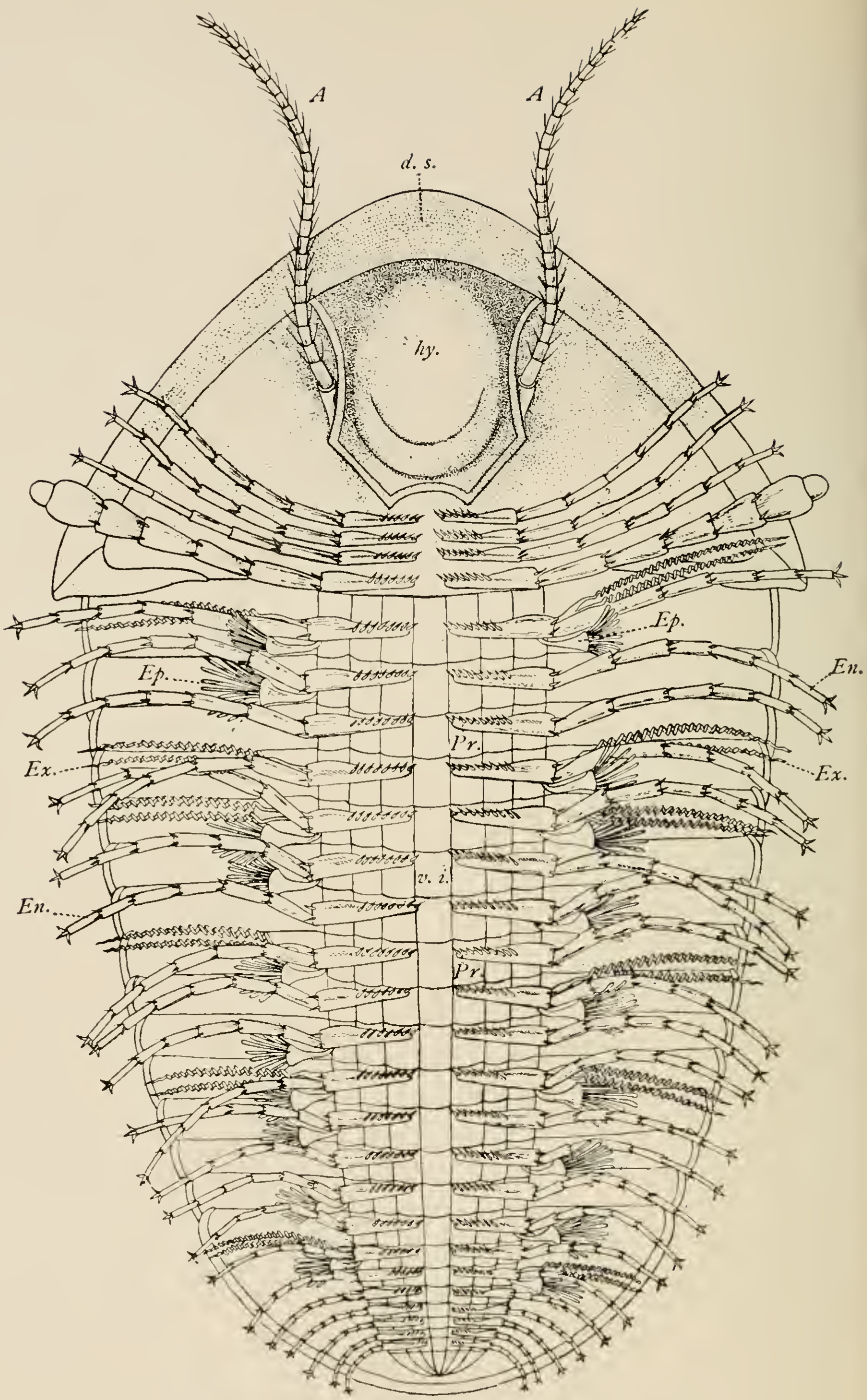
The restoration has quite a different aspect from that made by Beecher although the essential elements of structure are the same. The protopodites are placed in what is considered to be their normal position and the flattened joints of the endopodite are given as nearly vertical instead of being on the plane of the ventral surface of the body of the trilobite. Beecher shows the protopodite, endopodite, and exopodite in their approximately natural position in his restored transverse sections of the thorax and appendages.

Observation.—In looking at the restoration the observer must recall that the limbs are seen from their narrow lower (ventral) side and that they are quite deep in their vertical section as shown by the transverse views (pl. 34, figs. 4-6) of the thorax.

This restoration should be compared with the restoration of the ventral side of *Neolenus* (pl. 31) and *Calymene* (pl. 33).



Restoration of ventral side of
TRIARTHRUS BECKI Green



Restoration of ventral side of
CALYMENE SENARIA Conrad

DESCRIPTION OF PLATE 33

Legend

d. s. = dorsal shield.	ep. = epipodite.
hy. = hypostoma.	ex. = exopodite.
a. = antennule.	pr. = protopodite.
en. = endopodite.	v. i. = ventral integument.

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Calymene senaria Conrad 147

FIG. 1. (About two and a half times the average size of the species.) This restoration is based on my studies of the ventral appendages of *Calymene senaria* from 1875-1880, and published in 1881. The restoration of 1881 is taken as the base and such changes made in it as the discoveries of antennules and long protopodites necessitate. Only a fragment of an antennule has been seen, but with fine antennules of *Neolenus* and *Triarthrus* for study I do not hesitate to put them in the restoration of this species. Through the kindness of Dr. Alexander Agassiz I had the opportunity of making a photograph of the original thin sections which I made 1875-1880. Some of these are reproduced on plate 29.

Observations.—In looking at the restoration the observer must recall that the limbs are seen from their narrow lower (ventral) side and that they are quite deep in the vertical section as shown in the view of the transverse section of the thorax, fig. 2, pl. 34. The latter view gives a side view of the entire limb.

This restoration should be compared with the restoration of the ventral side of *Neolenus* (pl. 31) and *Triarthrus* (pl. 32).

DESCRIPTION OF PLATE 34

Legend

d. s. = dorsal shield.	exi. = exite.
en. = endopodite.	int. = intestinal canal.
ex. = exopodite.	pr. = protopodite.
ep. = epipodite.	v. i. = ventral integument.

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Ceraurus pleurexanthemus Green 148

FIG. 1. (× about 5.) Transverse diagrammatic sketch of one of the anterior thoracic segments presenting a side view of the ventral appendages as far as known. Some of the sections affording data on the limbs of *Ceraurus* are illustrated on pls. 26, 27.

Calymene senaria Conrad (See pl. 33) 147

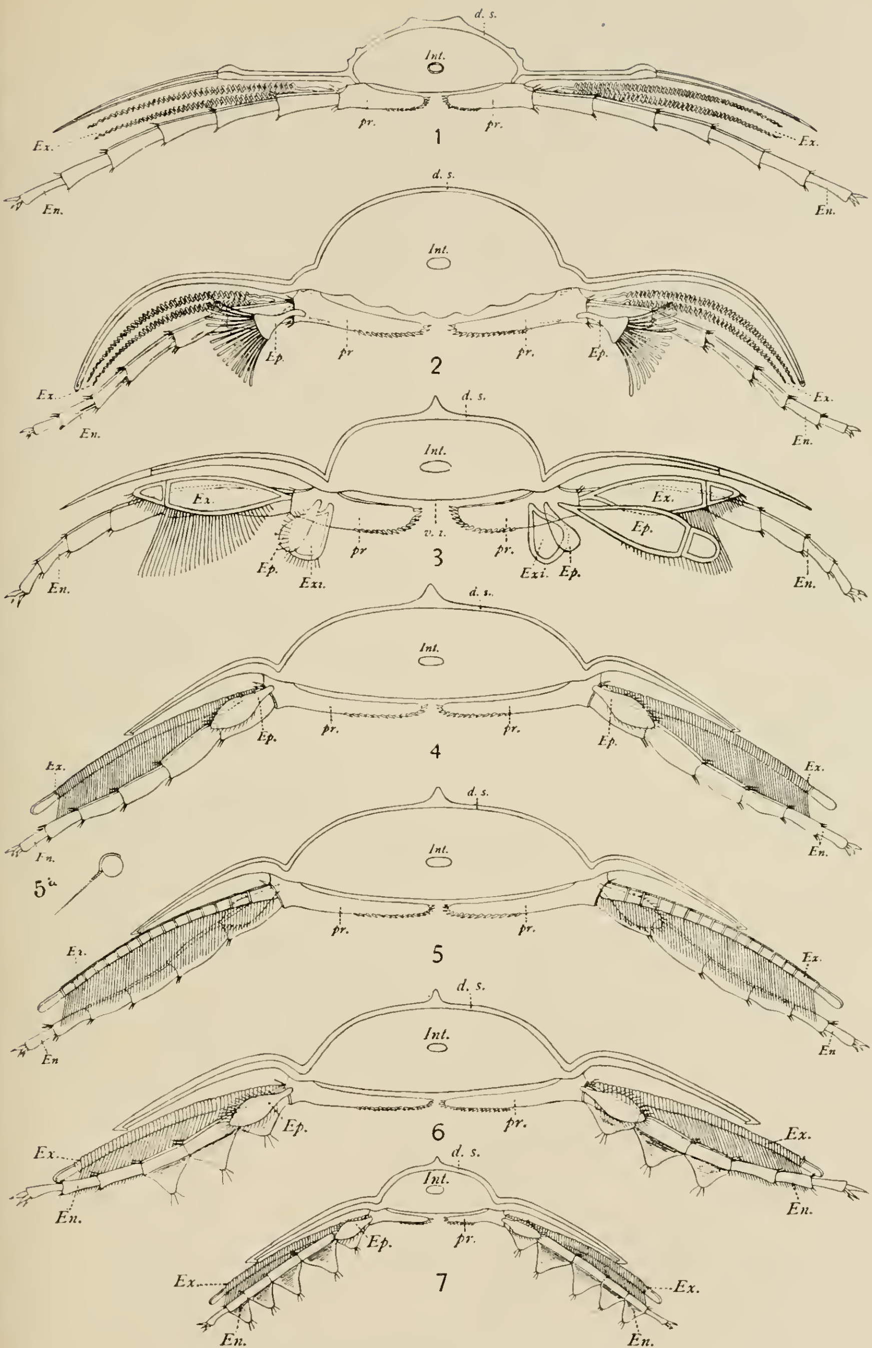
FIG. 2. (× about 5.) Transverse diagrammatic sketch of one of the anterior thoracic segments presenting a side view of the ventral appendages as far as known. Some of the sections affording data on the limbs of *Calymene* are illustrated on pls. 26, 27.

Neolenus serratus (Rominger) (See pl. 31) 126

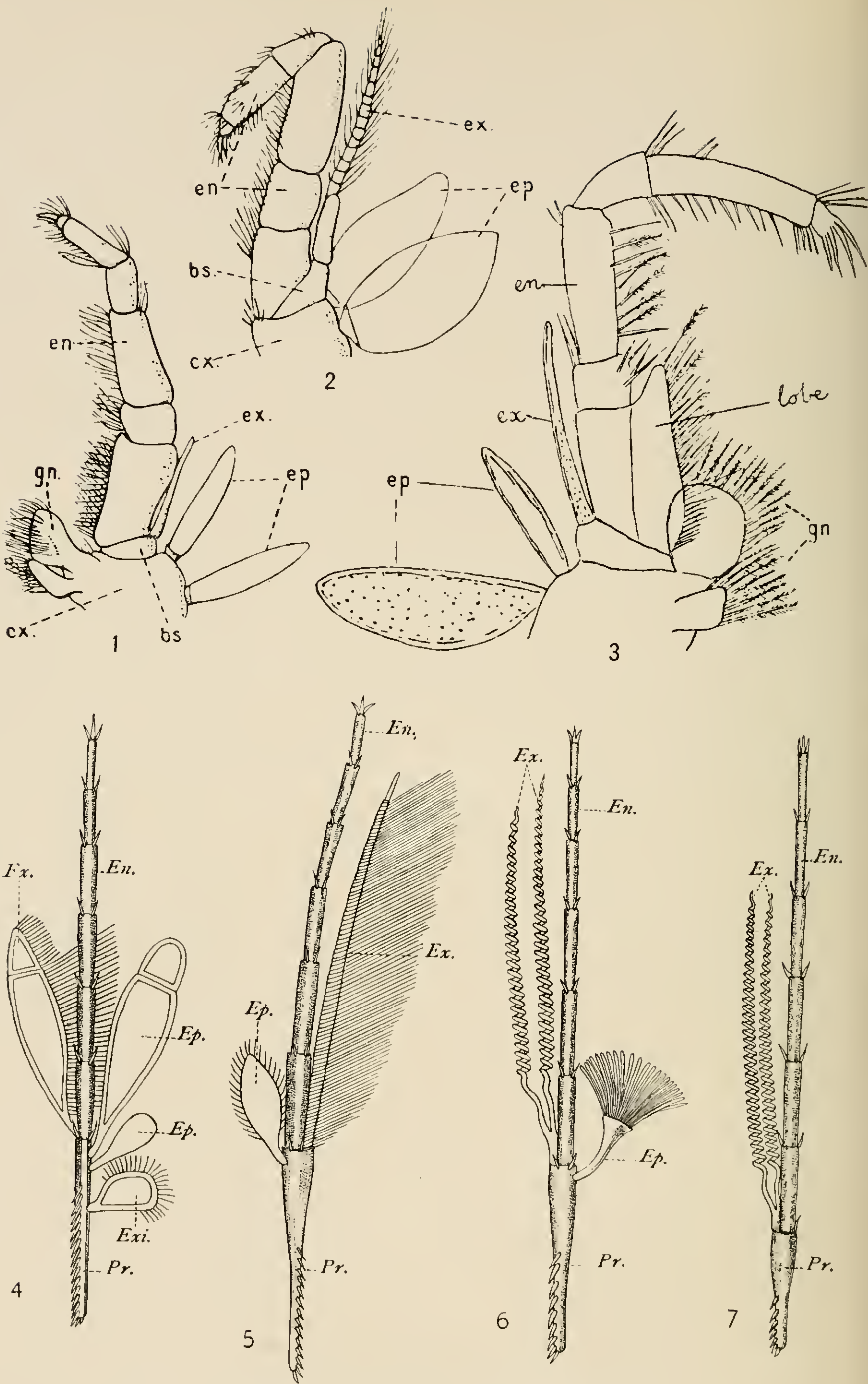
FIG. 3. (× about 3.) Transverse diagrammatic sketch of an anterior thoracic segment presenting a side view of the ventral integument and the limbs.

Triarthrus becki Green (See pl. 32) 135

FIGS. 4-7. (× about 5.) Transverse diagrammatic sections of thoracic segments and appendages. Fig. 4 = posterior side of third segment, showing the strong, jointed arm of the exopodite and its attachment to the distal end of the protopodite; 5 = anterior side of the third thoracic segment and limbs, showing the setiferous exopodite, the endopodite, and the small epipodite; 5*a* = section of the arm of the exopodite, showing the manner in which the setæ are attached to it; 6 = anterior side of the eighth thoracic segment with three enlarged joints on the leg (endopodite); 7 = posterior view at the third segment of limbs of pygidium; the endopodite has five expanded joints and a slender distal joint.



CAMBRIAN AND ORDOVICIAN TRILOBITES
with ventral appendages
Transverse diagrammatic sections



DIAGRAMMATIC SKETCHES OF THORACIC LIMBS

TRILOBITES AND RECENT CRUSTACEANS

DESCRIPTION OF PLATE 35

Legend

en. = endopodite.	bs. = basopodite.
ex. = exopodite.	exi. = exite.
ep. = epipodite.	gn. = gnathobase.
cx. = coxopodite.	

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Anaspides tasmaniæ G. M. Thomson (See text fig. 1, p. 171) 170

FIG. 1. Enlarged diagrammatic outline of second thoracic limb. (After Calman.)

2. Enlarged diagrammatic outline of first thoracic limb. (After Calman.)

Paranaspides lacustris Smith (See text fig. 3, p. 172) 170

FIG. 3. Enlarged diagrammatic outline of first thoracic limb. (After Smith, Proc. Royal Soc. London, Ser. B, Vol. 80, 1908, p. 471, fig. 6.)

Neolenus serratus (Rominger) 126

FIG. 4. Diagrammatic sketch of a thoracic limb to illustrate the several parts and their supposed position in relation to the protopodite.

Triarthrus becki Green 135

FIG. 5. Diagrammatic sketch of a thoracic limb showing the protopodite, exopodite, and supposed epipodite.

Calymene senaria Conrad 147

FIG. 6. Diagrammatic sketch of thoracic limb, showing the protopodite, endopodite, spirals of exopodite, and setiferous epipodite.

Ceraurus pleurexanthemus Green 148

FIG. 7. Diagrammatic sketch of thoracic limb, showing the protopodite, endopodite, and spirals of exopodite.

The diagrammatic sketches of the thoracic limbs of the four genera were prepared for the purpose of comparing them with each other, and also to form the basis of comparison of the limb of *Neolenus* with that of *Anaspides*, text fig. 1, p. 171, and *Koonunga*, text fig. 2, p. 171, *Paranaspides*, text fig. 3, p. 172.

DESCRIPTION OF PLATE 36

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Crustacean limb, genus and species undetermined........................ 154

FIG. 1. (× 20.) Drawing based on photographs of several jointed legs which are preserved on the surface of a small slab of shaly limestone. They are light brown in color and have a polished surface similar to the chitinous legs of recent crustaceans.

1a. (× 20.) Transverse section of a third joint that has been worked out of the rock.

2, *2a-d.* (× about 8.) Reproduction of photographs of several of the legs on the slab of limestone. Fig. 2 has eight joints, fig. *2a* six, figs. *2b* and *2c* eight; fig. *2d* is a fragment preserving four joints. The distal joint has been outlined in fig. *2c*. U. S. National Museum, Catalogue No. 65532.

Formation and locality.—Ordovician: (Trenton) *Cynthiana* limestone. Bank of Ohio River below Covington, Kenton County, Kentucky.

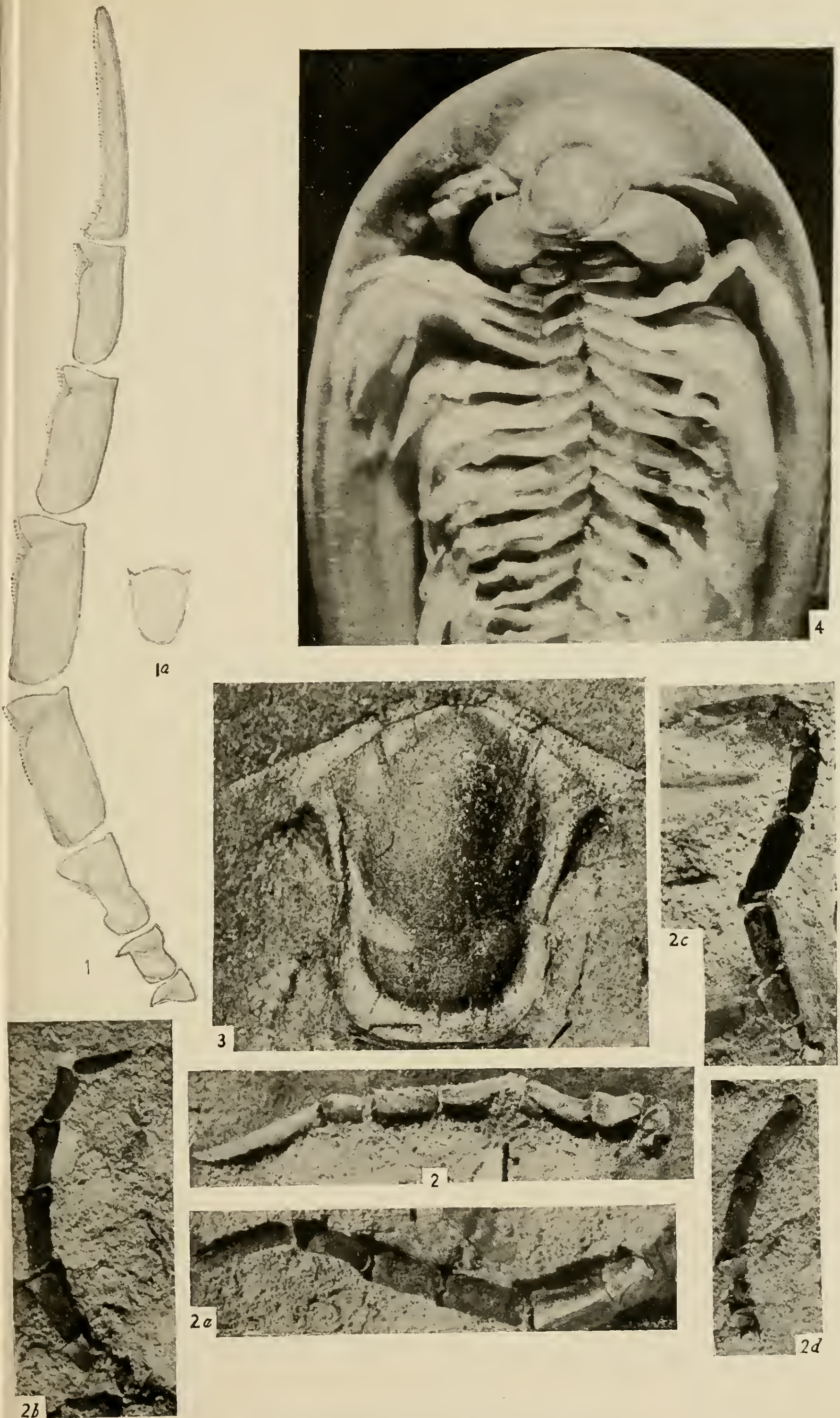
Neolenus serratus (Rominger).................................... 126

FIG. 3. (× 8.) A small, nearly entire hypostoma enlarged. U. S. National Museum, Catalogue No. 65533.

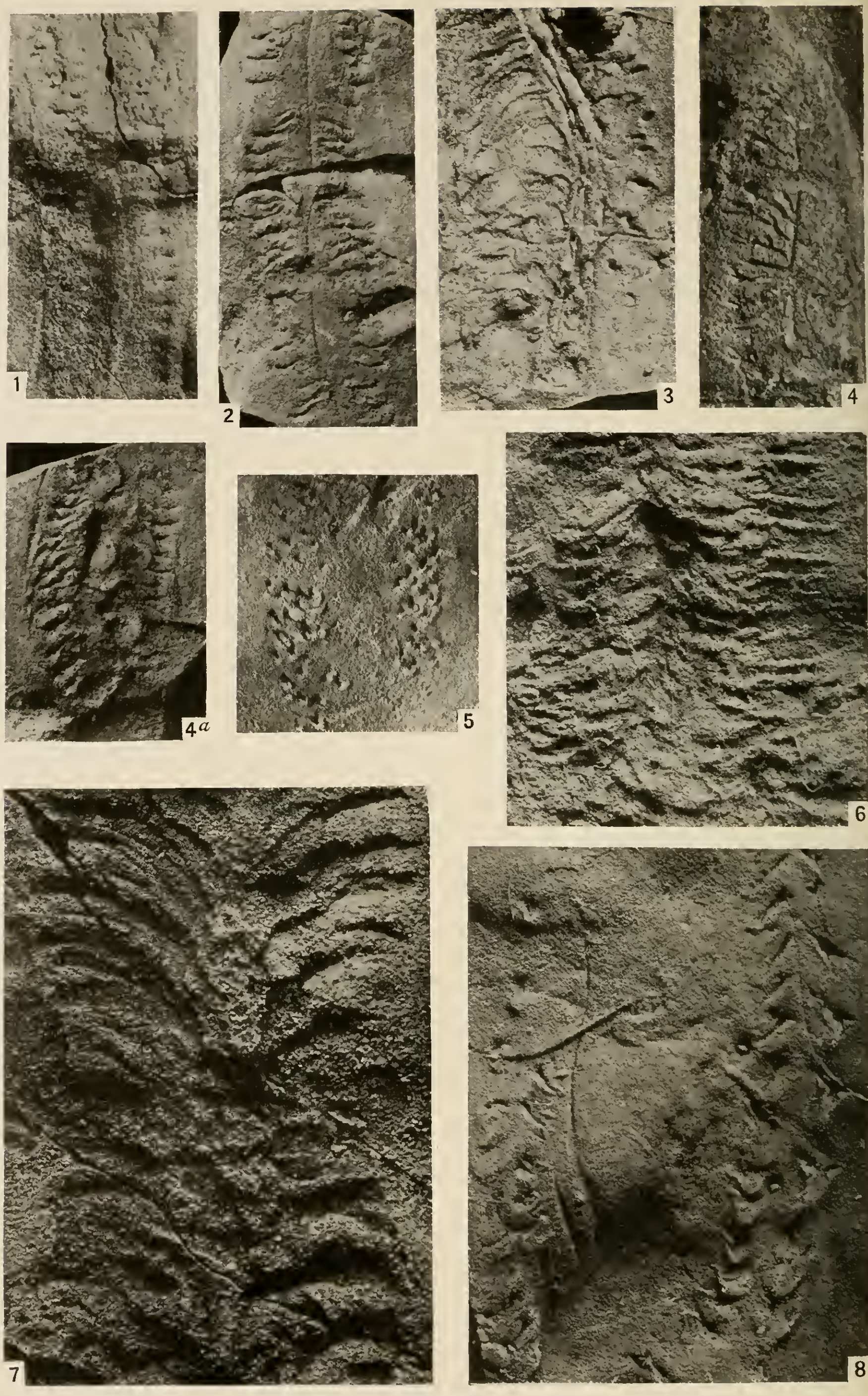
Formation and locality.—**35k**, Middle Cambrian: Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, above Field, British Columbia, Canada.

Apus lucasana Packard.. 169

FIG. 4. (× 6.) Ventral view of carapace with hypostoma, cephalic and 12 pairs of the trunk limbs slightly pushed over so as to show their form and arrangement. The *Apus* is from a pond near Aurora, New York.



CRUSTACEAN LIMB, NEOLENUS AND APUS



TRILOBITE TRACKS AND TRAILS

DESCRIPTION OF PLATE 37

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Trilobite tracks and trails.. 174

FIG. 1. (Natural size.) Trail on surface of fine compact sand where the legs were used to push the dorsal shield along while the edges of it were resting on the sand, thus leaving a slight marginal groove and a central groove made probably by the median projection at the end of the pygidium. U. S. National Museum, Catalogue No. 66136.

2. (Natural size.) Imprint of short strong legs with an apparent bifurcation at the outer end. Some of them are tripartite which indicates a central claw with the two spines. U. S. National Museum, Catalogue No. 66137.

3. (Natural size.) Trail where the legs on the left side left their imprint for nearly their entire length, and on the right side only the distal joint and terminal claw touched the sand. After the trilobite had made the trail a worm came up through the sand and followed along in the center of the trail for some distance. U. S. National Museum, Catalogue No. 66138.

4. (Natural size.) A trail essentially similar to that of fig. 2, but with the imprint of the leg from the median line out to its distal extremity. The division of the impression near the outer end may have been caused by one of the other legs leaving its impression at a different angle, or it may have been that the exopodite had a sufficiently strong supporting arm to make an impression. U. S. National Museum, Catalogue No. 66139.

4*a*. (Natural size.) Trail cut deeper into the sand than those represented by figs. 1-4. U. S. National Museum, Catalogue No. 66140.

The specimens illustrated by figs. 1-4, 4*a*, are from locality **73**, Middle Cambrian: Tapeats sandstone; Tonto group; Quagunt Valley, Grand Canyon of the Colorado River, Arizona.

5. (Natural size.) This track was made by the claw and end of the distal joint of the legs when the animal was ascending a slight muddy slope. U. S. National Museum, Catalogue No. 66142.

The specimen represented by fig. 5 is from locality **8u**, Middle Cambrian: Flathead sandstone and shales; 4 miles (6.4 km.) above Walker's ranch in canyon, North Fork of Dearborn River, Lewis and Clark National Forest, Montana.

5. (Natural size.) Cast of a trail made by the protopodites and legs, the latter showing to the right beyond the cast of the deep, narrow impressions made by the protopodites. U. S. National Museum, Catalogue No. 66141.

From locality **3j**, Middle Cambrian: Wolsey ? shale; about 6 miles (9.6 km.) west-northwest of Scapegoat Mountain on the Continental Divide between Bar Creek and the headwaters of the south fork of the North Fork of Sun River, Powell County, Montana.

Trilobite tracks and trails—Continued.

FIG. 7. (Natural size.) Trail over relatively soft surface of sand where the protopodites have sunk into the sand, crowding it up along the median line. There are a few traces of the leg beyond portion of the trail illustrated. U. S. National Museum, Catalogue No. 66143.

The specimen illustrated is from the Middle Cambrian: Tapeats sandstone, on Shinimo Creek, below Powell's Plateau, Grand Canyon of the Colorado River, Arizona.

8. (Natural size.) Trail made on surface of ripplemarked, very fine sand, where only the ends of the legs touched the sand. U. S. National Museum, Catalogue No. 66144.

From locality **73a**, Middle Cambrian: Tapeats sandstone; in Chuar Valley, Grand Canyon of the Colorado River, Arizona.

DESCRIPTION OF PLATE 38

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Trilobite tracks and trails.. 174

FIGS. 1 and 2. (× 3.) Track where the legs appear to have burrowed down into the sand so as to leave a relatively deep impression. U. S. National Museum, Catalogue No. 8616.

The specimen illustrated is from the Tonto shale, above the Tapeats sandstone; Grand Canyon of the Colorado River, Arizona.

This specimen was illustrated by Dr. C. A. White in Palæontology, Geog. and Geol. Expl. and Surv. west 100th Merid., Pt. 1, Vol. IV, 1878, pl. 1, figs. 6*a-b*.

3. (Natural size.) Trail in which the impressions made by the protopodites are preserved, also the edge of the dorsal shield. There are no traces of the imprints of the legs beyond the dorsal shield. U. S. National Museum, Catalogue No. 66145.

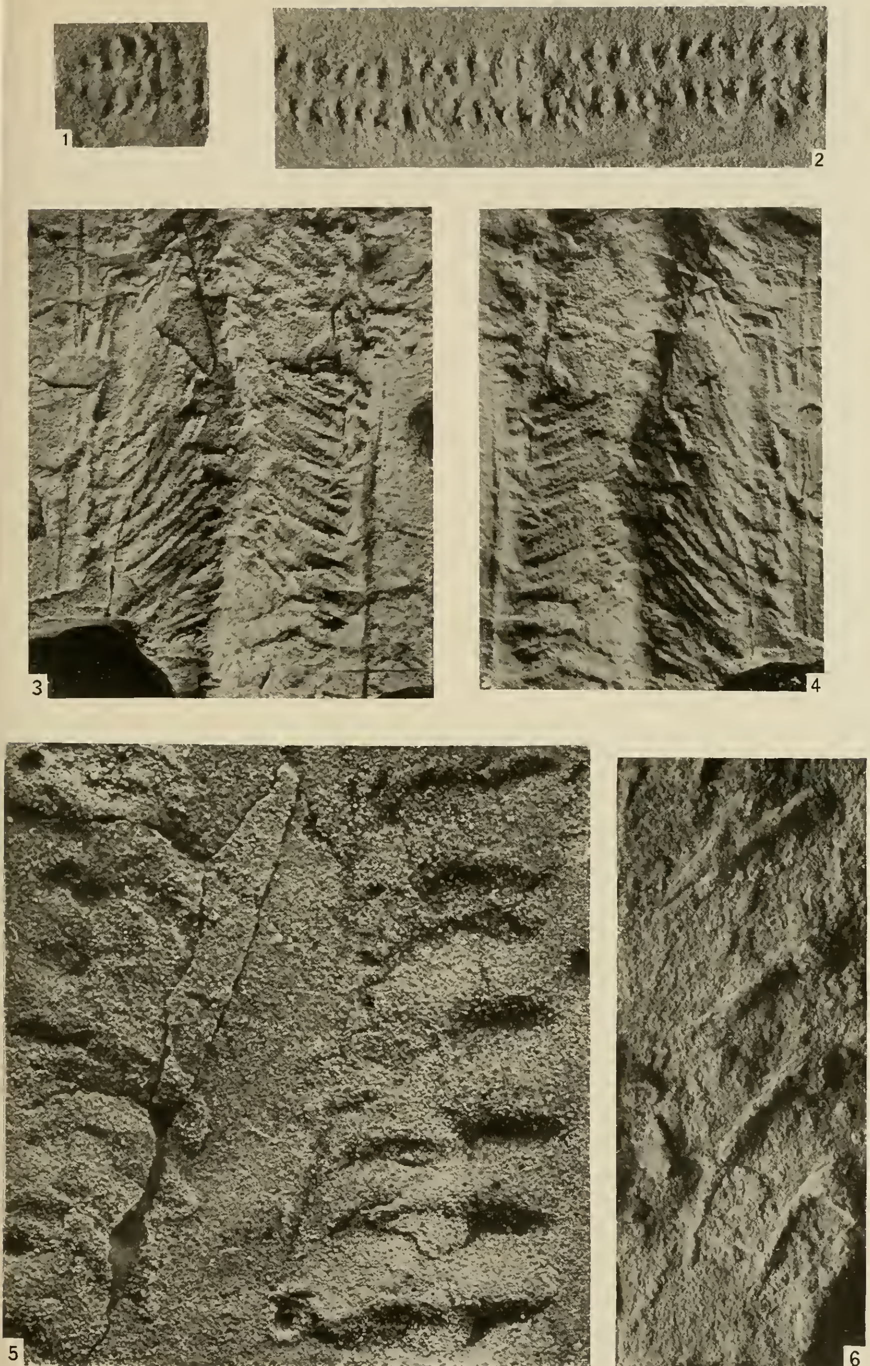
The specimen illustrated is from locality **115**, Upper Cambrian: Lower beds at L'Anse Cove, east side of Great Belle Isle, Conception Bay, Newfoundland.

4. (Natural size.) Photograph of the cast of the trail represented by fig. 3.

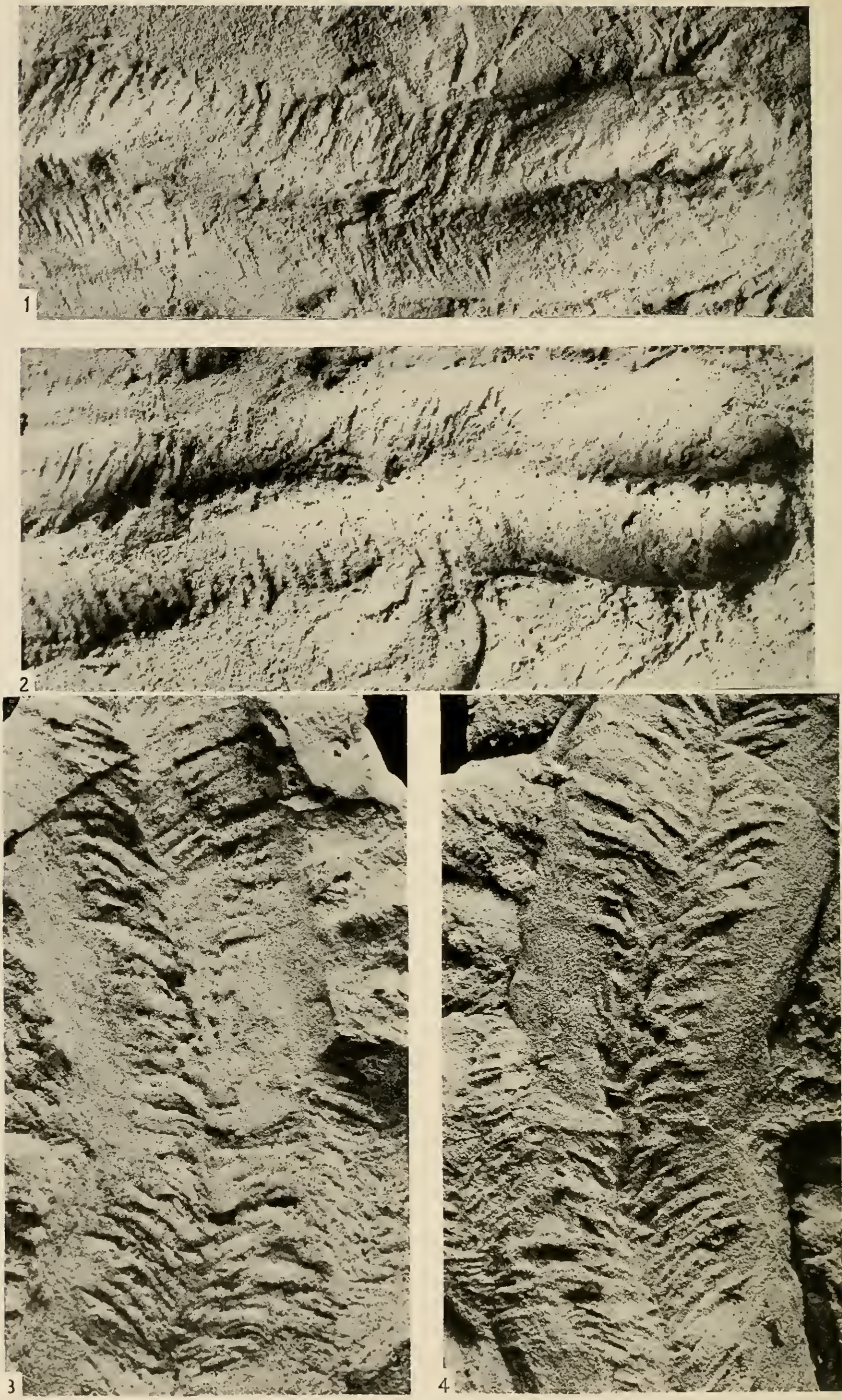
5. (Natural size.) Portion of a trail in which the imprints of the protopodites and part of the inner joints of the leg are preserved. U. S. National Museum, Catalogue No. 66146.

6. (× 2.) Fragment of a trail preserving the cast of the impression of the end of the protopodite and portions of the legs. U. S. National Museum, Catalogue No. 66147.

The specimens represented by figs. 5 and 6 are from the Middle Cambrian: Tapeats sandstone, on Shinimo Creek, below Powell's Platêau, Grand Canyon of the Colorado River, Arizona.



TRILOBITE TRACKS AND TRAILS



TRILOBITE TRACKS AND TRAILS

DESCRIPTION OF PLATE 39

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Trilobite tracks and trails.. 174

FIG. 1. (Natural size.) Natural cast of a trail in which at the right of the figure the trilobite evidently burrowed deeper into the sandy mud. It then moved a short distance and again went deeper into the mud. This is better shown by the fig. 2, which is of a cast made of the specimen represented by fig. 1, and which represents the actual trail made by the animal. U. S. National Museum, Catalogue No. 66148.

2. (Natural size.) Plaster cast made of the natural cast illustrated by fig. 1. This shows the original trail of the animal made on the surface of the muddy sand.

The specimen represented by figs. 1 and 2 is from locality **73a**, Middle Cambrian: Tapeats sandstone; in Chuar Valley, Grand Canyon of the Colorado River, Arizona.

3 and 4. (Natural size.) Trail made on the surface of the sand and natural cast of it represented by fig. 4, which shows the form of the endopodites that made the impressions shown by fig. 3. Fig. 3 is made from a cast made of the natural cast represented by fig. 4. U. S. National Museum, Catalogue No. 66149.

From locality **8u**, Middle Cambrian: Flathead sandstone and shales; 4 miles (6.4 km.) above Walker's ranch in canyon, North Fork of Dearborn River, Lewis and Clark National Forest, Montana.

DESCRIPTION OF PLATE 40

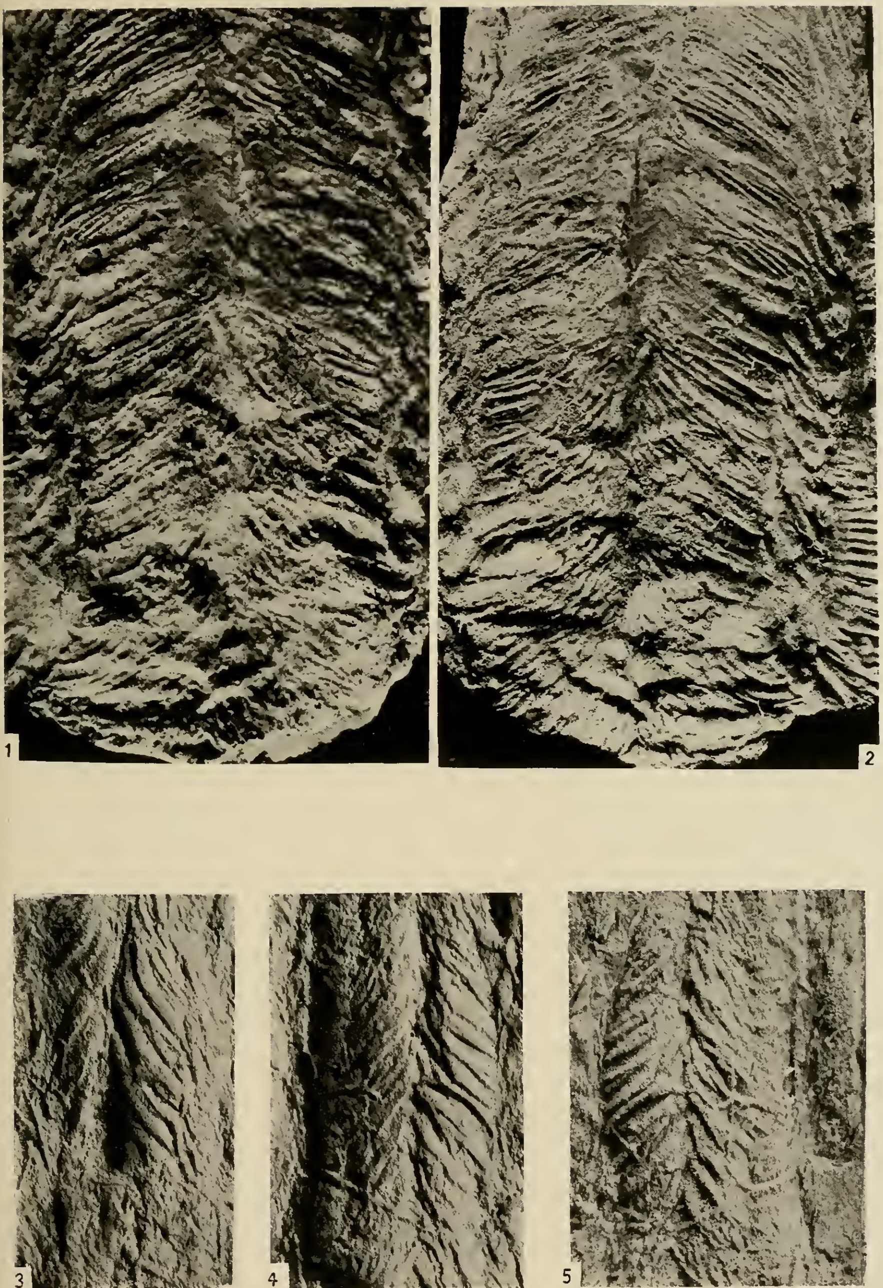
FIGS. 1 and 2. (Natural size.) Fig. 1 is from a photograph of a cast made of the natural cast represented by fig. 2 of a trail in which the protopodites have left their impressions; also on the left side there are traces of the legs (endopodites). Fig. 2 reproduces the ventral side of the appendages making the impressions. U. S. National Museum, Catalogue No. 66150.

From locality **114b**, Lower Ordovician: sandstone 1 mile (1.6 km.) north of L'Anse Cove, Great Belle Isle, conception Bay, Newfoundland.

3, 4, and 5. (Natural size.) Figs. 3 and 4 represent portions of the natural cast of a trail which is unlike any of the other trails illustrated. The natural trail is shown by fig. 5. U. S. National Museum, Catalogue No. 66151.

From locality **366n**, Upper Cambrian: Lower *Lingula* flags at Portmadoc, Merionethshire, North Wales.

This track is described as *Cruziana semiplicata* by Salter.



TRILOBITE TRACKS AND TRAILS

TRILOBITE TRACKS AND TRAILS

DESCRIPTION OF PLATE 41

FIGS. 1 and 2. (Natural size.) Fig. 1 is a natural cast of a large trail crossed by a smaller one where the animal was half burrowing along in relatively soft sediment, stopping frequently and leaving a trail such as that shown by fig. 2.

It must be recalled that frequently trails were made in semiplastic mud and that later on sand was washed into the trails, thus making casts, in which when the subsequently formed rock is exposed to weathering the shale formed by the mud dissolves and disappears, leaving the cast of the trail as shown in this instance by fig. 1. U. S. National Museum, Catalogue No. 66152.

From locality **73a**, Middle Cambrian: Tapeats sandstone; in Chuar Valley, Grand Canyon of the Colorado River, Arizona.

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DESCRIPTION OF PLATE 42

Trilobite tracks and trails.. 174

FIGS. 1 and 2. (Natural size.) Right and left side of a portion of a broad track (13 to 15 cm.) showing trifid termination of the individual imprints formed probably by the claw and spines of the distal extremity of the leg. The central portion of the track has been cut out in order to bring the imprints of the two sides within the limits of the plate. U. S. National Museum, Catalogue No. 58593.

The specimen represented is from locality **220b**, Upper Cambrian: Potsdam sandstone; near Beauharnois, Province of Quebec, Canada.

These tracks were illustrated on pl. 47, Vol. 57, Smithsonian Miscellaneous Collections, 1912.

3. (Natural size.) Photograph of a natural cast of annelid trails, trilobite trails, etc., which illustrate the abundance of annelids in and on the muddy surface of the bottom over which the trilobite was foraging for food. U. S. National Museum, Catalogue No. 66153.

From locality **8u**, Middle Cambrian: Flathead sandstone and shales; 4 miles (6.4 km.) above Walker's ranch in canyon, North Fork of Dearborn River, Lewis and Clark National Forest, Montana.

1

2

3

TRILOBITE TRACKS AND ANNELID TRAILS

INDEX

The references in **heavy-face** type refer to the pages upon which the genera and species are described and figured.