SOME NEW MIDDLE CAMBRIAN FOSSILS FROM BRITISH COLUMBIA

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The Middle Cambrian faunas of British Columbia, particularly the marvelous assemblage of organisms from the Burgess Pass, discovered by Dr. Charles D. Walcott in 1910 and studied by him throughout the remainder of his life, continue to afford most interesting subjects for research. A small group of these fossils from the Burgess shale and the Stephen formation was sent me some time ago by the authorities of the United States National Museum for further study. In their general appearance they suggest graptolites, and as such had been laid aside for future study by Doctor Walcott. Upon close study, however, they have proved to be an unusually interesting and at the same time difficult assemblage of fossils, none of which belong to true graptolites. It is with the full realization of the tentative nature of the determinations that the following results of my studies are published.

ALGAE

DICTYOPHYCUS GRACILIS, new genus and species

Plates 1, 2

This form consists of a reticulate network of delicate fibers, which, looked at with the naked eye, strongly suggests *Dictyonema*. With the aid of a microscope, however, the organism is seen to have no trace of thecae or of any other graptolitic structure except a number of irregularly distributed circular pores, the occurrence of which may or may not be accidental. The fibers themselves lack the strong consistence and glossy appearance that the chitinous tests of graptolites, as a rule, possess and suggest rather the softer tissue of plant life.

A study of the changes that take place in recent algae when decay sets in reveals the fact that in a form such as *Chlorodictyon foliosum* J. G. Agardh, one of the Caulerpaceae, the originally flat, broad, leaflike expansions of the thallus become so perforated by the decay

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of the interstitial tissue that the remaining portion is left as a network of fibers. The same thing happens in algae like *Dictyoneuron californicum* Ruprecht, whose broad leaf-like thallus bodies, provided with a reticulate system of strengthening ribs, upon decay form reticulate masses of fibers. Dr. H. D. House, State botanist of New York, informs me that such algal remains are very common along seashores.

It would be quite possible to refer this form to either *Chlorodictyon* or *Dictyoneuron* if it were not for the fact that one of the specimens retains a broadly oval, brownish, carbonaceous film within the network of fibers, making it probable that the form had a continuous thallus expansion, a feature that would distinguish it from either genus. (See pl. 2, fig. 3.)

Description.—Thallus oval to broadly flabelliform—attaining in the largest specimen, not wholly preserved, a width of 5 cm. and a height of 4 cm.—strengthened by a close network of supporting ribs or fibers, which, as a rule, are the only parts preserved. These fibers are for the most part entirely smooth and range in width from 0.25 mm. to 0.5 mm. In some portions pores are present, which, since they lack a regular arrangement and are the same size as the grains of the rock, are probably not a part of the organic structure but are merely due to the rock texture. The arrangement of the fibers varies from very irregular meshes in some portions to quite regularly rectangular meshes in others.

Since the bases of all specimens are broken, no rhizoids have been observed; nor has anything suggesting sporangia been seen.

Occurrence.—Middle Cambrian, Burgess shale (Loc. 35K), Burgess Pass, near Field, British Columbia.

Holotype and paratypes.—U.S.N.M. No. 83483.

Remarks.—Although we have compared the organism here described with *Chlorodictyon*, one of the Caulerpaceae, and with *Dictyoneuron*, one of the Laminariaceae, no definite characters that would permit one to refer the fossil to either of the two families have been noted. We consider it probable, however, that if the fossil is an alga it must belong to one of these two families, which are so prominent in the marine flora of to-day.

H. DROZOA

CHAUNOGRAPTUS SCANDENS, new species

PLATE 2, FIGURES 4 TO 6; PLATE 3, FIGURE 3; PLATE 4, FIGURE 1

Grouped about a specimen of the sponge *Tupoia lineata* Walcott are some rhabdosomes of a "graptolite" that quite obviously used the

sponge to climb upon. Since one specimen of this graptolite has both sides preserved, it is referred on the basis of its habitus to *Chaunograptus*.

Description.—Rhabdosomes consisting of slender (0.12 mm. wide), straight stems (hydrocaulus 25 mm. long), which branch either very infrequently or only near the base. Thecae short, conical, narrowing distinctly toward base (projecting portion 0.7 mm. long), alternating on the hydrocaulus and projecting irregularly at various angles ranging from 90° to 20°; though most often at right angles they are at times sharply curved upward. Aperture circular, slightly expanded. Periderm apparently smooth. Gonothecae not distinguished.

Occurrence.—Middle Cambrian, Burgess shale (Loc. 35K), Burgess Pass, near Field, British Columbia.

Holotype and paratypes.—U.S.N.M. No. 83484.

Remarks.—This species resembles *C. novellus* Hall, the genotype, more than any of the other species referred to the genus. (Ruedemann, 1908, p. 223.) Though all the species are repent upon foreign bodies, *C. scandens* seems not to have been so closely attached as the others.

In the description of the graptolite *Mastigograptus* (1908, p. 213) I pointed out the fact that it was closer to the hydrozoans in the character of its thecae than any other form. Later (1919) Chapman described two species (*Archaeolafoëa longicornis* and *Archaeocryptolaria skeatsi*) from the Ordovician of Australia, which, on the basis of the form of the hydrothecae and the discovery of the gonothecae attached to the hydrosome, in at least the first of the two, he unhesitatingly referred to the hydroid coelenterates of the order Calyptoblastea and the family Lafoëidae. He likewise placed *Mastigograptus* Ruedemann in the same order and family, and pointed out that *Chaunograptus* also approaches his forms so closely that it is referable to the same group.

In the basal constriction of the thecae and the irregular angles of divergence of the thecae from the hydrocaulus the new species of *Chaunograptus*, even more than those previously described, suggests relationship to the hydroids of the campanularid type. It differs sharply in this respect from the true graptolites, the Dendroidea and Graptoloidea, which according to evidence now accumulating belong to an entirely different phylum.

The fragments reproduced in Plate 2, Figures 4 and 5, indicate the presence in the Burgess shale of a hydroid larger than *Chaunograptus scandens*. The fossil is, however, too fragmentary to warrant a description.

CRUSTACEA

MARRIA WALCOTTI, new genus and species

PLATE 4, FIGURES 2, 3; PLATE 5

Two specimens (from the famous fossil bed on Mount Stephen, Loc. 14s), when seen with the naked eye are amazingly suggestive of a graptolite such as *Nemagraptus gracilis*. They were laid aside by Doctor Walcott with the other supposedly Cambrian graptolites. After the study of these two specimens on which the following description and discussion are based, further search yielded five more incomplete ones, most of which had been regarded as fragments of the sponge *Pirania muricata* Walcott.[1]

When the specimen selected as the holotype was studied under the microscope it lost its graptolitic aspect and revealed itself as the segmented body of a crustacean with large regularly jointed arms, each joint of which gives rise to a side branch. In other words, it is a bizarre crustacean, its immense swimming feet serving to distinguish it from all other Cambrian crustacean genera.

Inasmuch as *Marrella* may become a synonym, if my subsequent contentions are sustained, and thus nullify the compliment that Doctor Walcott wished to pay his friend Prof. John E. Marr, of St. Johns College, Cambridge University, I am calling this new crustacean *Marria* in order to perpetuate the compliment.

Description.—Body small (7.5 mm. long and 3.5 mm. wide in compressed condition), elliptical in outline, with truncated front. Carapace of head (or cephalothorax?) of subquadrangular outline (about 3.25 mm. long and 3.5 mm. wide) occupying half of the body. Postcephalic portion (either thorax + abdomen or abdomen only) consisting of seven (or possibly eight) simple segments, the first of which is 0.7 mm. long, the others decreasing slightly in length as well as regularly in width. There is no trace of a telson or of caudal styles. The frontal portion of the supposed head possesses a subtriangular depression, the base of which is in front. Near the apex is a small tubercle with a central depression, strongly suggesting the presence of an eye. Since the surfaces of the head and segments show no sculpture, they were apparently smooth. On the head, to the left and right and behind the eye, are several irregular nodes, which may be incidental to the preservation. There is also a pair of black spots or minute tubercles on either side of the eye. A distinct tubular depression, suggesting the alimentary canal, begins behind the eye, where it is somewhat wider, and extends backward to the first segment.

The most important feature of this organism is the presence of the two pairs of immense swimming appendages, both of which

[1] Walcott, C. D., Smithsonian Misc. Coll., vol. 67, p. 298, pl. 79, fig. 1, 1920.

proceed from the anterolateral corners of the head. Both are fundamentally biramous, dividing into two principal branches, which in turn send out a series of secondary, filamentous branches bearing setae on one side. The first pair, which is the shorter, is directed forward, the second sideways. Only one of the first pair (on the right side) of swimming appendages is preserved. The protopodite is short and stocky. One of the branches (exopodite) has only the base preserved; the other branch (endopodite) bears four or five (one displaced) long, flexuous, secondary branches and shows the base of a fifth or sixth. The series of secondary branches on the exopodite from the four bases shown on the stump in front of the head, as drawn in the restoration (pl. 5), are conjectural. We can not determine whether this first pair of appendages represents the first pair of antennae or the second; if the latter, the first pair of antennae may have been small or very tenuous.

The second pair of swimming appendages is by far the larger of the two and may either represent the second pair of antennae or may correspond to the mandibular foot of the nauplius. (See under Relationships.) The protopodite is again short and powerful and appears to consist of two joints. The forward division of the foot, which we take to be the exopodite, is extended horizontally and reaches a length of 20 mm.; the number of its joints can not be definitely established. On one side it bears 7 to 11 thin flexuous subbranches (exites) and on the other about 6, which branch off nearer the base. The posterior division of the swimming foot, according to our view the endopodite, curves backward nearly parallel to the body, giving off about 10 slender, thin endites, about 14 mm. long, on the outer side of the branch, and terminates in a similar but shorter (9.5 mm.) endite.

All the exites and endites are provided with short setae on one side. These, however, may be only the bases of longer bristles, since there is one fragment that retains long stiff setae on the portion of the swimming appendage preserved.

On the left side are three simple legs, two of which undoubtedly proceed from the underside of the head, and the third (not drawn on restoration) appears to do so. On the right side are the bases of what appear to have been abdominal feet, the stumpy second, however, being doubtful. There is no evidence of a biramous structure or of gills, the exopodites apparently alone protruding beyond the body.

Occurrence.—Middle Cambrian, Stephen formation (Loc. 14s), Mount Stephen, British Columbia.

Holotype and paratypes.—U.S.N.M. No. 83485.

Relationships of Marria.—There is no fossil crustacean that can be directly compared with *Marria walcotti.* The only fossil form that

to our knowledge in a general way resembles it is the grotesque *Bostrichopus antiquus* Goldfuss of the lower Carboniferous (Culm.) of Nassau, Germany. (See fig. 1.) The one specimen known to have been found is preserved in the Bonn collection. Good figures are given in part 1 of Roemer's Lethaea geognostica (1876), pl. 38, figs. 10a–b, and recently (1929) Steinmann has redescribed it, giving a restoration. According to Goldfuss's figure this minute crustacean is surrounded by a corona of 60 extremely thin, flexuous, filamentous appendages, radiating from three (or four?) short basic appendages, located behind the head. Steinmann reconstructs the form as having the filamentous feet distributed evenly in pairs on the segments of the body and concludes that the species belongs to an entirely extinct class of crustaceans. Even though the swimming feet have a similar structure, our species is still different in the form of the body, especially of the head, which bears two large eyes in *Bostrichopus*.

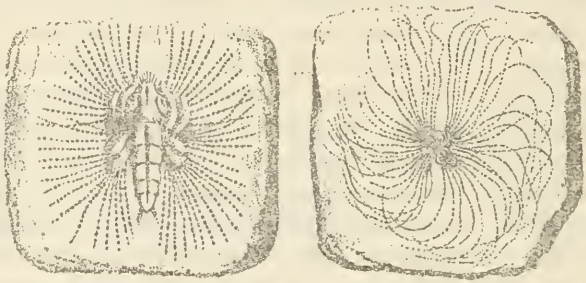

FIGURE 1.—*Bostrichopus antiquus* Goldfuss. Right figure, entire specimen, natural size; left, enlargement of body and bases of limbs. (After Roemer)

The outstanding characters of *Marria* are the very simple body and the enormous development of the antennae (see *postea*), which indicates an extreme adaptation of an otherwise primitive form.

The great age of the form and the fact that a similar development of the antennae (at least of the second pair) takes place in at least two orders of the Branchiopoda, namely, the Phyllopoda and the Cladocera, as well as in the next order, the Copepoda, make it probable a priori that the species represents a generalized type, not directly referable to any of the recent orders of crustaceans. Positive determination of its relationship is prevented by the fact that the mandibles and maxillae remain unknown and that the subdivisions of the body can not be definitely made out. How uncertain are the determinations of Cambrian crustaceans from incomplete remains is clearly evidenced by the fact that Walcott's determinations of the Burgess shale crustaceans were challenged by Fedotov (1925) and Fedotov's in turn by Henricksen (1928).

Other important characters of *Marria* are the immense development of two swimming arms (first and second pair of antennae, see *postea*), the large unsegmented head with carapace (possibly cephalothorax) bearing a single eye, five pairs (or less) of legs, a simple abdomen, consisting of about seven segments, and the absence of a telson.

It is customary to refer the earlier Paleozoic crustaceans to the suborder Phyllopoda of the order Branchiopoda, because these are the oldest and most primitive crustaceans. [The recent genus *Apus*, or *Lepidurus*, has been traced to the Permian (Ruedemann, 1922).] There is indeed a close resemblance to the family Limnadiidae of the Phyllopoda—particularly to *Limnetis* in the biramous, strongly developed second antennae, the single (not bivalved) carapace, the fused compound eyes in the middle of the head, and the small number of thoracic feet. Although a telson is present in *Limnetis*, in *L. brachyura* it is so small that this species appears but little different from our specimens in this respect. The body of the Limnadiidae is, however, laterally compressed and the carapace covers most of it.

According to common consensus of opinion the Limnadiidae lean toward the second suborder of the Branchiopoda, the Cladocera. *Marria* also has important characters in common with Cladocera, namely, the strong development of the biramous second antennae into principal organs of locomotion, the fused compound eyes, and the short body with a small number of thoracic limbs. Though the Cladocera have a telson, it is variable in size and in some species much reduced. The carapace is likewise variable, for while it is most frequently a bivalve shell inclosing the whole postcephalic region of the body, it may be reduced to a mere brood pouch, as in Leptodora. The segmentation of the body is little pronounced, if not obscure, the thorax bearing as many pairs of limbs as there are segments; the abdomen having but three segments, bearing no limbs, but with a telson. The head in the Cladocera, however, is always bent downward so that the first pair of antennae and the median eye are on the ventral side.

It will be seen that our form, though not directly referable to the Cladocera, agrees well with that order in the development of the second antennae, the carapace (aside from its common bivalve form in the Cladocera), the fused eyes, the small number of segments, and thoracic limbs. It would seem to differ in not possessing the downward bend of the head or a telson.

Our species also invites comparison with the second order of crustaceans, the Copepoda, in regard to the possible retention of the single nauplius eye, the strongly developed biramous second pair of antennae, and the possible absence of a carapace. The Copepoda

differ from *Marria* in having five pairs of biramous feet, the first of which is attached to the cephalothorax and the others to the thoracic somites. On the other hand, the strong development of plumed hairs in the pelagic forms may well be duplicated in *Marria*. Some of the members of the family Peltiidae of the suborder Podoplea have even flattened bodies, somewhat like isopods and probably *Marria*.

Finally, the close resemblance of our form to the nauplius of many crustaceans, among them even the Cirripedia and Malaco-

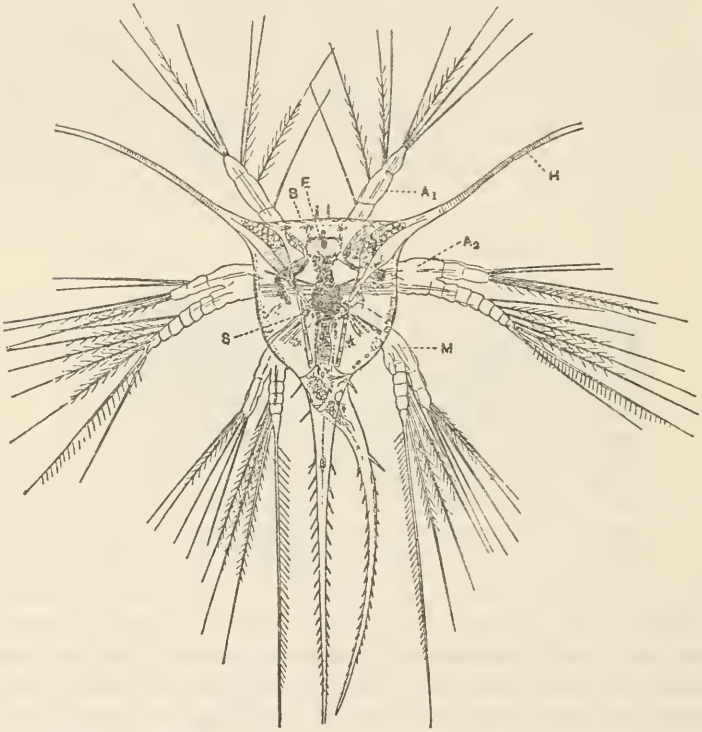

FIGURE 2.—Nauplius larva of *Lepas fascicularis*, ×10. A_1, A_2, First and second antennae; B, brain; E, eye; H, frontolateral horn; M, mandible; S, stomach. (After Groom)

straca, is undoubtedly most striking. These bear not only a single eye but also two pairs of large biramous swimming legs, formed by the second pair of antennae and the mandibles. These biramous limbs, as, for example, in the nauplius of *Lepas* (see fig. 2), bear a large number of long spines, which in turn are set with stiff setae, the whole producing an organ strangely resembling that of *Marria* in which the spines are further developed into jointed secondary branches (endites and exites). As we can not be certain that the two pairs of swimming limbs of *Marria* represent the first and

second pairs of antennae, it is possible to assume that they may be the second antennae and mandibles and that we see in the nauplius, and still more so in the following protozoaean larva of the Eucarida, a recapitulation of an ancestral *Marria*. We can visualize our species making its way through the water in a jerky or saltatory and more or less irregular manner, like most of the crustaceans that have large biramous swimming legs and short bodies.

As none of the crustaceans here used for comparison, except the nauplius and protozoaean stages of later crustaceans, possesses a like development of the two large biramous swimming limbs, it appears necessary to consider *Marria* not only as a member of a new family, the Marriocaridae, but even of a distinct suborder of the Entomostraca, the Marriocarida.

MARRELLA SPLENDENS Walcott

PLATE 3, FIGURES 1, 2; PLATES 6, 7

Marrella splendens WALCOTT, Smithsonian Misc. Coll., vol. 57, p. 193, pls. 25, 26, 1912.

Marrella splendens RAYMOND, Mem. Connecticut Acad. Sci., vol. 7, p. 155, fig. 32, 1920.

Marrella splendens WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 4, p. 170, 1921.

By far the most striking and bizarre crustacean discovered by Walcott in the Burgess shale is *Marrella splendens*. In contrast to its small carapace are its two pairs of massive curved hornlike appendages, the anterior pair of which projects sideways, and the posterior pair is directed backward. Walcott placed this form with the trilobites in a separate family of an unknown order, stating (1912, p. 192) that this family (Marrellidae) "is less primitive than the Apodidae and may be considered as near the Trilobita." This determination has been challenged by some of the authors who have discussed the crustaceans of the Burgess shale. Raymond (1920, pp. 115–117) states: "None of the illustrations so far published shows biramous appendages on the cephalon. This, coupled with the presence of tactile antennae, makes its reference to the Trilobita impossible, but the present interpretation indicates that it was closely allied to them." Raymond places *Marrella* with the Isopoda and gives a restoration of the ventral side (fig. 32, p. 116), showing two similar pairs of antennae (antennules and antennae) and three pairs of simple legs (the mandibles, first and second maxillae) on the cephalon. Another authority, Fedotov (1925), also removes the genus from the trilobites, considering it a typical phyllopod of the order Conchostraca, very close to the Cladocera but more primitive than the recent forms. K. L. Henricksen (1928), according to Richter's review, arrived at the following conclusions: *Marrella* does

not possess a carapace, and as a result of a wrong determination of an unmovable head spine as "antennule" the appendages of the head have been misunderstood. The only character it has in common with the trilobites is that all segments of the trunk bear legs. All other characters, among them the possession of A_2, oppose its reference to the trilobites and point rather to the Notostraca (with exception of the strong development of A_2, the division of the legs, the absence of a carapace). Fedotov's suggestion of the relationship of *Marrella* with Conchostraca and Cladocera is nullified by such characters as the flat, free head, the widely separated eyes, and other features. If Walcott considered *Marrella* more highly developed than *Apus*, he reversed the facts, since the lack of division of the legs of *Apus* is a later development. (Fig. 3.) There is nothing similar to it among the trilobites, especially now that Barrande's figure of *Bohemilla*, which could perhaps have been quoted, has been corrected by Klouček. *Marrella* is therefore a primitive branchiopod of still simpler structure than the Notostraca [Richter].

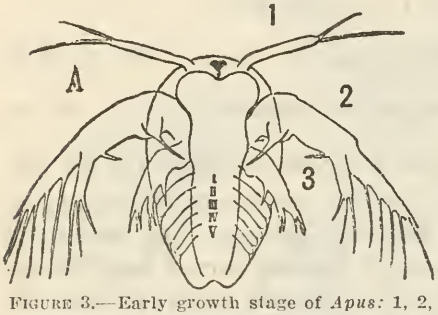

FIGURE 3.—Early growth stage of *Apus:* 1, 2, 3, Cephalic appendages; I, II, III, IV, V, body segments. (From Lang's Comparative Anatomy)

This brief survey shows that *Marrella* has thus far remained a very fractious puzzle and that any additional knowledge concerning it would be most welcome. In fact, a study of the large quantity of material now made available, with the new ultra-violet light method, is most desirable. For, as we shall see presently, here is a Cambrian trilobite freshly molted and exhibiting all its body anatomy!

In the small suite of slabs containing the problematic fossils from the Burgess shale, suggestive of graptolites, was one bearing several specimens of *Marrella splendens*. When these, with the supposed neighboring graptolite, were brought under the Lapworth-Parkes microscope, not only the amazing delicacy of the body but also the distinct identity of the appendages with those of a trilobite became apparent. Likewise the absence of any protecting carapace was too evident to be overlooked. All these observations point toward the fact that the fossil may represent a freshly molted trilobite. Following up this clew, the writer recalled having previously read of such a suggestion, and a search of the literature revealed that Edgar Dacqué, in his brilliant Vergleichende biologische Formenkunde der fossilen niederen Tiere (1923, p. 703), incidental to the discussion of the fact that many trilobite carapaces, especially when heaped

together, are the cast-off tests of molting individuals, had remarked: "It is possible that, among others, the soft-shelled crustaceans described by Walcott from the North American Middle Cambrian as *Marrella* and *Molaria*, whose systematic position could not be established thus far, may be soft-shelled crustaceans, namely, trilobites immediately after molting" (translation).

Working with this suggestion in mind, the writer found from Walcott's figures and the material in the New York State Museum the following evidence:

(1) The tests were so delicate that the animals clearly had insufficient protection. Walcott (1912, p. 194) states that in camp the fossils were called the "lace crab" because of their delicate tissue. It is probable that these young freshly molted individuals, in seeking the protection of deeper and darker places, as molted crustaceans do, had the misfortune of sinking into the trap formed by the water charged with carbonic acid that filled the particular depression in which the Burgess shale with its amazing number of species was deposited, just as the other amazing accumulation of organisms was formed.

(2) Walcott saw the distinguishing characters of his family Marrellidae in the "small subquadrangular carapace," "the two posterolateral spines comparable with the lateral lobes of the carapace of Apodidae," and "the five pairs of appendages of the head."

It is these appendages that furnish the solution of the problem. Though the antennae are clearly the same as those described in the trilobites, the strangest appendages and those most divergent from trilobites are the two pairs of long, thick horns. Walcott termed the first of these "antennulae (?)" and the other "the posterior spines or lobes of the carapace."

In most specimens the first pair projects horizontally, or sideways, coinciding exactly with the frontal margin of the trilobite cephalon, including the genal spines. The other pair is most frequently turned so far backward that it flanks the two sides of the trunk. There are, however, many specimens, and among them some that have suffered little disturbance in preservation, that have the "posterior" spines projecting sideways, as in Walcott's Plate 26, Figures 3 and 5. In this position they correspond exactly in location and outline with the posterior margin of the cephalon.

These two pairs of appendages may, therefore, very well have been the strands of thicker connective tissue, supplied with blood vessels and nerves that lay under the frontal doublure and the posterior furrowed margin of the cephalon and between which the thin membrane of the cheeks was stretched out. This assumption is well supported by the fact that the posterior margins of the anterior appendages and the anterior (outer) margins of the posterior appendages distinctly

show jagged edges, indicating that there a connecting membrane was torn away. This is well shown on the anterior appendages in Walcott's Plate 25, Figures 2 and 6, and Plate 26, Figures 5 and 6, and for the posterior appendages in Plate 26, Figures 1 (fig. 4 and pl. 6, fig. 1, of this paper) and 4.

Still more convincing is the fact that one of the specimens figured by Walcott (pl. 25, fig. 3) retains, on the left side, the cheek of the cephalon itself, together with the eye cavity (ventral side), which shows from under the "appendage" that has separated from the test.

Therefore, if the two pairs of appendages are placed in their normal position, as in the accompanying diagram (fig. 5), the margin of the head of the trilobite is fully outlined. The head in proportion to the trunk is very large—a fact that corresponds to the supposed larval age of the individuals—and the posterior appendages extend into the genal spines.

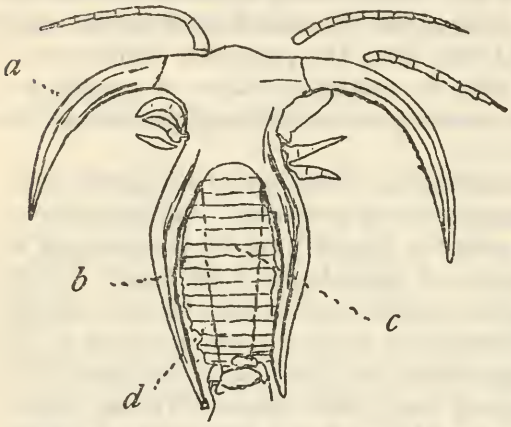

FIGURE 4.—*Marrella splendens*. Walcott's Plate 26, Figure 1. (Letters correspond to those in fig. 5)

The backward direction of the "posterior spines of the carapace" is therefore only a post-mortem position of the fossils.

(3) The antennae (*a''* in Walcott's drawings) are the same as in the other trilobites, as drawn by Beecher and Walcott. They are like those of *Neolenus serratus*, even to the rows of setae.

The so-called "mandibles" (*m*) of Walcott are the same as "the posterior spines of the carapace," when they are in their normal horizontal position, clearly seen in his Plate 26, Figure 5.

The maxillulae (*m'*) and maxillae (*m''*) are the four pairs of longer limbs on the last segments of the carapace, and the same as in *Neolenus serratus* from the Burgess shale and other trilobites.

This brings all "five pairs of appendages" of *Marrella splendens* in complete agreement with the trilobites.

(4) The "strong, small subquadrangular carapace" of *Marrella splendens* is the compressed mass of organs, notably the stomach, contained in the glabella of the trilobite. This is shown in Walcott's excellent Figure 2 of Plate 25, in which the intestine is seen extending backward from the stomach and, where torn, exhibits the intestinal cavity.

(5) The "labrum" (*lb* in pl. 26, fig. 2) is a typical trilobite hypostoma, similar to that of *Neolenus serratus* and *Ogygopsis klotzi.*

(6) The muscle attachments, shown as rows of tubercles on the axial lobe of the abdomen (in pl. 25, figs. 1 and 5; pl. 26, figs. 3 and 4) are exactly the same as repeatedly figured for trilobites, for example, by Hall and Clarke [2] from specimens where the test was either exfoliated or transparent.

(7) According to our material and Walcott's drawings, the legs, both of the carapace and abdomen, are the same as those of trilobites. The gills of the third to fifth legs of the head are, for instance, well

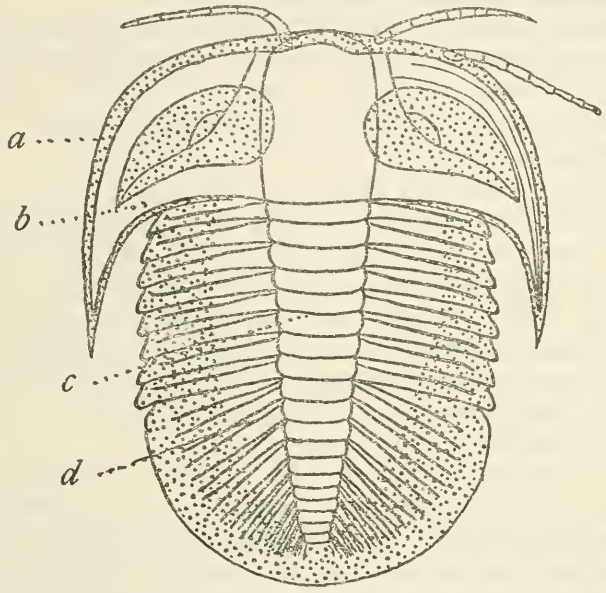

FIGURE 5.—A young trilobite with large cephalon, showing in white the portion preserved in the specimen of *Marrella splendens: a,* Frontal tissue strand of cephalon; *b,* posterior tissue strand of cephalon and genal spines; *c,* axial lobe of thorax; *d,* proximal portion of pleura

shown in Plate 25, Figure 3—on the right side—also in Plate 26, Figures 3 and 4. All legs possess "the jointed leg-like endopodite, a jointed setiferous exopodite, and expanded gill-like epicoxite," which Walcott recognized only for those of the abdomen.

(8) The abdomen in the molted specimens retains only the axial lobes without the pleura, a feature that has aided strongly in obscuring the trilobite nature of *Marrella.* It is probable that, as in the case of the cephalon, the pleura were represented by thin soft membranes, which later in life gave rise to the harder chitinous shell. (Fig. 5.) Possible traces of thicker tissue strands in these pleural

[2] Paleontology of New York, vol. 7, pl. 23, fig. 8; pl. 25, fig. 8; 1888.

membranes may be seen in Plate 26, Figures 4 and 6, on the right side, while the specimen shown on Plate 26, Figure 1, retains the thin tests of the pleura themselves on both sides of the axis.

(9) Finally, we have a specimen from our State Museum collection clearly showing the pygidium as a fine carbonaceous film (see pl. 3, fig. 2), a result of the retention of the thin pygidial membrane after molting.

Combining all these facts, we have no hesitation in considering *Marrella splendens* a trilobite in a young, freshly molted stage—probably *Neolenus serratus*, which possesses the same general outline, especially in the carapace and pygidium.

The caudal rami found by Walcott in *Neolenus* and probably doubtless also present in other trilobites have not yet been seen in *Marrella splendens*. They are, however, exceedingly delicate appendages that may well have been lost in the molting, or rather in fossilization.

From lack of material I have not taken up the supposed relationship of *Molaria spinifera* to the trilobites, suggested by Dacqué.

Half a year after the preceding discussion had been written, Dr. C. E. Resser, of the United States National Museum, informed me that considerable additional material on *Marrella splendens*, including a number of photographs, had been found and should be used. Some of these excellent pictures, which bring out additional features of *Marrella* worth recording, are reproduced herewith. They have not been retouched.

Plate 6, Figure 1, is an enlarged portion of Walcott's Plate 26, Figure 1. It shows the distinct outline of the glabella with the glabellar furrows and a narrow portion of the fixed cheeks, the remainder of which has been torn away along the jagged edge. The flatter occipital ring is recognizable posterior to the glabella. From it proceed the posterior thickened margins of the cephalon, which are here turned backward. The anterior converging sections of the facial suture are preserved where it crosses the frontal margin of the cephalon.

Plate 6, Figure 2, is a somewhat obliquely compressed specimen. It also shows the glabella, the axial lobe of the thorax with the muscular attachments of the legs, and the pygidium. The latter clearly exhibits the axial lobe extending three-fourths of the length, and also the marginal doublure on the left.

Plate 6, Figure 3, again shows the cranidium with the short sectors of the facial suture on the broad frontal "horns" (margins of carapace). This specimen demonstrates the fact that with the exception of the pair of antennules there are no antennae, mandibles, or maxillae, which Walcott had been led to believe were present, but only biramous cephalic and thoracic legs, the endopodites of which are

developed into gills as in the classic *Triarthrus becki*. In contrast to this the adjoining figure shows the thoracic feet stripped of the endopodites, and therefore looking like cephalic appendages. Some of Walcott's drawings (pl. 25, fig. 6, and pl. 26, figs. 2–4) also show cephalic feet with gills. Where Walcott figures antennae, mandibles, maxillulae, and maxillae (pl. 25, fig. 1, and pl. 26, figs. 1 and 5), the posterior margin of the cephalon, as shown before, is mistaken for the mandible, and the cephalic feet, which have lost their endopodites by poor preservation, for maxillulae and maxillae. This misconception led Raymond (1920, p. 116, fig. 32) to an erroneous restoration of *Marrella splendens*, showing five pairs of uniramous cephalic appendages, and to the statement (*ibid.*, p. 143) that *Marrella* forms "an intermediate stage between the Trilobita and the higher Crustaceae."

Plate 7, Figure 1, gives a ventral view. exhibiting the frontal doublure and the hypostoma. The transversal suture just behind the frontal margin appears to represent the frontal portion of the uniting facial sutures, with a rostral plate posteriorly to it. The most distinctive feature is the presence of white strands of connective tissue extending sideways from the anterior margin of the oval hypostoma into the frontal thickened margins of the free cheeks. Behind the glabella a portion of the intestine is seen, and behind this the internal view of the axial lobe of the thorax. The lower half of the picture shows more clearly the crowded, partly overlapping joints (segments of Raymond) of the posterior portion of the thorax.

Plate 7, Figure 2, is important in shedding light on the character of the supposed "large crescentiform sessile eyes," which "occur on the anterior margin just within the base of the anterior spines." (See Walcott's pl. 25, figs. 4 and 5.) Raymond speaks (p. 115) of "large marginal sessile eyes." Figures 3 and 4, which are further enlargements of the "eyes" in Walcott's Figures 4 and 5, show these bodies to be really circular to oval in outline. In both specimens they are squeezed out of place with respect to the thin test of the carapace, in the original of Figure 3 laterally and in that of Figure 4 anteriorly, both specimens showing oblique compression by their general outlines. In Figure 4 a triangular patch of the test adhering to the gland on the right and in Figure 3 the gland on the right (partly cut) are distinctly integral parts of the test. In Figure 2 they are in their normal position, which is under the cephalon at both sides of the glabella. This location, as well as their outline, the indications of their composition of concentric or spiral ducts (as seen especially in fig. 3), and their prominence directly after the molting suggest their nature as shell glands rather than as digestive glands or hepatic ceca. It is quite probable that

these same shell glands are also retained in peculiar cranidial depressions of full-grown trilobites, as, for example, in the "lunettes" of *Bumastus*. Anyone who has observed the prominent shell glands in the carapace of an *Apus* or noted their location in such other primitive crustaceans as *Branchipus* and *Daphnia* (fig. 6) or the prominent development of the maxillary or shell glands in the larval forms of the Branchiopoda, Ostracoda, Copepoda, and Cirripedia will expect to see shell glands as a distinct feature in the freshly molted trilobites and will not be surprised to see their markings retained on the inside of the carapace of mature individuals.

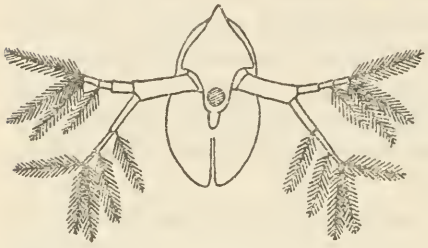

FIGURE 6.—*Daphnia longispina* O. F. Müller. Frontal view. (After Woltereck)

Plate 6, Figure 1, as well as Plate 7, Figures 1 and 2, shows clearly the torn and ragged posterior (interior) edges of the frontal "horns," which though considered appendages by Walcott and Raymond, are in reality the frontal doublure of the cephalon.

Occurrence.—Middle Cambrian, Burgess shale (Loc. 35K), Burgess Pass, near Field, British Columbia.

Plesiotypes.—U.S.N.M. No. 83486.

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EXPLANATIONS OF PLATES

PLATE 1

Dictyophycus gracilis, new species

FIGURE 1. Holotype, ×2. Portion of frond with well-preserved regular network of fibers.
2. Small group of fibers compressed on another indistinct fossil. ×2.
3. Largest specimen observed, probably composed of several thalli. ×2.

PLATE 2

Dictyophycus gracilis, new species

FIGURE 1. Portion of network drawn with Lapworth-Parkes microscope to show irregular character of meshes. ×4.
2. Portion of network with fine pores; also traces of parallel lines. ×4.
3. Specimen retaining softer part of the thallus besides the network of ribs. ×4.

Chaunograptus scandens, new species

FIGURES 4, 5. Opposite sides of another hydrozoan, with larger hydrothecae. ×4.

6. Camera drawing of type to show character of hydrocauli and hydrothecae. ×4.

PLATE 3

Marrella splendens WALCOTT

FIGURE 1. Camera drawing of freshly molted specimen in New York State Museum, showing hypostoma (*a*), fine parallel sculpture lines of crustacean carapace, bifurcation of legs (*c*), and thin epidermis film of pygidium (*p*). ×4.

2. Unretouched photograph of same specimen, showing the lateral compression of pygidium. ×4.

Chaunograptus scandens, new species

3. Photo of counterpart of type specimen, slightly retouched. ×4.

PLATE 4

Chaunograptus scandens, new species

FIGURE 1. Another slab retaining mostly hydrocauli and a few hydrothecae. ×4.

Marria walcotti, new species

2. Photo of holotype, not retouched. ×2.

3. Drawing made with Lapworth-Parkes microscope to bring out details of structure. ×4.

PLATE 5

FIGURE 1. Restoration of *Marria walcotti*, new species.

PLATE 6

Marrella splendens WALCOTT

FIGURE 1. Cranidium of original of Walcott's Plate 26, Figure 1. ×9.

2. View of obliquely compressed specimen, showing glabella and pygidium. ×3.

3. Dorsal view of specimen showing glabella, frontal sections of facial sutures, gills on cephalic appendages (left upper side), and axial lobe of thorax. The axial segments appear to continue into the pleura on the right side, beyond which traces of the feet are seen. ×3.

PLATE 7

Marrella splendens WALCOTT

FIGURE 1. Ventral view of specimen. ×3.

2. Dorsal view showing shell glands in position. ×3.

3. Frontal portion of glabella with shell glands. ×9. Portion of Walcott's Plate 25, Figure 4.

4. Frontal margin of glabella, with shell glands. Portion of Walcott's Plate 25, Figure 5. The frontal lobe of the glabella is forced beyond the white transversal doublure of the cephalon and embraces the circular shell glands. ×9.

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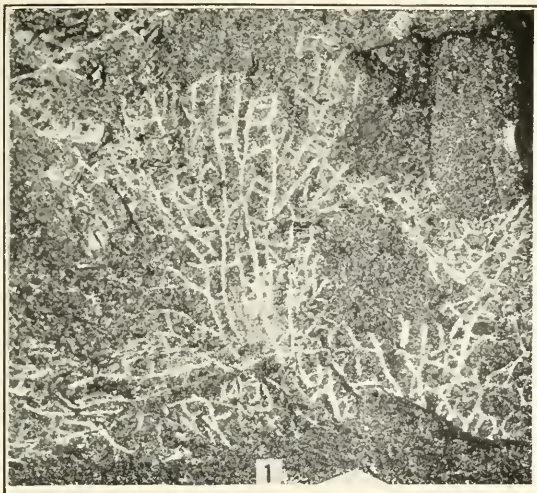
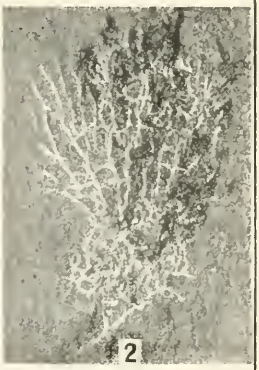
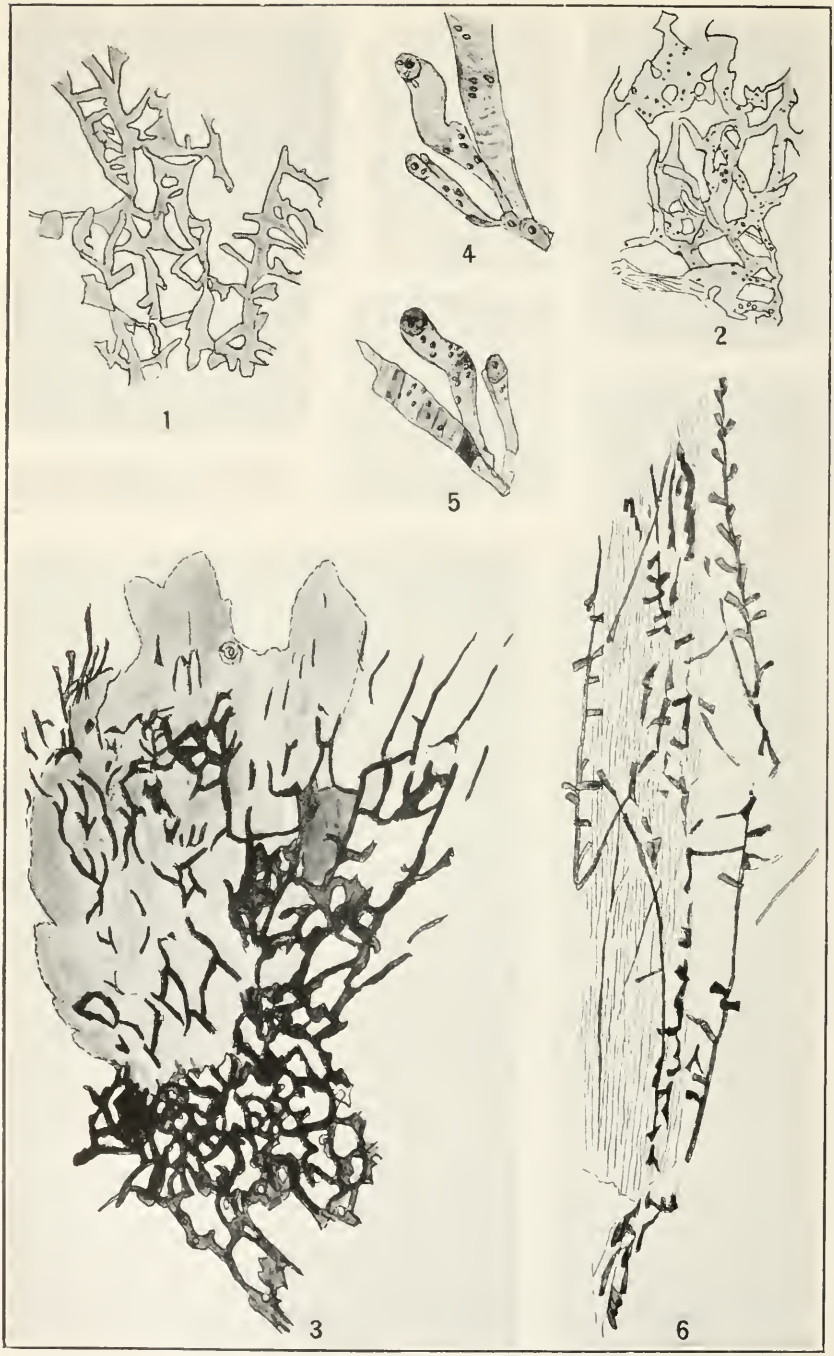




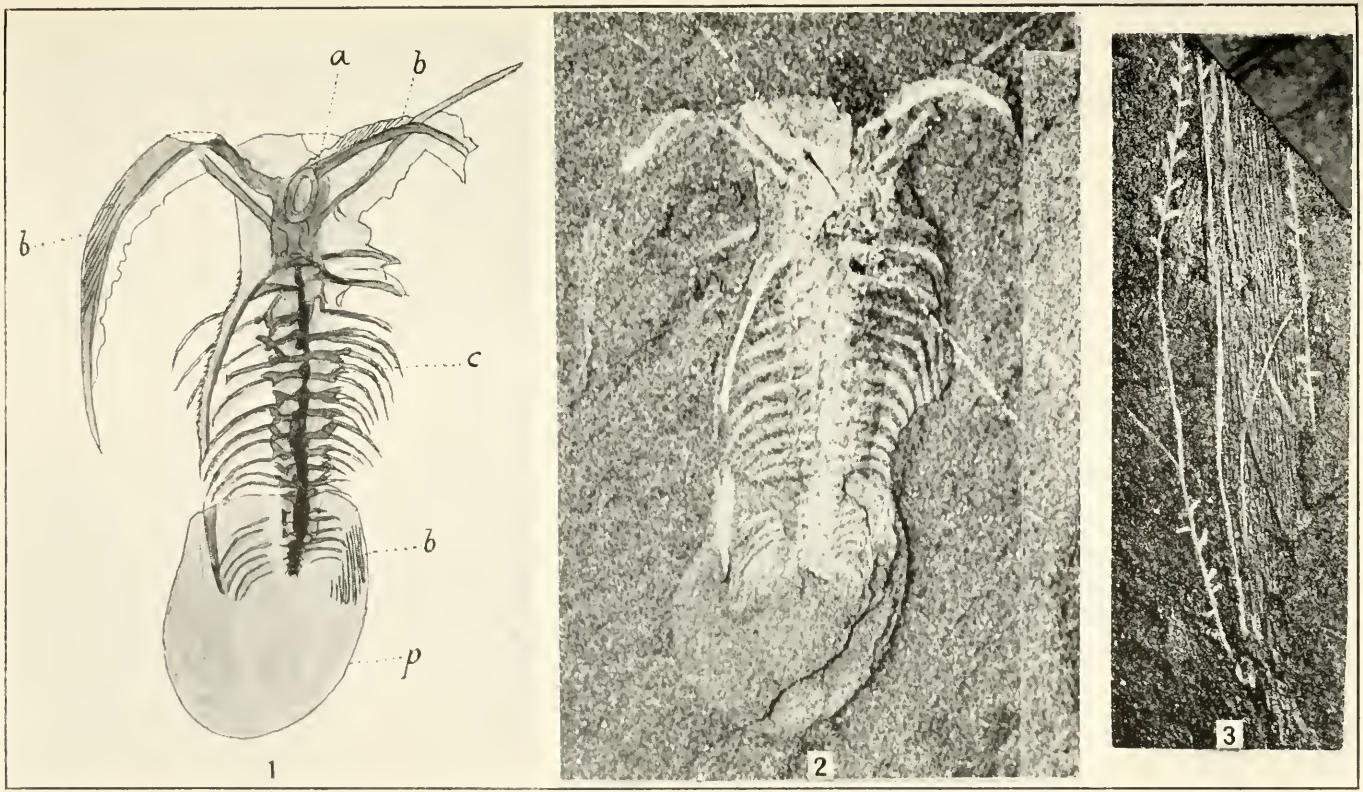
DICTYOPHYCUS GRACILIS, NEW SPECIES

FOR EXPLANATION OF PLATE SEE PAGE 17.



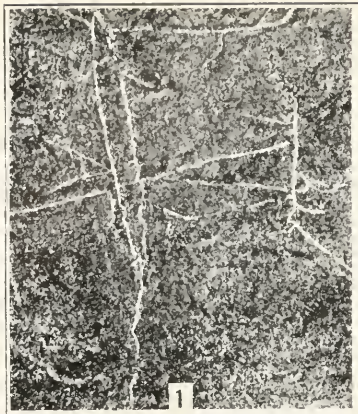
DICTYOPHYCUS GRACILIS, NEW SPECIES, AND CHAUNOGRAPTUS SCANDENS, NEW SPECIES

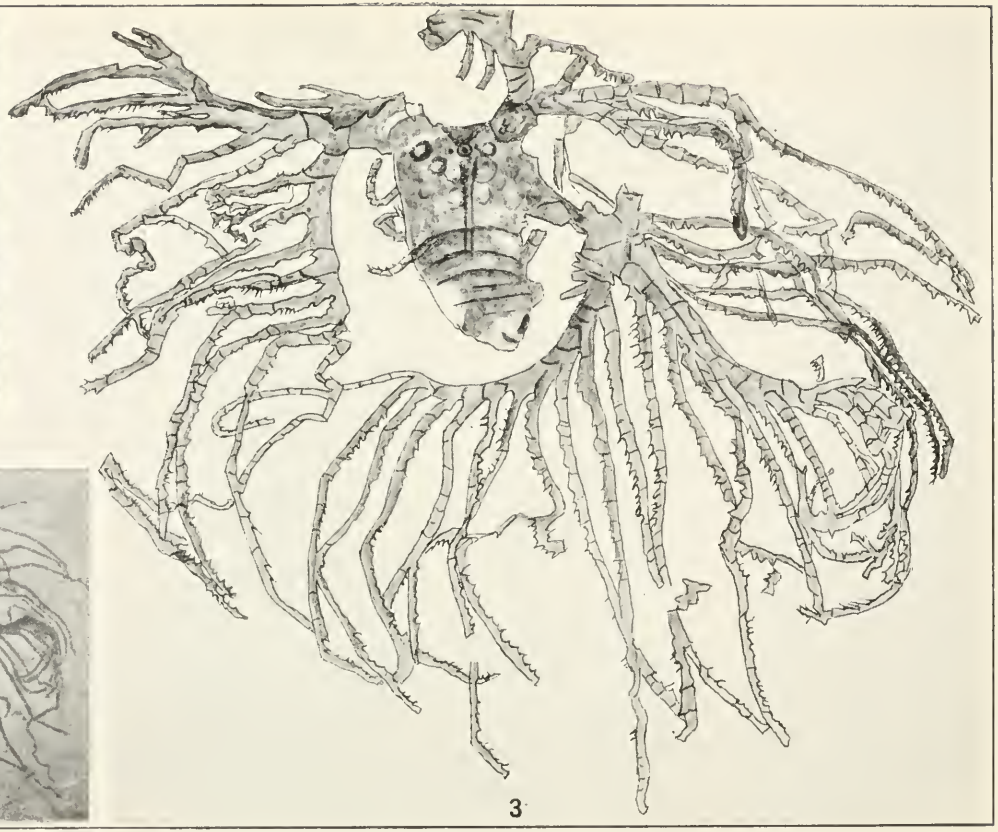
FOR EXPLANATION OF PLATE SEE PAGES 17, 18.



MARRELLA SPLENDENS WALCOTT AND CHAUNOGRAPTUS SCANDENS, NEW SPECIES

FOR EXPLANATION OF PLATE SEE PAGE 18.





CHAUNOGRAPTUS SCANDENS, NEW SPECIES, AND MARRIA WALCOTTI, NEW SPECIES

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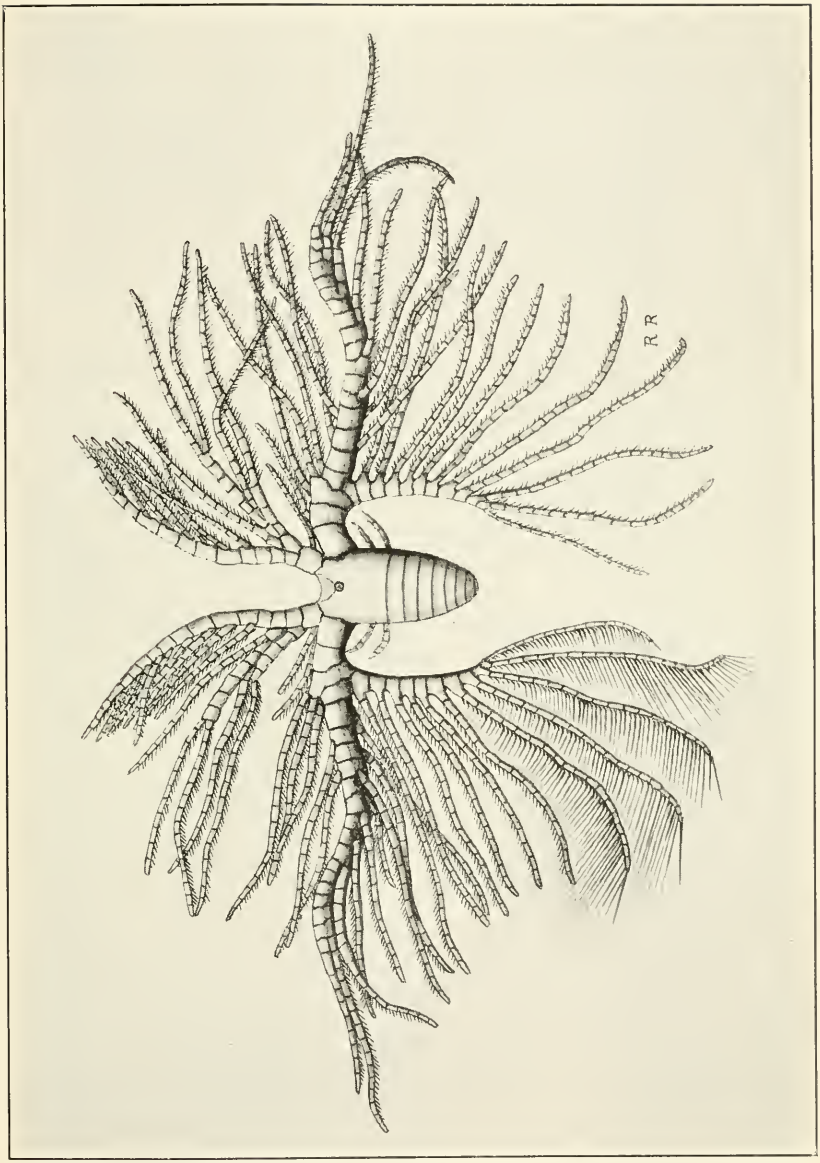

MARRIA WALCOTTI, NEW SPECIES

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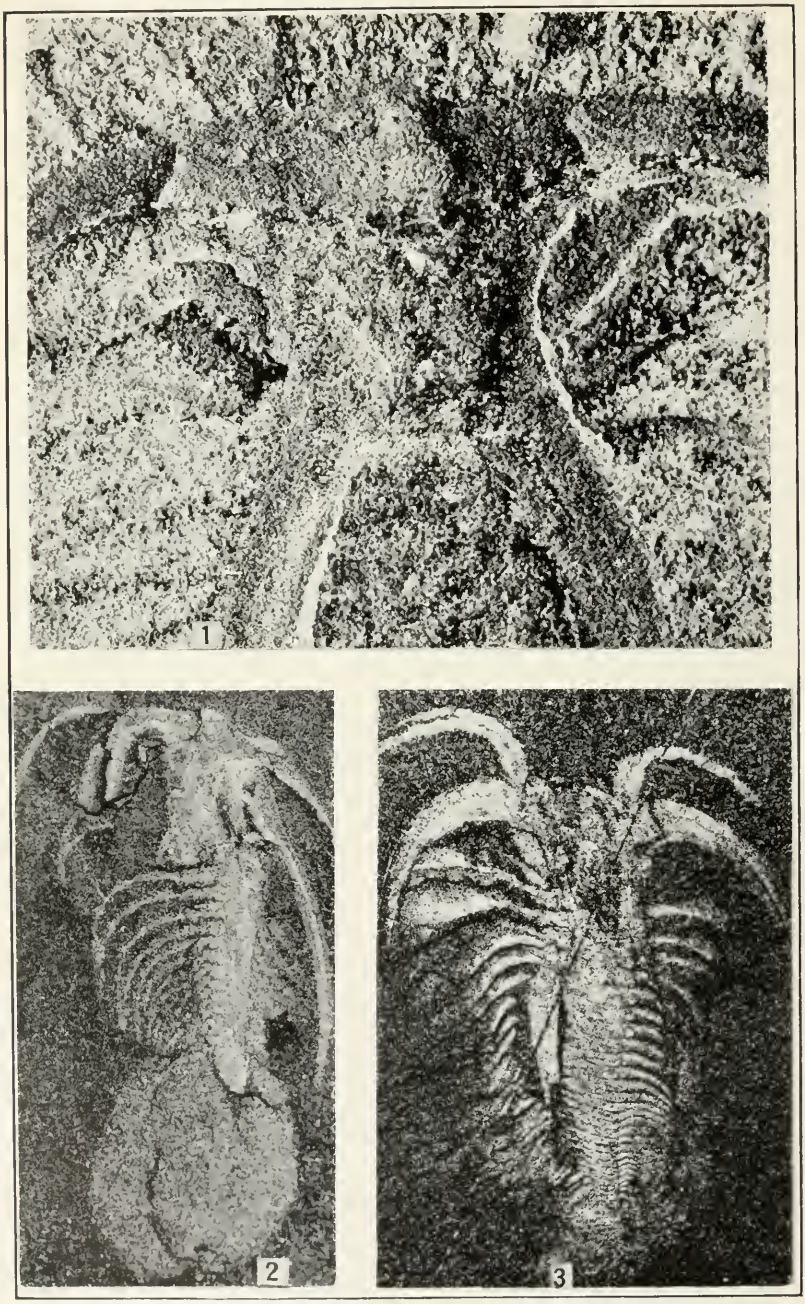

MARRELLA SPLENDENS WALCOTT

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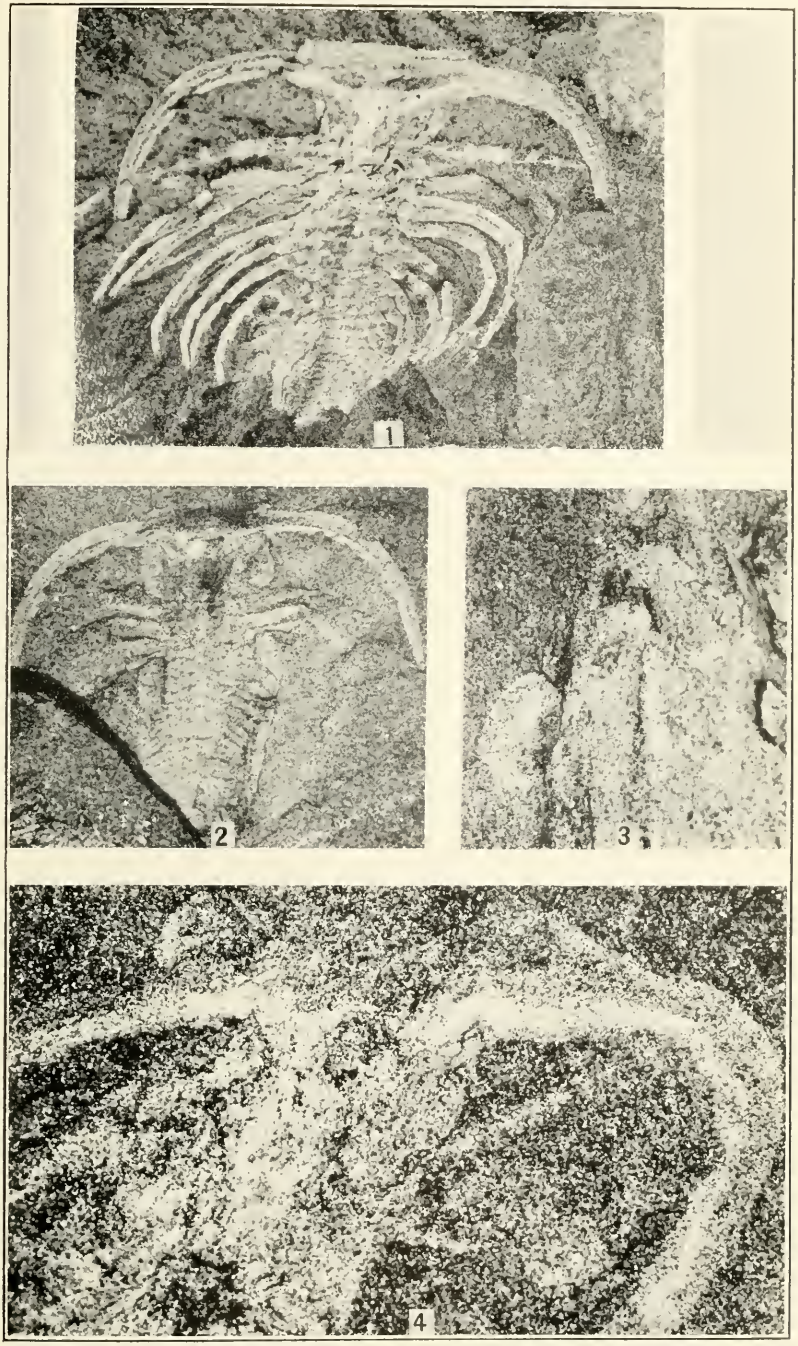

MARRELLA SPLENDENS WALCOTT

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