

THE VENTRAL ANATOMY OF THE UPPER
CARBONIFEROUS EURYPTERID
ANTHRACONNECTES MEEK AND WORTHEN

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ABSTRACT. All the known species of Upper Carboniferous eurypterids appear to have had so similar a dorsal anatomy that they have been thought to belong to one genus which has gone under three names. Of *Adelophthalmus* Jordan and von Meyer 1854, *Lepidoderma* Reuss 1855 and *Anthraconnectes* Meek and Worthen 1868, only the last is founded on a specimen showing both the ventral organs (in the holotype) and the dorsal (in the counterpart). *Anthraconnectes* is therefore preferred (though the other names have priority) until it is known whether the ventral anatomy of either of the others is the same as that of *Anthraconnectes*.

The ventral anatomy of the genus is described from the holotype and topotypes of *A. mazonensis* Meek and Worthen and *A. moyseyi* H. Woodward. Particular attention is paid to the 1st or genital operculum as revealed in the natural casts and in etched specimens. Sexual dimorphism is described and deductions made from several examples displaying Stormer's Type A median genital organ and two showing his Type B. In Type A the 1st and 2nd opercula resemble Type A of *Eurypterus fischeri* Eichwald, as described by Holm 1898 and by Wills 1964. Type B is less well documented, but one specimen of this type is shown to resemble Type B of *E. fischeri* in having clasping organs. Internal evidence indicates that Type A was the female and Type B the male, as was claimed by Holm to be the case in *E. fischeri*.

Nothing was discovered about the structure of the gills or their position on the body, except that there are small spots devoid of scale-ornament on the opercula, which may provide an indication of the positions on the roofs of the overlying gill-pouches where, by analogy with *Eurypterus*, the gills themselves were sited.

THE present study originated as a result of the application of new embedding and etching techniques to specimens of *Eurypterus fischeri* Eichwald (see Wills 1964) in which the chitinous skin is preserved in a silty limestone from Oesel in Esthonia. I described the discovery of the position of the gills on the under-surface of the mesosomatic segments, their protection by the underlying opercula or *Blattfüsse*, and their intimate structure, which latter had been discovered by G. Holm but never published. New discoveries relating to the external sex-organs were also made. I applied the same techniques to some of the Upper Carboniferous eurypterids, but found the ferrous carbonate more intractable than the limestone, and the chitinous skin often more broken and less perfectly preserved than in the Silurian fossils.

THE HISTORY OF THE NOMENCLATURE OF
UPPER CARBONIFEROUS EURYPTERIDS

All the fossils here described belong to a group of eurypterids which has gone under three different names given independently in (a) Germany (the Saar)—*Eurypterus* (*Adelophthalmus*) Jordan and von Meyer 1854-6 (the paper dated 1854); (b) Czechoslovakia (Bohemia)—*Eurypterus* (*Lepidoderma*) Reuss 1855-6; (c) America (Mazon Creek, Illinois)—*Eurypterus* (*Anthraconnectes*) Meek and Worthen 1868.

(a) and (b) were founded on the dorsal features, and (c) upon the ventral anatomy.

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In 1907 English specimens were described by Henry Woodward as *Eurypterus moyseyi* which, with others, were later shown by Moore (1936) to belong to *Anthraconectes* Meek and Worthen, sharing distinctive ventral features with the American species.

In 1912 Clarke and Ruedemann described the dorsal features of *Anthraconectes*, having discovered the counterpart of the actual specimen of *A. mazonensis* which Meek and Worthen had figured and described. It thus became the first Upper Carboniferous eurypterid of which a fairly complete picture of the whole animal was known.

There have been revisions:

- (a) of the holotype of *Adelophthalmus granosus* Jordan and von Meyer by Guthörl (1934) who postulated a carapace with large compound eyes, although Jordan and von Meyer were so convinced that the animal was blind that they gave it a name meaning 'no obvious eye';
- (b) of the English specimens, originally referred to *Eurypterus*, by Moore (1936), already mentioned;
- (c) of the American and English Upper Carboniferous eurypterids by Kjellesvig-Waering (1948), who referred all the species to *Lepidoderma* (This paper also reproduces the original figures of *Lepidoderma imhofi* Reuss);
- (d) of the holotype of *Lepidoderma imhofi* Reuss by Přibyl (1955), in which he claims that *Lepidoderma* is a synonym of *Adelophthalmus* (Kjellesvig-Waering (1958b, 1959) accepts this claim);
- (e) of the genus *Adelophthalmus* by van Oyen (1956), who also accepts Přibyl's contention that this name has priority over *Lepidoderma* and *Anthraconectes*. This contention has also been admitted as correct by Kjellesvig-Waering (1958b, 1959). Van Oyen's approach to the taxonomy is unusual, for his material, from a single layer in the Dutch coalfield, consisted of a very large number of specimens of one species which he measured and analysed statistically. He found a wide range in the proportions of various selected features, and concluded that only eleven of the twenty-six named species and subspecies were valid, and that the remaining fifteen were synonyms of *Adelophthalmus imhofi* Reuss. These include *A. mazonensis* Meek and Worthen 1868 and *A. moyseyi* H. Woodward 1907, which form the subject of the present paper.

In my work on fossil scorpions I have been impressed by the similarity of the dorsal features of chelicerates possessing very different ventral anatomies; and I feel that the same may be true in the group of Carboniferous *Eurypterus*-like creatures with the above name.

Since none of the revisions, except those of Moore (1936) and Kjellesvig-Waering (1948), make any reference to the ventral surface of the animals, it appears advisable to retain *Anthraconectes* for the American and English species in which the ventral organs are known to agree, but with a proviso that if *Adelophthalmus* is found to have similar ventral organs, that name has priority. Meek made the same proviso in 1868.

MATERIAL

With one exception, the specimens to be described are preserved in clay ironstone nodules which have been split into two halves. These are rarely exact part and counterpart, but more often display the cast of the dorsal surface and the cast of the ventral

surface respectively, with adherent bits on one that belong to the other. In some cases the two halves are so different that one must postulate that a natural cast of the body (which is rarely completely flattened) must have been lost when the specimen was collected. The two halves are best thought of as (1) the dorsal seen from the ventral side and (2) the ventral seen from the dorsal, bearing in mind the possibility that the first may show only ventral structures seen from the ventral side; and that the second may show nothing but dorsal features seen from the dorsal side; and that both may show a mixture of dorsal and ventral organs pressed together. The chitinous skin may still survive virtually unaltered, but is usually very fragmented (as in the Carboniferous scorpions preserved in ironstone—Wills 1959, 1960) and consequently is more difficult to extract than the skin of *Eurypterus fischeri* from the limestone of Oesel (see Holm 1898, Wills 1964). The external ornament, however, is often seen, either as scales on the chitin or as little pits on the surface of the cast. This has proved a valuable aid in deciding whether one is seeing the fossil from within or from the outside. It is noteworthy that only those parts of the skin have been preserved that were in life fully exposed to outside influences. In this they differ from the Oesel eurypterids, in which the excessively thin skin of the linings of the gill-pouches may be perfectly preserved.

The facts set out above have not always been recognized by the palaeontologists who have described these rare fossils, and their descriptions and measurements may consequently be misleading and difficult to understand.

The Specimens

American specimens. These are all examples of *A. mazonensis* Meek and Worthen from the famous Upper Pennsylvanian locality of Mazon Creek, Illinois.

(1) A latex-rubber cast of the holotype of *A. mazonensis*, showing the venter as seen from below, amplifies and supplements Meek and Worthen's description and figure. The holotype is UI X345.

The two half-nodules containing the holotype of *A. mazonensis* have had a curious history. In the original description written in 1868, Meek and Worthen (p. 544) state 'The only specimen of this interesting fossil we have seen, consists merely of the impression of the ventral side'. In 1884 James Hall described a Mazon Creek specimen displaying the dorsal surface of a eurypterid as *A. mazonensis* without realizing that it was the other half of the type specimen. In 1912 Clarke and Ruedemann (p. 223) learnt from Professor Whitfield that Hall's specimen was in the American Museum of Natural History and was the counterpart which Meek and Worthen had never seen; they described and figured it on pl. 26, fig. 1, and text-fig. 51. They added a footnote 'A drawing of this counterpart was given by Hall *loc. cit.*'; and they included in their synonymy '*Eurypterus (Anthraconectes) mazonensis* Hall, Pennsylvania 2nd Geol. Surv. Rep't Progress, PPP, 1884, p. 25, fig. 2, 3'. In their description there is nothing to suggest that they had seen Meek and Worthen's half-nodule, or knew of its whereabouts. Through the courtesy of Dr. N. D. Newell (American Museum of Natural History), I have been able to see a splendid cast of the counterpart (AMNH 8538).

Kjellesvig-Waering (1948), in revising the genus as *Lepidoderma* Reuss, devoted six plates to *L. mazonensis*, but appears to have assumed that Meek and Worthen's holotype was lost. However, Dr. Isles Strachan, when at the University of Illinois in 1957, found it in a store-cabinet in a drawer labelled 'Meek and Worthen's types'. He made a splendid latex-rubber cast of it which he sent to Dr. C. D. Waterston of the Royal Scottish Museum, Edinburgh, who has kindly made it available to me for re-description.

(2), (3). Among the Mazon Creek specimens figured by Kjellesvig-Waering as *Lepidoderma mazonensis* were two in the Museum of Comparative Zoology, Harvard College (MCZ 7162, 7163), which Professor H. B. Whittington has generously allowed me to develop by the techniques referred to above. I etched one half of each to display the ventral features, but with only partial success, owing to indifferent preservation of the chitinous skin. Each, however, supplies some information about the external genital organs.

(4) Excellent casts of another specimen of *A. mazonensis* in the Chicago Natural History Museum (CNHM PE5094) were loaned to me by Dr. Kjellesvig-Waering.

English specimens. Those referred to are all examples of *A. moyseyi* H. Woodward from the Nottinghamshire-Derbyshire coalfield.

(a) The 'Nottingham Beetle'. The first example came into my possession in 1914 and has long been known as the 'Nottingham Beetle' since its discovery by a miner, the late Mr. W. M. Hodgson, in the Nottingham Coalfield. The horizon is unknown. Originally preserved in shale, thin layers of which were impregnated by ferrous carbonate, it displayed the dorsal surface of the carapace and mesosoma with fragments of the appendages. Recently, with the consent of Professor F. W. Shotton, I embedded it in 'Marco' and then etched out the ventral parts. Now part of the specimen remains in the transparent Marco block like an insect in amber, and the parts that had been isolated by the etching are mounted as micro slides (BU 751/1 to /32), which show an amazing wealth of detail.

(b) All the specimens of *A. moyseyi* that were found at the Shipley clay-pit near Ilkeston, Derbyshire, by the late Dr. L. Moysey and presented by him to the Geological Survey, have been made available for study through the courtesy of Dr. F. W. Anderson. The horizon of the claypit is below the Top Hard Coal in the Ammanian Coal Measures. They include Woodward's holotype (GSM 30193) and paratype (GSM 30194), and a topotype (GSM 30249 and 30250) figured in a revision of this species by Moore (1936). All of these show ventral features.

Terminology. In my description of *Eurypterus fischeri* (Wills 1964) I used two German terms, 'Blattfuss' and 'Zipfel', that had been employed by Holm (1898), whose classic paper I was supplementing. Of these I propose to retain *Zipfel* for the external median genital organ, Z1 on the 1st operculum of both sexes, and Z2 on the 2nd in the supposed female; but I here use *operculum* instead of *Blattfuss* for the mesosomatic flap-like appendages. My reason is that I found in *E. fischeri* that the *Blattfüsse* functioned as the floors of the gill-pouches in the same way as do the branchial opercula of the king-crab, *Limulus*, although the gills in the fossil form were attached to the roof of the pouch and not to the opercula as they are in *Limulus*. There is every reason to believe that their general structure and function in *Anthraconetes* was the same as in *Eurypterus*.

In my *Eurypterus* paper *gill-tract* was used for the part of the ventral body-wall that was modified for respiration, one pair of tracts representing a pair of gills on each of the five mesosomatic branchial segments. Such tracts have not been preserved in any of the present specimens, but there are features in the distribution of the ornament on the opercula that suggest the position of the gill-tracts on the roof of the overlying gill-pouch. These features are here termed *gill-spots*.

Spatula is used in place of Meek and Worthen's 'spatulate plates' and of Caster and Kjellesvig-Waering's 'lateral lobe' for a sclerite that occurs on either side of the *Zipfel* on the 1st operculum. The rest of the laminate part (lamina) of the operculum is termed the *ala*. (In my *Eurypterus* paper, following Holm I used 'lateral lobe' for the whole bilobed laminate part of the genitally modified opercula).

Other new or unusual terms are defined in the text.

Orientation. In the descriptive section, R. and L. indicate the true Right and Left of the animal (unless otherwise stated); 'above' and 'over' imply 'dorsal to' or 'dorsad'; 'below' and 'under' imply 'ventral to' or 'ventrad'.

Abbreviations used in the illustrations. Adult body-segments numbered in roman numerals.

A1-A VI, prosomatic appendages 1-VI; *al*, ala; *ant*, anterior; *as*, ant. strip, op. 1; *ca*, cast; *car*, carapace; *?cg*, supposed aperture of coxal gland; *ch*, chelicera; *cl*, clasping organ; *cox*, coxa; *dz*, distal joint of Z1; *d. op. 1*, doublure of op. 1; *do. met.*, doublure of metastoma; *dor*, dorsal; *ga*, genital aperture, supposed position of; *gb*, gnathobase; *gp 1-5*, gill-pouch above op. 1-op. 5; *gs 1-5*, gill-spot on op. 1-op. 5; *gt*, gill-tract, supposed position of; *H2, H3*, suspension hinges of op. 2, op. 3; *has*, hastate end of Z1; *L*, true Left side; *maz*, main joint of Z1; *me*, median eye (ocellus); *met*, metastoma; *mjz*, middle joint of Z1; *mm*, the points behind which the spatulae and Z1 moved independently and hung free from the body; *ms*, middle strip of op. 1; *mn*, the points on op. 2 behind which the alae and Z2 moved independently and hung free from the suspension hinge on segment IX; *op. 1 (VII+VIII)*, 1st operculum on adult segments VII, VIII; *op. 2 (IX)-op. 5 (XII)*, 2nd to 5th opercula on adult segments IX-XII; *pdo*, posterior doublure; *pl*, pleural spine; *R*, true Right side; *s XIII, s XIV*, sternal plate of metasomatic ring

of adult segments XIII, XIV; *sm*, smooth; *spa*, spatula; *sut*, suture; *T VII—T XII*, tergites of adult segments VII—XII; *Z1*, 1st *Zipfel*, on op. 1; *Z2*, 2nd *Zipfel*, on op. 2.

Repositories. The following abbreviations are used throughout:

- AMNH = American Museum of Natural History, New York.
- BU = Geology Department, University of Birmingham.
- CNHM = Chicago Natural History Museum.
- GSM = Geological Survey and Museum, London.
- MCZ = Museum of Comparative Zoology, Harvard College, Cambridge, Mass.
- UI = Geology Department, University of Illinois, Urbana.
- USNM = United States National Museum, Washington.

Segmentation. The segments of the adult are indicated in roman numerals. As in *E. fischeri* the 1st operculum is regarded as composite, genital (vii) plus 1st branchial (viii). This numbering, which is based on what can be seen in the fossil, differs from that employed by zoologists in which the genital is regarded as viii, which is its number in the embryo, the viith or pregenital being usually greatly reduced or lost in the adult chelicerate (see Wills 1947, 1959, 1960).

The sex problem. *Anthraconectes* was probably sexually dimorphic. Individuals with long, three-jointed 1st *Zipfel* (Størmer's Type A) are here regarded as female, on account of the complexity of the genital modifications which affect two opercula, in a way closely similar to that found by Holm and myself to occur in *E. fischeri*. The full case for this determination, which differs from that propounded by Størmer (1935), has been set out in my paper on *E. fischeri*, and is further discussed on p. 504.

Acknowledgements. My thanks are due to Professor H. B. Whittington, Drs. C. D. Waterston, F. W. Anderson, E. Kjellesvig-Waering, N. D. Newell, and E. S. Richardson Jr., for placing at my disposal these rare specimens (or casts of them) from the collections in their keeping, and to Professor F. W. Shotton and Dr. Isles Strachan for help and encouragement throughout. I am also very grateful to Mrs. M. Darley for typing, to Mr. L. Vaughan for valuable assistance with the photography, and to my daughter for raising only a few mild objections to the use of hot acid and balsam on her cooking stove.

Genus ANTHRACONECTES Meek and Worthen 1868

DIAGNOSIS OF THE VENTRAL ORGANS

The 2nd joint of chelicera about two-thirds the length of metastoma; prosomatic appendages II–V increase in length backwards from coxa; three or four joints to coxa and seven joints (with paired spines on the distal joints and a pointed terminal spine) on each leg. Coxae with spined or toothed gnathobases. Prosomatic appendage VI (a paddle) has very large coxa with toothed gnathobase and rod-like ?flabellulum on dorsal side, five joints, and a blade of three pieces and one small terminal piece. Metastoma oval, slightly emarginate in front. Ventral skin of coxae of appendage VI and of the mesosomatic opercula covered with close-set small and very small triangular scales except where overlapped. Venter sexually dimorphic:

Type A, ♀. No clasping organs known. Metastoma more than half the length of the carapace. 1st operculum long, with long median three-jointed rod-like 1st *Zipfel* with rounded, slightly emarginate distal end, flanked by a pair of spatulae extending dorsad to it. Spatulae fused to the alae except at their posterior ends. Alae sutured to one another and to the hastate proximal end of the *Zipfel*. Slight indications only of triangular areas in front of *Zipfel*, but no defining sutures. 2nd operculum with median anterior projection covered with hairs; lamina of bilobed alae continuous in front of 2nd *Zipfel*, which consists of an unpaired proximal part and a distal pair of terminal spikes, lying dorsad

to the 3rd joint of the 1st *Zipfel*. 3rd–5th opercula without median sutures, and with or without unornamented gill-spot near each lateral end: so also on 1st and 2nd opercula.

Type B, ♂. Clasping organ on 3rd leg (appendage iv). Metastoma less than half the length of carapace. 1st operculum short with short median three-jointed *Zipfel* having a bifid distal end projecting slightly behind the posterior margin of the spatulae. Anterior end of *Zipfel* not hastate, but passing squarely without any suture into the median part of the lamina. Spatulae short. 2nd operculum without genital adaptations and similar to 3rd–5th opercula of both sexes.

DESCRIPTION

The present-day consensus of opinion is that *A. mazonensis* and *A. moyseyi* are certainly congeneric, and specifically very close, if not identical (Moore 1936, Kjellesvig-Waering 1948, van Oyen 1956). These views have been based mainly on the dorsal features, and little attention has been paid to the ventral organs, our knowledge of which has been derived chiefly from the holotype of *A. mazonensis*. It seems advisable, therefore, to redescribe the American species first, although the 'Nottingham Beetle' gives fuller information.

A. The American Species

A. mazonensis Meek and Worthen 1868

I. The Holotype, an individual with *Type A* genital organs.

A rubber cast of the holotype which is in the Geology Department, University of Illinois, UI X345, forms the basis of the following description (see Pl. 77, fig. 1; text-fig. 1).

This cast reproduces the features of the actual ventral surface of the animal which is seen in low relief and with the details of the skin-ornament wonderfully displayed. So much is this the case, that parts originally unornamented and smooth can generally be recognized with certainty. The same perfection is, however, not found in the front of the prosoma, the distal parts of the legs and some parts of the metastoma. In text-fig. 1 the ornament is perforce shown semi-diagrammatically, for the squamation on many parts is too small to be represented to true scale. Most of it is hardly visible on the photograph (Pl. 77, fig. 1).

A comparison of the rubber cast of the holotype with that of the counterpart (AMNH 8538) shows that a natural rock-cast of the body together with the actual chitinous skin was lost when the nodule containing the fossil was broken open. This can be verified by noting the complete difference between text-fig. 1 and Clarke and Ruedemann's pl. 26, fig. 1 (1912). It is quite certain that the skin was originally there; for on both rock specimens there are little pits representing the finest details of the ornament of scales, which show up beautifully as projections in the rubber casts.

While Meek and Worthen's figure (1868*a*, p. 21) is in general correct, the rubber cast throws further light on a number of points:

1. There are two indistinct features near the front of the prosoma, which may represent the two chelicerae (text-fig. 1).

2. The coxa of the R. 1st leg (appendage II) is present.

3. Most of the paddle (appendage VI) shown in Meek and Worthen's figure is no longer visible. A large protuberance visible on the left side of the photograph (Pl. 77, fig. 1) represents a gap in the holotype where a piece of the nodule has broken away. This piece must have been in place in 1868, for they not only figured the paddle but referred to it specifically in their description. Clarke and Ruedemann's figure of the counterpart of the holotype shows only the same proximal joints that can be seen in the rubber cast of the holotype.

Half-moon-shaped and pointed scales can be seen on the proximal joints of the prosomatic appendages and elongate linear and obtuse ones on the metastoma, but the cast does not show the full pattern of ornament figured by Meek and Worthen on the latter.

4. The post-metastomal waist (which is the ventral expression of the major hinge between the prosoma and the mesosoma) is clearly shown by the relief. The prosoma lies stretched forward so that virtually the whole of the 1st operculum is displayed. The coxae of appendage VI are broken away behind, but what remains shows that they, like the metastoma which is completely preserved, lay in a plane well below that of the operculum. I have elsewhere suggested that the metastoma may have been boss-shaped in life, whereas it generally appears as a flat plate in the fossils. Even in this extended state the waist is distinct, and must have been much more accentuated when the body was contracted, as it is in MCZ 7163 (Pl. 77, fig. 2).

5. The ventral parts of the mesosoma and the first two sternal plates of the metasoma are covered by close-set minute scales wherever the organs were fully exposed to the elements, with the exception of the distal part of the *Zipfel*, which is bare of ornament. Where the front of each operculum was normally protected by the overlap of the preceding one or, in the case of the 1st operculum, by the overlap of the metastoma and coxae VI, the ornament is diminutive or non-existent. An example of this can be seen on the left side of the 5th operculum where part of the 4th has been broken away.

The sternal plate of the 2nd metasomal ring (text-fig. 1, *S XIV*) appears almost bare of ornament, but this may be due to the fracture that divided the nodule having, at this point, passed along the inside instead of the outside of the skin.

The two unornamented patches between the broken ends of the gnathobases of appendage VI and the front of the 1st operculum are probably casts of the thin skin of the upper sides of those parts of the gnathobases that have been lost.

6. The 1st operculum is seen to have consisted of three strips—anterior (*as*), middle (*ms*), and posterior strips (*ps*)—as in *Eurypterus*, but the strips are separated by slight

EXPLANATION OF PLATE 77

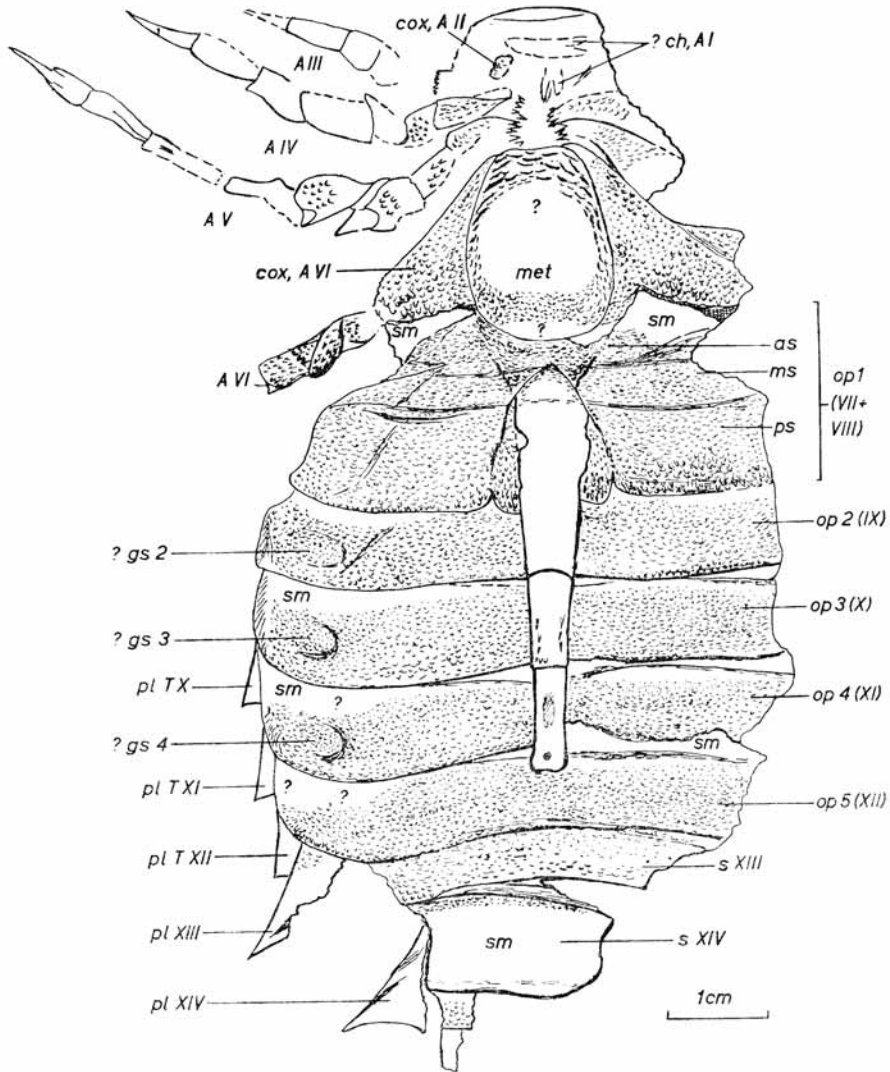
Anthraconectes mazonensis Meek and Worthen 1868 (photographed by reflected light).

Fig. 1. Ventral view of the ventral surface (cf. text-fig. 1). A latex-rubber cast of the holotype, UI X345. Type A, natural size.

Fig. 2. Ventral view of ventral organs of prosoma and part of mesosoma. The distal part of 1st *Zipfel* broken away, revealing end of 2nd *Zipfel*. Type A, MCZ 7163, after development, $\times 1.8$.

Fig. 3. Ventral view of a type B individual, MCZ 7162, after development (cf. text-fig. 3). Apart from the prosomatic appendages, most of the ventral skin is missing. $\times 1.8$.

Fig. 4. Ventral view of part of 1st operculum of Type B, showing the *Zipfel* and R. spatula, isolated from MCZ 7162 (cf. text-fig. 4b). Slide MCZ 7162/1, $\times 10$.



TEXT-FIG. 1. *A. mazonensis* Meek and Worthen, Type A, UI X345. Ventral view of a latex-rubber cast of the holotype. For key to abbreviations, see p. 477.

ridges and not by lines of elongate mucrones. The ridges resemble those seen along the front of the exposed part of each of the remaining opercula. The anterior strip is an obtuse triangle with its apex immediately behind the metastoma, to the doublure of which it was no doubt connected by thin skin. The base of this triangle is much shorter than the full width of the 1st operculum, since it contributed to the post-metastomal waist. So in a lesser degree did the middle strip. The posterior strip closely resembles the exposed portions of the other opercula, but is divided behind by a notch on either side of the *Zipfel* into an inner spatula and an outer ala. Until recently spatulae were only known from *A. mazonensis* and *A. moyseyi*, but similarly placed plates are now recognized in *Dolichopterus* Caster and Kjellesvig-Waering 1956, and *Parahughmilleria* Kjellesvig-Waering 1961. (Holm 1898, pl. 4, fig. 23 of *Dolichopterus laticeps* shows the spatulae clearly.) The two spatulae extend under the *Zipfel*.

The *Zipfel* has a triangular 'hastate' end to its main joint. The bases of the triangle appear to coincide with the points at which the *Zipfel* and the spatulae began to be free from the body, and at which the posterior ends of two lines diverge forward across the middle and anterior strips. These lines are shown in Meek and Worthen's figure, and have been regarded by more recent workers as corresponding to the sutures which define the pair of 'pentagonal' or 'deltoidal' plates in *Eurypterus* and *Dolichopterus*. Close examination shows that the line on the true Left of the holotype is conspicuous because of a fold and fracture, and that that on the Right is barely recognizable. There is, at most, a slight interruption of the continuity of the ornament. The lines do not extend across the anterior strip. In *A. moyseyi* the corresponding parts can be examined by transmitted light and show no sign of sutures (p. 498, Pl. 78, fig. 3; Pl. 79, fig. 1). Possibly the lines in the holotype represent the position of the anterior boundary of the 1st gill-pouch along which the free-hanging portions of the operculum parted company from the fixed sternal portion. This interpretation is based on my discoveries in *Eurypterus* (Wills 1964).

EXPLANATION OF PLATE 78

- Anthraconectes moyseyi* H. Woodward 1907. All the figures refer to parts of one specimen, BU 751. Figs. 3-7 photographed by combined reflected and transmitted light: Figs. 1, 2, 8 by reflected light.
- Fig. 1. Dorsal view of dorsal surface before development, now in Marco block (cf. text-fig. 6A), $\times 2.25$.
- Fig. 2. Progress-photo of the ventral organs, less most of the 2nd operculum which had been extracted. Some organs outlined in white (cf. text-fig. 6B). $\times 2.25$.
- Fig. 3. Ventral view of most of the 1st operculum with parts slightly displaced at the sutures. Note absence of triangular or deltoidal plates and the position of the gill-spots (cf. text-fig. 10). Slide BU 751/18, $\times 4$.
- Fig. 4. Ventral view of most of the 2nd operculum with the distal part of the 2nd *Zipfel* restored to its original position (cf. text-fig. 10). Slide BU 751/1, $\times 4$.
- Fig. 5. True dorsal view (ventral as found) of the endostoma with its bristles shown pointing forward (cf. text-fig. 9B, D). Slide BU 751/19, $\times 7.5$.
- Fig. 6. The true ventral view (dorsal as found) of the same. The bristles are shown pointing forward, but the backward pointing granules of the carapace also point forward (not clearly seen in photo) (cf. text-fig. 9A, C), $\times 7.5$.
- Fig. 7. Dorsal view of the metastoma and parts of the vth and vith prosomatic appendages with the vith gnathobase outlined (cf. text-fig. 8B). For ventral view see Pl. 79, fig. 4. Slide BU 751/16, $\times 2$.
- Fig. 8. Dorsal view of the median eye-node showing the lenses of the two ocelli. Slide BU 751/10, $\times 10$.

In the present specimen it can be seen conclusively that the spatulae and alae are united except for a short distance at their posterior edges. On the other hand I find no indication on the alae of the 1st or any other operculum of a modification of the pattern of scale ornament comparable to the unornamented or barely-ornamented patches (gill-spots) seen on all the five opercula of *A. moyseyi* (p. 496).

The *Zipfel* is extremely well preserved, and is remarkable for its enormous length, its tip lying over the anterior edge of the exposed part of the 5th operculum. Meek and Worthen picture it divided by three sutures into four joints, but state that they are doubtful about the existence of the most anterior of the sutures (their No. 3). The rubber cast, presenting the evidence as a positive, shows quite clearly that their No. 3 and No. 2 exist, but that No. 1 is absent. The jointing of the *Zipfel* thus matches closely the arrangement in *A. moyseyi* (cf. text-figs. 1 and 10A).

The proximal main joint has a hastate triangular anterior end. Except for a few narrow scales at the very front it is devoid of ornament. From the base of the anterior triangle backwards, it can be seen to have had a narrow flange at either side, which underlay and was free from the spatula. It tapers backwards to end in a curved articulation that lines up with the back of the 2nd operculum. The next (middle) joint tapers slightly, and may, before compression, have been narrower than it now appears, for there are, near either side, three elongate scales that may have defined its original width. The second articulation is nearly straight and shows three or four mucrones out of what was a transverse row (cf. pp. 499, 501) on its ventral side. The third joint is nearly parallel-sided, but expands slightly at the end into two blunt lobes. As Meek and Worthen state 'the extremity . . . is slightly expanded, truncated or somewhat rounded and not bipartite'. Just in front of the extremity is a tiny pimple, and in front of this is a depression (in the cast), the counterpart of which in the specimen they mistook for an articulation (their No. 1).

7. The 2nd-5th opercula are splendidly displayed. The maximum breadth of the animal occurs at the 2nd and 3rd opercula, behind which it decreases gradually to the 5th. The exposed part of each is gently rounded at the post-lateral corner and here the ornamentation consists of long, narrow ridges, sub-parallel to the end of the segment. Elsewhere, as already noted, there is an overall ornament of small semilunar scales that are coarsest behind, and become progressively smaller in front, until they are a mere dusting and finally disappear from the part overlapped by the preceding operculum.

On each of the 2nd, 3rd, and 4th opercula there is a small oval depression, ill-defined by slight folds, near to their R. ends (the L. ends are not preserved). The pattern of tiny scales passes without interruption across the areas. Nevertheless the depressions probably correspond to the unornamented gill-spots described in *A. moyseyi* (BU 751, p. 501), where they are to be interpreted as indications on the operculum of the positions of the gills which, by analogy with *Eurypterus*, would be sited on the roof of the gill-pouch floored by the operculum. In this specimen, however, there is no change in the pattern of scales as there is in *A. moyseyi*.

The 2nd operculum has its median portion covered by the 1st *Zipfel*, and consequently does not show whether or not it was bilobed and had a 2nd *Zipfel*. The 3rd and 4th opercula also have their median parts concealed by the 1st *Zipfel* but probably were devoid of a median suture, as is the 5th.

8. The relation of the opercula to the tergites. In the rubber cast of the ventral surface (text-fig. 1) the only part of the dorsal skin that can be seen is the post-lateral doublures

of the sharp pleural spines (*pl*, x-xiv) of the 10th-14th tergites, which are better displayed in the ventral view of the counterpart AMNH 8538, figured by Clarke and Ruedemann (1912, pl. 26, fig. 1). Each of the 10th-12th spines lies rather behind the rounded post-lateral corner of the corresponding operculum, namely the 3rd, 4th, and 5th. As in *E. fischeri*, the opercula were probably hinged to the body along their front edges, and, except along these hinges, were separated from the dorsal skin (the tergites) by the body itself (covered by the thin skin of the posterior and lateral doublures of the tergites), and by the water-spaces of the gill-pouches.

9. The metasoma (last abdominal segment XIII and tail segments). The exposed part of sternal plate XIII is shorter than the exposed part of any of the opercula, but it carries a similar ornament of small scales. Its pleural spine appears as a particularly formidable structure, though its connexion to the sternal plate of the body-ring is missing. Its connexion to the tergal plate is, however, well preserved in the counterpart (Clarke and Ruedemann 1912, pl. 26, fig. 1), where it is also seen in ventral view, as here. In the counterpart too, the next two pleural spines and their supporting, relatively narrow, tergal plates are clearly displayed; whereas in the holotype (text-fig. 1) only parts of the XIVth sternal plate and its pleural spine can be seen. The plate appears devoid of ornament, probably because one is looking at a cast of its inner surface. There is finally a scrap of the XVth sternal plate with scale ornament along its front.

II. *Topotypes of A. mazonensis Meek and Worthen*

(i) *MCZ 7163a, b* (having Type A genital organs)

Both half-nodules were depicted by Kjellesvig-Waering (1948). His pl. 4 and pl. 5, fig. 3 showed a dorsal view of the dorsum and some fragments of appendages as preserved in 7163*a*, and his pl. 5, fig. 4 depicted the counterpart, 7163*b*. The chitin, where it can be seen (for example on the carapace) is fragmented into tiny bits set in white kaolin, a feature recalling some of the Carboniferous 'scorpion' skins (Wills 1959, 1960). The counterpart shows a natural cast of the dorsal skin with pits representing the ornament of scales. There is a slight indication of an axial knob on the 2nd tergite, similar to those described by Clarke and Ruedemann. The counterpart also shows the ends of the first three opercula on the L. side. These can be seen in Kjellesvig-Waering's pl. 4.

I embedded and etched 7163*a*, extracting intact the five distal joints of the L. appendage v (the 4th leg) with the terminal and other smaller spines still attached (text-fig. 2, slide MCZ 7163/1). I also mounted a fragment of the posterior edge of a tergite with a brush of setae that lined the posterior doublure (slide MCZ 7163/2). Of the ventral structures, the R. chelicera and the tip of the 1st *Zipfel* were not to be seen; but little else was missing.

Unfortunately the matrix proved very difficult to wash away from the skin, and consequently many details remain obscured. The skin is now embedded in a Marco block and can be examined from either side, the dorsal showing the features pictured by Kjellesvig-Waering (pl. 4); the ventral is shown by my Pl. 77, fig. 2.

At one stage of the etching I noticed about ten circular markings about 3 mm. in diameter on a bedding plane. These I thought might be embryos—possibly at a stage corresponding to the trilobite-larva of *Limulus*. I painted them with Durofix and extracted 8 or 9, but I failed to mount any of them satisfactorily. The best ones seemed to show two linear structures, one on either side of the circle, which might represent rudimentary paddles. Two poor mounts are numbered MCZ 7163/3 and /4.

The ventral parts, now in the Marco block, are not easy to see or interpret, because of the general opacity due to adherent matrix.

The L. chelicera was visible, but during the final embedding it was displaced from the position shown in Pl. 77, fig. 2, so that it now lies transverse to the body. The broadish hand and narrow fingers measure about 8 mm. in length.

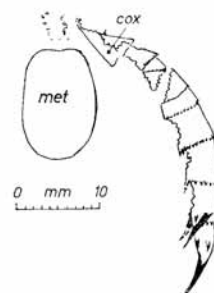
The coxae and proximal joints of most of the legs and paddle are preserved, and display their denticle-covered jaws around the oral cavity. Of the denticles, most point backwards, but a few project ventrally (cf. *E. fischeri* as figured by Holm 1898). No clasping organs can be seen. The coxa and first two joints and part of a third joint of the 4th L. leg (A v) remain in place, and complete the picture of that appendage, for the rest of it was extracted in one piece, as already noted (p. 484, text-fig. 2). The appendage consisted of the coxa, seven joints (the last two with spines), and a large terminal spine carrying two smaller ones on its ventral side.

The metastoma and coxae of the paddles (appendage vi), as seen in ventral view, overhang the 1st operculum, giving the appearance of a waist; but most of that operculum is visible (Pl. 77, fig. 2). Its structure resembles that seen in the holotype except as regards the *Zipfel*, which was certainly much shorter than the gigantic organ of the type. The tip, however, was broken away, and the exact length is unknown (see p. 483). The loss of the terminal joint and part of the 2nd joint has revealed two narrow structures which are the bifid end of the 2nd *Zipfel* on the 2nd operculum. This organ was unknown in *Anthraconectes* until my development of *A. moyseyi* (BU 751), but its discovery was not unexpected in view of the known existence of a 2nd *Zipfel* in the form of *Eurypterus* that has a long 1st *Zipfel* (Type A).

Owing to the retention of parts of both the 1st and 2nd *Zipfel*, it is not possible to see whether the 2nd operculum was bilobed, but in view of the structure discovered in *A. moyseyi*, bilobation may be safely postulated. There is no indication of bilobation in any of the remaining opercula, nor is their preservation good enough to permit the detection of gill-spots.

(ii) MCZ 7162a, b (having Type B genital organs)

Both half-nodules of this small but very complete specimen (half the size of the holotype) were figured by Kjellesvig-Waering (1948). His pl. 3, fig. 3 and pl. 5, fig. 2 show the dorsal aspect of the dorsum as exhibited by 7162a. The fragmentation of the chitin and its retention by kaolin, and the ornament of the tergites, are well shown on his pl. 3, fig. 3. I embedded and etched this half-nodule to reveal the ventral organs (Pl. 77, fig. 3; text-fig. 3). The prosomatic appendages were found complete, with the exception of the R. chelicera; but unfortunately for my study of the genital and respiratory organs, the opercula of the mesoma had disintegrated badly before fossilization, and only parts of the 1st operculum were recovered. The chitin of the sternal plates of the first

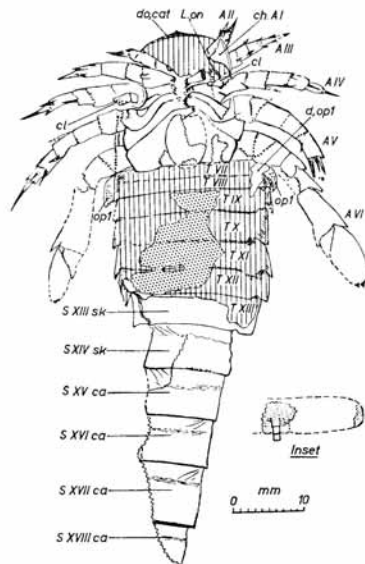


TEXT-FIG. 2. *A. mazonensis* Meek and Worthen, Type A, MCZ 7163. Ventral view of Appendage v, the coxa and 2nd, 3rd, and part of 4th joint as seen in the Marco block of MCZ 7163, in present relation to the metastoma. Half of 4th and 5th-8th joints and terminal spine in slide MCZ 7163/1. For key to abbreviations, see p. 477.

two metasomatic rings is fairly well preserved, but most of the tail is represented by a cast of the inside of the sternal plates (text-fig. 3).

The following features are noteworthy:

1. There is a sharp triangular spine on the midline of the front of the carapace. In this specimen it points almost vertically downwards at a place where there are traces of the



TEXT-FIG. 3. *A. mazonensis* Meek and Worthen, Type B, MCZ 7162 after etching. Ventral aspect of (1) the inside of the dorsal organs (ruled); (2) the prosomatic appendages except the R. chelicera; (3) parts of the ventral skin and of internal casts of the metasomatic segments. *Inset*, reconstruction to the same scale of the 1st operculum, based on slide 7162/1 and on the ends of *op 1* shown on the main figure. Parts obscured by matrix stippled. For key to abbreviations, see p. 477.

anterior doublure. A similar spiny process is mentioned in Kjellesvig-Waering's (1948, p. 20) general description of *A. mazonensis*. The Geological Survey's specimen of *A. moyseyi* (GSM 30250) also shows one and Clarke and Ruedemann (1912, text-figs. 44, 116) figure a similar, but forwardly directed spine in *A. mansfieldi* C. E. Hall. It is therefore probably a normal feature of these Carboniferous eurypterids that is rarely seen owing to its ventral inclination.

2. The basal joint of the L. chelicera cannot be recognized, but the pincer with its fixed and movable finger is well displayed. It lies on its side, and is roughly triangular in outline with the fingers in sufficient relief to show them to be of equal size and slightly curved. Evidently this example lies in a position at right angles to the posture of the chelicera figured by Kjellesvig-Waering (1948, pl. 1, fig. 3). There is no ornament visible.

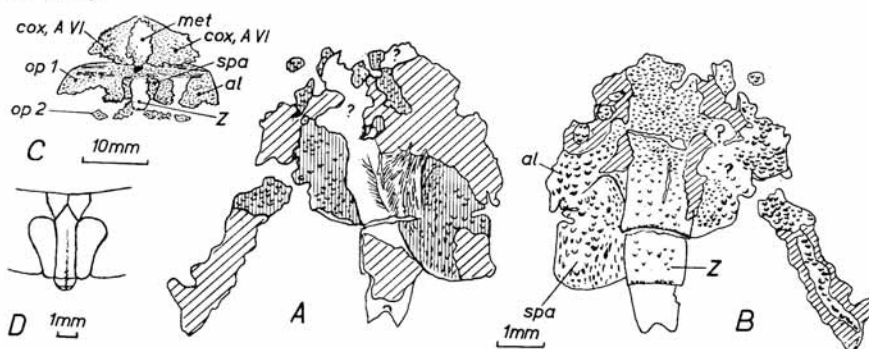
3. The four 'legs' are well preserved, but it is not possible to be certain about the exact number of joints in each, nor about the precise shape of the coxae, though their mandibular denticles are clearly seen surrounding the oral cavity. As pointed out by Kjellesvig-Waering (1948), the appendages increase in length backwards. Each of the legs ends in a long pointed spine that appears to be articulated to the last joint, which itself has two fixed spines near its distal end. The penultimate joint may also carry fixed spines. The distal ends of the joints show an edging of mucrones and here and there a small spine.

The number of joints excluding the terminal spine, but including the coxa, increases backwards; the 1st leg (A II) having four or five; the 2nd leg (A III) six; the 3rd (A IV) six or seven; and the 4th (A V) eight. There is thus a close match with the arrangement in *E. fischeri* as figured by Holm (1898, pl. 2, fig. 1), but the first three legs here are less obviously food-gatherers than in *Eurypterus*.

4. On both of the 3rd legs (A IV) there is a curious structure projecting from the first or possibly the second joint after the coxa. That on the R. side is the better exposed. It has an ornament of pointed granules and the appearance of being two jointed, which is probably due to a fold resulting from the flattening. These organs are almost certainly

claspers, and, as such, are evidence that this individual was a male (Holm 1898, Størmer 1934, Wills 1964).

5. The paddle appendage (A vi) is modelled on very similar lines to the paddle in *E. fischeri* (Holm 1898, pl. 2, fig. 1) and to that of *A. mazonensis* as figured by Kjellesvig-Waering (1948, pl. 1, fig. 1). It consists of an enormous coxa and five joints followed by the actual paddle-blade made up of three large elements and one tiny piece at the end. As preserved, the plane of the blade on each side of the animal makes an angle of about 30° to the general plane of the mesosoma, sloping inwards and downwards in relation to the body.



TEXT-FIG. 4. *A. mazonensis* Meek and Worthen.

A, B. Parts of the 1st operculum of Type B isolated from MCZ 7162. Slide 7162/1. A, Dorsal view. Dorsal structures left plain. The hairs in the centre are probably on the internal dorsal skin of the *Zipfel*. Vertical ruling, ventral skin with scales showing through; diagonal ruling, parts obscured by matrix on their dorsal side. B, Ventral view showing ventral structures, whether they are exposed on the dorsal or ventral side. Diagonal ruling, parts obscured by matrix on both sides.

C, Ventral view of parts of the 1st and 2nd opercula of a supposed Type B, as seen in a latex-rubber cast of CNHM PE5094. Zigzag lines are fractured edges; stippled where ornament can be seen; large black spot, matrix. The spatulae, lying dorsad to the *Zipfel*, are partly hidden by it. Its distal end is not visible, being covered by matrix in the actual fossil.

D, ? Young example of Type A. Outline of the median part of the 1st operculum of USNM 38866, copied from Kjellesvig-Waering 1948, pl. 1, fig. 6, for comparison with figs. A-C.

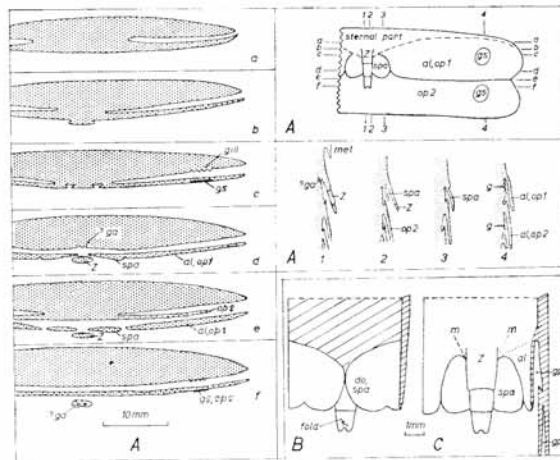
For key to abbreviations, see p. 477.

6. The 1st operculum was etched out in several small detached fragments, the greater part of it having disintegrated during entombment. Luckily one piece retaining the whole of the *Zipfel*, and one spatula with some of the laminate anterior part to which these organs were attached, was recovered and mounted (slide MCZ 7162/1). This can be examined from either side, but is badly obscured in places by adherent matrix (Pl. 77, fig. 4; text-figs. 4, 5). The short *Zipfel* consists of three joints, but there is no triangular hastate front end, the organ merging squarely into the anterior part of the operculum without any suture or interruption of the ornament. The second joint ends in line with the posterior edge of the R. spatula, and the terminal joint projects only a very short distance behind this line. The ventral surface of the main and second joint carries a fair number of pointed scales, and each has a line of mucrones at its posterior end; but the terminal joint is unornamented. It is strongly emarginate and has the appearance of

ending in two lobes. On its dorsal surface there is a sharp fold in the skin just in front of the base of the lobes, but one cannot determine whether or not the fold marks the position of the actual apertures of the genital ducts.

The dorsal surface of the proximal part of the originally cylindrical *Zipfel* probably carried the long, flexuous hairs which can be seen when the slide is examined from the dorsal side (text-fig. 4A). Those on the R. have the appearance of underlying the surviving spatula, which suggests the possibility that they were attached to its dorsal side. However, in *A. moyseyi* (BU 751) it is certain that similar hairs were attached to the dorsal side of the *Zipfel* (see text-fig. 10A), and for that reason I favour assigning these to that position.

I regard the *Zipfel* as an example of Type B belonging to an adult male (according to Holm 1898). The question of sex is further discussed below.



TEXT-FIG. 5. *A. mazonensis* Meek and Worthen, Type B.

A, Tentative reconstruction of opercula 1 and 2 in ventral view based on analogy with *E. fisheri* with diagrammatic sections. 1 to 4, lines of longitudinal sections; a-f, lines of transverse sections.

B, Dorsal view of the reconstructed middle part of the 1st operculum; wide ruling, soft parts of the body cut away to below the roof of the 1st gill-pouch; close ruling, vertical section.

C, Ventral view of B with section through the ala and body. Dotted line, anterior pocket of the 1st gill pouch.

For key to abbreviations, see p. 477.

The spatulae appear to have been short, oval, laminate organs that were continuous with the alae except for a very short distance on their posterior sides. The ornament of the one that has survived in place is depicted on text-fig. 4B. The other spatula was extracted (slide MCZ 7162/2). The internal edges of the two spatulae must have almost met above the *Zipfel*. The spatulae, the alae, and the *Zipfel* all began to hang free from the body at about the same point (text-fig. 5C, *mm*).

Text-fig. 5 is an attempt to show by means of diagrammatic reconstructions and sections what can be deduced from the scraps of skin recovered, about the relations of the

Zipfel, the spatulae and alae to one another, to the body and to the possible sites of the genital apertures and the gills.

No remains of the 2nd and subsequent opercula were found.

(iii) *CNHM PE5094* (having Type B genital organs)

Dr. Kjellesvig-Waering has kindly lent me three latex-rubber casts of this small specimen (carapace length: 15 mm.). One cast shows the ventral surface seen from the ventral side, being a cast of the external impression of the fossil on the rock. By courtesy of Dr. E. S. Richardson, Jr. (Chicago Natural History Museum) and of Dr. Kjellesvig-Waering, I give a sketch of the 1st operculum and remains of the 2nd operculum in text-fig. 4c. Dr. Kjellesvig-Waering had exposed the greater part of the *Zipfel*, of which only the anterior end was originally visible. The cast shows that:

- (a) The unornamented *Zipfel* has no hastate anterior end, but passes forward squarely into the ornamented lamina, exactly as in MCZ 7162.
- (b) The *Zipfel* appears to be fairly short. Its distal end is hidden but what is visible reaches to well behind the posterior edges of the spatulae. It is therefore relatively longer than the *Zipfel* in MCZ 7162 and in USNM 38866 (below).
- (c) The spatulae are short and rounded in front, and appear to be sutured to the alae.
- (d) There are no triangular areas in front of the *Zipfel*.
- (e) The 2nd operculum is poorly preserved, and one cannot be certain about its structure.

This specimen is regarded by Kjellesvig-Waering (*in litt.*) as an example of a Type B individual, and I agree on the grounds that its 1st operculum seems to resemble that seen in MCZ 7162 and to differ from the operculum of USNM 38866. This last, however, was regarded as a Type B individual by Kjellesvig-Waering (1948).

(iv) *USNM 38866* (? a young example of Type A)

I have not had an opportunity to see this fossil or a cast of it. The following remarks are based upon the description and illustrations in Kjellesvig-Waering (1948); an enlarged drawing of the median part of the 1st operculum is given on his pl. 1, fig. 6 (copied here, text-fig. 4d). The whole fossil (his pl. 6, fig. 1) has much the same proportions as MCZ 7162, but is smaller, having a carapace length of 11.8 mm. as against 15.6 mm. It differs from it in the following respects:

- (a) The *Zipfel* has a hastate anterior end which is ornamented (cf. Type A in the holotype and in *A. moyseyi*).
- (b) On either side of the hasta of the *Zipfel*, triangular areas are shown, comparable with those to be seen in the holotype (Type A) and in some examples of Type A of *A. moyseyi* (below).
- (c) The 2nd and 3rd joints of the *Zipfel* are very much smaller than the 1st, and the 3rd joint is unique in having a rounded termination without any emargination; whereas in MCZ 7162 the three joints are sub-equal in length and the 3rd is strongly emarginate (Pl. 77, fig. 4).

The 1st operculum of USNM 38866 appears therefore to differ from that organ as developed on adults of both Type A and Type B, but to have more affinity with Type A

Ventral anatomy

General. The elucidation of the venter was my chief aim. In text-fig. 6B I have indicated its parts in the approximate positions they occupied in relation to the carapace, tergites, and bits of appendages that were originally visible. In some cases the position of a part, as shown in the figure, may have resulted from displacement during fossilization, but in others it records the arrangement after etching and mounting—for example, coxa v was originally concealed by coxa vi when the progress photo was taken (Pl. 78, fig. 2), but as mounted on slide BU 751/16, it lies well in front of coxa vi and exhibits its hair-clad ventral face. It is shown in this position on text-fig. 6B. There is also some uncertainty about the identification of some of the isolated fragments of appendages as named in the figure.

Prosoma

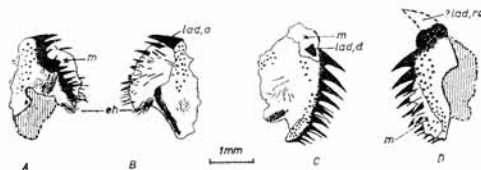
(a) *The body-skin.* In one or two places (in the Marco block and on slide BU 751/11) the lateral doublure of the carapace is seen. As in *E. fischeri* (Holm 1898, pl. 3, fig. 17) it is beautifully ornamented by elongate brown thickenings that run parallel to the edge of the carapace in contrast to the scales on its dorsal surface, which always point backwards. None of the thinner ventral skin to which the appendages were attached has been preserved.

(b) *The appendages 1-vi (A 1-A vi).* The chelicerae (A 1) were not found. Of the four legs only the 4th pair (A v) is well preserved (text-fig. 6B). It is clearly a walking leg comparable to the 4th leg of *A. mazonensis* (above, p. 484 and text-fig. 2) and also to the same leg in *E. fischeri* (Holm 1898, pl. 2, fig. 1). Its coxa (of the R. side) is well displayed in slide BU 751/16. It carries a gnathobase with large sharp denticles, which had been bent on itself in fossilization (text-fig. 8B). It is shown restored to its original shape in text-fig. 8A. That part of the coxa which moved above the gnathobase of the paddle is well exposed. It is covered with setae. The dorsal-facing parts are obscurely displayed, but a curious round cavity can be recognized (text-fig. 8B, e, cg), which may be compared with the circular hole on coxa v of *E. fischeri*. I have suggested (Wills 1964) that the latter may mark the site of the opening of the coxal gland. A similar cavity is well displayed on a detached and damaged coxa that is thought to belong to the vth appendage of the L. side (slide BU 751/8).

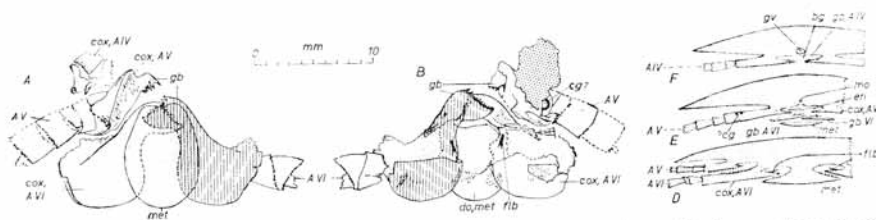
In addition to the gnathobase on coxa v, three rather similar gnathites were extracted, of which the smallest was the foremost, but it is not known to which coxa each belonged. Two (slides BU 751/3, /5) are figured in text-fig. 7. Each has its inner edge armed with large thorn-like denticles and long hair-like movable setae which occur on both the upper and lower surfaces. Some are still attached but many are witnessed only by their facets. The denticles, largest in front, pointed inwards and backwards (in a double row in BU 751/5, text-fig. 7A, B) comparable to the arrangement in the 2nd coxa (A III) in *E. fischeri* (Holm 1898, pl. 2, fig. 9). The majority of the denticles in the two gnathites figured seem to lie more or less in the same plane as the surfaces of the sclerite, but it is possible that this appearance results from compression, and that some may have pointed ventrally like those described in *A. mazonensis* (above, p. 485) and in *E. fischeri* (Holm 1898, pl. 2, fig. 4). On slide BU 751/5 there is towards the posterior end a bunch of fine hairs, labelled as 'epicoxal hairs', on the supposition that the bunch is comparable to one of the hair-covered epicoxites of *Eurypterus* described by Holm (1898, pl. 2,

figs. 3, 4, 9, 15.) but in this case there is no indication that the hairs were borne by a separate sclerite as they were in that genus.

In slide BU 751/3 the front end of the gnathite is heavily chitinized as if it were adapted to crushing, suggesting that the specimen may be part of the R. 3rd coxa. The foremost denticle is probably bent back on itself in the matrix, and may originally have pointed forwards, roughly as indicated in text-fig. 7D. (cf. Holm 1898, pl. 2, fig. 4 of 3rd coxa of *E. fischeri*.)



TEXT-FIG. 7. *A. moyseyi* H. Woodward. Type A. A, dorsal; B, ventral view of gnathobase on the coxa of ?L. 2nd leg (A III) or possibly of 1st leg. Slide BU 751/5. C, ventral; D, dorsal view of gnathobase of ?R. 3rd leg (A IV). Slide BU 751/3. *eh*, ?epicoxal hairs; *lad, d*, large anterior denticle, ? displaced in matrix; *lad, o*, ditto, in original position; ?*lad, ro*, ditto, restored to original position; *m*, matrix with denticles and hairs showing through.



TEXT-FIG. 8. *A. moyseyi* H. Woodward. Type A. The metastoma and associated appendages IV-VI. Slide BU 751/16.

A, Ventral view. Stipple, metastoma; ruling, L. coxa and gnathobase of A VI. The hair-covered part of coxa v originally overlay the R. gnathobase of A VI. Its toothed gnathite is shown restored to its original position.

B, Dorsal view, showing the reversal of the toothed gnathite of A v, as it is preserved. Light stipple, ventral skin seen from within; ruling, dorsal skin of L. coxa and gnathobase. *flb*, ?flabellulum (full black) on the internal strips of both coxae; unstippled, surviving part of the dorsal hair-clad skin of the R. coxa A VI and of the doublure of the metastoma. Heavy stipple, matrix.

D-F, Diagrammatic transverse sections. D, through the middle of the metastoma showing its attachment to the body and the position of the flabellulum; E, through the front of the metastoma, the gnathobases of A VI, coxae of A v, the endostoma, the mouth (*mo*); F, further forward through the buccal groove (*bg*), the gullet (*gv*), and coxa and gnathobase of A IV.

For key to other abbreviations, see p. 477.

(c) The metastoma and great coxae of the paddle (A VI) with their gnathobases were extracted together (slide BU 751/16; Pl. 78, fig. 7; Pl. 79, fig. 4; text-fig. 8). The metastoma shows no new features apart from the hairs on its broad doublure. In text-fig. 8D it is interpreted as a boss, pendent from the body, with water-spaces above the doublure, in which the coxae of the paddle were free to move, their toothed gnathobases projecting

beyond the front of the metastoma (text-fig. 8A), just as they do in *A. mazonensis* (MCZ 7162, text-fig. 3, and the example figured by Kjellesvig-Waering 1948, pl. 1, fig. 1); but since the preparation shows both sides of these organs, their structure is for the first time fully revealed (a detached coxa vi of *A. imhofi* Reuss, showing one surface admirably, is figured by van Oyen (1956, pl. 19, fig. 196a, b). The coxa is dorso-ventrally flattened and almost circular in outline behind, with a large mandibular process, the actual gnathobase, projecting forward. The external skin is thick and covered with scale ornament; the internal skin is thin and hair-clad in places. The whole coxa was pivoted to the body, at a point not far from its centre, by muscles that entered it from above (text-fig. 8D). On the internal lateral dorsal surface near this point there is on each coxa a minute rod-like process protruding into the space, mentioned above as existing between the body and the dorsal skin (doublure) of the metastoma (text-fig. 8B, D, *flb*). Perhaps this rod may be a homologue of the flabellulum on appendage vi of *Limulus*. Distally the dorsal and ventral skins of the coxa part company to provide the socket of the articulation of the first joint of the paddle, the 1st and 2nd joints of which are still in place on the L. side.

The mandibular process (the gnathobase) is a heavily chitinized arm projecting forwards to expand into a saw-edged jaw with ten sharp teeth and one rounded one at the inner end. As preserved, the R. and L. jaws cross one another, the actual biting edges touching one another only near the front (text-fig. 8B, E), but an outward swing of the whole coxa would bring the two edges into one straight transverse line, just behind the buccal groove. By analogy with *Eurypterus*, it was just here that the broad endostoma (below) lay immediately above the jaws (text-fig. 8E). The surfaces of the gnathobases that moved across one another are covered with hairs.

The above features are hard to describe with clarity, but they are elucidated in text-fig. 8 by accurate drawings of the two aspects and by diagrammatic sections. It is only possible to represent diagrammatically the numerous minute hairs.

(d) *The endostoma* (slide BU 751/19, Pl. 78, figs. 5, 6; text-figs. 8E, 9). This specimen was not seen in its natural relation to any part of the body, but was discovered among the final washings. It presents a general resemblance to the endostoma of *E. fischeri* (Holm 1898, pl. 1, figs. 7-10; Wills 1964, text-fig. 1), which was a lip-shaped structure with a ventral covering of skin that turned over at the front to form the ventral lining of the gullet. But in this specimen difficulties arise from its present orientation, which can be established in the following way. One side of the double-skinned organ is partially concealed by a thin layer of matrix, which in turn is covered locally by bits of the carapace exhibiting numerous mucrones and scales which are known always to point posteriorly. However, the shape of the organ and the distribution of hairs on it, when compared with the endostoma of *Eurypterus*, show that the closure or turnover from its ventral to its dorsal skin, which should point forwards, here points in the backward direction indicated by the mucrones, and that the layer of skin nearest to the underside of the carapace is not the dorsal skin which lined the gullet, but the ventral one against which the gnathobases of the paddle worked. This anomaly can be explained by postulating rotation of the sclerite during fossilization on an axis transverse to the body in such a way that the true front of the endostoma was brought to face backwards and its true ventral surface came to lie dorsally upwards, as indicated diagrammatically in text-fig. 9F. Such a rotation is not improbable, since other organs around the mouth were found

to have been displaced. [In one dissection of *Eurypterus fischeri* the endostoma was found displaced in the matrix within the body just below the 5th tergite (Wills 1964).] Text-figs. 9A and B show the present orientation, in relation to the carapace, of the two sides of the endostoma in so far as they are visible. Text-figs. 9C and D are reconstructions of the corresponding sides (C, the true ventral; D, the true dorsal) as they would appear after the suggested rotation. Unfortunately there is not enough of the ventral skin preserved to allow its complete restoration. In both C and D the distribution of hairs is known partly from setae still in place and partly from the facets to which they were attached.

If the rotation hypothesis is held to be inadmissible, it follows that in life the organ lay in its present position and orientation with regard to the carapace; that the ornament on the latter suggests a part of the carapace in line with the median eyes; and therefore that the organ belonged to the front rather than to the back of the oral cavity and was an anterior lip or *labrum*. I would reply that the *labrum* of a Eurypterid has never been found, but must have been a small structure in view of the shortness of the adjacent coxae; that the present specimen could scarcely be functional as a *labrum*; that its dimensions are appropriate to the width of the metastoma and the gape of the jaws of the gnathobase; and if rotated it would be functional as the posterior lip of the oral cavity and as a filter to exclude large particles from ingestion. Also if rotated, a general match of its structure can be established with the endostoma of *E. fischeri*, about whose position and orientation there is no question.

The endostoma was a forwardly directed transverse lip about 2 mm. long and 5.5 mm. wide. By analogy with *Eurypterus*, it lay across the back end of the buccal groove and formed the lower surface of the actual mouth (text-fig. 8E). Its dorsal or buccal surface led into the gullet, and its ventral surface overlay the jaws of the great gnathobases of the paddle. The turnover from the ventral to the dorsal skin constituted the actual lip, which seems to have been thin and fairly sharp-edged. In outline it is slightly embayed in the middle, and here the skin is thickish. A similar but deeper embayment in *E. fischeri* marks the point at which the ventral skin passed into the lining of the gullet.

EXPLANATION OF PLATE 79

Anthraconectes moyseyi H. Woodward 1907. All the figures refer to parts of one specimen, BU 751, photographed by combined reflected and transmitted light.

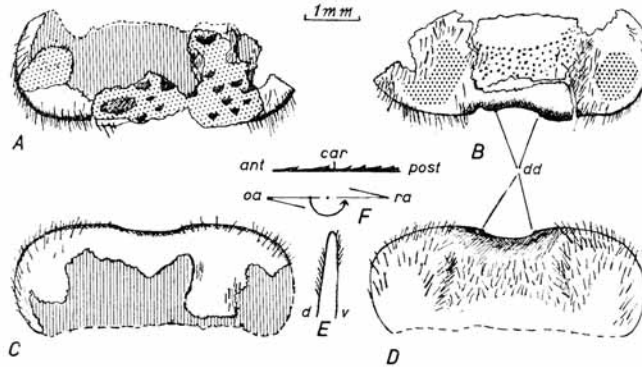
Fig. 1. Dorsal view of median part of the 1st operculum with ornament and hairs showing through in places, and a band of setae belonging to the front edge of the 2nd operculum near the back margin of the alae and spatulae (cf. text-fig. 10A). BU 751/18, $\times 10$.

Fig. 2. Dorsal view of median part of the 2nd operculum with ornament and hairs showing through in places, and a band of setae belonging to the front edge of the 3rd operculum pressed against matrix near the back margin of the alae (especially clear on L. side). Note the inner edges of the alae overlapping dorsad to the *Zipfel* (restored to its original position), and the hair-clad nature of the median triangular projection passing back into the unornamented ventral skin of the front of the *Zipfel* (cf. text-fig. 10B). Slide BU 751/1, $\times 10$.

Fig. 3. Dorsal view of part of the same (with the overlapping alae removed) and the dorsal skin of the proximal part of the *Zipfel* (slide BU 751/4) restored to its original position (note how far forward it extends), $\times 10$.

Fig. 4. Ventral view of metastoma and the proximal parts of appendages IV-VI. Coxae A IV and A V have been displaced forward in mounting. The gnathobase of coxa A V was bent back during fossilization (cf. text-fig. 8A). For dorsal view see Pl. 78, fig. 7. Slide BU 751/16, $\times 5$.

The two ends of the lip are, on both surfaces, thickly covered with setae which cluster near the margins to form a projecting brush, but the skin adjacent to the embayment is bare, except for a pair of minute denticles at either end (text-fig. 9D, *dd*). Further back, the middle of the dorsal surface is covered with forward pointing hairs like those at its two ends, but its most posterior part seems to have been bare. The middle part of the ventral surface has been lost, but there are indications that the whole of the ventral skin may have been hairy, except just behind the embayment of the lip.



TEXT-FIG. 9. *A. moyseyi* H. Woodward. Type A. The endostoma. Slide BU 751/19.

A, Dorsal view of the specimen showing adherent bits of the carapace (stipple), the original ventral skin facing dorsally (plain), and the inside of the dorsal skin (ruled).

B, Ventral view of the specimen showing the inverted dorsal or buccal skin (plain) with hairs and hair-facets, matrix (heavy stipple); thickened lip and denticles (*dd*) (shaded).

C, Restoration of the ventral skin, as far as preserved (plain), in its original orientation. Inside of dorsal or buccal skin (ruled).

D, Restoration of the dorsal or buccal skin and hairs, in its original orientation.

E, Longitudinal section based on C and D. *d*, dorsal; *v*, ventral.

F, Diagram to illustrate the hypothesis of reversal of the endostoma prior to fossilization. *car*, carapace; *oa*, the original anterior end rotated to the reversed position (*ra*), as found.

The structure of the endostoma, as here interpreted, differs in detail from that of *E. fischeri* (Holm 1898, pl. 1, figs. 7-10; pl. 8, figs. 1, 2; Wills 1964, text-fig. 1). In particular the whole organ must have projected forwards more freely on either side of the buccal cavity, and the setae situated at the two sides must have joined forces with those on the gnathobases of the coxae of the legs to form a still more efficient sieve than that possessed by *Eurypterus*.

The post-metastomal waist. The metastoma and coxae of the paddle, when first exposed, concealed the front part of the 1st operculum (Pl. 78, fig. 2), indicating that the body was contracted when entombed. In this position the post-metastomal waist (p. 480) was virtually non-existent.

Mesosoma

(a) *The ventral skin of the body.* As already noted there has been no preservation of that part of the body-skin which lay within the gill-pouches and which, by analogy

with *Eurypterus*, bore a pair of gill-tracts within each pouch (Wills 1964). However, there is wonderful preservation of the chitin of the outer and inner skin of the *Zipfeln*, of the outer skin of the opercula and of marginal parts of their inner skins (the doublures), and of many of the setae and hairs that were attached to the inner surfaces of both *Zipfeln* and opercula. The setae to be described in the following section as lying within the intersegmental folds have survived even though the skin that bore them has disappeared completely.

(b) *Relation of the ventral to the dorsal organs.* In the mounted 1st operculum (slide BU 751/18) it can be seen that there are pressed against its dorsal surface two features that do not belong to it, both of which are of value in determining its relationship to the rest of the body. The first and most conspicuous is a band of closely packed parallel setae running across the alae and spatulae near their hinder edges (Pl. 79, fig. 1, *ant. do. op 2*). Originally these setae were almost certainly attached to the anterior doublure of the 2nd operculum, thus recording the position of its front in relation to the 1st, and giving an indication of the small amount of overlap of the 1st over the 2nd operculum. A similar band representing the front of the 3rd operculum runs across the dorsal side of the 2nd operculum (slide BU 751/1; Pl. 79, fig. 2). Both these bands are very conspicuous, and tend to obscure the distribution of the hairs on the internal lateral doublures of the opercula on to which they have been pressed.

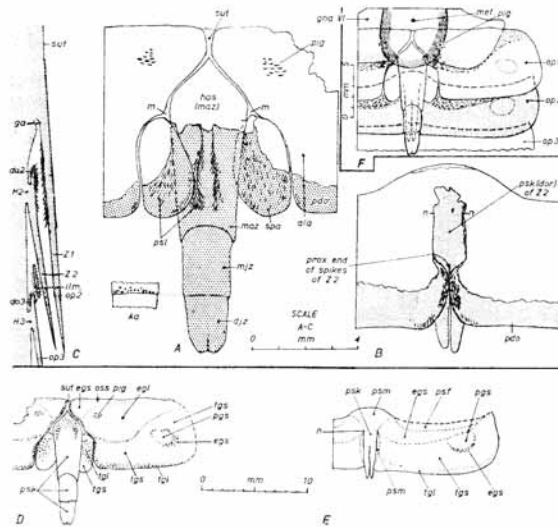
The second feature is seen on the dorsal side of the front end of the L. ala. It is a strip of skin with the heavy mucronate ornament belonging to the posterior margin of the carapace. The position of this important dorsal landmark in relation to the 1st operculum has been utilized in constructing text-fig. 6B, in which an attempt has been made to place the ventral organs in their correct position *vis-à-vis* the dorsal ones. There has been only a slight displacement of the opercula from their original positions, which was: the 1st operculum (VII+VIII) under tergites VII and VIII, and the 2nd-5th opercula (IX-XII) under tergites IX-XII (text-fig. 6B). The exposed part of each overlapping operculum is just about as long as the exposed part of the corresponding tergite (or two tergites in the case of the 1st operculum). The dimensions of the concealed parts can be established for the 2nd and 3rd opercula (text-fig. 10F).

(c) *The opercula.* The 1st and 2nd opercula which were extracted and mounted as slides BU 751/1, /4, /18, are bilobed with the two halves separated by the 1st and 2nd *Zipfeln* respectively. In the 1st operculum the two halves are each divided into a spatula and an ala. The 3rd, 4th, and 5th remain in the Marco block. They show no signs of a median suture or of bilobation. In this respect they differ conspicuously from *Eurypterus*, in which there is no doubt that the five opercula represent a set of paired branchial appendages, branchial in that each operculum floored a gill-pouch with a pair of gills in its roof (Wills 1964).

The part of each operculum normally exposed is covered by a dense ornament of small scales, except for a small bare oval area near each lateral end (these are termed gill-spots below); but the part normally underlain by the preceding operculum has less ornament or none. In the 1st and 2nd opercula the very front is thin and has a few hairs; possibly the anterior strip is missing from the 1st; but in any case, by analogy with *Eurypterus*, no anterior doublure is to be expected here. In the 2nd operculum the anterior edge turned over into the anterior doublure which, as already noted, was thickly coated with setae.

The complex genital modifications of the 1st and 2nd opercula match in many respects the adaptations found in Type A individuals of *Eurypterus*. They demand detailed description.

(d) *The 1st operculum* (slide BU 751/18; Pl. 78, fig. 3; Pl. 79, fig. 1; text-figs. 10A, D, F) is a large structure, measuring (without the *Zipfel*) about 6.5×25 mm. Before etching, its front half was concealed from ventral view by the metastoma and coxae of the paddle (text-fig. 10F). The slide shows the operculum to have consisted of five parts—the mesial



TEXT-FIG. 10. *A. moyseyi* H. Woodward. Type A. Slides BU 751/1, /4, /18.

A, Dorsal view of the median part of 1st operculum (dorsal skin stippled); *Aa*, Ventral view of the distal articulation on the middle joint of Z1. B, Dorsal view of the median part of 2nd operculum (the dorsal skin of 2nd *Zipfel* and the surviving doublure of the alae with hairs are stippled), slightly reconstructed. C, Sagittal diagrammatic section. D, E, Ventral views of 1st and 2nd opercula with the distribution of ornament and setae outlined: only large or conspicuous scales indicated. The areas labelled separately are not sharply defined. F, Ventral view of metastoma, coxae of A VI and opercula 1, 2, 3 in their original relative positions, as deduced from a progress-photo and from the positions of the bands of setae marking the anterior edges of opercula 2, 3.

do 2, do 3, anterior doublures of op. 1, 2; *egl*, large elongate scales; *egs*, small ditto; *H2, H3*, suspension hinges of op. 2, 3; *ilm*, internal lateral margin of ala of op. 2; *oss*, thin skin with small scales and setae; *pgs*, unornamented gill-spot; *pig*, pigmented scales; *psf*, plain thin skin without setae; *psk (dor) Z2*, plain dorsal skin of Z2; *psl*, plain dorsal skin with long flexuous setae; *psm*, ditto with many short setae; *tgl*, triangular scales, large; *tgs*, ditto, small. For key to other abbreviations see p. 477.

three-jointed *Zipfel* on either side of which is first a short narrow spatula and then a broad ala. The exact shape of the front of the ala cannot be determined in this or any of the other examples of *A. moyseyi*; but it was probably much the same as in the holotype of *A. mazonensis*, where a still more anterior strip is seen (p. 482; text-fig. 1) which can be matched in *Eurypterus* and *Dolichopterus*. On this view the anterior part seen in

slide 751/18 would correspond to the middle strip in those genera. The two alae are sutured to one another on the middle line, to the hastate anterior end of the *Zipfel*, and to the outer sides of the spatulae, by narrow bands of thin unornamented skin, fragments of which have survived despite the fracturing which took place along the sutures during extraction and mounting. There is no change in the pattern of ornament, apart from a deeply pigmented spot (below) to suggest the presence of paired 'triangular', 'pentagonal', or 'deltoidal' plates in front of the hasta of the *Zipfel*, nor is there any trace of sutures to define such plates.

This observation confirms the conclusion reached about the corresponding parts in *A. mazonensis* (p. 482), and makes it improbable that the triangular areas visible in some specimens of *A. moyseyi* (p. 504) represent discrete plates. I suggest that the lines appearing to define these areas on their outer sides were produced during fossilization by unequal compaction as between the sternal part of the ala and its free-flapping opercular part that underlay the gill-pouch.

The alae of the 1st operculum are considerably longer and more completely covered by scales than the other four opercula. The gill-spots are perhaps a trifle smaller than those on the latter. Very little of its original anterior and lateral outline can be seen. Apart from bits of the posterior doublure, the internal skin of the alae has not been preserved.

Dorsad to the alae I searched for, but failed to find, any remains of internally directed tentacle-like horns, such as occur in *Eurypterus* and *Dolichopterus*.

Ornament. The anterior hastate end of the *Zipfel* is covered with medium-sized triangular scales, passing behind into two bands of large transversely elongate ones, but the rest of its surface is plain (text-fig. 10D). The whole of the spatulae and most parts of the alae are closely covered by small scales of two types—transversely elongate and triangular. The general distribution is shown in text-fig. 10D. The elongate scales, small near the middle line and somewhat larger elsewhere, cover most of the front part, which in life was underlain by the coxae of the paddle (text-fig. 10F). On this strip (the supposed 'middle strip', see p. 480), half-way between the front and the spatula, is a patch of particularly pigmented scales that lay above the point at which coxa VI passed above the edge of the metastoma (text-fig. 10A, D, F). Apart from this pigmented patch, the pattern sweeps from the mid-line towards the side of the operculum with no interruption.

The boundary of the area of elongate scales is not sharp, nor is there a band of large mucrones to divide the ala into strips, as in *Eurypterus*. It passes in front of the gill-spot. Behind the boundary is the posterior strip, in which the ornament consists of predominantly triangular scales, with the exception of the gill-spot itself which is an oval patch of bare skin lying toward the side of the ala. Around the spot are a few elongate scales that serve to accentuate its bareness. The ornament around the edges of the spatula and adjacent ala is heavy and limbate, and near the posterior end of the former the scales are drawn out into linear ridges parallel to the length of the animal.

Though the distribution of the two types of scale ornament was probably conditioned by the overlap of the metastoma and coxae of the paddle, behind which there was freer contact with the outside elements (a similar distribution of ornament is found in the 2nd operculum, where the relation of the area of overlap to the area of elongate scales is even closer), it is not impossible that the boundary between the two strips also coincided roughly with the limit between those parts of the *Zipfel* and alae that were a sternal

portion of the animal's ventral body-wall, and those parts that hung free. This boundary would then indicate the front of the gill-pouch. The position of the gill-spots suggests that the site of the gills themselves was further towards the side of the animal than in *Eurypterus*.

The *Zipfel* was a long, three-jointed rod that projected freely backwards and downwards from its hastate proximal end which was a sternal part of the body-wall. In front of the hasta the alae met at a median suture, and, as already mentioned, there are no suture-defined triangular areas comparable with the pentagonal plates of *E. fischeri*, which Holm regarded as the paired basal joint of the *Zipfel*.

(i) The main joint (proximal) is more than half the length of the appendage. Its ornamented hastate proximal end (text-fig. 10D) is defined on either side by sutures as far back as the points at which they divide around the front ends of the spatulae. These points (text-fig. 10A, *mm*) also mark the end of the fixed (sternal) hastate part and the beginning of the free hanging rod: for distal to these points the skin of the *Zipfel* can be seen to have been tubular. Its ventral surface is thick and devoid of ornament; its dorsal side has thin skin which is folded (in its present flattened state) into a median groove and two lateral ridges which carry long posteriorly directed hairs (Pl. 79, fig. 1; text-fig. 10A). The tubular part of the main joint hung below and quite free from the spatulae, and projected backwards for a considerable distance behind them (Pl. 78, fig. 3; Pl. 79, fig. 1; text-figs. 10A, D).

(ii) The middle joint, also free from ornament and tubular, was articulated to the main joint along an almost semicircular line. Its other end is straight and marked on the ventral side by a line of small mucrones (text-fig. 10A) similar to those outlining the distal ends of the joints of the legs.

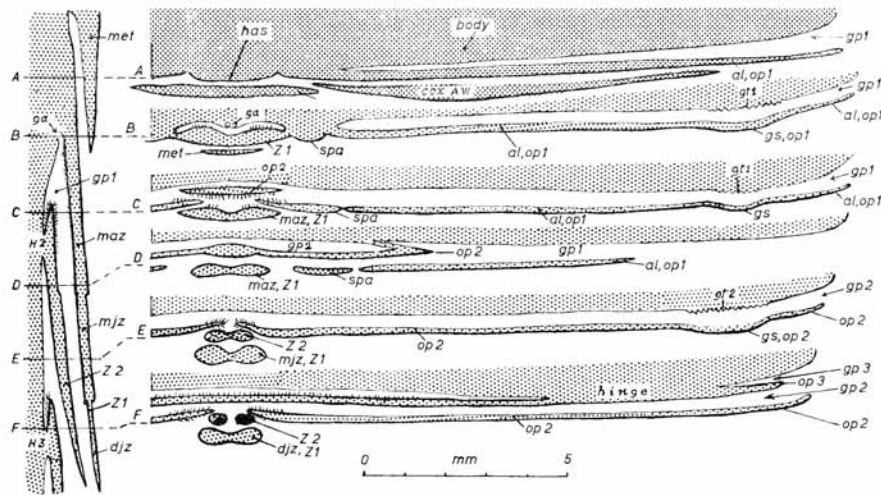
(iii) The terminal joint was also free from ornament and tubular, but sealed at its distal end, which is thickened and devoid of any opening. The end is emarginate, the excavation being continued forward for a short distance by a groove that gives the impression that the tube originated through the fusion of the two parts of a paired organ.

On neither the main nor middle joint is there a pair of spurs, as there is in *Eurypterus*; the terminal joint takes the place of the pair of furcae in that genus. The *Zipfel*, however, resembles the 'type A' *Zipfel* of *Eurypterus* in that no aperture can be seen on it. Following Holm (1898) I contend in my 1964 paper that the paired genital aperture was sited on the body wall at the base of the inside of the *Zipfel*. It is in this position that I have shown the openings in the diagrammatic sections (text-figs. 10C, 11, section B).

The spatulae were each a short narrow oval-elongate lamina attached to the body along its front, where the soft tissues originally merged into those of the main joint of the *Zipfel* on the one hand, and into those of the alae on the other. All three organs began to hang free from the body at this point (text-fig. 10A, *mm*). The outer skin of the spatula was ornamented with scales (p. 498) and its inner skin was very thin and covered with long hairs (shown diagrammatically in text-fig. 10A) which also show the extent to which the internal skin has been preserved.

The internal lateral edge of each spatula was not attached to the *Zipfel*, but overlapped it dorsally (the R. spatula was displaced ventrally in mounting, and is so shown in text-fig. 10A). The other edge was sutured to the ala for some distance, but how far back the union extended cannot be determined now, since the parts became separated during extraction. In the holotype of *A. mazonensis* and those specimens of *A. moyseyi* that show the ventral surface (see p. 504), the notch between spatula and ala extends for about a third or half the length of the spatula, but I got the impression, when developing the present example, that most of it was free to flap independently of the ala, for when first seen, the L. ala overlapped the L. spatula, but the R. ala was overlapped by the R. spatula.

In searching for a homologue of the spatulae, I thought at first that they might equate with the tentacle-like 'horns' of *Eurypterus* (nothing directly comparable having been found during the preparation); for the two organs hung from the body at just the same point, namely, between the base of the hasta of the *Zipfel* and the inner edge of the laminate part of the operculum. They are, however, directed posteriorly and downwards away from the body, whereas the horns in *Eurypterus* pointed forwards and upwards in such a way that they always remained within the gill-pouch.



TEXT-FIG. 11. *A. moyseyi* H. Woodward. Type A. Diagrammatic sagittal and transverse sections to show the structure and relationship of the 1st and 2nd opercula. The sections are based on the flattened skins; but the spaces within the animal occupied by tissues (stipple) and the gill-pouches occupied by water, have been expanded vertically. In life, both were larger still, and surfaces here shown flat may have been strongly curved. Thick lines represent skin that is actually preserved in the fossil or skin evidenced by setae visible in the matrix. Short thin lines represent setae; long thin lines represent the ventral skin of the body, the gill-tracts (zigzag lines) and the internal skin of the opercula, none of which, except bits of marginal doublures, has been preserved. For key to abbreviations see p. 477.

Dolichopterus jewetti, as described by Caster and Kjellesvig-Waering (1956, p. 22, fig. 1) had a 1st operculum displaying both 'internal tubes' (= horns) and 'lateral lobes' (= spatulae). The latter are much narrower than in *A. mazonensis* and *A. moyseyi*, and are said to be sutured to the posterior strip of the laminate part of the operculum. This recent discovery of the two organs on the same appendage invalidates my hypothesis.

(e) *The 2nd operculum* (Pl. 78, fig. 4; Pl. 79, figs. 2, 3; text-figs. 10B, E, F). This organ was the first part that I isolated (slide BU 751/1). I left in place its R. ante-lateral corner (progress-photo, Pl. 78, fig. 2), which can still be seen in the Marco block. On it is the R. gill-spot. The rest of the operculum was mounted as slides BU 751/1, /4.

During development the distal spikes of the *Zipfel*, together with a bit of the dorsal skin of its main joint, became detached from the rest of the operculum. I mounted the

spikes on the same slide as the main part of the operculum (slide BU 751/1); but, thinking that the other bit was only in accidental association, I mounted it separately as slide BU 751/4. Close examination has made it clear that this fragment is a piece of skin that fits exactly over the ventral skin of the main joint in slide 751/1 at a point where its dorsal skin is missing. When the posterior half of the fragment has been thus positioned, its anterior half overlies the rear part of the fan-shaped median process of the operculum (Pl. 79, fig. 3). In constructing this figure, photographs made to the same scale were used to reproduce the original dorsal aspect of the *Zipfel*. In Pl. 79, fig. 2, only the posterior ends of the spikes are shown, because the more anterior parts lay ventrad to the alae and were concealed by them in dorsal view.

As already noted, the conspicuous band of parallel setae (Pl. 79, figs. 2, 3, *ant do, op 3*) visible in dorsal view near the posterior margin (omitted from the text-figs.), belonged to the anterior doublure of the 3rd operculum. Its position shows that the 2nd operculum did not greatly overlap the 3rd (text-fig. 10F).

The whole operculum is a roughly rectangular strip with a forwardly directed median fan-shaped process that is covered with fine hairs (Pl. 78, fig. 4), and a small ante-lateral process at either end (text-fig. 10E). It measures without the *Zipfel* about 6×26 mm. The strip is divided by the median 2nd *Zipfel* into a pair of lobate alae which merge into one another without any suture in front of the *Zipfel* on the fan-shaped process. The whole operculum is thus closely similar in structure to the 2nd *Blattfuss* of *Eurypterus* (Holm 1898, pl. 4, fig. 21). In both genera the operculum was attached to the body by a suspension-hinge (text-fig. 10C, *H2*) that was lined in front by the anterior doublure, which was deep from back to front above the process and narrow elsewhere. This doublure was covered by the band of setae referred to above, p. 496, as being now pressed against the dorsal side of the 1st operculum. Thus suspended, the alae and 2nd *Zipfel* hung free from the body, and formed the floor of the 2nd gill-pouch. The tip of the *Zipfel* projected about 1 mm. behind the lobate hind edges of the alae, which, as preserved, meet one another *dorsad* to its two terminal spikes (Pl. 79, fig. 2; text-fig. 10B). This is the position in the flattened fossil, but in life the alae may have curved upwards along the sides of the *Zipfel*, and the latter organ may have been capable of upward and downward movement between them. Their inner edges would have tended to box in the two halves of the 2nd gill-pouch. The ventral side of the 2nd *Zipfel* lay directly above the dorsal side of the 1st *Zipfel*, which concealed it from ventral view. For this reason the 2nd *Zipfel* has not been observed previously in *Anthraconectes* or in any other eurypterid except *E. fisheri*. The two *Zipfeln* terminated at about the same point (text-fig. 10C), though the 2nd ended a little in front of the 1st when the body was in the contracted state (text-fig. 10F).

By analogy with *Eurypterus* the posterior side of the suspension-hinge would have formed the anterior pocket of the gill-pouch, but the only part of the inner skin of the operculum that has survived is the dorsal skin of the *Zipfel* (Pl. 79, fig. 3; text-fig. 10B, *psk*) and parts of the posterior doublure (*pdo*).

The alae are ornamented by close-set small scales, some transversely elongate and some triangular in shape. In text-fig. 10E are shown the two strips on each ala covered predominantly by one or other of the two types, and their relation to the unornamented areas of the gill-spots. The latter are larger than those on the 1st operculum. There is no conspicuous line of mucrones between the strips, such as is found in *Eurypterus*; but it

will be seen in text-fig. 10F that, as in *Eurypterus*, the anterior strip was the part that was overlapped by the 1st operculum.

Text-fig. 10E also indicates five areas of thin unornamented skin carrying setae of various kinds, which are often preserved, but more generally are evidenced by small holes (hair-facets). The areas are:

(a) The median fan-shaped area (*psm*) in front of the *Zipfel*, thickly covered with smallish setae (some visible in Pl. 79, figs. 2, 3), exactly as in *E. fischeri* (Holm 1898, pl. 4, fig. 21). This area is continued into:

(b) A pair of anterior strips (*psf*) which probably joined one another around the semi-circular edge of the fan. The setae on strips (*b*) are longer and more flexuous than those on (*a*), and probably spread on to the anterior doublure, which was densely covered by a strip of parallel, medium-sized setae (now adherent to the 1st operculum, p. 496);

(c) A pair of narrow strips (*psm*) on the internal-lateral edge of each ala. Here, in the front part, the setae are short and form an extension of the close-set hairs on (*a*). (The setae of the fan also spread for some distance in amongst the scales of the anterior strip of ornamented skin, whereas elsewhere that skin shows no hair-facets, except widely scattered ones that are unusual in that each is sited on the apex of a scale.) On the hinder part of (*c*) bordering the internal-lateral expansion of the alae, where they almost overlap above the terminal spikes of the 2nd *Zipfel*, there are numerous, very long, posteriorly directed, flexuous hairs on both the external and internal surfaces. Those in the external surface would have remained concealed by the *Zipfel*, had not that organ become detached by the etch. The hairs on the inner (dorsal) surface are indicated in text-fig. 10B, and some are visible in Pl. 79, fig. 2, though most of them are too slender and too mixed with the band of setae belonging to the anterior doublure of the 3rd operculum to be recognized clearly in the photograph. A few stragglers from (*c*) can be seen on the posterior doublure of the ala (text-fig. 10B).

The *Zipfel* (*Z2*) consisted of a cylindrical main joint that passed backwards without any break or suture into two terminal, acutely conical spikes which are a little longer than the main joint. They show no openings. On no part of the *Zipfel* is there any ornament or hairs, except two or three very tiny setae on the dorsal side. On the ventral side the front of the main joint is defined by the change from the very hairy skin of the fan-shaped process to the completely hairless skin of the *Zipfel*. The line dividing the two types of skin runs between the points *nm* in text-figs. 10B, E, where the alae become separate from the *Zipfel*. Attention has already been called to the forward extension of the dorsal skin in front of the line *nm*, which extension proves that the *Zipfel* and the alae passed into the suspension-hinge near the anterior edge of the whole appendage, and that they were free to move together as a single flap as far back as the line *nm*, beyond which they could move independently.

The relations of the 1st and 2nd opercula to one another, to the genital apertures and to the gill-pouches are illustrated diagrammatically in text-figs. 10C, F, and 11, and may be summarized as follows:

(i) The front of the 2nd operculum lay not far behind the point at which the 1st began to hang free from the body. They were separated by a water-space.

(ii) The 2nd *Zipfel* lay above the broader and longer 1st *Zipfel*, but the two organs ended at about the same distance behind the metastoma.

(iii) The long hairs on the dorsal surface of the main joint of the 1st *Zipfel* were in close juxtaposition to the short setae on the fan-shaped process of the 2nd operculum and the longer setae on its anterior margin and anterior doublure. This implies that the hairs and setae were on the lower and upper walls, respectively, of a water-space which adjoined the most probable site of the genital apertures, namely, at the internal base of the 1st *Zipfel* (see Holm 1898, Wills 1964).

(iv) The hairy dorsal surface of each spatula was in a position where it could help to close the sides of that water-space. At the same time each spatula could form an internal-lateral wall to the 1st gill-pouch that lay above the adjacent ala of the 1st operculum.

(v) The long hairs on the dorsal surface (doublure) of the internal-lateral edges of the lobes of the alae of the 2nd operculum, and the lobes themselves, tended to form a similar wall to the 2nd gill-pouch.

(vi) The long hairs on the ventral surface of the internal-lateral edges of the alae of the 2nd operculum lay above and alongside the two terminal spikes of the 2nd *Zipfel*, which in turn lay above the distal joints of the 1st *Zipfel*.

(vii) The mutual relationships of the 1st to the 2nd *Zipfel*, of the spatulae to the 1st *Zipfel* and to the 1st gill-pouch, of the internal-lateral lobes of the alae of the 2nd operculum to the 2nd *Zipfel* and to the 2nd gill-pouch, and of the hair-clad parts to one another and to the *Zipfeln* and gill-pouches, all accord with the view that the two *Zipfeln* (like those in *E. fischeri*, as described by me (Wills 1964)) could have functioned as an almost tubular ovipositor lined with hairs in its proximal parts. This composite organ was separated, partly by hairs, partly by the spatulae of the 1st operculum, and partly by the hair-clad internal lateral lobes of the alae of the 2nd operculum, from the adjacent 1st and 2nd gill-pouches.

If the above interpretation be correct, this Type A individual was a female. The absence of horns from the 1st operculum (possibly due to an accident of preservation), constitutes the only serious difference between the organization of the genitally modified opercula of supposed females of *Anthracopterus* and *Eurypterus*.

The unmodified opercula 3–5 have already been covered by the general description given on p. 496.

2. The Geological Survey Specimens

Among the half-dozen or so specimens collected by Moysey from the Shipley Clay Pit, and now in the Geological Survey Museum, are three (each a part and counterpart) which have been figured as *A. moyseyi* by H. Woodward (1907) and Moore (1936). These authors have demonstrated that a close comparison of the organs seen in the three individuals can be made with the corresponding parts of *A. mazonensis*.

A careful examination of the originals and of rubber casts made from them, confirms the accuracy of previous descriptions, especially that of Moore. With the knowledge of the anatomy gained from the specimens described above, one can recognize traces of the 2nd *Zipfel* in GSM 30194 and 30249. In the latter a fairly well-defined gill-spot is visible. It is also possible to see the extent of the notch between the spatula and ala in both. In the rubber cast of 30249 the two 'triangular pieces' of Moore (1936, p. 370) are defined by lines which are seen to be the inner ends of the alae of the 1st operculum that

have become separated by an entombment fracture along the sutures that originally ran between their inner terminations and the hastate end of the 1st *Zipfel*. This implies that there are no 'triangular' or 'pentagonal' or 'deltoidal' plates in this specimen, which is thus seen to resemble, in this respect, the Birmingham specimen of *A. moyseyi* (BU 751) and the holotype of *A. mazonensis*, as here interpreted (pp. 482, 498).

It is noteworthy that all those specimens of *A. moyseyi* in which the genital operculum has been seen are individuals of Type A. There is therefore no positive evidence that the species was sexually dimorphic.

DETERMINATION OF SEX

All eurypterids are thought to have been sexually dimorphic, because at least five genera (*Eurypterus*, *Anthracopterus*, *Hughmilleria*, *Pterygotus*, and *Slimonia*) have been proved to be so. In each of these the most obvious sexual adaptation is the shape of the *Zipfel* on the 1st operculum. Forms with a long narrow *Zipfel* have been termed Type A, those with a short *Zipfel* Type B (Størmer 1934); but the shapes of the *Zipfel* vary greatly from one genus to another, and with the age of the animal (*Eurypterus*, Holm 1898; *Slimonia*, Waterston 1960). Other sex-controlled modifications have received little attention.

According to Holm (1898), Type A was the female; but Størmer's view, based on studies of other genera, is that it was the male. Tentatively advanced in 1934, this determination of the sex has later been extended by him to all eurypterids (1935, 1949, 1955). Much confusion has consequently arisen in papers on eurypterids (including *Anthracopterus*) published since 1934. The controversy is discussed in my 1964 paper.

Only in *Eurypterus fischeri* are the sexual differences known from dissections of nearly complete individuals and in sufficient detail to provide reliable anatomical evidence about the sex. In the paper cited above, I have redescribed the sex-modifications of the two Types, using hitherto undescribed preparations made by Holm and others made by myself of specimens of *E. fischeri* from the original locality in Oesel, with the conclusion that Holm's determination of Type A as the female is correct. In reaching this assessment the principal features relied upon are as follows:

For Type A individuals, the greater complexity of the organization of the 1st and 2nd opercula, the suitability of the external genital organs for egg-laying, and the absence of clasping organs from any prosomatic appendage;

For Type B individuals, the greater simplicity of the organization of the 1st operculum and its suitability for semination, the want of modification of the 2nd operculum and the presence of clasping organs which, in the only living marine chelicerate, *Limulus*, are a male prerogative.

In the following discussion it is recognized that *A. mazonensis* and *A. moyseyi* agree so closely in their general proportions and genital modifications (so far as these are known) that data drawn from either species can be safely used in defining the sexual characteristics of the genus. (This postulate is logically questionable because, so far, no specimen of Type B of *A. moyseyi* has been found.)

The importance of the discoveries resulting from the etch-dissections of the three

examples of *Anthraconectes* described in the present paper lies in the demonstration that a second genus of eurypterids possessed genital modifications in its Type A individuals that are remarkably similar to the better documented organs in *Eurypterus* of Type A: in particular the existence of a 2nd *Zipfel* and bilobation on the 2nd operculum. The general layout of the 1st and 2nd operculum (including the distribution of setae) in *Eurypterus* and *Anthraconectes* is, in fact, so similar that arguments in favour of the former being the female are applicable with confidence to the latter. On the other hand, no horns have been found on the 1st operculum. This can perhaps be explained as resulting from non-preservation or from non-discovery during the etching. The absence of clasping organs from Type A individuals is also less well authenticated in *Anthraconectes* than it is in *E. fischeri*, for only two specimens of Type A (MCZ 7163 and BU 751) have been etched so as to reveal the details of parts of the prosomatic appendages. So far as can be seen, no clasping organs appear to be present.

For Type B of *Anthraconectes* our information is less exact, for no individual of that Type of *A. moyseyi* has so far been found, and of the three examples of *A. mazonensis*—(a) USNM 38866, (b) MCZ 7162, (c) CNHM PE5094—that have claims to be regarded as Type B, (a) has been only partially developed by mechanical means, and is here regarded as a young individual of Type A (p. 489); (b) has been etched, but its opercula were found to be imperfectly preserved (p. 488); and (c) in its undeveloped state exposes only part of the genital region (p. 489).

In the genital region:

(i) (b) and (c) each appears to exhibit a short 1st operculum and short *Zipfel*. The *Zipfel* is fairly heavily ornamented with scales; it passes forward into the laminate part of the operculum squarely and without a hastate anterior end and defining sutures; and its distal end is emarginate—all features differing from their counterparts in Type A. However, the *Zipfel* in (b) resembles the 1st *Zipfel* in Type A in the number of its joints, their general proportions, and in the band of mucrones at the end of the 2nd joint.

(ii) The 2nd operculum is missing from (b), and its median part is concealed in (c). In this way we are deprived of important evidence; for, by analogy with *Eurypterus*, the 2nd operculum in Type B should not be bilobed nor provided with a *Zipfel*.

Apart from the genital region:

(i) (b) shows clasping organs on the 3rd leg (A iv). This is definitely a male attribute, appropriate to Type B.

(ii) Differences in the relative sizes of various parts of the animal that are due to sexual dimorphism depend for their proof on accurate measurements which are difficult to make and to interpret, because the specimens vary so much in size, amount of compression, and state of preservation. After various attempts I can find no reliable data in the few examples in which the sex is known, apart from the following (which are given, for what they are worth, as confirmation that (a) is a young individual of Type A, and (b) and (c) older specimens of Type B):

1. The percentage ratio of the length of the free hanging part of the *Zipfel* to the length of the carapace is: (a) c. 32, (b) 21, (c) ?33; whereas in undoubted Type A examples of *A. mazonensis* the ratio is 94 in the holotype and ?56 in MCZ 7163, and in undoubted Type A of *A. moyseyi* it ranges from 73 to ?65.

2. The percentage ratio of the length of the metastoma to the length of the carapace.

Type A (in <i>A. mazonensis</i>)		Type B (in <i>A. mazonensis</i>)	
(a) USNM 38866 56	(b) MCZ 7162 44
Holotype, UI X345 55	(c) CNHM PE5094 ?46
AMNH 8538 55		
MCZ 7163 c. 52		
Type A (in <i>A. moyseyi</i>)			
BU 751 53		
GSM 30249/50 50		
GSM 30192/3 c. 52		
GSM 30194/5 ?50+		

It is likely that the males were smaller and narrower than the females, but this cannot be proved since reliable measurements are unobtainable.

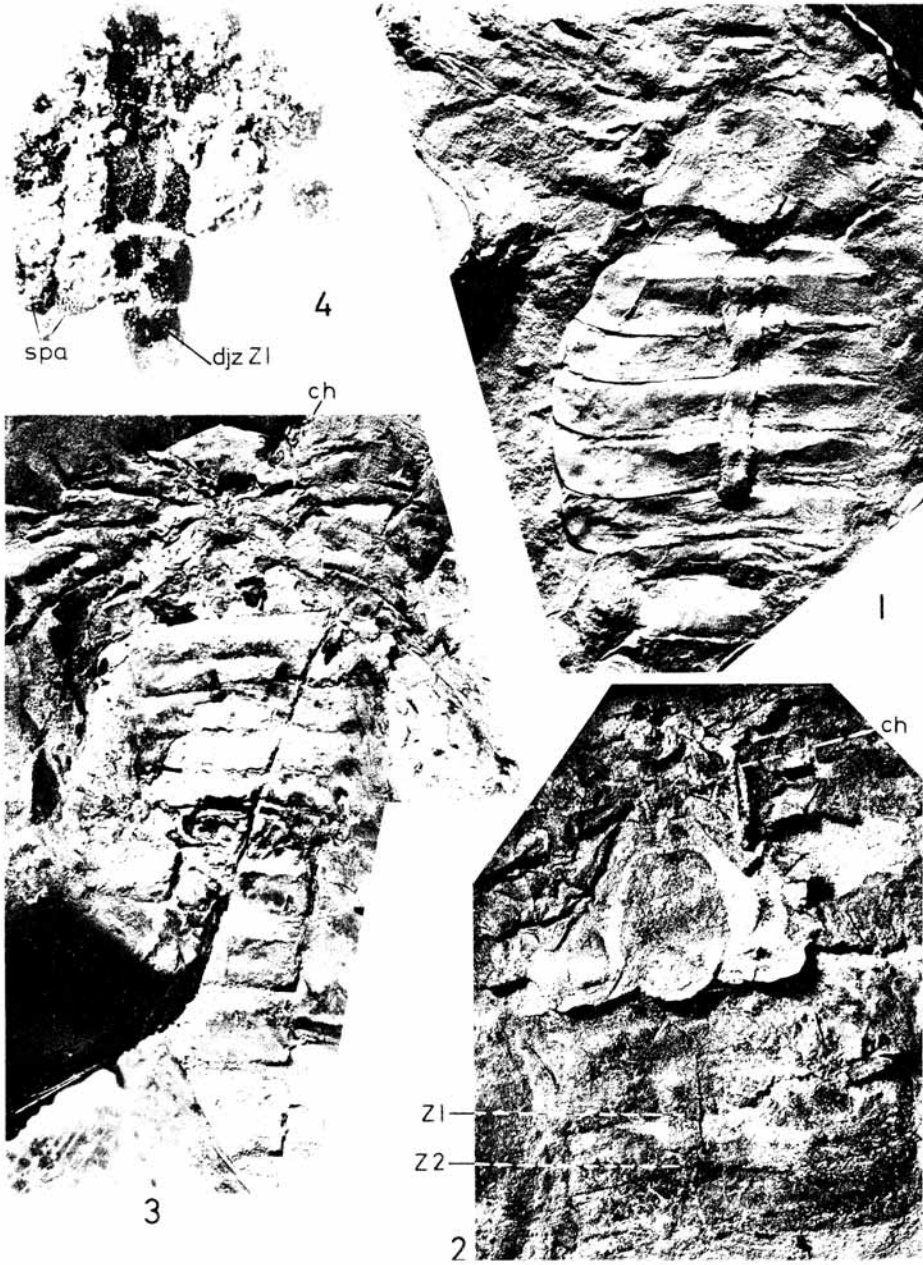
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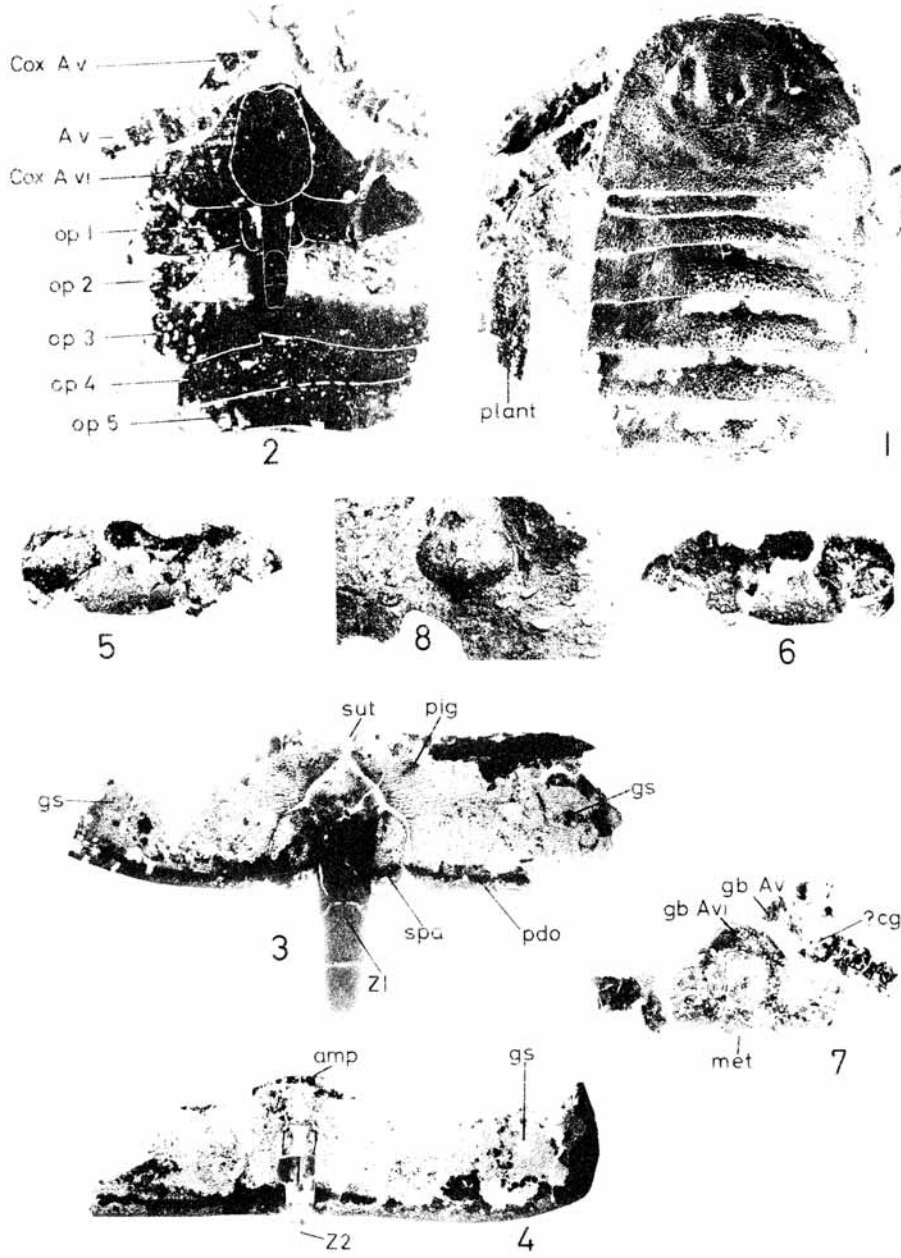
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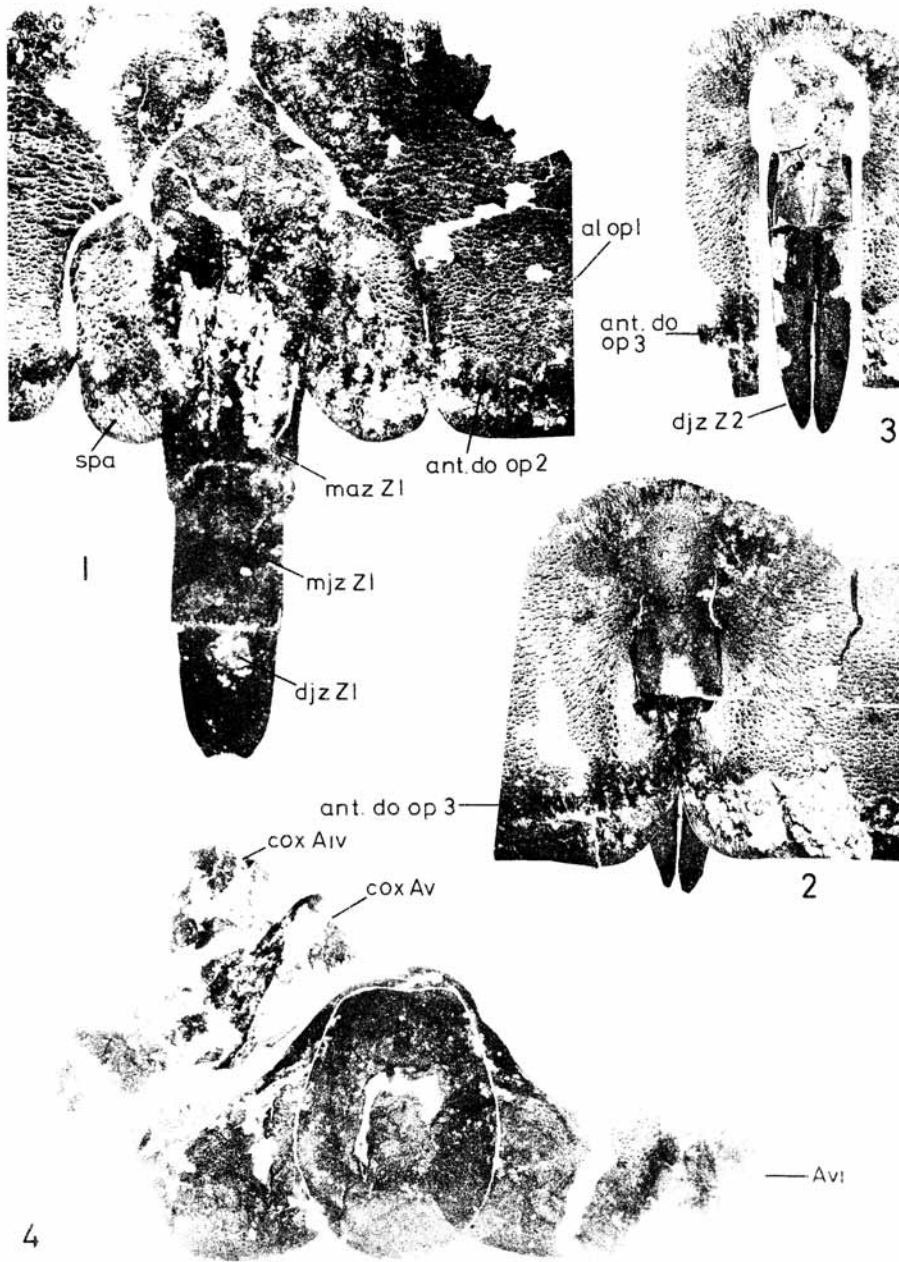
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