THE MEDIAN ABDOMINAL APPENDAGE OF THE SILURIAN EURYPTERID *SLIMONIA ACUMINATA* (SALTER)

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ABSTRACT. The results of a study of a series of specimens exhibiting the median abdominal appendage of *Slimonia acuminata* (Salter) from the Upper Silurian of Logan Water, Lesmahagow, Lanarkshire, are given. The anatomy of the opercular appendage of both sexes is redescribed in the light of knowledge obtained from recent work on related structures in other eurypterids, and the segmented nature of the appendages demonstrated. Stages in the development of the appendage in both sexes in ontogeny are described for the first time.

INTRODUCTION

SEXUAL dimorphism was first noted in eurypterids by Woodward (1866–78, p. 61) who described two forms of median abdominal appendage in *Pterygotus bilobus* Salter. Later in the same work, Woodward (pp. 114–19) gave a description of both types of sexual appendage in *Slimonia acuminata* (Salter) and compared them with the opercular structures of *Limulus*. Since the appearance of Woodward's monograph, much detailed research has been done on eurypterid anatomy in Europe and America and important works dealing with the form of the median appendage and its function have been published. An historical summary of earlier work has been given by Størmer (1934*a*, pp. 43–50) who later published two masterly descriptions of the opercular appendages of German Lower Devonian eurypterids: *Grossopteris overathi* (Gross) (1934*b*, pp. 289–90) and *Pterygotus rhenaniae* Jaekel (1936, pp. 14–23). Recent detailed descriptions of American eurypterids, in which particular attention is given to the sexual appendage, include Kjellesvig-Waering (1948, pp. 22–23) on the Carboniferous *Adelophthalmus mazonensis* (Meek and Worthen), and Caster and Kjellesvig-Waering (1956, pp. 22–27) on the Upper Silurian form *Dolichopterus jewetti* Caster and Kjellesvig-Waering.

The purpose of the present work is to re-examine the opercular structures of *Slimonia acuminata* in the light of our greatly increased knowledge of related structures in other eurypterids, and to describe the growth stages of the median appendage of both sexes, an aspect which appears to have received little attention from previous workers. The study has been made possible by the large size of the appendages in *Slimonia* which are often excellently preserved in the Upper Silurian mudstones of Logan Water, Lesmahagow, Lanarkshire, from which locality all the specimens examined have come. The relatively large number of available specimens having the opercular appendage preserved has also facilitated the work.

History of previous work. Neither in Salter's original description of the species (1856, p. 29) nor in Page's original figure of the genus (1856, p. 135, fig. 3) is the form of the median appendage of *Slimonia acuminata* recorded. Huxley and Salter (1859, pp. 59, 60), however, figured both types of genital appendage. The type A appendage, using Størmer's

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classification (1934*a*, p. 46), was regarded as a portion of the epistoma of a species referred with hesitation to '*Pterygotus*' *acuminatus*, and the type B appendage was regarded as the epistoma of that species.

The sexual significance of the central lobe of the operculum was first realized by H. Woodward (1866–79, pp. 114–20) who figured both types of appendage and compared them with the opercular structures of *Limulus*. Unfortunately the supposed sexual dimorphism which he recognized in *Limulus* was based on two distinct species (Pocock 1902, p. 259, footnote). Woodward regarded the tricuspid type A appendage as being female and the type B appendage as male, and in both he figured what he regarded as genital openings on the deltoidal plates of the operculum. (For definitions of parts see text-figs. 1, 3.) Sutures were not noted in the type A appendage, but in the type B form, Woodward described the transverse furrows which occur at the distal end of the appendage and which he thought were variable in number and were due to there being a number of similar appendages lying one on top of another, the end of each projecting beyond that of the one above it. Laurie (1893, pp. 512–15) adds little to Woodward's description of the type A appendage, except to refute the idea that *Parka decipiens*, sometimes found in association with it, represents egg-capsules, a supposition which had been used by Slimon and Woodward to support their claim that the type A form was female. Laurie gave a careful account of the type B appendage which he regarded as being a single structure, the distal end of which was eversible. The variation in the number of furrows, a fact which Laurie did not question, he regarded as being due to the different extent to which it was protruded in different cases. In neither appendage did Laurie mention the genital openings described by Woodward, and their existence was queried by Clarke and Ruedemann (1912, p. 64), who quoted the findings of Woodward and Laurie and adopted the sex determination given by Woodward. In describing the type B appendage, they stated that there are two transverse furrows at the distal end.

Gaskell (1908) had compared the opercular appendages of eurypterids with those of living members of the Arachnida, and concluded that the type A appendage of *Eurypterus* belonged to the male, and not the female, as had been previously supposed. Størmer (1934*a*) found the occurrence of secondary sexual characters in eurypterids, such as clasping organs, to support Gaskell's sex determination, and figured the two types of genital appendage of *Slimonia* accordingly. Through a knowledge of the position of transverse sutures in the type A appendage of other eurypterids, Størmer indicated sutures in his drawing of the tricuspid appendage of *Slimonia*, although these are not repeated in his later figure (1955, fig. 21, 2*c*).

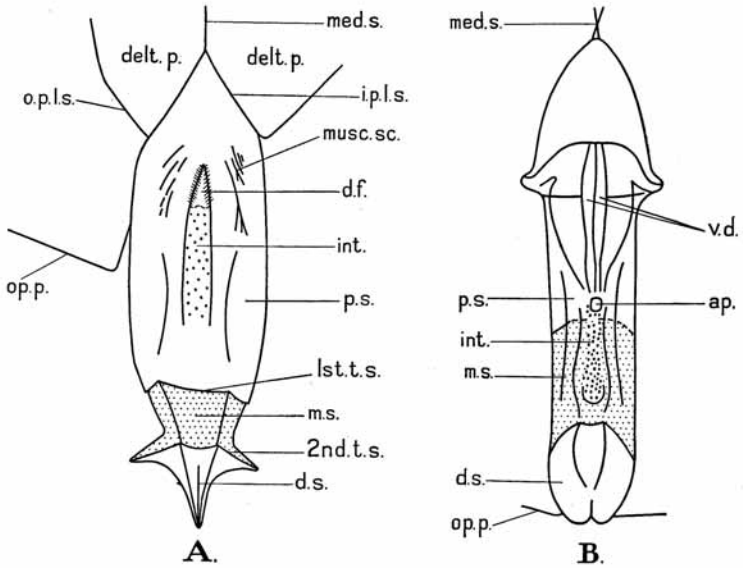
In a paper concerned primarily with the gill-like structures of eurypterids, P. F. Moore (1941, p. 66) figured a type A appendage of *Slimonia acuminata* in which two pairs of ridged areas, interpreted as muscle scars, are indicated near the base of the appendage. Moore did not indicate the presence of transverse sutures on the specimen which he figured.

THE TYPE A APPENDAGE

Anatomy of the adult appendage. The appendage is situated behind the paired deltoidal plates (delt.p., text-fig. 1) of the operculum. The anterior part of the appendage is hastate, the hastation being bounded anteriorly by the inner post-lateral sutures (i.p.l.s.) of the deltoidal plates. The sutures meet at the anterior tip of the median appendage and

continue anteriorly as a single median suture (med.s.), separating the paired deltoidal plates, to the anterior margin of the operculum. The deltoidal plates meet the opercular plates (op.p.) in the outer post-lateral sutures (o.p.l.s.) which may be straight or angled causing the deltoidal plates to be four- or five-sided.

The shape of the type A appendage is broadly fusiform, the point of greatest breadth being approximately level with the posterior margins of the opercular plates. The length



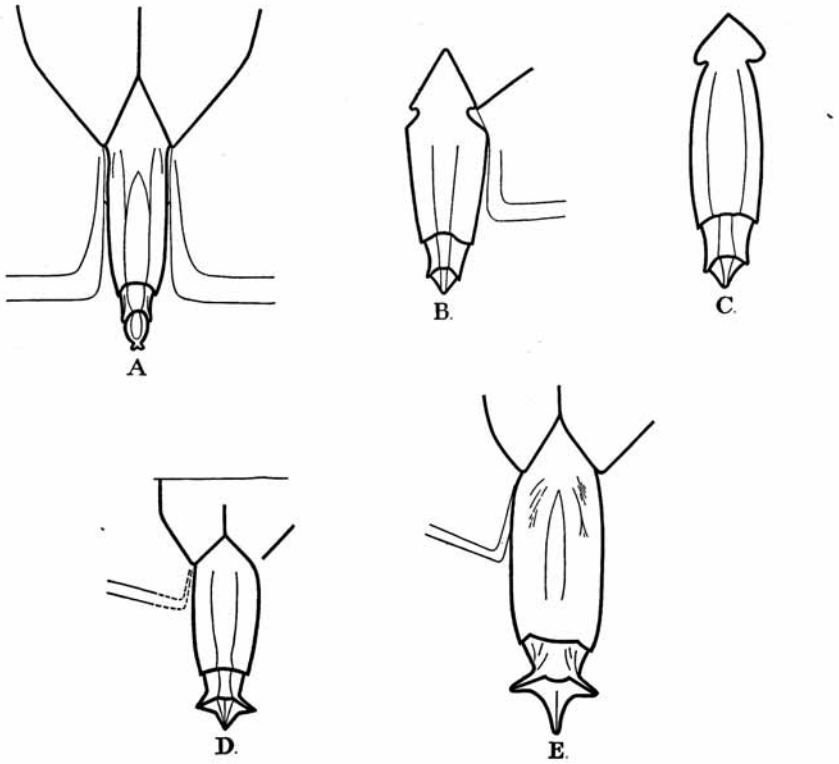
TEXT-FIG. 1. A, Reconstruction of the dorsal surface of the type A median abdominal appendage of *Slimonia acuminata* (Salter) ×¾. B, Reconstruction of the dorsal surface of the type A median abdominal appendage of *Pterygotus rhenaniae* Jaekel, after Størmer, ×2 approx. ap. = male gonopore, d.f. = dorsal furrow, d.s. = distal segment, delt.p. = deltoidal plate, i.p.l.s. = inner post-lateral suture, int. = thin integument, m.s. = middle segment, med.s. = median suture, musc.sc. = muscle scar, o.p.l.s. = outer post-lateral suture, op.p. = opercular plate, p.s. = proximal segment, v.d. = median canals or *vasa deferentia*?, 1st.t.s. = first transverse suture, 2nd.t.s. = second transverse suture.

is between three and four times the breadth. The anterior part of the appendage is hastate, the posterior portion is trispinate. The posterior spine is normally slightly longer and more acute than the paired spines which extend farther laterally than the greatest breadth of the appendage. A marked feature is the asymmetry of the paired spines, one being more posteriorly directed than the other, which is set slightly angled towards the posterior from the normal of the long axis of the appendage.

A longitudinal median ridge extends posteriorly from the rear of the hastate portion of the appendage. The margins closely follow the outline of the appendage and taper to a narrow keel in the posterior median spine. The median ridge occupies about one-third of the width of the appendage.

The type A appendage is divided into three segments by two transverse sutures. The

first separates the proximal segment from the middle segment, the former making up at least two-thirds of the total length of the adult appendage. The form of the suture varies throughout ontogeny (see text-fig. 2), but in adult specimens it is divided into three parts. The median section is curved as the suture passes over the median ridge, which



TEXT-FIG. 2. Growth stages of the type A median abdominal appendage of *Slimonia acuminata* (Salter). A, Kelvingrove Museum .09. 123. aa, ×2. B, Kelvingrove Museum .09. 123. aca, ×1. C, Geological Survey Museum 87280, ×1. D, British Museum (Natural History) 45157, ×½. E, Royal Scottish Museum 1859. 35. 5, ×½.

is wide at this point since the edges of the ridge flare outwards as the posterior margin of the proximal segment is approached. The two lateral sections of the suture also curve outwards as they are traced posteriorly to the margins of the appendage. The form of the suture appears to vary in different specimens owing to the accident of flattening of the median ridge during preservation. The second suture separates the middle segment from the distal segment. It also has a median curved portion passing over the median ridge, which again broadens as it approaches the posterior margin of the middle segment. The lateral parts of the suture pass outwards to the tips of the lateral spines in a

straight line bisecting them into unequal portions. The part of the spine formed by the middle segment is narrower than the posterior portion formed by the distal segment.

Størmer (1934*a*, text-fig. 19) indicated possible positions for the transverse sutures of the type A appendage, basing his figure on an illustration given by Woodward (1866–78, pl. 17, fig. 2). Examination of this specimen (B.M.N.H. 45157) shows a crack running across the appendage almost midway down the proximal segment which was shown in Woodward's figure and interpreted by Størmer as a suture. The position of the first suture is, however, correctly shown in Woodward's illustration in the more distal position, while the central part of the second suture is drawn between the lateral spines. The sutures are particularly well seen in specimens exhibiting the dorsal side of the appendage.

With regard to the finer structures of the type A appendage, Woodward (1866–78, p. 116, text-fig. 35) figured two circular openings, one on each of the deltoidal plates, which he interpreted as ovipores. These are not mentioned by Laurie (1893) and a re-examination of the figured specimen (B.M.N.H. 44445) does not support Woodward's claim. What were thought of as gonopores appear as two very small wrinkles in the integumen which are neither rounded nor pore-like. It is true that other workers, for example Holm (1898, p. 43) and Clarke and Ruedemann (1912, p. 66 and text-fig. 122), have described what they regard as gonopores as occurring in a rather similar position in other genera. These, however, occur at the lateral points of the hastate basal portion of the proximal segment of the median appendage and not on the deltoidal plates. They are thus not homologous to the pores described by Woodward. In the course of the present study many perfectly preserved specimens have been examined and no similar structures have been seen. They are therefore regarded here as merely an accident of preservation.

In the description of the median ridge it has been stated that it extends posteriorly from the rear of the hastate portion of the appendage. Preparation of one specimen (R.S.M. 1859. 35. 5) suggests that the median ridge may be accompanied by a complementary median furrow in the dorsal surface of the appendage, the opening of which does not extend as far as the ridge itself. The specimen displays a mould of the interior of the dorsal surface of the appendage, and the median ridge was broken away at the midline of the proximal segment rather less than half-way from the anterior tip of the segment. Where the ridge was broken away, two natural margins were revealed converging anteriorly, where they meet to form the boundaries of a lanceolate groove. Hair-like thickenings of the integumen occur along these margins, the hairs being directed posteriorly and diagonally inwards towards the mid-line. The hairs appear to extend beyond the margins and protrude into the groove.

The ridged areas regarded by Moore (1941) as muscle scars flank the median ridge on the proximal segment posterior to the hastation. On Moore's specimen (Sedgwick Museum A 16236) two pairs of ridged areas are seen, the larger being anterior to the smaller, which has a more central position on the appendage (see Pl. 42, fig. 2). Similar areas may be seen in the Geological Survey Nos. 87282, 87283, and 87285; in the Royal Scottish Museum 1859. 35. 5; and in part in the Kelvingrove Museum .09. 123. pi. The areas are marked by narrow branching ridges radiating in a post-lateral direction with intervening smaller, parallel ridges which may be very numerous (see Pl. 42, fig. 3). An examination of the muscular attachments on the dorsal surface of the operculum of *Limulus* has confirmed, in the writer's opinion, Moore's view that the areas represent

muscular attachments. The pattern of the markings compares closely with that of the attachment of the 'branchial muscles' in *Limulus* (Benham 1885), although the muscles of the type A appendage of *Slimonia* cannot be regarded as homologous with these.

Development of the type A appendage. Examination of a series of type A appendages has shown how different growth stages, exhibiting very different shapes, are related to one another. It has thus been possible to work back from the known adult appendage to the previously unrecognized nepeonic and juvenile forms.

The smallest type A appendage seen has a total length of 24·0 mm. and a maximum breadth of 6·0 mm. and is preserved in the Slimon collection of the Kelvingrove museum No. .09. 123. aa. (see text-fig. 2A, and Pl. 42, figs. 4–6). The maximum width of the appendage is at the posterior angles of the hastation, from which it tapers posteriorly. The proximal segment comprises over three-quarters of the total length of the appendage, as compared with two-thirds in adult examples, and its posterior margin, marked by the first suture, is anterior to the rear margins of the opercular plates. The latter feature has been noted in a nepeonic example of the type A appendage of *Eurypterus fischeri* Eich. by Holm (1898, p. 43, pl. 1, fig. 11). The suture is curved, the convexity towards the anterior, and the post-lateral angles are acute. Lateral spines are not developed, the middle segment tapering towards the posterior, where the post-lateral angles are more acute than in the proximal segment and are posteriorly directed. The second suture, like the first, is curved with the convexity towards the anterior. The distal segment is elliptical, being longer than it is broad, and divides into two minute points at the posterior extremity of the appendage. The median ridge extends from the rear of the hastation to the distal segment, where it terminates before reaching the posterior margin. The opercular plates of this specimen are interesting in that they indicate the transverse fused suture extending laterally from the posterior points of the deltoidal plates, a feature which is rarely seen in *Slimonia* (Pl. 42, fig. 4).

The next growth stage is shown in the Kelvingrove Museum specimen No. .09. 123. aca., in which the length of the appendage is 39·0 mm. and the maximum breadth 14·0 mm. The broadest part lies in the proximal segment behind the hastation. The proximal segment still constitutes about three-quarters of the total length of the appendage. The first suture, however, lies posterior to the rear margins of the opercular plates (see text-fig. 2B). In the post-lateral angles of neither the proximal nor the middle segment is the angle so acute as in the smallest form, although they are still posteriorly directed. The middle segment at this stage is proportionately longer in relation to the other segments than in any other stage in ontogeny, comprising about one-sixth of the total length of the appendage as compared with one-ninth in the smallest specimen. The distal segment is triangular, tapering posteriorly to a point, showing no indication of the small paired

EXPLANATION OF PLATE 42

Figs. 1–6. *Slimonia acuminata* (Salter). Median abdominal appendage Type A. 1, Entire appendage. ×$\frac{3}{4}$, R.S.M. 1859.35.5. 2, Entire nepeonic appendage. ×3, Kelvingrove .09.123.aa. 3, Distal part of the nepeonic appendage showing the distal, middle and part of the proximal segments. Alcohol immersed ×6, Kelvingrove .09.123.aa. 4, Diagrammatic representation of fig. 3. 5, Part of the proximal segment to show the two pairs of muscle scars. ×1$\frac{1}{2}$, Sedgw. Mus. A16236. 6, Part of the proximal segment to show muscle scars. ×1$\frac{1}{2}$, R.S.M. 1859.35.5.

horns noted at the posterior extremity of the smallest specimen. The length of the distal segment is smaller than the maximum breadth.

An appendage exhibiting a slightly later stage in development is Geological Survey 87280, counterpart 87281, which is probably the specimen which was figured by Huxley and Salter (1859, pl. 15, fig. 3) as a problematical fragment. The length is 48·0 mm. and the maximum breadth 13·0 mm., but the point of maximum breadth lies midway down the length of the proximal segment instead of at its anterior as in smaller examples (text-fig. 2C). In other respects this specimen resembles No. .09.123 aca., except that the median ridge is more pronounced, and as a consequence the sutures have become divided into a central and lateral parts such as is seen in the more adult specimens. The relationship of the first suture with the posterior margins of the opercular plates is not seen, since the appendage has become separated from the rest of the operculum.

The British Museum specimen B.M. (N.H.) 45157 is small but exhibits adult characters (text-fig. 2D). The posterior margins of the opercular plates are now level with the mid-point of the length of the proximal segment. The trispinate distal feature is present although not fully developed. The post-lateral angles of the middle segment have been produced to form the anterior portion of the lateral spines. The antero-lateral parts of the distal segment have also been expanded to form the posterior portions of the lateral spines, angles being developed in the lateral margins of the distal segment between the lateral spines and the posterior median spine. All three spines are less acute than in adult specimens, in which they are still further produced (text-fig. 2E).

In summary, the development of the type A appendage appears to exhibit the following features:

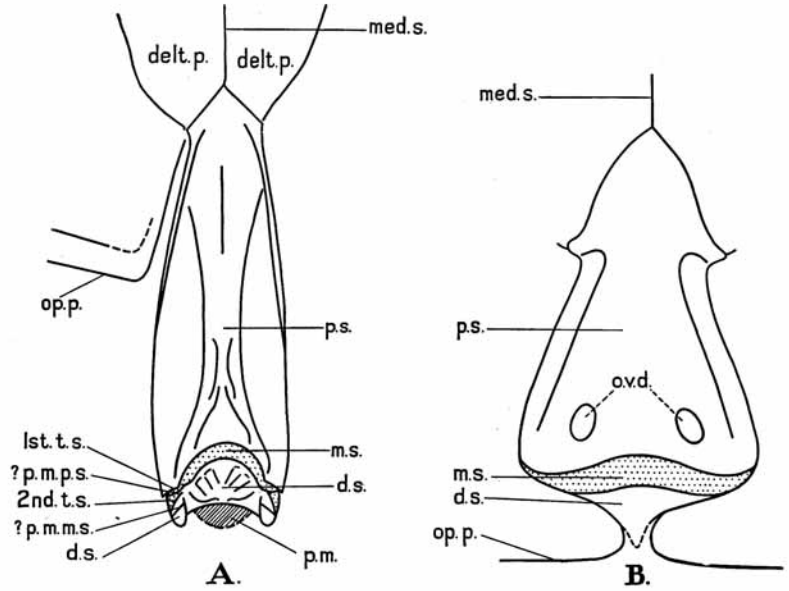
1. A greater growth rate in the length of the proximal segment in relation to the length of the opercular plates from the condition seen in the nepeonic form, in which the proximal segment does not extend beyond the posterior margins of the opercular plates, to the adult condition in which the rear margins of the opercular plates are approximately on a level with the mid-line of the proximal segment.
2. The gradual posterior migration of the point of maximum breadth in the proximal segment from the anterior part of the segment to half-way down the length.
3. The reorientation of the post-lateral angles of the middle segment from a posterior to a postero-lateral or lateral direction, with their elongation to form the anterior parts of the lateral spines.
4. The changing shape of the distal segment from elliptical to triangular, and finally to the expansion of the antero-lateral parts to form the posterior portions of the lateral spines, and the production of the posterior tip to form the median spine.
5. The early loss of the paired horns at the posterior of the nepeonic appendage.
6. The growth of the median ridge with the consequent change in shape of the sutures from a simple curve to central and lateral parts.

THE TYPE B APPENDAGE

Anatomy of the adult appendage. Relationships between the deltoidal plates, the opercular plates, and the hastate anterior part of the median appendage are the same as those in the type A appendage.

The shape of the type B appendage is fairly narrow and conical, the point of greatest breadth approaching the posterior. It is made up of three segments of which the proximal is by far the largest, comprising approximately eight-ninths of the whole. A median ridge extends across the proximal segment from the lateral points of the hastation to the first suture. The ridge is waisted towards the centre of the segment, but flares out laterally in an ogee curve towards the rear of the segment, and occupies over two-thirds of the width of the segment at the posterior margin. In the Royal Scottish Museum

specimen 1859. 35. 7 longitudinal folds of the integumen commence within the median ridge at the posterior third of the proximal segment, and after running parallel for a short distance in the mid-line, curve outwards towards the post-lateral extremities of the median ridge in a more accentuated ogee curve than that followed by the margin of the ridge. This gives the appearance of two ducts or channels passing downwards and out-



TEXT-FIG. 3. A, Reconstruction of the dorsal surface of the type B median abdominal appendage of *Slimonia acuminata* (Salter), ×¾. B, Reconstruction of the dorsal surface of the Type B median abdominal appendage of *Pterygotus rhenaniae* Jaekel, ×2 approx. d.s. = distal segment, delt.p. = deltoidal plate, m.s. = middle segment, med.s. = median suture, o.v.d. = female gonopores, op.p. = opercular plates, ? p.m.p.s. = ? posterior margin of the proximal segment, ? p.m.m.s. = ? posterior margin of the middle segment, p.s. = proximal segment, 1st.t.s. = first transverse suture, 2nd.t.s. = second transverse suture.

EXPLANATION OF PLATE 43

Figs. 1–6. *Slimonia acuminata* (Salter). Median abdominal appendage Type B. 1, Invagination of the right side of the distal segment of the nepeonic form showing the striate ornament. ×144, Kelvingrove .09.123.aav. 2, Distal part of the adult appendage showing part of the proximal, the middle, and the distal segments with post-lateral complexes, note radial fold pattern in integumen of distal segment. ×1½, R.S.M. 1859.35.7. 3, Distal part of a flattened adult appendage showing part of the proximal, the middle, and distal segments with post-lateral complexes, note radial fold pattern in integumen of distal segment. ×1½, Geol. Surv. Scot. 6643. 4, The entire adult appendage, ×¾, R.S.M. 1859.35.7. 5, Distal part of the juvenile form showing part of the proximal segment, the middle segment, and the distal segment with lateral spurs. ×3, Kelvingrove .09.123.vq. 6, Entire appendage of the nepeonic form. ×3, Kelvingrove .09.123.aav.

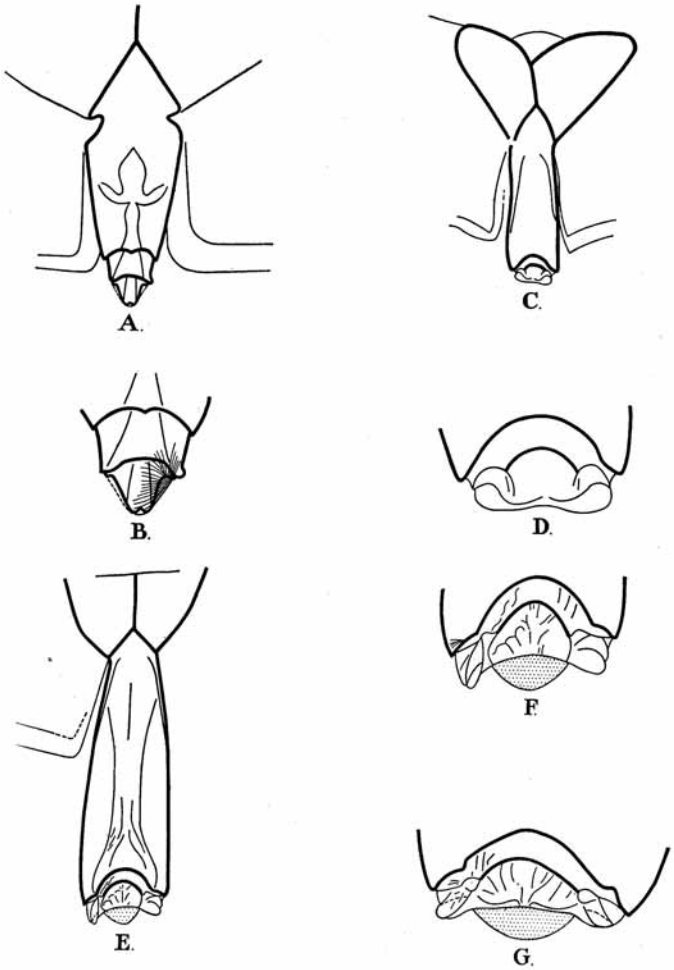
wards to the post-lateral points of the median ridge (see text-fig. 4E, and Pl. 43, fig. 5). The first suture is semicircular in the area of the median ridge, with the convexity towards the anterior. The lateral parts of the suture curve outwards to the post-lateral angles of the proximal segment in shallower curves the convexities of which are also directed anteriorly. The centre part of the second suture is also semicircular, and concentric to the first, thus confining the median portion of the middle segment to a narrow semicircular band. The central part of the distal segment has the form of a half-circle, being bounded anteriorly by the curved second suture, whereas the posterior margin is almost straight. Paired sigmoidal ridges extend laterally from the centre of the segment, near the posterior margin, to join the post-lateral complexes of the appendage.

Previous authors have described the type B appendage as terminating distally in a more or less truncated cone, which is marked by two or three deep furrows (Laurie 1893, p. 513). Laurie advances a convincing argument for refuting Woodward's idea that the type B appendage consists of three similarly shaped median plates, lying one on top of another, the end of each projecting a little beyond the one above, and correctly interprets the transverse furrows as structures belonging to a single median appendage. In addition to claiming that there may be two or three such furrows, Laurie says that the preservation of markings on the remains of these animals seemed to him to depend so much on the details of fossilization, and perhaps also on the condition of the animal at death, and that their presence on some specimens, and absence on others, is not of much weight as an argument. The writer sympathizes with this view since there is a great deal of variation in the appearance of the distal structures of the type B appendage due to the accidents of fossilization, and particularly to the flattening of a three dimensional structure. Careful examination of many adult specimens, however, makes it clear that throughout the variation there can be traced constant features which are due to the original form of the appendage and not to accident. Of these, the presence of two transverse sutures is one constant feature, and the occurrence of what are here termed the post-lateral complexes is another.

The form of the median portions of the two transverse sutures, or furrows, which divide the appendage into proximal, middle, and distal segments has been described. Posterior to the appendage, however, there occurs in some specimens (e.g. R.S.M. 1859. 35. 7 and Geol. Surv. Scot. 6643) a semicircular piece of integumen which probably served to attach the distal part of the appendage to the abdomen of the animal (see text-fig. 4E, F, G). The furrows which exist between the integumen and the posterior margin of the distal segment is probably what Laurie regarded as the third furrow, but is not a true suture.

The post-lateral complexes occur in all specimens which have been examined and are made up of structures developed from the lateral parts of the middle and distal segments. The complexes occur in the post-lateral angles of the appendage. Since their anatomy is more easily understood when their development through ontogeny is known, the description of these features is included in the following account of the development of the type B appendage.

Development of the type B appendage. A small appendage exhibiting the dorsal surface, which is here identified as a type B appendage in the nepeonic condition, is in the Slimon Collection, Kelvingrove Museum No. .09. 123 aav. (text-fig. 4A; Pl. 43, figs. 1, 2). Its



TEXT-FIG. 4. Growth stages of the Type B median abdominal appendage of *Slimonia acuminata* (Salter). A, Kelvingrove Museum .09. 123. aav, ×2. B, Distal portion of Kelvingrove Museum .09. 123. aav, ×4. C, Kelvingrove Museum .09. 123. vx, ×1. D, Distal portion of Kelvingrove Museum .09. 123. vx, ×4. E, Royal Scottish Museum 1859. 35. 7, ×½. F, Distal end of Royal Scottish Museum 1859. 35. 7, ×1. G, Geological Survey Scotland 6643, distal end ×1.

total length is 22·0 mm. and the maximum breadth, which occurs just posterior to the hastation, is 8·0 mm. Behind the hastation the form of the appendage is obconical. The proximal segment does not extend beyond the posterior margins of the opercular plates, and the bounding first suture is arcuate in form. The middle segment is broadest at the

anterior and tapers posteriorly, but flares slightly at the post-lateral angles. The second suture is in the form of a simple arch. The distal segment is broadly triangular in form. Embayments or invaginations occur in the dorsal surface of the distal segment, one on each side near the margins. That on the right side is more clearly seen than the one on the left owing to a slight anticlockwise twist in the specimen. The invaginations are situated towards the anterior of the segment and are bounded anteriorly by spurs which are seen immediately behind the second suture. From the lateral tips of the spurs, which form the antero-lateral angles of the segment, the margins are continued in a straight line towards the posterior tip of the segment. A remarkable feature, which has been seen in this specimen only, is the ornament of extremely fine striae which it exhibits. This is best seen on the right-hand side of the distal segment where the striae radiate across the surface of the segment from the inner margin of the invagination. Those striae, which extend anteriorly, cross the second suture without interruption and continue on the right postero-lateral portion of the middle segment. Striae which originate within the invagination at the posterior margin of the spur extend parallel to the edge of the segment in a posterior direction and then sweep diagonally across the rear part of the segment (text-fig. 4B; Pl. 43, fig. 1). Ornamentation can be traced also on the left posterior angle of the hastation, where striae radiate across the appendage from a point near the re-entrant angle at the rear of the hastation, and continue across the suture and over the left deltoidal plate. It would appear most probable that in life the entire surface of the appendage was sheathed in a fine integumen bearing striated ornament.

The 'median ridge' divides anteriorly into three lobes on the proximal segment of the appendage. There is a larger central lobe which does not extend forwards as far as the hastation, whereas the two lateral lobes almost reach the margins of the segment antero-laterally. The lobes unite at a point about one-quarter of the length of the segment from its posterior margin, and continue rearwards as a single median ridge which extends over the middle and distal segments. The margins of the ridge flare outwards at the sutures and it terminates posteriorly on the distal segment in two lobes.

The next growth stage is exhibited by the Kelvingrove specimens .09. 123. vq and .09. 123. vx. The latter (text-fig. 4C) has a length of 30·0 mm. and a maximum breadth of 8·0 mm. A similar growth stage is shown in R.S.M. 1865. 11. 11, Geol. Surv. 87287, Geol. Surv. Scot. 11825 and 11826. At this stage the shape of the appendage has already assumed the conical form of the adult, the point of greatest breadth being near the posterior of the proximal segment. The proportions of the segments and the form of the sutures are also similar to those of the adult. Differences occur, however, in the form of the post-lateral complexes, which are much simpler than in the mature appendage. The centre part of the distal segment is approximately semicircular in form, being bounded anteriorly by the median-curved portion of the second suture, and posteriorly by an almost straight margin. From this central region two lateral curved spurs or horns are developed from the distal segment, one on each side of the segment. They extend antero-laterally from the sides of the semicircular median part of the segment and then curve so that their tips are directed laterally or slightly post-laterally. Their anterior margins form a simple curve, convex towards the anterior, whereas the posterior margins are sigmoidal, the inner ends terminating near the median line of the appendage. The median-curved portion of the second suture terminates against the anterior margins of the spurs, and is presumably coincident with these margins as it is traced laterally.

Intermediate growth stages such as are shown in specimens Geol. Surv. 87288, 87289, and B.M. (N.H.) 59653, occur between that just described and the adult form. These, however, demonstrate only the constancy of the conical form of the appendage after the nepeonic stage has been passed, and a gradual increase in the complexity of the post-lateral regions.

The finest adult type B appendages seen are R.S.M. 1959. 35. 7 and Geol. Surv. Scot. 6643 (text-fig. 4E, F, G). Here the lateral horns of the distal segment, after growing antero-laterally, appear to curve fairly sharply until they are growing in a post-lateral direction. They extend post-laterally until their tips are posterior to the rear margin of the central part of the distal segment. In Geol. Surv. Scot. 6643 the appendage has been greatly flattened, and where the lateral spurs curve round from an antero-lateral to a postero-lateral direction they have been flattened upon themselves at the points of curvature, to form two round bodies (Pl. 43, fig. 6; text-fig. 4G). This is not seen in R.S.M. 1859. 35. 7, which has not suffered such severe flattening.

The lateral margins of the middle segment appear to extend posteriorly from the post-lateral angles of the proximal segment to the posterior part of the antero-lateral margin of the spurs of the distal segment. The supposition finds support in the simpler conditions seen in the juvenile forms (text-fig. 4C, D). A margin traverses the spurs of the distal segment and terminates laterally at the point where the lateral margins of the middle segment meet the distal spurs. This margin is rather indistinct and is interpreted by the writer as the posterior margin of the middle segment on the ventral side of the appendage. On the dorsal side, the posterior margin of the middle segment would appear in its lateral parts to coincide with the antero-lateral margin of the spurs of the distal segment. Another indistinct margin may be traced extending from the post-lateral angles of the proximal segment to a point just anterior to the position of curvature of the spurs of the distal segment. It is possible that this parallels the margin seen traversing the distal spurs and represents the posterior margin of the proximal segment on the ventral side of the appendage.

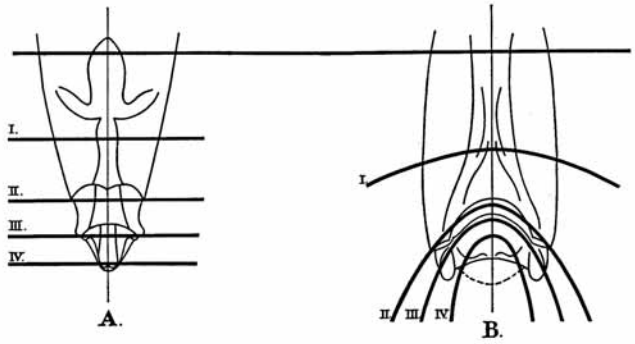
In summary, four features appear to be common to each of the post-lateral complexes of the adult type B appendage:

1. A distal member in a post-lateral orientation, which is regarded as a post-lateral extension of the spur of the distal segment clearly seen in juvenile forms.
2. Another member in a post-lateral orientation, lying anterior to the distal spur and posterior to the post-lateral angle of the proximal segment, which is thought to represent the lateral portion of the middle segment.
3. A margin traversing the posterior part of the distal spur, which is regarded as the posterior margin of the middle segment.
4. A margin traversing the middle segment between the post-lateral angle of the proximal segment and a point anterior to the position of curvature of the distal spur, which is regarded with hesitation as the posterior margin of the proximal segment on the ventral side of the appendage.

Although these features appear to be constant despite variation in the condition of preservation of the specimens, the interpretation of the structures presents many difficulties owing to the degree of specialization attained in *Slimonia*.

The form of the nepeonic type B appendage may be related to that of the adult appendage by the differential growth-rate diagram of text-fig. 5. The lines superimposed upon the outlines of the appendages have been constructed in the following ways. I, crosses the proximal segment three-quarters of its length from the anterior margin and

is of purely diagrammatic significance. II, touches the post-lateral angles of the proximal segment, between which it crosses the middle segment. These points are not in doubt in either form. III, touches the post-lateral angles of the middle segment, between which it crosses the distal segment at the anterior margin of the invaginations. There is no difficulty in constructing this line in the nepeonic form, but to do so in the adult form requires the assumption that the spurs, which lie anterior to the invaginations and posterior to the second suture in the nepeonic appendage, become extended in the adult to form the posterior member of the post-lateral complex. If this is allowed, then the



TEXT-FIG. 5. Diagram to illustrate the possible relationship through differential growth-rates of the form of the nepeonic (A) and adult (B) median abdominal appendage, type B, of *Slimonia acuminata* (Salter).

points about which the distal spurs are curved in the adult must represent the anatomical equivalent of the invaginations of the nepeonic form. IV, is a line crossing the posterior lobes of the distal segment. Support is given for the validity of the assumptions made in construction by the regular pattern which emerges in the resulting diagram. While the lines are parallel with and at right angles to the long axis of the appendage in the nepeonic form, they form a symmetrical series of curves in the adult which become more intense as the posterior of the appendage is approached. The adult form would therefore appear to be derived from the nepeonic form by greater differential growth at the margins of the distal part of the appendage as compared with a smaller growth-rate in the median region.

SEX AND FUNCTION OF THE APPENDAGES

While dimorphism of the median abdominal appendages of eurypterids is obvious, the determination of sex has proved difficult since no direct comparison can be made with closely related living forms. Following the work of Pocock (1902) on the secondary sexual characters among Xiphosura, and Gaskell's (1908) comparison of the opercular structures of eurypterids with those of *Thelyphonus*, Størmer (1934*a*) argued that the type A appendage was male and the type B female. He found support for this view principally in the secondary sexual characters seen in eurypterids such as clasping organs of *Mixopterus* and *Eurypterus*. More direct evidence became available in the wonderfully preserved genital appendages of the lower Devonian *Pterygotus rhenaniae* Jaekel,

which is of particular interest for the present study, since the genital appendages of *Slimonia acuminata* may be compared closely with this form.

The type A appendage of *P. rhenaniae* is narrowly lanceolate and is made up of three segments (text-fig. 1). The form of the appendage is less specialized than in *Slimonia* but is very similar to the nepeonic condition of the Scottish species, particularly in the shape of the distal segment with its terminal incision dividing the posterior margin into two lobes. On the dorsal side of the German species, Størmer (1936) was able to detect a central aperture towards the posterior of the proximal segment which he regarded as probably the combined aperture of the *vasa deferentia*. This hypothesis is supported by the occurrence in *P. rhenaniae* of two parallel canals anterior to the opening. While no trace of *vasa deferentia* or genital aperture has been seen on the type A appendage of *Slimonia*, it may well be that the male aperture opened into the dorsal furrow which occurs on the proximal segment of the appendage in an equivalent anatomical position to the male gonopore of the German species.

The type B appendage of *P. rhenaniae* is broad and pear-shaped, and is also made up of three segments whose proportions are very similar to those of the adult type B appendage in *Slimonia* (text-fig. 3). Towards the posterior of the proximal segment, two fairly large ovate openings occur which may be ovipores. Similar openings have not been seen in *Slimonia*. On the other hand, post-lateral complexes, which are a specialized feature of the *Slimonia* type B appendage, have not been described from *P. rhenaniae*.

The comparison which can be made between the appendages of *Pterygotus rhenaniae* and *Slimonia acuminata* is sufficiently close to leave no doubt that the trispinate appendage of *Slimonia* is equivalent to the lanceolate appendage of *Pterygotus rhenaniae*, and Størmer's determination of a male sex for these appendages is here adopted. In the same way the similarities between the pear-shaped or conical appendages in both species are sufficient to prove their equivalence, and a female sex is presumed for this type. The differences in the more detailed features of the anatomy, however, suggest that the functioning of the appendages was distinct in the two species.

It is reasonable to suppose that the post-lateral complexes of the type B appendage of *Slimonia* may represent ovipositor mechanisms. This appears not unlikely when the longitudinal median structures of the proximal segment are considered. As has been stated above these structures have the appearance of two ducts or channels which pass posteriorly and laterally in ogee curves on either side of the hinder portion of the proximal appendage, and terminate in the region of the post-lateral complexes. These channels could be regarded as genital ducts leading to the post-lateral complexes. In *P. rhenaniae*, however, the ovipores are found on the proximal segment. If the post-lateral complexes of *Slimonia* are regarded as fulfilling an ovipository function, it is necessary to postulate the participation of the middle and distal segments in the female genital system, in addition to the proximal segment of the appendage. Laurie (1893) regarded the distal portion of the type B appendage of *Slimonia* as being eversible. The writer favours this suggestion because of the regular radial fold pattern that is found on the median part of the distal segment in nearly all specimens of the type B appendage. Were the distal part of the appendage eversible it would appear to favour the supposition that the function of the post-lateral complexes was ovipository.

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REFERENCES

BENHAM, W. B. S. *in* LANKESTER, E. R., BENHAM, W. B. S., and BECK, E. J. 1885. On the muscular and endoskeletal systems of Limulus and Scorpio: with some notes on the anatomy and generic characters of scorpions. *Trans. Zool. Soc. London*, **11**, 311–84.

CASTER, K. E. and KJELLESVIG-WAERING, E. N. 1956. Some notes on the genus *Dolichopterus* Hall. *J. Paleont.* **30**, 19–28.

CLARKE, J. M. and RUEDEMANN, R. 1912. The Eurypterida of New York. *Mem. N.Y. St. Mus.* **14**.

GASKELL, W. H. 1908. *The origin of Vertebrates*. London.

HOLM, G. 1898. Über die Organisation von *Eurypterus Fischeri* d'Eichwald. *Mem. Acad. Sci. St. Petersb.* 8th ser. **8**, 2.

HUXLEY, T. H. and SALTER, J. W. 1859. On the anatomy and affinities of the genus Pterygotus. *Mem. Geol. Surv. Monogr.* **1**.

KJELLESVIG-WAERING, E. N. 1948. The Mazon Creek Eurypterid. A revision of the genus *Lepidoderma*. *Illinois Sci. Pap.* **3**, no. 4.

LAURIE, M. 1893. The anatomy and relations of the Eurypterida. *Trans. Roy. Soc. Edinb.* **37**, 509–28.

MOORE, P. F. 1941. On gill-like structures in the Eurypterida. *Geol. Mag.* **78**, 62–70.

PAGE, D. 1856. *Advanced text book on Geology*, 1st ed. Edinburgh.

POCOCK, R. J. 1902. The taxonomy of Recent Limulus. *Ann. Mag. Nat. Hist.* (7), **5**, 256–66.

SALTER, J. W. 1856. On some new Crustacea from the uppermost Silurian rocks. *Quart. J. Geol. Soc. London*, **12**, 26–34.

STØRMER, L. 1934*a*. Merostomata from the Downtonian Sandstone of Ringerike, Norway. *Skr. Norske Vidensk. Akad.*, I.M.-N-Kl. 1933. 10.

—— 1934*b*. Über den neuen, von W. Gross beschriebenen Eurypteriden aus dem Unterdevon von Overath im Rheinland. *Jb. Preuss. Geol. L.-A.*, **55**, 284–91.

—— 1936. Eurypteriden aus dem Rheinischen Unterdevon. *Abh. Preuss. Geol. L.-A*, N.F. h. 175.

—— 1955. Merostomata in *Treatise on invertebrate paleontology*, Part P, pp. P4–41. Lawrence, Kansas.

WOODWARD, H. 1866–78. British fossil Crustacea belonging to the order Merostomata. *Palaeontogr. Soc.*

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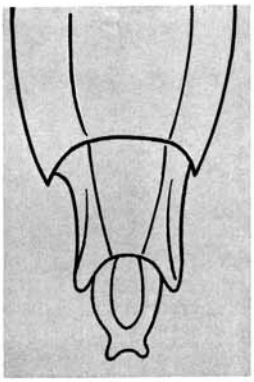

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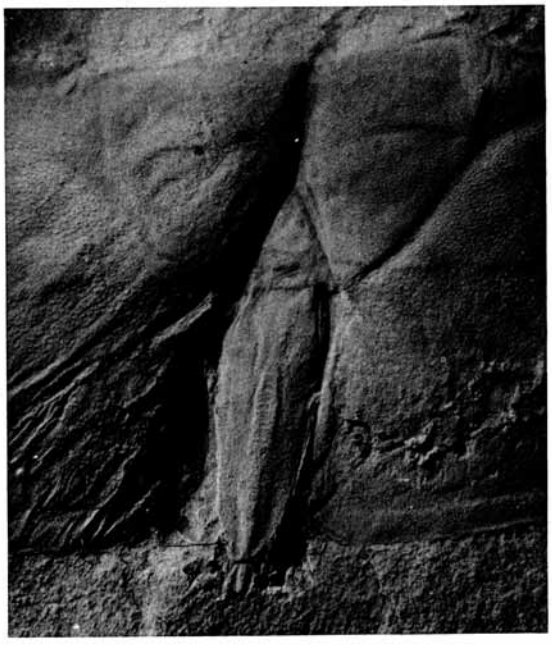

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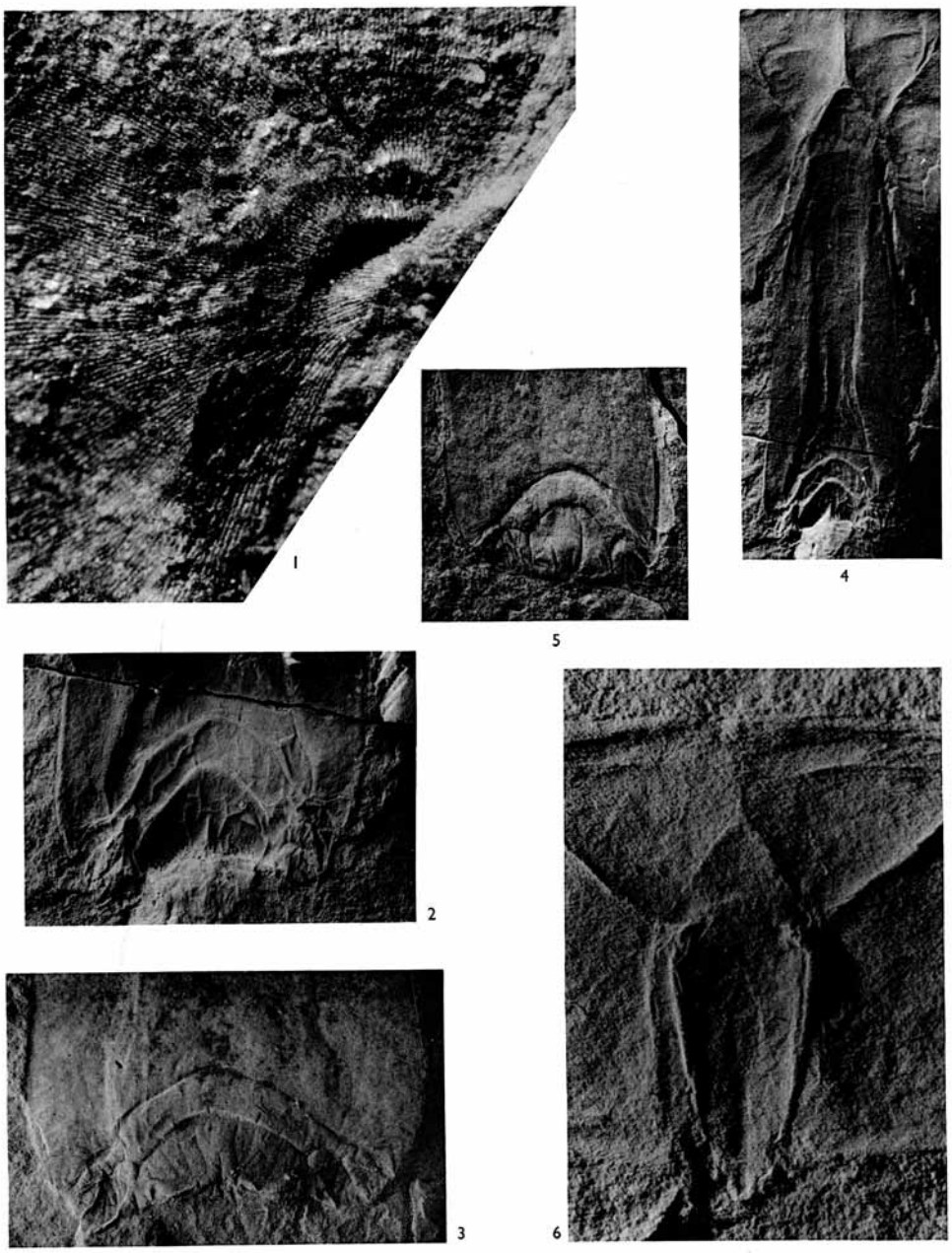
WATERSTON, *Slimonia acuminata* (Salter)



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