
Articulation and Exuviation in Cambrian Trilobites

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SUMMARY

Articulation of the exoskeleton is reviewed in trilobites where the inner portion of the thoracic pleura was horizontal. Devices enabling articulation in the thorax of the olenelloid *Holmia*, and of species of *Paradoxides* are described. The thoracic pleura in these taxa did not have the inner portion horizontal, but the body could be enrolled. Arching of the body, and opening of the cephalic sutures, are considered to have been essential preliminary manoeuvres in exuviation, allowing egress anteriorly of the newly moulted animal. Inversion of the free cheeks and rostral-hypostomal plate beneath the thorax in exuvial configurations of *Paradoxides* and *Ogygopsis* may be explained by such manoeuvres. There is no compelling evidence for an opening between cephalon and thorax in these specimens, and such an opening does not appear to have been necessary in freeing the vital soft parts and facilitating emergence. Exuviae consisted of the mineralized exoskeleton, held together by articulatory membranes and the unmineralized cuticle that had covered the ventral side of the body and the appendages. Consideration needs to be given to how such exuviae came to be buried and partially preserved, to the effects of progressive decay of unmineralized cuticle before burial, and of transport before or during burial, before claiming that a particular specimen is an exuvial configuration. The criteria for recognizing such a specimen are problematical, but it is considered that the symmetrical inversions described here may be such configurations.

1. INTRODUCTION

A renewed interest in moulting in trilobites has been accompanied by drawings showing the body strongly arched in the initial stages of exuviation. It has been thought that species of the important Cambrian groups of olenelloids, paradoxidids and redlichiods behaved in this way. Specimens of taxa of any of these groups showing flexure of the body are exceedingly rare, and it has been stated that olenelloids could not enrol. I have recently described articulatory devices in the thorax of *Olenellus*, and here describe those in the olenelloid *Holmia* and in species of *Paradoxides*. These taxa did not have the horizontal, transverse hinge between sclerites that characterizes the majority of trilobites, but evidently they could arch the body,

sufficiently to bring the pygidium close beneath, or possibly into contact with, the cephalon.

Strong arching of the body in exuviation has been invoked to explain a specimen of an entire exoskeleton in which particular sclerites are inverted below it in a symmetrical arrangement. Three examples of such supposed moult configurations are again described here, which show the free cheeks and rostral-hypostomal plate inverted beneath the thorax. Such a configuration is unlikely to occur by chance, but if it is the remains of exuviae abandoned on the surface of the substrate, how was it preserved with so little disturbance? Thus the recognition of a moult configuration raises questions of behaviour in trilobites, of the precise morphology that would have enabled such behaviour, and of the circumstances of burial and

preservation of exuviae. Here I outline the possible behaviour, during exuviation, of a species of *Paradoxides*, bearing in mind that the animal was casting the entire exoskeleton, mineralized and unmineralized. Opening of the cephalic sutures would have freed the vital soft parts, and allowed the newly moulted animal to emerge, without needing manoeuvres to create an opening at the back of the cephalon. If exuviation took place on the surface of the substrate, decay of the unmineralized cuticle would have caused progressive disintegration of the remains. Only rapid burial could have resulted in preservation of a moult configuration. The processes of burial, and possible effects of incidental disturbance and transport, need consideration. It may not be valid to assume that inversion of portions of the exoskeleton, relative to the remainder, is an infallible criterion for recognition of exuviae. Such arrangements may have been preserved after decay and disturbance of exuviae or carcasses.

Terminology follows Harrington *et al.* (in Moore 1959) and, in addition, I have used *thoracopygon* for the articulated exoskeleton of thorax and pygidium, and *axial shield* for that in which the cranium is articulated to the thorax and pygidium, after Henningsmoen (1975). The term *exsagittal* (abbreviated as *exs.*) refers to the direction parallel to the median, sagittal (*sag.*) line, and *transverse* (*tr.*) is at right angles to the sagittal line. I have used *enrolment* and *enrolled* in a general sense to include arching the body to varying degrees, without necessarily implying that the pygidium was brought into contact with the cephalon.

2. ARTICULATION OF THE EXOSKELETON

In most trilobites articulation between segments of the thorax (figure 1), and between cephalon, thorax and pygidium was facilitated by the following devices.

1. In the axial region, the articulating half ring,

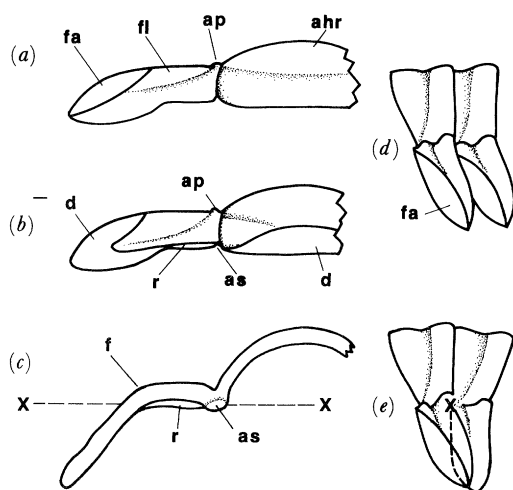


Figure 1. Articulation devices between left halves of thoracic segments in a fulcrate trilobite: (a) dorsal; (b) ventral; (c) posterior, (d) (e) left lateral views, latter showing flexed position about axis and dashed outline of facet of second segment. ahr, articulating half ring; ap, axial process; as, axial socket; d, doublure of axial ring and pleura; f, fulcrum; fa, facet; fl, flange; r, recess; x, axis of rotation of segment.

which extended beneath the doublure of the next anterior ring or the occipital ring;

2. An axial process at the anterior margin of the axial furrow, which fitted into a socket on the adjacent posterior margin;

3. The pleura was abruptly flexed at the fulcrum, dividing it into an adaxial, horizontal inner portion about which adjacent sclerites could hinge;

4. The anterior edge of the inner portion of the pleura fitted below the posterior edge of the corresponding portion of the segment in front, or of the posterior cephalic border. This anterior edge has the form of a narrow (*exs.*) flange, which fitted into a recess on the posterior edge, and thus acted as a hinge;

5. The outer portion of the pleura sloped downward and outward, was underlain by a doublure, lobate or pointed in form, a spine or blade. To enable these outer portions to swing one below the other during enrolment the antero-lateral edge was bevelled to form a facet to facilitate this overlap.

In these trilobites, therefore, articulation between sclerites was precisely guided by a straight, transverse, horizontal hinge which extended between the axial articulating process and the fulcrum. In life an articulating membrane would have extended between the anterior margin of the articulating half ring and the doublure of the ring in front, and between the anterior edge of the flange and the edge of the recess in front. In describing the articulating devices Whittington & Evitt (1954, pp. 21–24, figures 3, 4, 9 and 27) showed that they were elaborated by a socket and process at the margin of the axial ring, and at the fulcrum. Since that time, descriptions of additional silicified material (see, for example, Palmer 1958; Whittington 1954; Whittington & Campbell 1967; Hunt; 1967; Chatterton & Ludvigsen 1976; Evitt & Tripp 1977; Chatterton & Perry 1983, 1984) have shown that thoracic segments of this type are present in trilobites throughout their range in time. The morphology is characteristically different between groups, for example, the wide (*tr.*) inner portion and narrow, steep outer portion of the pleura in *Cryptolithus* (Campbell 1975) and harpetids, or the arched segment of *Bumastus* (Chatterton & Ludvigsen 1976) with its wide axis, exceedingly narrow (*tr.*) inner portion of the pleura, and wider outer portion that continues the slope of the axial ring.

Öpik (1970, p. 3) observed that the pleura in the Cambrian *Redlichia* lacked the fulcrum, and was curved down to an almost vertical attitude at the tip. Thus there was no horizontal inner portion of the pleura to give a transverse hinge between sclerites of the exoskeleton. Öpik also referred to the pleural guide, a short process at the anterolateral corner of the pleura, which acted to keep it in place during flexure between sclerites, and to the absence of the facet. Bergström (1973a, pp. 16–17, plate 2, figures 3, 4 and 7) noted the lack of the fulcrum in olenelloids, and showed both an axial process and the pleural guide. In *Olenellus* (Whittington 1989, figures 1, 17 and 18) the anterior margin of the pleura was extended by a flange, the angulate anterolateral corner of which may have acted as a pleural guide. The narrow flange in *Holmia*

(figures 14 and 19) was concave, and fitted below the narrow strip of doublure that extended along the posterior edge of the next anterior segment. Similar devices have been shown in *Wammeria* (Whittington 1989, figures 28 and 32). Conflicting statements have been made about the form of the pleurae, and the articulation devices in paradoxidids, but enrolled specimens have long been known (see, for example, Pompeckj 1896, plate 16, figure 1). Bergström (1973a, p. 18) refers to the presence of an axial articulating process, and to the fulcrum in certain species, whereas Bergström & Levi-Setti (1978, p. 9) remarked on the absence of the fulcrum and horizontal inner portion of the pleura in *Paradoxides davidis* and its subspecies. The present investigation suggests that in this species and others of *Paradoxides* (figure 21) the fulcrum and facet were absent, and that articulation was facilitated by a flange that underlay a narrow strip of doublure on the next anterior segment, and a distal projection or pleural guide. Thus in olenelloids, redlichiods and paradoxidids adjacent sclerites of the exoskeleton probably swung about the axial articulating process, the pleura guided by the flange (figure 21). This form of articulation was termed non-fulcrate by Öpik (1970, pp. 4–5), to distinguish it from the fulcrate type with the transverse hinge (figure 1). Non-fulcrate articulation is not confined to the three taxa mentioned above, for it was present in *Olenoides* (Whittington 1980, figure 3), regarded (in Moore 1959) as a corynexochoid. Other genera in this taxon, such as *Ogygopsis* (figures 9 and 11), appear to have been fulcrate, however, and the short outer portion of the pleura was faceted. In his study of xystridurids, Öpik (1975, p. 23) showed that this family included fulcrate and non-fulcrate species, and referred to other groups showing the same phenomenon. He also referred to *Paradoxides* as having the fulcrum in anterior, but not in posterior segments, a statement that I cannot substantiate.

More information is needed on the articulatory devices of the pleurae of Cambrian trilobites, and of the original convexity of the exoskeleton, before the significance of the distinction between fulcrate and non-fulcrate articulation may be assessed. The cranidium of species of *Redlichia* (Öpik 1958, plate 3, figures 1–7; 1970, plate 10, figures 1–4) was convex, but entire specimens figured by Öpik and by Zhang *et al.* (1980) are extended and flattened. Whether or not there was a flange on the pleura, the shape of the pleural guide and form of the doublure, are not revealed. McNamara (1986, p. 412) recorded the axial process and socket in *R. forresti*.

Illustrations of enrolled or partly enrolled post-Cambrian trilobites are frequently given, those of Cambrian species rare. Agnostoids and eodiscoids enrolled closely, and Stitt (1983) figured late Cambrian examples from other taxa. It seems evident that almost all trilobites could enrol at least partly, if not completely, and the statement (Harrington in Moore 1959, p. O102) that olenelloids and other Lower Cambrian species with small pygidia could not enrol is misleading. I have described two examples of species which could not enrol, but such examples are rare. In

the Ordovician remopleuridid *Hypodicranotus* (Whittington 1952), the fork of the hypostome reached back to the pygidium. The thorax of *Hypodicranotus* was fulcrate, like that of other remopleuridids, the segments having the articulating half ring, fulcral process and socket, and facet. Evidently some flexibility of the thorax was provided for, severely limited by the rigidly attached hypostome. In the upper Cambrian *Schmalenseeia* (Whittington 1981) the segments show no evidence of the articulating half ring, are not fulcrate, and lack the facet. It was concluded that the exoskeleton was not articulated.

3. EXUVIATION

(a) General considerations

Study of the hypostomes of *Holmia*, and of forms such as *Paradoxides* that had the rostral plate and hypostome fused into a single plate, has shown (Whittington 1988) that the hypostome was firmly braced against the dorsal exoskeleton. It formed part of a capsule that enclosed the vital organs of the head, including the U-shaped anterior end of the alimentary tract, the mouth backward-facing and situated at the posterior border of the hypostome. These considerations strongly support Henningsmoen's (1975, p. 182) view that the cephalic sutures were a special provision to facilitate ecdysis. Opening of the sutures opened the capsule protecting the vital organs, and freed the delicate eye surface. The newly moulted animal may then have emerged forwards, through an anterior opening, enabling it to withdraw from backwardly directed spines of the exoskeleton, and from the appendages, which were presumably swung back to facilitate this shedding. This mode of emergence would have been possible for trilobites with a marginal suture or a facial suture that traversed the eye lobe. A special case is that of certain phacopinids (Richter 1937, 1942; in Moore 1959, p. O462; cf. Henningsmoen 1975, pp. 189–191) in which the facial suture was ankylosed in the adult. Richter explained the exuvial configuration of the cephalon (inverted and backward-facing) lying in front of the hypostome and thoracopygon, as having resulted from the moulted animal emerging after opening of the hypostomal suture and a split at the back of the cephalon. The cephalon was inverted as the animal emerged, in what has been termed the 'Salterian' mode of exuviation. This mode of moulting occurred only in the adult stages, in earlier stages of development the facial suture was functional, as it was in the adults of other phacopinids.

The exuviae would have consisted of the mineralized exoskeleton, articulatory membranes and the cuticle that had covered the animal ventrally, including the limbs. This non-mineralized cuticle was continuous, extending inward from the inner margin of the doublure of the cephalon (including the rostral plate), to the doublure of the hypostome, and inward from the doublure of the thoracic segments and pygidium, and sheathing all the limbs. These cast remains were therefore a unit, all the sclerites of the mineralized exoskeleton having been linked together by unmineralized cuticle. Decay of the latter would have been

rapid, perhaps a matter of days, and would have led to progressive disintegration of the exuviae and scattering of the mineralized sclerites. No doubt their usual fate was complete dismemberment. If the exuviae were shed on the surface of the substrate, only rapid burial could have preserved them. Depending on how soon burial took place, exuviae may have been complete, partly or wholly disintegrated. Thus complete, or almost complete, exuviae may have been preserved as an entire exoskeleton, or one with some displacement or sclerites missing. Such a specimen would be difficult to distinguish from that provided by a buried carcass. Öpik (1970, p. 13), Henningsmoen (1975) and Speyer (1987) have discussed the criteria for discriminating between such specimens. Prominent among the criteria is the rare occurrence of a peculiar arrangement of the portions of the exoskeleton, and particularly of a configuration in which certain portions are inverted relative to the remainder. Examples of such occurrences described in recent years include one of the Ordovician *Carolinites* by Fortey (1975), various Lower Palaeozoic species by McNamara & Rudkin (1984), of Devonian *Phacops* by Speyer (1985), and of Cambrian *Redlichia* by McNamara (1986). In these examples inversion of one or more portions of the exoskeleton (cranidium, free cheek, hypostome), relative to the thorax and pygidium, is taken as evidence of a moult configuration. I have re-examined the original specimens of *Ogygopsis klotzi* and *Paradoxides davidis trapezopyge* of McNamara and Rudkin, and conclude that there is evidence that not only the free cheeks but also the rostral-hypostomal plate, are inverted beneath the thorax in at least two of these specimens. The symmetrical arrangement of the free cheeks, and of the rostral-hypostomal plate, in these configurations argues against their being accidentally arrived at during transport and burial. I accept that these inversions resulted from manoeuvres of the animal in moulting, but have re-examined the possible form of such manoeuvres, bearing in mind the role of the cephalic sutures, the nature of exuviae and their fate.

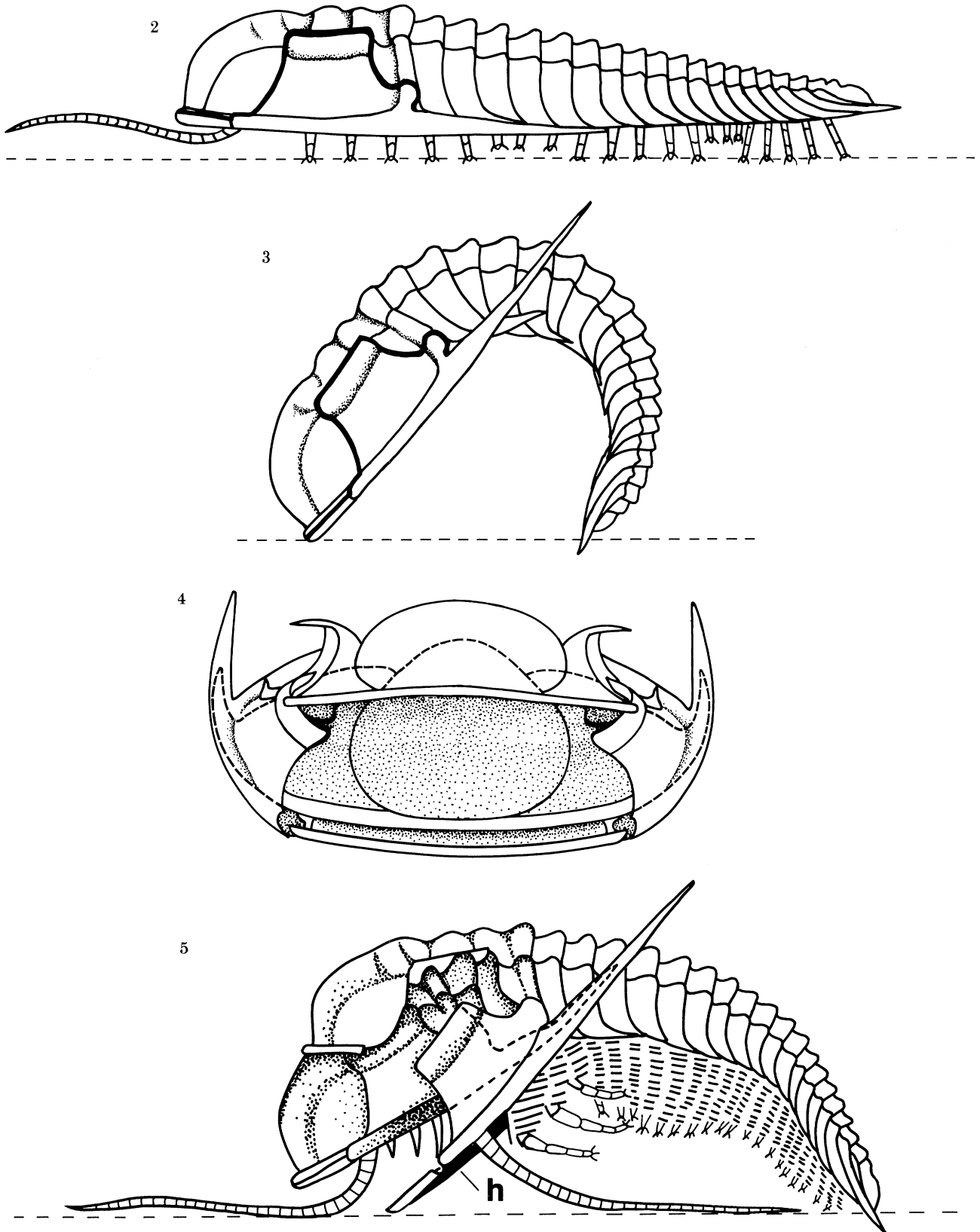
Other aspects of ecdysis in trilobites, such as the detection of moults in large samples, and the number during an individual lifetime (Hunt 1967; Sheldon 1988), are not discussed here. Examples of what are considered to be newly moulted trilobites are rare. In that of *Olenoides serratus* from the Burgess Shale (Whittington 1980), the exoskeleton is wrinkled, shows little relief, and lacks any mineralization. In those of *Phacops rana* (Miller & Clarkson 1980; Speyer & Brett 1986) the exoskeleton is thin and wrinkled, and the former authors comment that in moulting trilobites shed the thickly calcified exoskeleton without any resorption, so that the calcite had to be reformed at each ecdysial cycle, a process requiring considerable metabolic effort.

(b) *Exuviation in Paradoxides*

Fortey (1975, p. 114, figure 15) was the first to portray flexure of the body through more than 180° as a preliminary manoeuvre in exuviation of the Ordovician *Carolinites*. Inversion of particular portions of

the exoskeleton were attributed to this action. McNamara & Rudkin (1984, figure 11) followed suite in portraying downward flexure of more than 90° of the cephalon and first three thoracic segments as explaining inversion of the free cheek beside and beneath the thorax in moult configurations of *Ogygopsis* and *Paradoxides*. In error in their portrayal, the free cheek was not inverted in their figures 11*c* and 11*d*, as it should have been if I have followed their text correctly.

Figure 2 is based on *P. carens*, the convexity given to the entire exoskeleton like that attributed to the cephalon (figure 20). Figure 3 shows the presumed initial flexure of the body above the substrate, the long pleural spines of thoracic segments 15–17 (Šnajdr 1958, plate 26, figure 10; plate 3, figure 1) assisting to hold it in position. Immediately preceding exuviation the epidermis would have been withdrawn from the old cuticle (mineralized and unmineralized), freeing muscles from attachment to apodemes, and ligaments linking the anterior fossula to the anterior wing of the hypostome. Opening of the facial and connective sutures (figures 4 and 5) would have allowed the emergence forward of the post-ecdysial animal. Emergence may have been accompanied by a relaxation and gradual extension of the body of the moulted animal. Flexible membranes that connected the anterior edge of each articulating half ring to the doublure of the ring in front, and the anterior edge of each flange to the doublure in front, held cranidium, segments and pygidium of the old mineralized exoskeleton together. The cephalon of the moulted animal would have been freed to emerge, not only from the dorsal exoskeleton, but also from the rostral-hypostomal plate, freeing the vital soft parts, including the anterior end of the alimentary canal and backward-facing mouth. Forward emergence was essential to this process, and also to withdrawal of the genal and pleural spines. The free cheeks would have been pushed aside, thus assisting to free the eye surface, and would have hung down beside the cephalon (figure 4). The ‘lower jaw’ of the ecdysial gape (as Henningsmoen (1975) termed it) was composed not only of the free cheeks and rostral-hypostomal plate, but also the cuticle that had extended inward from the inner edge of the doublure and which sheathed the limbs. In the cephalon this cuticle would have extended between the inner edges of the doublure of the free cheeks and the doublure of the rostral-hypostomal plate, holding these portions of the exoskeleton together despite the opening of the connective sutures to allow space for the new animal to emerge (figure 4). The connective sutures played an important role in providing this space, in that they enabled the cast free cheeks to be pushed aside by the emerging animal. The ventral cuticle connecting free cheeks and rostral-hypostomal plate would have had to be flexible and somewhat elastic to permit such an emergence without rupture. Provided this was so, the rostral-hypostomal plate would have been swung down with the free cheeks. As the animal continued to withdraw from the old cuticle, the anterior limbs would have extended to touch down on the substrate (figure 5). An impression of the cast cuticle that had covered the presumed antennae and biramous limbs is



Figures 2–6. *Paradoxides* sp., suggested manoeuvres during exuviation. Exoskeleton based on *P. carens*, which has 18 thoracic segments, convexity similar to that of *P. davidis* (Whittington 1988; figure 8). 2. Left lateral view showing antenna and assumed walking legs; thick line indicates suture lines. 3. Flexure of body above substrate, using the pleural spines of thoracic segments 15–17 to dig into sediment. Limbs omitted. 4. Anterior view of ecdysial gape in cephalon, as sutures opened and cephalon of moulted animal (stippled and dashed outline) began to withdraw from old exoskeleton and emerge. 5. Left lateral view of moulted animal (stippled with dashed outline of cephalon and anterior three walking legs indicated) as it emerged from exuvia, which included the rostral-hypostomal plate (h) and appendages shown diagrammatically.

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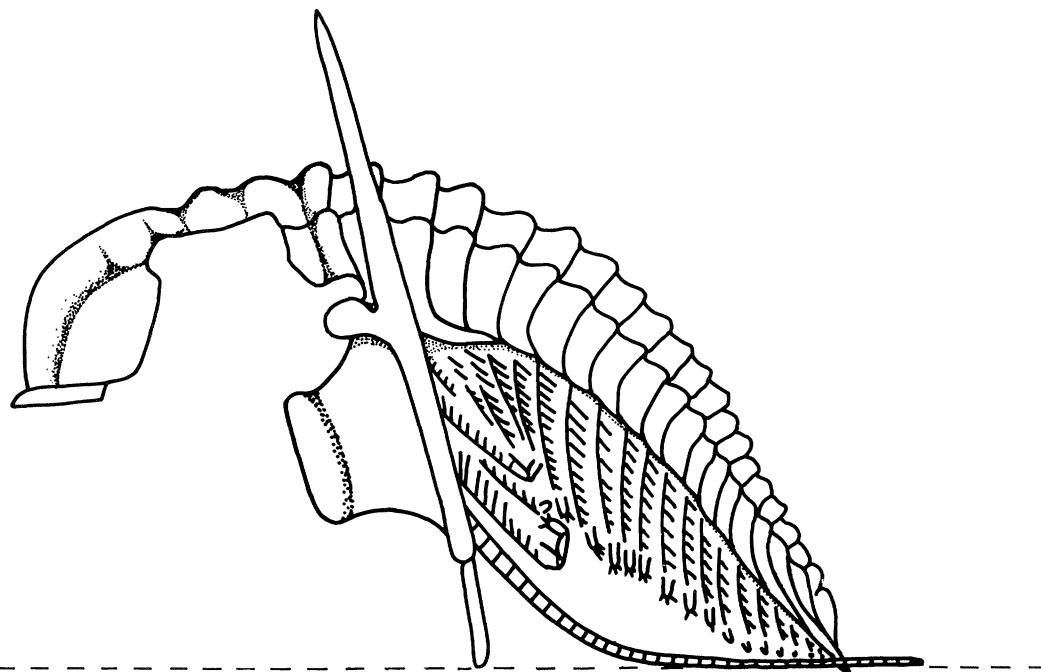


Figure 6. Exuviae after emergence of moulted animal, which included mineralized exoskeleton, cast ventral cuticle and cuticle of appendages. Portrayed perched on substrate, free cheeks and rostral-hypostomal plate having been rotated back from position shown in figure 5.

shown hanging below the old mineralized, axial exoskeleton. The rostral-hypostomal plate and free cheeks were attached to the rest of the exuviae by the unmineralized ventral cuticle, and swung down about a transverse fold in this cuticle.

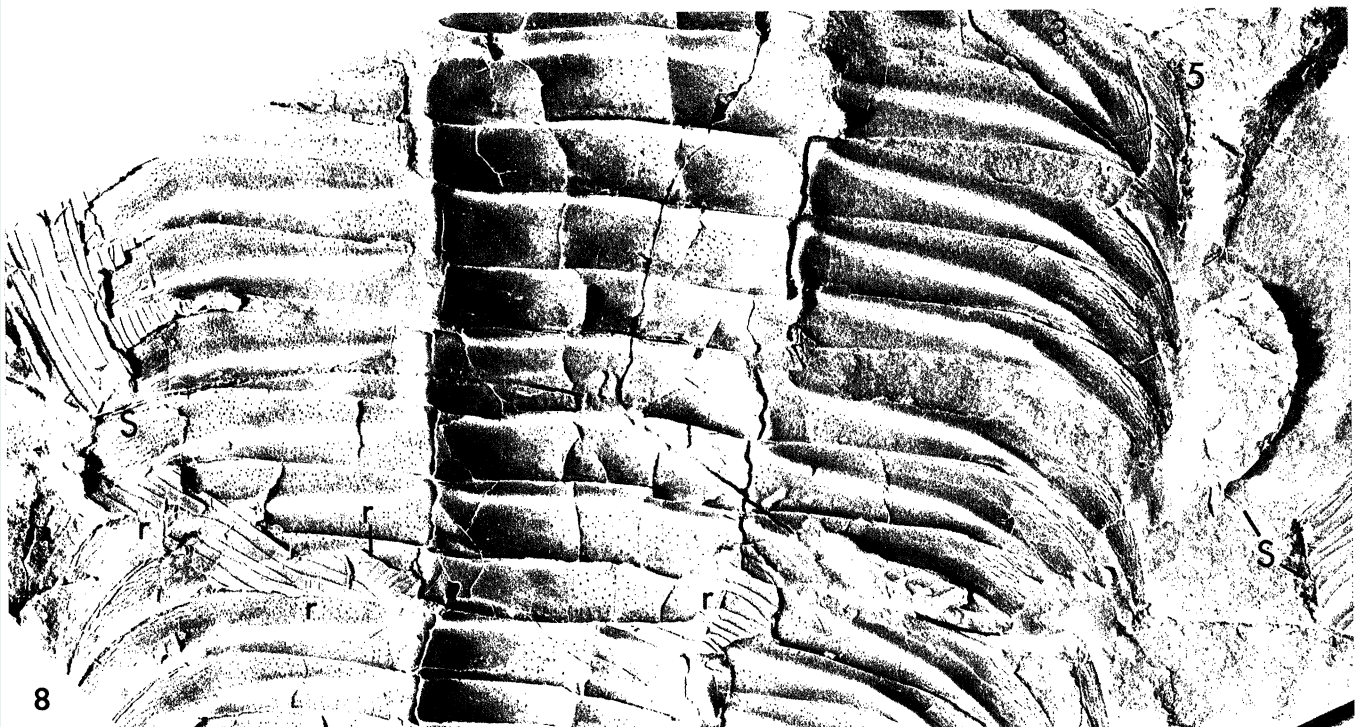
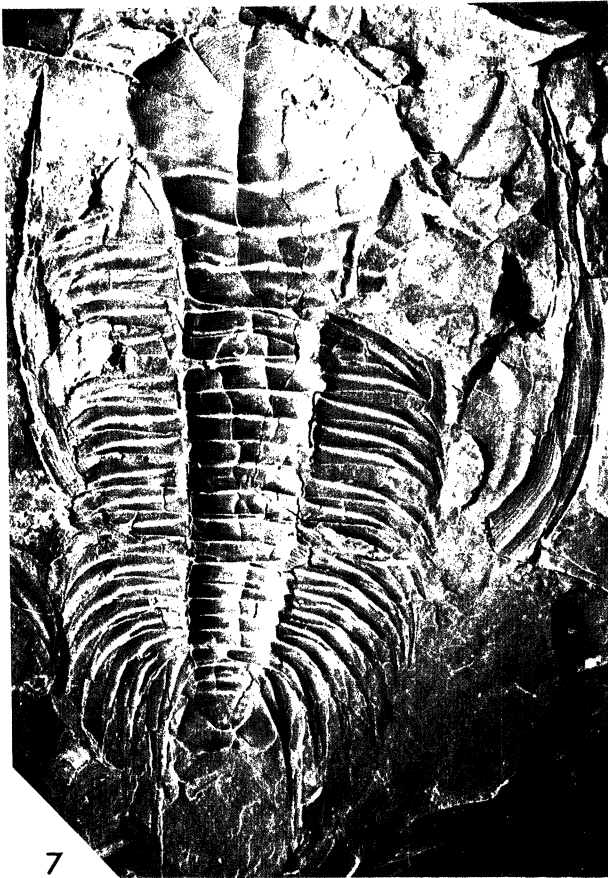
Continued forward movement of the animal, and completion of exuviation would have left the exuviae (figure 6). It is presumed that this continued forward movement of the newly moulted animal dragged the axial exoskeleton forward, causing the free cheeks and rostral-hypostomal plate to be tilted up vertically or even overturned, the anterior margin of the plate held by the substrate. The amount of rotation possible was limited to the amount shown, by the doublure of the free cheek coming into contact with the tips of the pleurae of the first two segments. The presumption is that the ventral cuticle was not ruptured, but continued to hold free cheeks and rostral plate together, but was further folded, as shown diagrammatically.

(c) *Preservation of the exuviae*

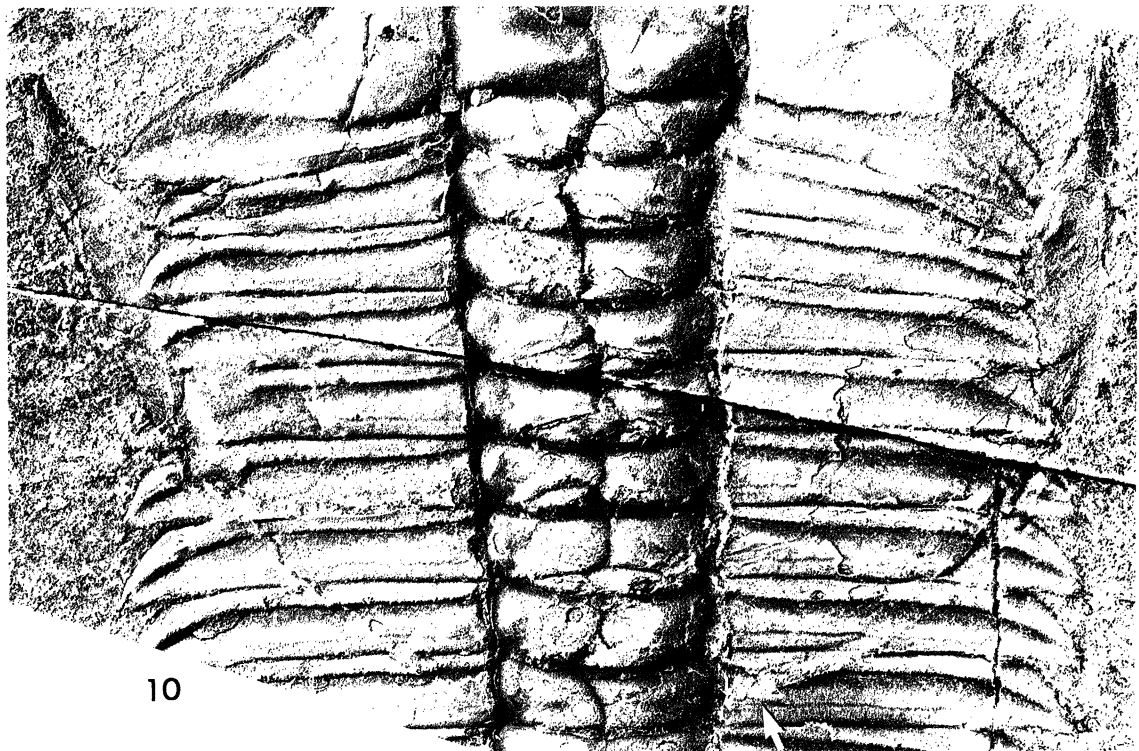
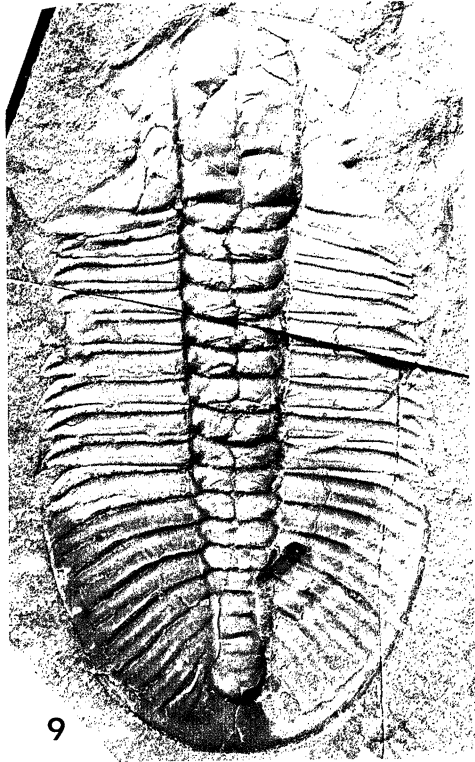
Figure 6 portrays exuviae abandoned on the substrate in a precarious position. Henningsmoen (1975, pp. 181, 188) mentioned that trilobites may have sought concealment for safety when preparing for ecdysis, and that exuviae, since they were not likely to have been dismembered by scavengers, had a greater potential for preservation intact than a carcass. However, though the remains (§3*a*) were originally a unit held together by non-mineralized cuticle, unless decay was inhibited by rapid burial, specimens showing characteristic inversions would have been dismembered. Little is known of the circumstances of burial of most specimens that have been regarded as exuvial configurations, with the exception of those described

by Speyer (1985, 1987). It may be imagined that exuviae like those portrayed here may have extended and collapsed within a short time so that they came to lie on the substrate, the dorsal side of the axial exoskeleton up, the free cheeks and rostral-hypostomal plate inverted beneath it. The original of figures 7 and 8, may be an example of such exuviae. It was collected by Dr R. Levi-Setti and his family between 1974 and 1978, from the interval 241 to 278 cm in the measured section of Bergström & Levi-Setti (1978, figure 1). These authors (1978, pp. 3–6, figure 2) noted the limited stratigraphical and size range of specimens (the example figured here is in the middle of this size range), and considered that entire exoskeletons were all exuviae. Predominantly they occur ventral side down, randomly orientated, not overlapping, Bergström & Levi-Setti refer to burial in quiet waters, below wave-base, and to sudden events of turbidite-type deposition. As §4*b* (iii) shows, in this specimen the cranium has been pushed back over the first three thoracic segments, bending these segments back on the right side and carrying with it, under the thorax, the free cheeks and rostral-hypostomal plate. The implication is that when this happened, probably in the course of burial, the unmineralized cuticle had not decayed, but held the exuviae together. Dissociated exoskeletal parts of the same species, some possibly broken, and portions of exoskeletons of other species, occur in the slab shown in figure 7. They may be explained as having been brought in with the sediment in which the exuviae were buried, and imply some transport of the fossils. Presumably it was during this transport and burial that the exuviae were partly telescoped.

If the exuviae (figure 6) had rolled upside-down before extending and collapsing, they may have come



Figures 7 and 8. *Paradoxides davidis trapezopyge* Bergström & Levi-Setti, 1978 cast bank of Manuels River, at Manuels, southeastern Newfoundland, from level 241–278 cm of Bergström & Levi-Setti (1978, figure 1); Middle Cambrian, ROM 41741. Original of McNamara & Rudkin (1984, figure 12). 7. External mould of dorsal exoskeleton, thoracic segment 5 numbered, magn. $\times 0.75$. 8. Portions of thoracic segments 3–16, and anterior portions of inverted free cheeks, showing anterior section of suture (s) and fragments of external mould of rostral-hypostomal plate (r) adhering to segments 12–14 (magn. $\times 2$).



Figures 9 and 10. *Ogygopsis klotzi* (Rominger, 1887), Stephen Formation, northwest flank of Mount Stephen, the famous 'fossil bed' (Rasetti 1951, p. 42; locality S8d, p. 128 and locality 1, p. 192); Middle Cambrian. ROM 41791, original of McNamara & Rudkin (1984, figure 9A). Internal mould of axial exoskeleton, respectively entire (magn. $\times 1$); enlargement showing inverted free cheeks and possible fragment of rostral-hypostomal plate (arrowed) beneath thorax (magn. $\times 2.5$).

to lie ventral side of the axial exoskeleton upward, the free cheeks and rostral-hypostomal plate inverted, or possibly not. In the latter case all the parts of the exoskeleton may have lain approximately in their original relationships, held together by unmineralized cuticle. The originals of Bergström and Levi-Setti's (1978) plate 6, figure 8, and plate 9, figure 3, have the exoskeletal parts little displaced, and may be examples of such exuviae. The inversion of the right free cheek in the holotype (Bergström & Levi-Setti 1978, plate 7, figure 2), and displacement of cranidium and free cheek, may have occurred during transport and burial of exuviae which had suffered slight decay. If such remains had lain on the surface of the substrate for even a few hours, decay of the unmineralized cuticle would have begun. Partial dismemberment might then have occurred as a result of any disturbance, and within a few days at most the sclerites of the exuviae would no longer be held together. Thus the usual fate of exuviae was disintegration and scattering, unless quiet conditions, and burial following swiftly on early stages of decay, resulted in preservation. The exuviae of figure 7 must be a rare accident of preservation.

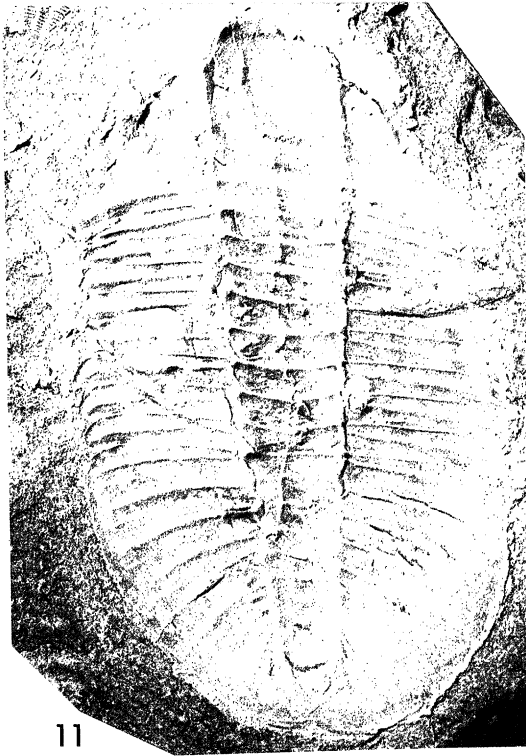
The initial sharp flexure of the anterior portion of the body in exuviation of *Ogygopsis* and *Paradoxides* was proposed not only to account for inversion of the free cheeks, but 'to facilitate splitting of the cephalon from the thorax' (McNamara & Rudkin 1984, p. 166, figure 11). However, such a split may have been a special provision for exuviation when the facial suture was ankylosed (§3*a*), and not one that occurred more widely in moulting. Opening of the cephalic sutures would have provided adequately (figures 4 and 5) for emergence forward of species of either genus. The moult configurations (figures 7–12) do not show evidence of such a split, rather they show that the cephalic sutures opened, and the flexure required by McNamara & Rudkin between the cephalon and each of the first three thoracic segments was so sharp as to have required dislocation of all these joints. I therefore propose a less abrupt flexure of the body at the beginning of exuviation (figure 3). A supposed moult configuration of *Paradoxides davidis intermedius* (Bergström & Levi-Setti 1978, plate 6, figure 3; McNamara & Rudkin 1984, pp. 169–170) consists of an exoskeleton lacking the cranidium, and showing displacement at the sutures. In exuviae (figure 6) the weakest link was between the large sclerite of the cranidium and first thoracic segment, by flexible membranes at the posterior edge, whereas the thoracopygon was held together not only by such membranes, but also by the ventral cuticle. The onset of decay would have weakened the attachment of the cranidium, and in the course of such transport as was associated with burial, the cranidium might have been dislocated, inverted, or carried away from the remainder of the exuviae. Thus specimens considered to be exuvial configurations, but lacking the cranidium, may not be evidence for a split at the back of the cephalon having aided exuviation. The particular specimen referred to here shows no inversions, and could be interpreted as derived from a carcass rather than from exuviae.

The above has emphasized the important influence

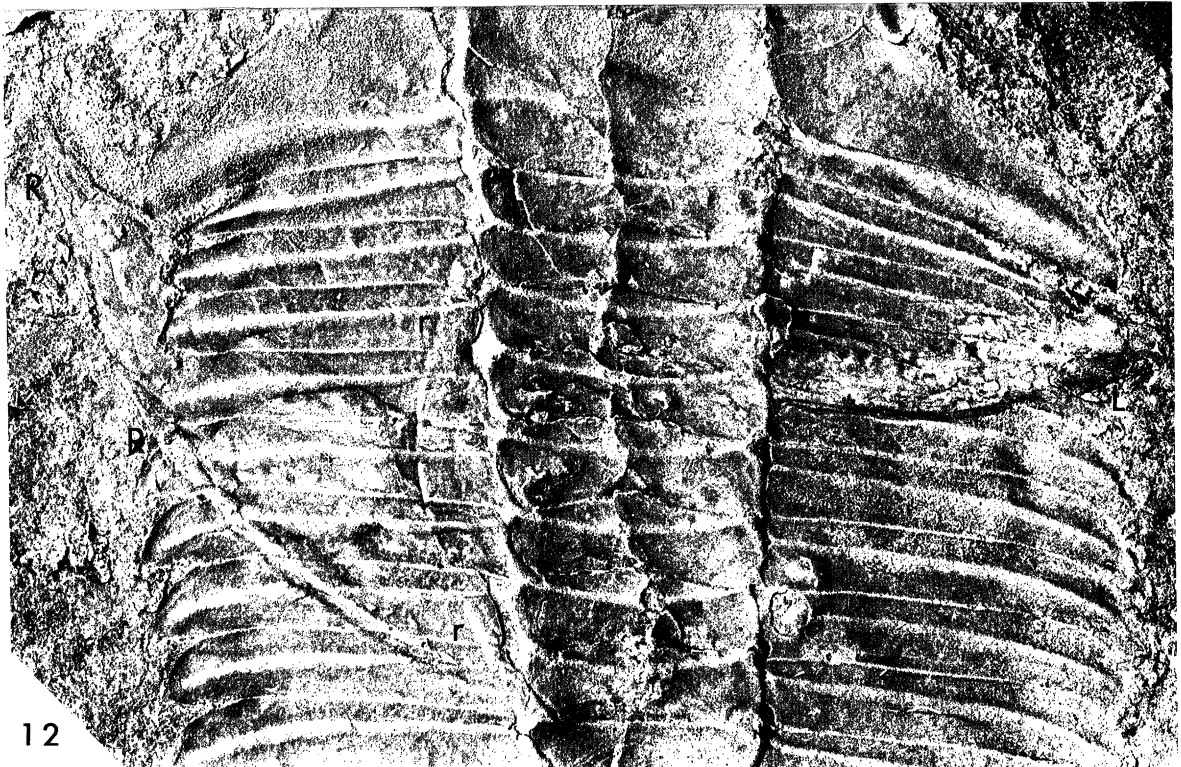
of the onset and progress of decay of unmineralized cuticle on the arrangement of mineralized sclerites preserved. The claim that a particular arrangement is an exuvial configuration needs detailed consideration. Any implication of no disturbance before or during burial is difficult to accept, because rapid burial by an influx of sediment appears essential to preservation. The difficulty of distinguishing between preserved exuviae and the remains of dead animals is evident. This is particularly the case with entire exoskeletons, examples of which, providing they show no peculiar or distinctive arrangement of exoskeletal parts, are considered by some authors to be the remains of carcasses. On the other hand, Bergström & Levi-Setti (1978, p. 5) appear to have regarded all complete specimens as exuviae, though no peculiar arrangement of parts is evident in some examples. The ventral cuticle and that which covered the limbs is rarely preserved, the unique example from the Burgess Shale (Whittington 1975, pp. 118–119) having been preserved under exceptional conditions. It shows portions of thoracic and pygidial appendages, the posterior cerci and a central, darker area (presumably the ventral cuticle) and is not associated directly with any mineralized exoskeleton. It could have been derived by the disintegration of exuviae or of a carcass.

(*d*) *Exuviation in other Cambrian trilobites*

McNamara and Rudkin (1984, figure 11) developed their proposed mode of exuviation to explain two specimens of *Ogygopsis klotzi*. In one (figures 9 and 10) the free cheeks have been inverted to lie beneath the thorax almost in their original relation to one another. It may be that the rostral-hypostomal plate lies between them, but this is uncertain. In the second specimen (figures 11 and 12) the free cheeks and rostral-hypostomal plate are inverted to lie beneath the thorax, but their original relationships have been altered. I suggest that these configurations may have resulted from behaviour in exuviation like that proposed for *Paradoxides* (figures 2–6). Opening of the cephalic sutures would have allowed the emergence forward of the newly moulted animal, inverting the free cheeks and rostral-hypostomal plate in the exuviae. Burial before decay of the unmineralized exoskeleton would have held the exuviae together in the original relationship (figure 9), or with modification resulting from folding and probably rupture of the ventral cuticle (figure 11). Specimens of the extended axial shield (Rasetti 1951, plate 29, figures 7 and 8) may be the remains of exuviae after decay of the ventral cuticle and consequent scattering of free cheeks and rostral-hypostomal plate before or in the course of burial. According to Lehmann (1960), this was Rasetti's belief. The specimen which Lehmann (1960, figure 1) described has the cranidium and first thoracic segment detached and inverted, lying beside the remainder of the axial shield. As Lehmann suggested, such a specimen could have resulted from further decay of exuviae leading to separation of portions of the axial shield, and inversion of them, prior to burial. Thus a decay series of exuviae could account for the features



11



12

Figures 11 and 12. *Ogygopsis klotzi* (Rominger, 1887), locality and formation as figures 9 and 10. ROM 41876, original of McNamara & Rudkin (1984, figure 9B (printed in reverse)). External mould of axial exoskeleton, respectively, entire (magn. $\times 1$); enlargement showing inverted left (L) and right (R) free cheeks and anterior edge of rostral-hypostomal plate (r) beneath thorax (magn. $\times 2.5$).

shown by different specimens, in all of which the cephalic sutures had opened.

A small specimen of the genicranidium and inverted perrostral plate and hypostome of *Olenellus thompsoni* were referred to by McNamara & Rudkin (1984, p. 167) as a possible exuvial configuration, following Hupé (1953, figure 18). Another probable configuration is the original (Whittington 1989, p. 137, plate 1, figure 8) of a specimen that has the inverted perrostral plate beneath the axial exoskeleton. The plate has been inverted so that the posterior tips lie almost exactly beneath their original position. The whereabouts of the hypostome are unknown. Such specimens are apparently rare, but led me to suggest that *Olenellus*, with its marginal, perrostral suture, may have moulted in much the same way as suggested for *Paradoxides* (figures 2–6). No inversion of the rostral plate and hypostome has been recorded in a specimen of *Holmia kjerulfi*, but the articulatory devices described here were like those of *P. carens* (figure 21), so that the body could have been enrolled. This species may have moulted in a similar manner. Inversion of free cheeks and rostral-hypostomal plate, as a unit or slightly displaced, has been figured by McNamara & Rudkin (1986, figure 13) in species of *Oryctocephalus*. Similar inversions in specimens of *Bathynotus holopygus* have been recorded (Whittington 1988, p. 584), with slight displacement at the sutures between the free cheeks and rostral-hypostomal plate. There are also examples in which these sclerites were not inverted. In §3a I have contended that the cast unmineralized cuticle, including that covering the limbs, was a continuous unit, and that opening of the cephalic sutures was essential for forward emergence of the moulted animal. If these specimens were derived from exuviae, then the ventral cuticle which had held the free cheeks and rostral-hypostomal plate together in their approximate original relationships would have to have separated by decay from the axial exoskeleton. Separation of these two portions of the exuviae, and shifting of them in the course of any transport during burial, could account for the resulting different configurations. Perhaps such a mode of origin is more likely than one from a carcass, in which decomposition of soft parts may have resulted in a greater dismemberment of exoskeletal sclerites.

The considerations outlined in §3a have led me to put forward a rather different mode of exuviation for species of *Paradoxides* and other genera, and to reject the necessity for an opening at the back of the cephalon. This general mode of exuviation may have obtained in paradoxidids, ogygopsids, olenelloids and other Cambrian trilobites, without necessarily resulting in inversion of cephalic sclerites. In addition, I suggest that the inversions of exoskeletal portions of specimens of *Redlichia* (McNamara 1986) may not have resulted from particular manoeuvres during exuviation, especially not from an initial backward movement. Rather than the cephalic sutures opened and allowed emergence forward, the different dispositions of portions of the exoskeletons being the effects of disturbance during transport and burial of perhaps partly decayed exuviae. It is difficult to determine the criteria by

which these specimens may be considered to have been derived from exuviae rather than from carcasses.

4. SYSTEMATIC PALAEOLOGY

(a) Family Holmiidae Hupé, 1953

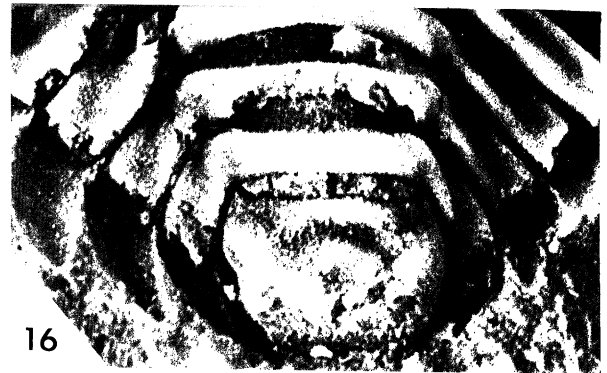
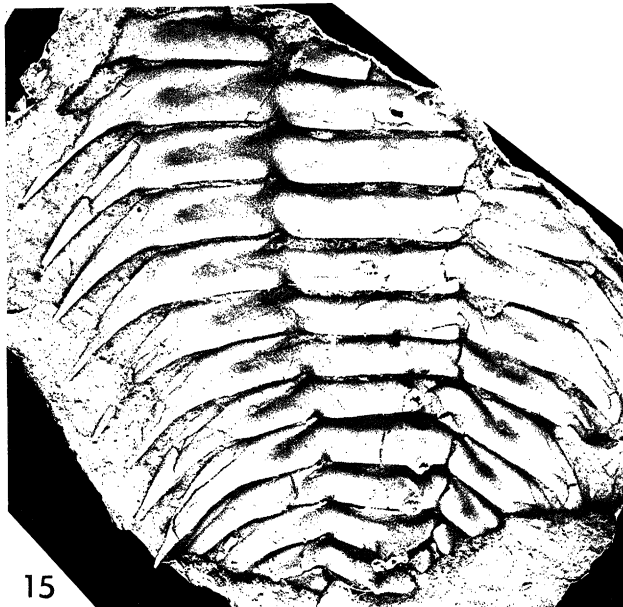
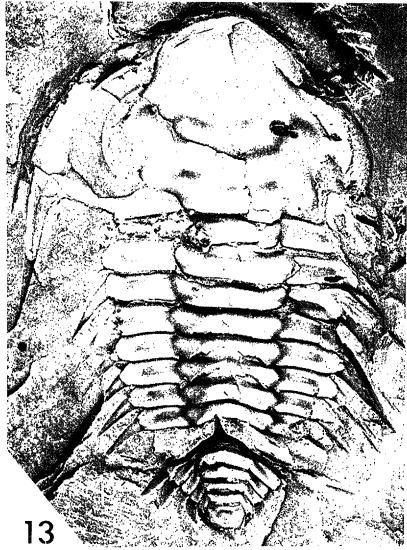
Genus *Holmia* Matthew, 1890

(i) *Holmia kjerulfi* (Linnarsson, 1871) (figures 13–19)

This species, the type, has been described by Holm (1887), Kiaer (1917), Bergström (1973*b*), Nikolaisen (1986) and Whittington (1988), the latter with reference to the hypostome. The morphology of the thorax and pygidium are dealt with briefly in the older works, here new details are given from some of the specimens studied by Kiaer. The axial ring of the thorax is inflated anterolaterally, most conspicuously in the more anterior segments, and there is a short median spine, beside and behind which the ring is flattened. This form is duplicated by the occipital ring (figure 13). The median spine increased in size progressively from the occipital ring to the 12th segment (figures 13 and 15), possibly that of the 14th was of similar size, but the spine was much reduced or absent on the last segment (figures 16 and 17). Beside each axial ring the axial furrow curves around the anterolateral inflation, is shallowest opposite the pleural furrow, and descends steeply posteriorly to the axial articulating socket. Where broken medially, internal moulds show the broad (sag.) articulating furrow and the half ring projecting forward beneath the axial spine (figures 14 and 18).

The convexity of the exoskeleton of *Holmia kjerulfi* was shown by Kiaer (1917, plate 7, figures 1–3). The pleura rose steeply from the axial furrow into the anterior and posterior bands, which were separated by a broad, shallow pleural furrow. The inner portion of the pleura sloped downward and outward, the spinose outer portion having been as steeply inclined. In the original of figure 13 the thorax is disarticulated behind segment 8, segments 12–16 and the pygidium preserved after a gap. Segment 12 has been flexed so that it is seen in oblique posterior view, in which it shows the axial spine and steep outward slope of the pleura and pleural spine. The pleurae changed progressively in form and direction, so that the posterior pair curved backward beside the pygidium (figures 15–18). The portion of the pleura impressed by the furrow is sub-parallel sided, the posterior margin curved back distally, then swinging forward to give both a slight backward projection of the posterior band, and a slight constriction at the base of the pleural spine. The doublure of the pleura (figure 19) extended inward beneath the pleural spine to a curved edge just outside and below the outer end of the pleural furrow; a narrow (exs.) strip, convex ventrally, extended inward below the posterior band of the pleura. Along the anterior edge of the pleura (figure 14) was a narrow (exs.) flange which was concave dorsally, and at the distal end had a small, angular projection. During flexure of the thorax this flange acted as a guide beneath the doublure of the pleura (or posterior border of the cephalon) in front.

The first axial ring of the pygidium (figures 16–18)



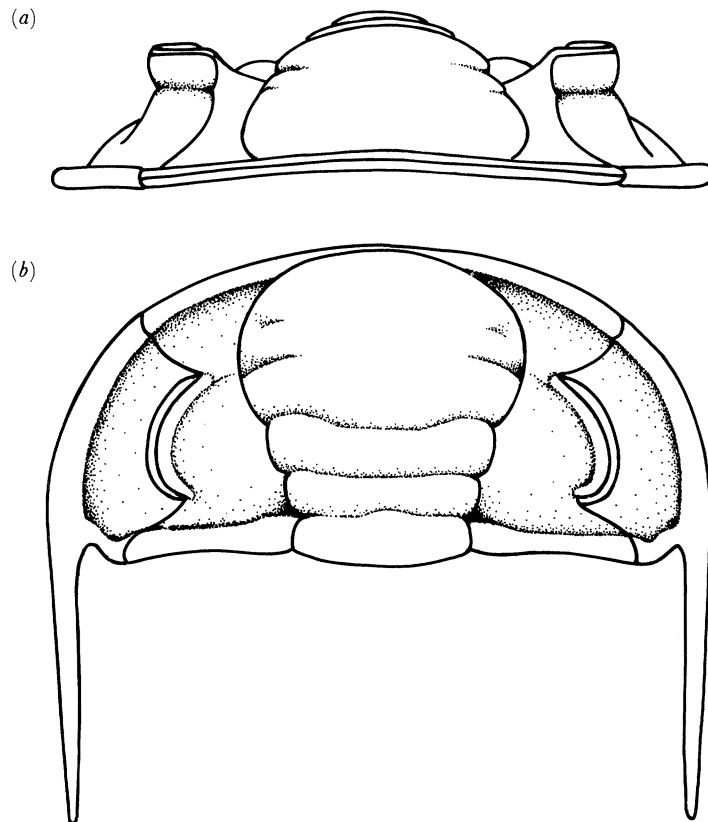


Figure 20. *Paradoxides (Hydrocephalus) carens* (Barrande, 1846). (a) anterior and (b) dorsal, views of cephalon, restored after Šnajdr (1958, figure 2 and 17 and plate 27, figure 5) and figures 22–24.

is clearly defined, behind it the axis was low, tapering and rounded posteriorly. The pleural region beside and behind the axis was gently inflated, not furrowed; the lateral margin convexly curved outward, the posterior having a slight convex-forward curvature so that the postero-lateral corner was bluntly spinose. At the antero-lateral corner is the prominent articulating process. Internal moulds show a relatively broad doublure underlying the pleural region beside and behind the axis.

The thorax of *Holmia kjerulfi* is like those of other olenelloids (Whittington 1989) in having the axial articulating process and socket, and pleural flange that fitted beneath the doublure of the pleura in front. It may be assumed that the thorax could have been flexed, and that the pygidium articulated with the posterior segment. Størmer (1942, plate 2, figure 4) showed a partially flexed specimen. The small pygidium was composed of more than one segment, and the doublure extended beneath the pleural region. *Holmia* does not display such distinctive features of

Olenellus as the division of the thorax, the macropleura of the 3rd segment, or the long axial spine on the 15th segment.

(b) **Family Paradoxididae Hawle & Corda, 1847**
Genus Paradoxides Brongniart, 1822

(i) *Paradoxides (Hydrocephalus) carens* (Barrande, 1846) (figures 20–27)

Discussion. This species was described in detail by Šnajdr (1958), who selected a meraspid specimen as lectotype; Šnajdr (1987) subsequently limited the name *carens* to specimens coming from the Skryje area. Those coming from the same formation in the Jince area were referred to a different species, the distinctions between the species based largely on the pygidium. The present examples lack the pygidium, but are referred to *carens* because they came from Skryje. The Bohemian material is partially flattened, and Šnajdr's many illustrations do not include lateral views or any reconstruction of the original convexity. An incomplete specimen (figures 22–24), though clearly partly flat-

Figures 13–19. *Holmia kjerulfi* (Linnarsson, 1871). *Holmia* Shale, Tømten, Norway; Lower Cambrian. 13, 14, 16. Incomplete, partly disarticulated internal mould of exoskeleton, (p) tip of pleura of 12th segment, PMO 74283. 13. Dorsal view (magn. $\times 1.5$). 14. Posterior portion of cephalon, and first four anterior segments, to show flange (f) of second segment (magn. $\times 4$). 16. Posterior three segments and pygidium (magn. $\times 9$). 15. Latex cast of external mould of thoracic segments 1–12, PMO 22984 (magn. $\times 3$); the internal mould was the original of Kiaer (1917, plate 8, figure 10, PMO 22985). 17 and 19. Internal mould of posterior thoracic segments 6–16 and pygidium, PMO 22390, original of Kiaer (1917, plate 8, figure 6). 17. Posterior three segments (14–16) and pygidium, showing doublure d (magn. $\times 10$). 19. Anterior segments, segment 9 excavated to show the doublure d, including the narrow strip below the posterior band (magn. $\times 6$). 18. Internal mould of posterior thoracic segments 14–16, and pygidium, showing doublure d, PMO 22974 (magn. $\times 10$). Original of Kiaer (1917, plate 8, figure 8).

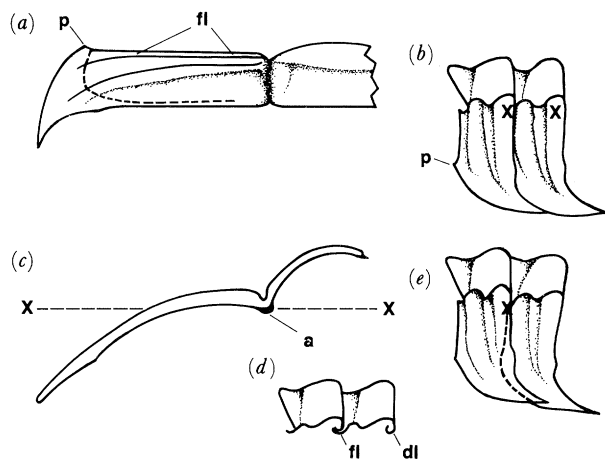


Figure 21. *Paradoxides (Hydrocephalus) carens* (Barrande, 1846). Articulation devices in the thorax of this non-fulcrate trilobite. (a) dorsal view of left half of segment; (b) left lateral view of two segments in the extended position; (c) posterior view of left half of segment; (d) as (b), inner portion of pleura shown in cross-section; (e) left lateral view of two segments in flexed position. a, axial articulating process; dl, cross-section of doublure; fl, flange; p, projection at antero-lateral corner of flange; x, axis of rotation. Dashed line in (a) shows position of inner edge of doublure, in (e) shows anterior edge of pleura.

tened and fractured, retains sufficient convexity to enable an estimate of the original form. That proposed for the cephalon (figure 20) is similar to that suggested for *P. davidis* (Whittington 1988, figure 8). The posterior view (figure 22) shows that the posterior border of the cephalon, and the pleurae, rose steeply from the axial furrow, then curved to slope at first gently, then abaxially more steeply, outward and downward. The inner portion does not appear to have been horizontal, nor is there evidence of a relatively abrupt flexure at a fulcrum, but rather an increasing downward curvature abaxially. The anterolateral portion of the pleura, outside the termination of the pleural furrow, is not flattened into a distinct facet. I regard the pleural spines (figures 22 and 24) as having been splayed out by compaction, and consider that originally they continued the downward slope of the adjacent portion of the pleura (figures 21a, c). Such a form would have been necessary to allow the spines to pass one below the other in enrolment (figure 3). Disarticulated pleurae (figures 26 and 27) reveal the narrow (exs.) flange along the anterior margin of the pleura, the anterior edge of which terminates in a small projection at the base of the pleural spine (figure 21a, b). The flange is concave dorsally, in the form of a groove adaxially that widens and flattens abaxially as it approaches the projection. The inner edge of the doublure of the pleura (figures 21a and 25) curves backward from a point adaxial to the projection, beneath the extremity of the axial furrow, and then continues inward parallel to the posterior margin of the pleura. Thus there was a narrow band of the doublure, convex on the ventral side, along the posterior edge of the pleura. The originals of figures 25–27 show that when the segments were articulated this band of the doublure lay directly above the flange of the pleura

following (figure 21d). It presumably acted as a guide during flexure of the thorax, keeping the pleura in position. Flexure (figure 21e) increased the overlap between the distal portions of the pleurae. The anterolateral projection may have acted as a guide for this overlap. The posterolateral margin of the pleura, behind the extremity of the pleural furrow, curves back to form a slight projection at the base of the pleural spine; this projection may have assisted in keeping the pleurae aligned correctly. The reconstruction (figure 21e) shows a flexure of 10° between adjacent segments, an amount that appears reasonable and is ample to allow enrolment of the entire exoskeleton.

Bergström (1973a, p. 18) cited figured examples of enrolled paradoxidids, and showed the flange and anterolateral projection of the pleura of *P. carens*. The present material shows in more detail the articulating devices of the thorax, including the articulating half ring, which was much longer (sag.) on the first thoracic segment (figure 23) than on those following. The axial furrow descended steeply beside the extremity of the articulating furrow, less steeply at the posterior edge of the axial ring. There was presumably an axial, articulating boss at the anterior edge, a socket at the posterior edge. It is suggested (figure 21b, c, e) that the axis of rotation passed through the articulating boss and along the adaxial portion of the flange. Abaxially the flange widened (exs.) and shallowed, presumably to allow for the downward inclination of the outer portion of the pleura.

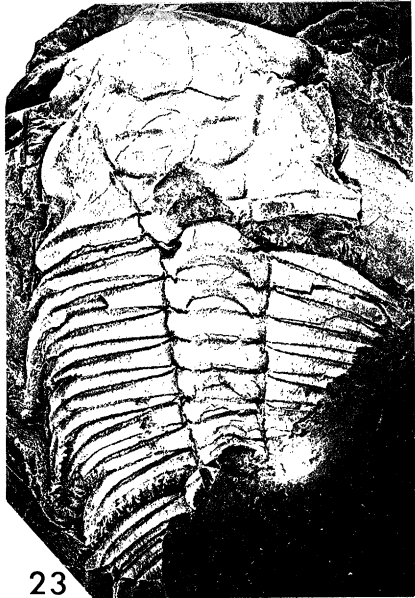
Hydrocephalus carens is the type of Barrande's genus *Hydrocephalus* and the name was brought back into use by Šnajdr (1958). The way in which this, and new generic names of Šnajdr (1958) have been used has varied (Sdzuy 1967, p. 91; Bergström & Levi-Setti 1978, p. 15; Courtessole 1973, p. 122; Dean (in Martin & Dean 1988, p. 18)). Here I have used *Hydrocephalus* as a subgenus.

(ii) *Paradoxides davidis* Salter, 1863 (figures 28 and 29)

This species and its subspecies were described by Bergström & Levi-Setti (1978) and the rostral-hypostomal plate by Whittington (1988). In a portion of the thorax (figure 28) the axis is gently convex, the pleurae having been flattened, and there has been some dislocation between segments and distortion postero-laterally. For convenience, some of the more complete segments on the left side (figure 29) have been lettered consecutively A–F. The specimen, preserved in a muddy concretion, has fragments of the exoskeleton adhering to it, for example on axial ring E, and in pleural furrows E and F. The sculpture of scattered, minute tubercles may be seen on the external surface. Exfoliation of the exoskeleton has resulted in much of the remainder of the exoskeleton being preserved as an internal mould. Dislocation has occurred between segments A–D, and between E and F, so that, for example, the articulating half ring of F has been brought to lie on the external surface of axial ring E. Along the anterior edges of pleurae B, C and D the concave flange has been exposed by the dislocation, and shows a slight angular projection at the distal end. The margin of the posterior band of each pleura swings



22



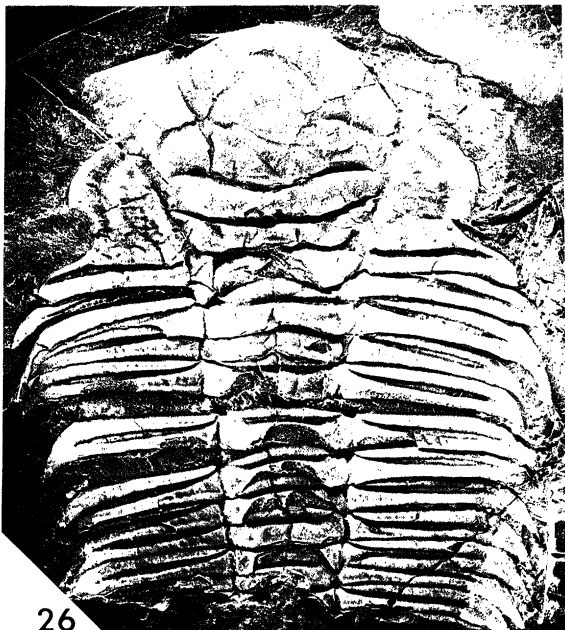
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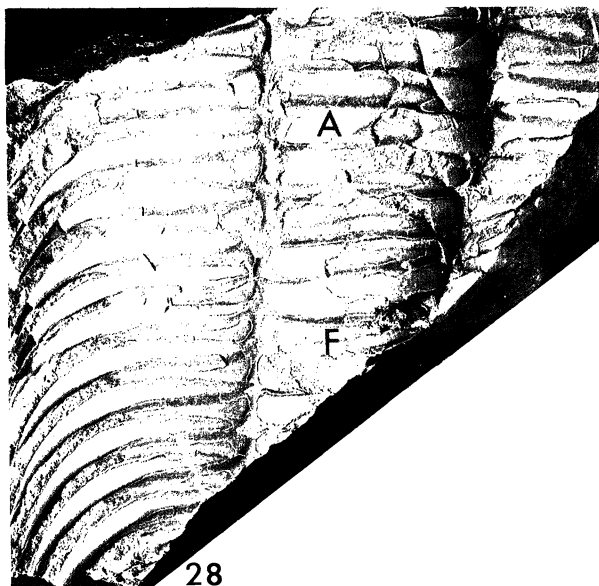


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Figures 22–27. *Paradoxides (Hydrocephalus) carens* (Barrande, 1846). Jince Formation, *Ecca**paradoxides pusillus* Zone, Skryje area, Bohemia; Middle Cambrian. 22–24. Internal mould of cranium and portions of the first twelve thoracic segments, oblique posterior, dorsal, left lateral views (magn. $\times 1$). 25. Left side of first nine segments, dorsal view, fifth segment excavated to show doublure, d, including narrow strip exposed below posterior band of pleura, (magn. $\times 4$); SM A 1546. 26 and 27. Internal mould of cranium and portions of the first eleven thoracic segments, SM A 1345. 26. Dorsal view (magn. $\times 1$). 27. Left pleurae of segments 2–8, the fifth and sixth disarticulated and showing the flange f (magn. $\times 4$).



Figures 28 and 29. *Paradoxides davidis* Salter, 1863, Manuels River Formation, 1.5 miles east of Elliot Cove and north of Foster's Point, Random Island, Newfoundland; Middle Cambrian, SM A 105191. 28. Portion of thorax, exfoliated, fragments of exoskeleton adhering in furrows, dorsal view, (magn. $\times 1$). 29. Left pleurae of segments A–F, disarticulation reveals the flanges on segments B to F (arrowed); flange of E overlain distally by posterior band of D, magn. $\times 4$.

back distally, then forward to the base of the pleural spine. This slight projection in segment D overlies the flange of segment E, which is exposed by exfoliation in the adaxial portion of segment E. The dislocation between segments E and F has not only brought the

articulating half ring of F to lie on the axial ring E, but also brought the flange (as seen abaxially) to lie above the posterior band of E. As Bergström and Levi-Setti noted (1978, p. 9), there was no fulcrum in *P. davidis*, but a progressive downward curvature abaxially, a

cross-section like that portrayed for *P. carens* (figure 21*c*). It appears that the articulating devices in these two species were similar.

(iii) *Paradoxides davidis trapezopyge* Bergström & Levi-Setti, 1978 (figures 7 and 8)

This specimen, originally figured by McNamara & Rudkin (1984, fig. 12), has the relatively broad, backward-widening pygidium characteristic of the subspecies. Only the counterpart is available, an external mould of cranium, thorax and pygidium, with which are associated the free cheeks, inverted and backward-facing with respect to the rest of the exoskeleton. Because it is an external mould of the dorsal exoskeleton, the left free cheek of the animal is on the right side of the specimen (and vice versa), orientations reversed by McNamara & Rudkin (1984, p. 168). In this account left and right refer to the original directions in the animal and not to those shown in figures 7 and 8. The external mould of the dorsal exoskeleton shows the scattered, minute granules of the external surface, and moulds of the terrace lines on the pleural spines. The left free cheek is preserved as an external mould of the doublure, and an internal mould of the genal field; the right free cheek is similarly preserved, but has fragments of the exoskeleton adhering posterolaterally. The moulds of right thoracic pleurae 1–3 lie nearer to the observer (figure 7) than does the mould of the cranium, and the mould of the right free cheek, together with the fragments of the rostral-hypostomal plate (figure 8), lie nearer to the observer than the mould of the thorax. In this configuration, therefore, the cranium had been pushed back to lie on the dorsal side of the anterior three thoracic segments. The free cheeks and rostral-hypostomal plate, however, were inverted to lie on the ventral side of the thoracic exoskeleton.

Right thoracic pleurae 1–5 are not displaced from one another, and 1–3 lie on the mould of the posterior portion of the right fixed cheek. Right pleurae 4 and 5 continue into axial rings 4 and 5, which lie immediately behind the occipital ring. To the left of the midline, axial rings 4 and 5 appear to be curved backward, and outside them are portions of left pleurae. The most complete of these lies diagonally across the dorsal side of left pleurae 5 and 6 (figures 7 and 8). The remainder of the thorax (segments 6–20) and pygidium are articulated together with only slight displacement, and almost complete.

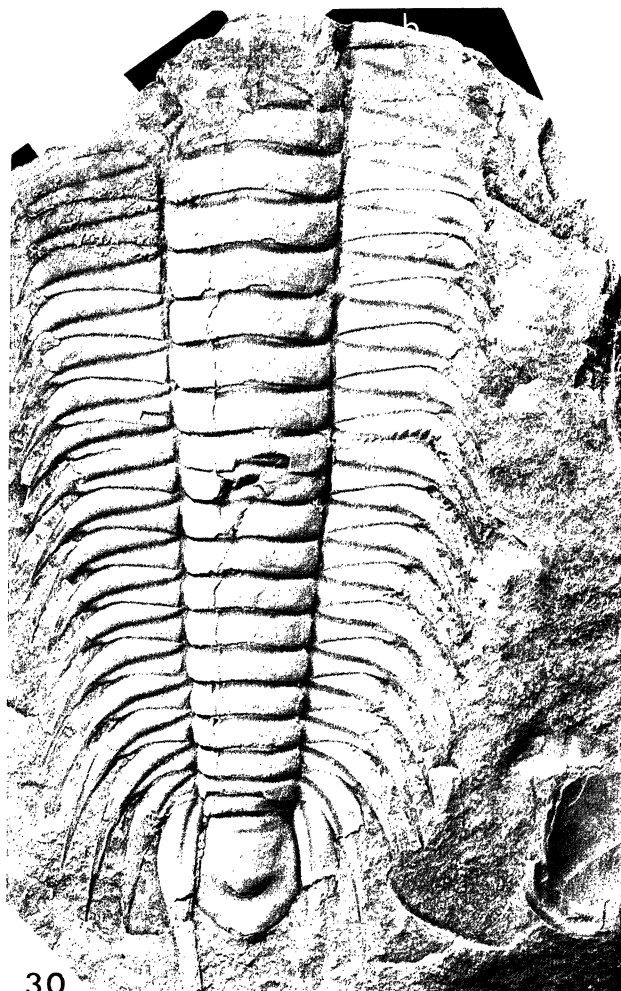
The posterior portion of the inverted right free cheek lies on the moulds of right pleurae 4–6, the dorsal exoskeleton preserved, the genal spine directed forward beside the cranium. Portions of the broad anterior doublure of the cheek, traversed by well-spaced terrace ridges, lie on the tips of pleurae 6–10 (figure 8). The inverted left free cheek lies immediately adjacent to the cranium and segments 1–10, the dorsal exoskeleton of the genal field preserved. The adaxial edges of this field are formed by the curved outline of the base of the eye lobe, and the sections of the facial suture. The external mould of the broad lateral doublure, with terrace ridges, is cut off anteriorly by the connective suture. Lying on the inner surfaces of right and left

pleurae 11–13 are fragments of an external mould impressed by strong, well-spaced terrace ridges (figure 8). I consider that these are impressions of parts of the rostral-hypostomal plate, which bore such terrace ridges (see also Whittington 1988, plate 53, figures 1–3 and 8). The curving lines of terrace ridges on the right distal fragments are similar to, but not aligned with, the curving lines on the free cheek doublure. I regard these as terrace ridges of the rostral plate. Adjacent to where this plate is fused with the hypostome, terrace lines on the latter run at right angles (see Whittington 1988, plate 53, figure 3). In the present specimen, the fragment of the mould on right pleura 13, adjacent to the axial furrow, shows terrace lines similarly disposed. The fragments beneath left pleurae 12 and 13 are probably impressions of a portion of the rostral plate close to its junction with the hypostome. McNamara & Rudkin (1984, p. 168) noted these fragments, but considered them to be part of the doublure of the free cheek. The course of the sutures in *P. davidis* (Whittington 1988, figure 8) precludes this interpretation, the left free cheek not being broken anteriorly, but showing the sutural boundary. I thus conclude that the rostral-hypostomal plate was present in this specimen, inverted and backward-facing relative to the cranium and thorax, detached from the free cheeks and slightly displaced relative to them.

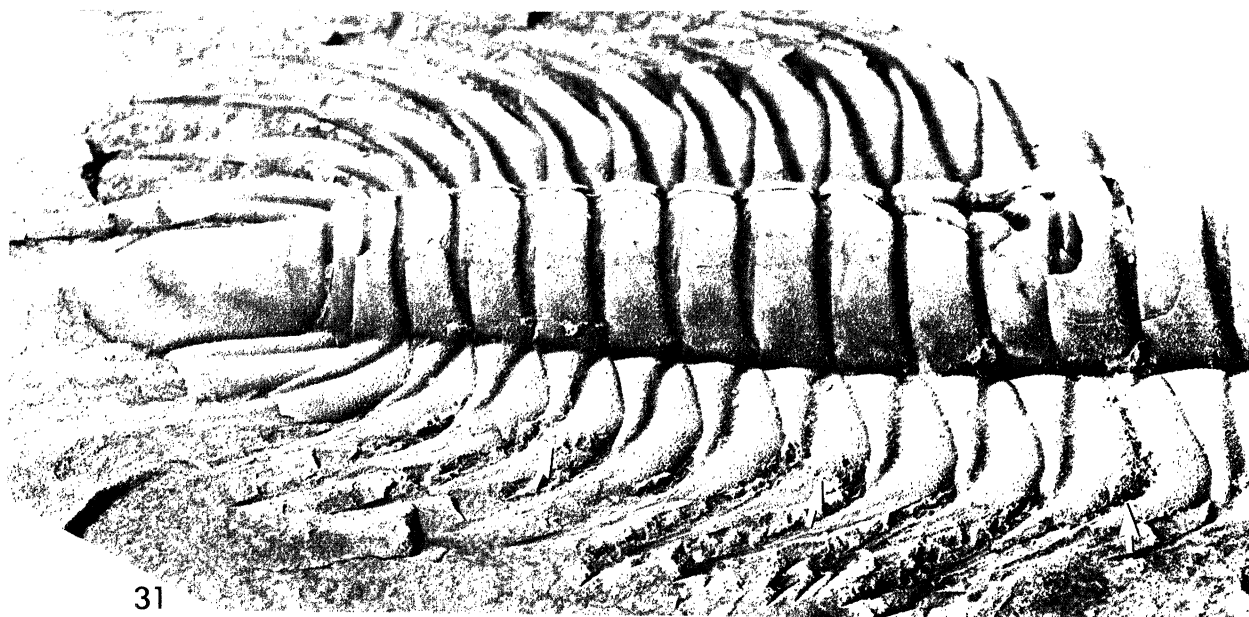
(iv) *Paradoxides gracilis* (Boeck, 1827) (figures 30, 31)

This species was described by Šnajdr (1958). The present specimen shows the complete thorax of 20 segments and the pygidium, the last segment having a long, posteriorly directed pleural spine. Like the specimens figured by Šnajdr, it has been flattened so that the convexity of the axial region was reduced, and pleurae and pleural spines are horizontal. The axial furrow was deepest beside the anterior and posterior margin of the axial ring, and there was presumably an axial articulating boss and socket. The pleura is parallel-sided, the posterior margin curving back abaxially, then swinging forward at the base of the pleural spine. A slight backward projection was thus formed at the outer end of the posterior pleural band. Excavation of this band of right pleura 9 (figure 31) has revealed the relatively wide (exs.) flange of pleura 10, defined by a downward flexure at the posterior margin, and having an angular projection at the anterolateral corner. This projecting angle of the flange lay beneath the backward projection of the posterior band of the next pleura. Excavation of right pleurae 13 and 16 has revealed the curved inner margin of the doublure, situated beneath the extremity of the pleural band. Where the posterior band of left pleura 8 and 9 is broken (figure 30), a portion of the flange of pleura 9 and 10 is exposed. The inner margin of the doublure has been exposed in left pleurae 10 and 19, and the narrow (tr.) flange of backwardly directed left pleura 20.

There is no evidence of fulcrum or facet in the pleurae of *P. gracilis*, and it seems probable that the pleurae, after rising steeply from the axial furrow, sloped downward abaxially, gently proximally and more steeply distally. Articulation between them was



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Figures 30 and 31. *Paradoxides gracilis* (Boeck 1827), Jince Beds, Jince, Bohemia; Middle Cambrian. PMO 15098. 26, internal mould of right posterior border (b) of cephalon, thorax and pygidium; g indicates mould of lower surface of genal spine, dorsal view, (magn. $\times 1.5$). 27, right oblique view of portion of thorax and pygidium, (magn. $\times 3$); flange of segment 10 and internal margin of doublure of segments 13 and 16 arrowed.

facilitated by the flange and its distal projection. It has not proved possible to reveal the doublure beneath the posterior band. The relatively broad (exs.), flat flange (resembling that of *Olenellus* (Whittington 1989, figure 19, plate 3)) contrasts with the narrow, concave flange in *P. carens* and *P. davidis*, but the form of the pleurae is similar. In *P. davidis*, as in *P. gracilis*, the last pleura of the thorax is backwardly directed, and a long (exs.) lateral facet on the pygidium facilitates articulation (see Dean, in Martin & Dean (1988, plate 4, figures 13–15, for an illustration of this facet in *P. davidis*). In the present specimen of *P. gracilis*, in dorsal view the boundaries between successive pleurae are directed forward and outward, so that at the base of the pleural spine the boundary lies transversely opposite the middle of the next anterior axial ring. Some, but not all, the larger specimens illustrated by Šnajdr (1958) have this appearance. Bergström & Levi-Setti (1978, p. 9) commented on this same appearance in flattened specimens of *P. davidis*, and it is evident in many (but not all, e.g. their plate 10, figure 7) of their illustrations. This outward and slightly forward direction of boundaries between pleurae appears to be an effect of compaction, and not original. Articulation would have been more effective between pleurae having transversely directed boundaries.

(c) **Family Ogygopsidae Rasetti, 1951**
Genus Ogygopsis Walcott, 1889

(i) *Ogygopsis klotzi* (Rominger, 1887) (figures 9–12)

In his description of this species, Rasetti (1951) stated that the rostral plate and hypostome were fused, and placed the genus in a separate family, because of characters of the hypostome. His subsequent diagnoses (in Moore 1959, p. O219) of family and genus are equivocal with respect to whether or not the rostral plate and hypostome were fused; here I accept that there was a rostral-hypostomal plate.

McNamara & Rudkin (1984) described two specimens, the first (figures 9 and 10) is a mould of the internal surface of the axial shield, to which cling fragments of a black layer in which the exoskeleton is preserved. On the anterior border of the cranidium, and the pygidial border, fine anastomosing terrace lines, directed subparallel to the margin, are preserved on the surface of the black layer. Remains of the free cheeks, in correct relative position to each other, lie beneath the pleurae of the thorax, inverted so that the genal spine is directed forward beside the posterior portion of the fixed cheek. The postero-lateral portions of the free cheeks have scraps of the black layer clinging to them, and show that each cheek is inverted, preserved as a faintly concave external mould in which is impressed the anastomosing terrace lines. The specimen has been strongly flattened, and the overlapping portions of the exoskeleton pressed into one another. It is therefore difficult to discern whether the posterolateral portion of the cheek lies upon, or below, pleurae 1–6. On balance I conclude it lies below, and the curving anterior portion of the border extends below pleurae 7 and 8 (figure 10). On the right side, adjacent to the axial furrow and below pleura 8, is a parallel-sided fragment bearing terrace lines, which

might be the external mould of the extremity of the rostral plate.

The second specimen (figures 11 and 12) is an external mould of the axial shield, showing impressions of the fine terrace lines around the margins. Beneath the impressions of right pleurae 1–8 is the poorly preserved right free cheek inverted so that the genal spine is directed forward beside the posterior portion of the fixed cheek. The posterior portion of the right free cheek is preserved as an internal mould, a fragment of a black exoskeletal layer clinging to the border shows the characteristic terrace lines. The anterior portion of the border is preserved as a groove, the external mould of the doublure. Adjacent to the axial furrow, beneath right pleurae 2–8 (figure 12), is a poorly preserved curved structure which is the size and shape of the rostral plate. If this assumption is correct, the plate has been rotated through 180°, the width (tr.) lying in an exsagittal line. The groove between the posterior margin of the plate and the hypostome is faintly outlined. A gently convex posterior portion of the internal mould of the left free cheek, aligned transversely, underlies left pleurae 1–4. It has a fragment of the black exoskeletal layer preserved at the base of the genal spine, which bears the fine, anastomosing terrace lines. This specimen, like 41791, has been strongly flattened.

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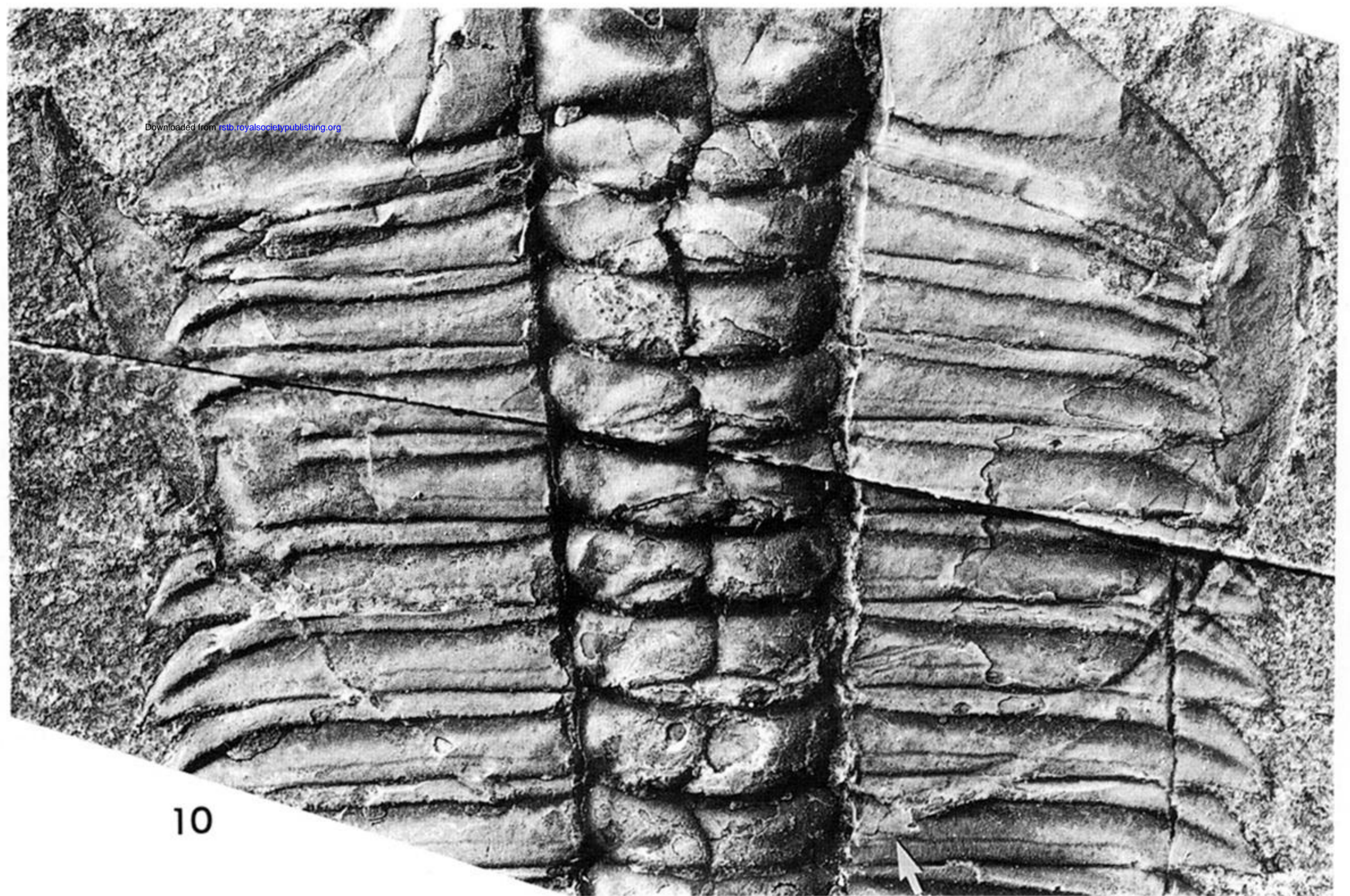
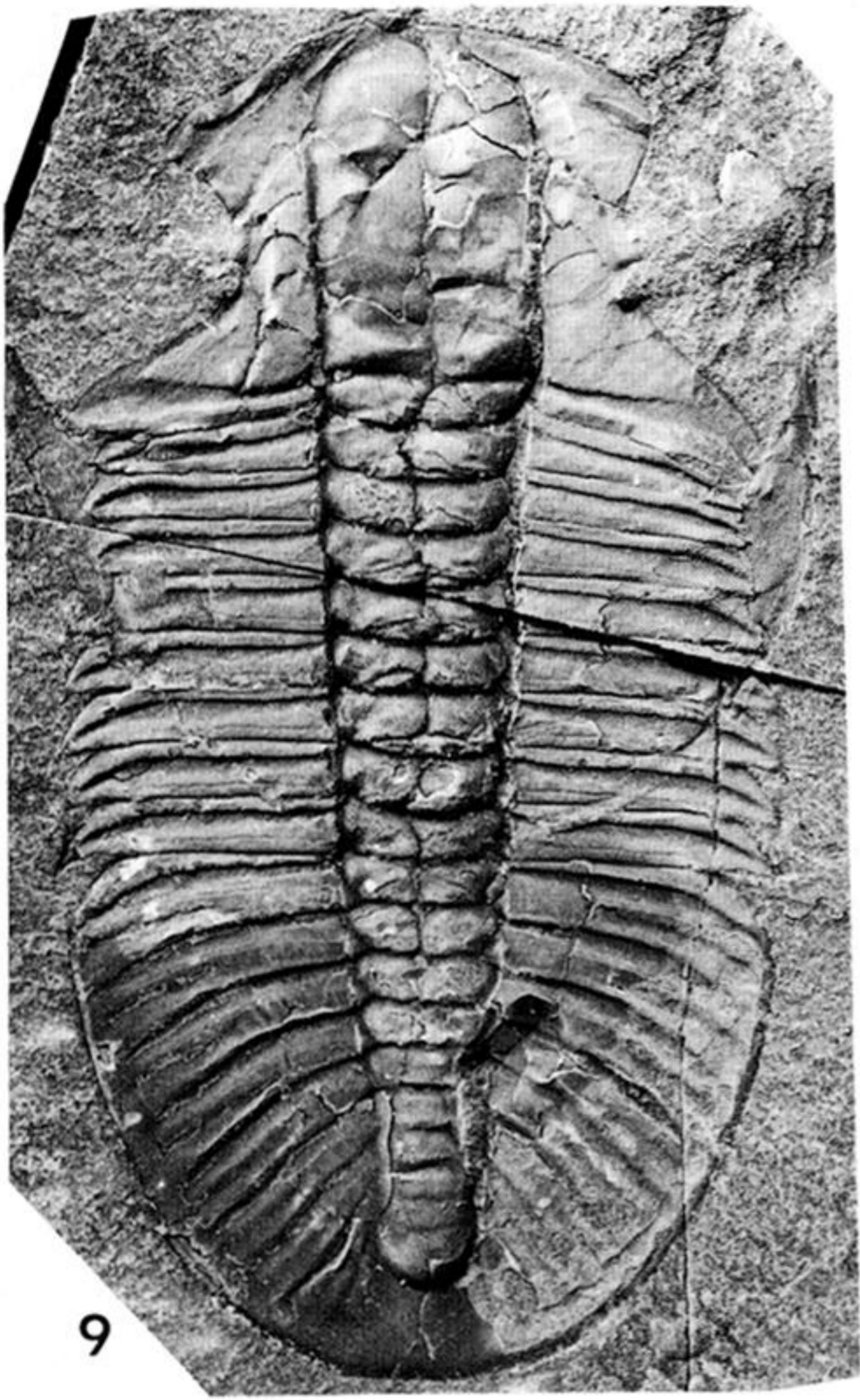


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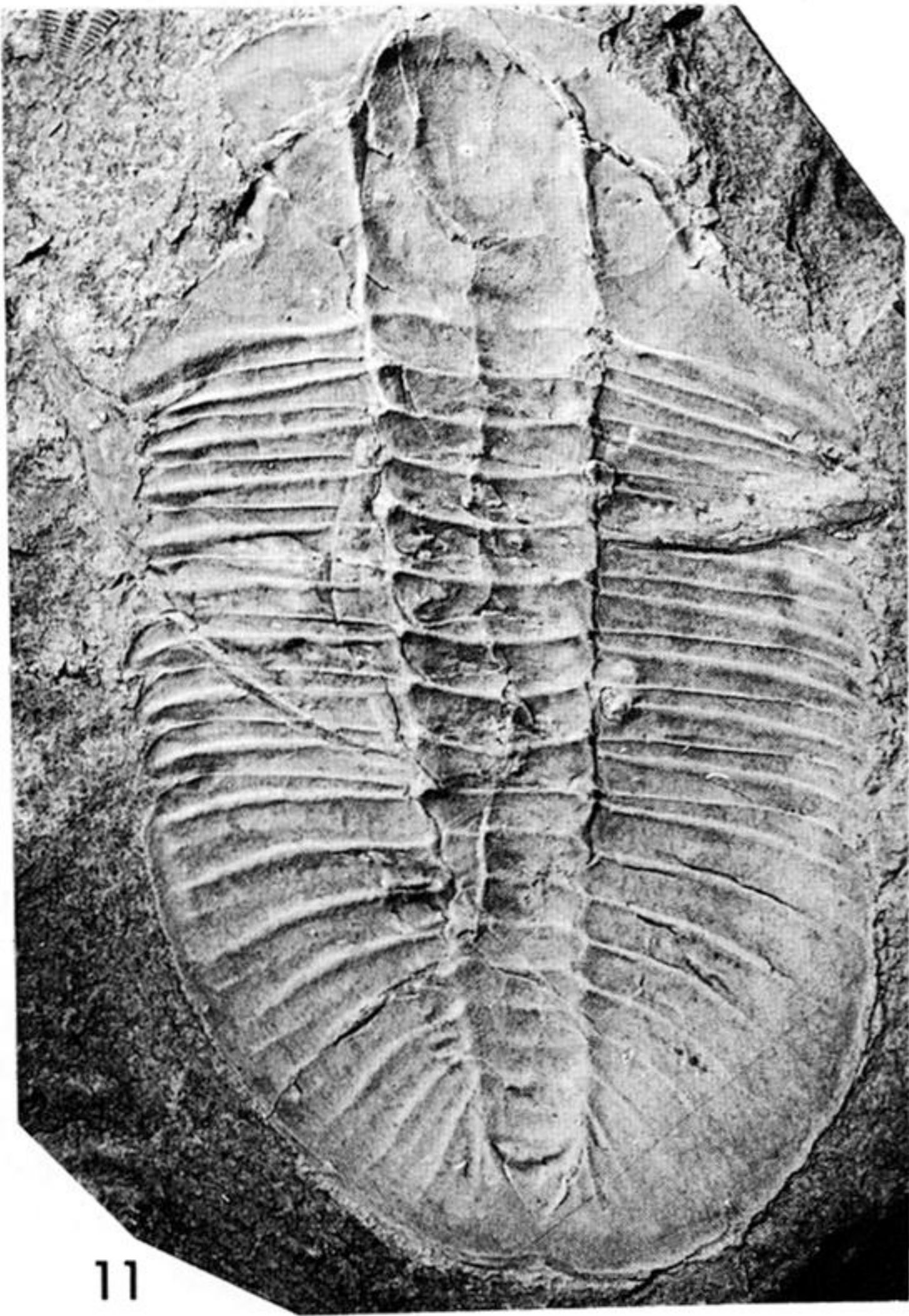


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Figures 7 and 8. *Paradoxides davidis trapezopyge* Bergström & Levi-Setti, 1978 east bank of Manuels River, at Manuels, southeastern Newfoundland, from level 241–278 cm of Bergström & Levi-Setti (1978, figure 1); Middle Cambrian, ROM 41741. Original of McNamara & Rudkin (1984, figure 12). 7. External mould of dorsal exoskeleton, thoracic segment 5 numbered, magn. $\times 0.75$. 8. Portions of thoracic segments 3–16, and anterior portions of inverted free cheeks, showing anterior section of suture (s) and fragments of external mould of rostral-hypostomal plate (r) adhering to segments 12–14 (magn. $\times 2$).



Figures 9 and 10. *Ogygopsis klotzi* (Rominger, 1887), Stephen Formation, northwest flank of Mount Stephen, the famous 'fossil bed' (Rasetti 1951, p. 42; locality S8d, p. 128 and locality 1, p. 192); Middle Cambrian. ROM 41791, original of McNamara & Rudkin (1984, figure 9A). Internal mould of axial exoskeleton, respectively entire (magn. $\times 1$); enlargement showing inverted free cheeks and possible fragment of rostral-hypostomal plate (arrowed) beneath thorax (magn. $\times 2.5$).

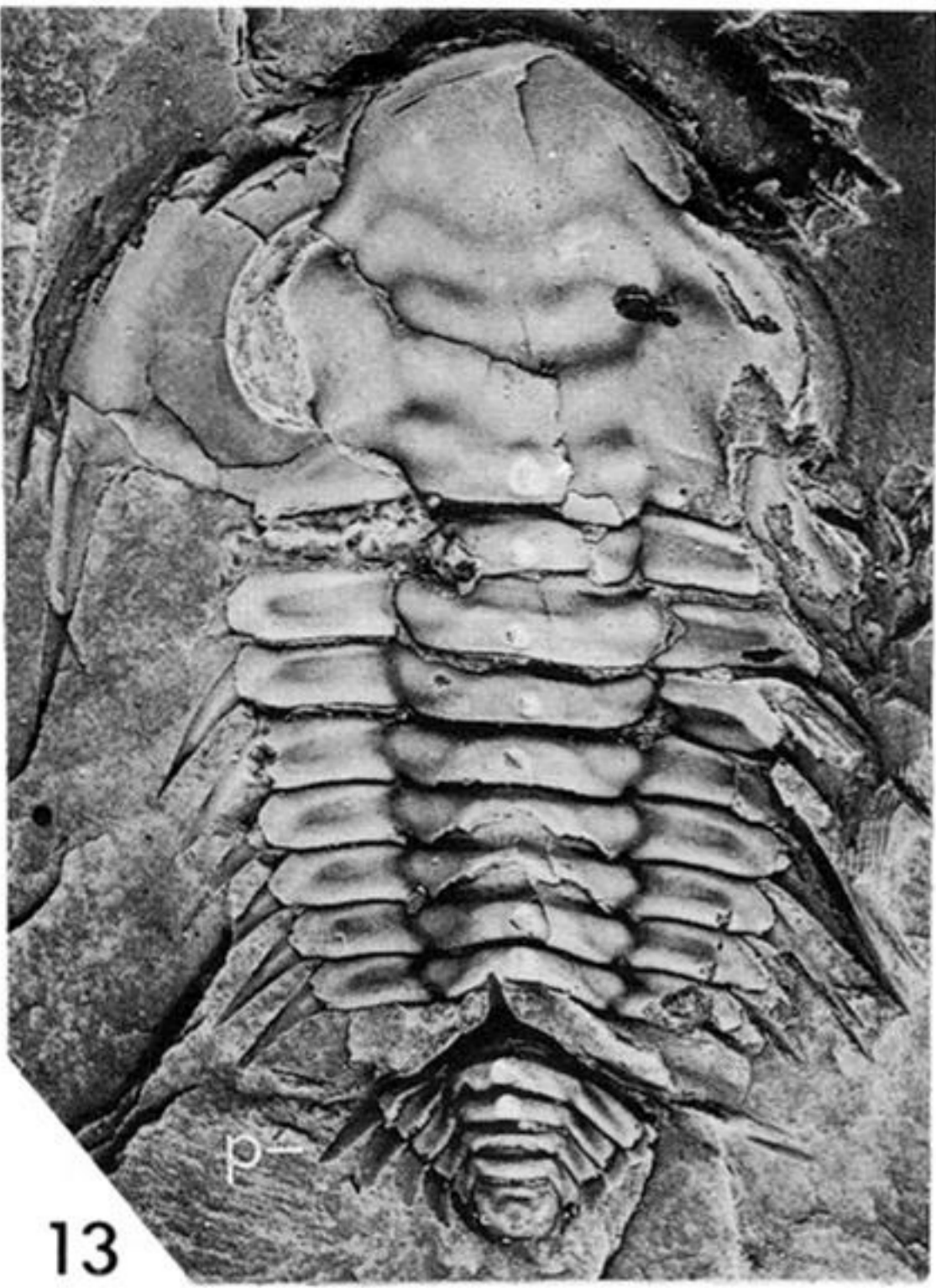


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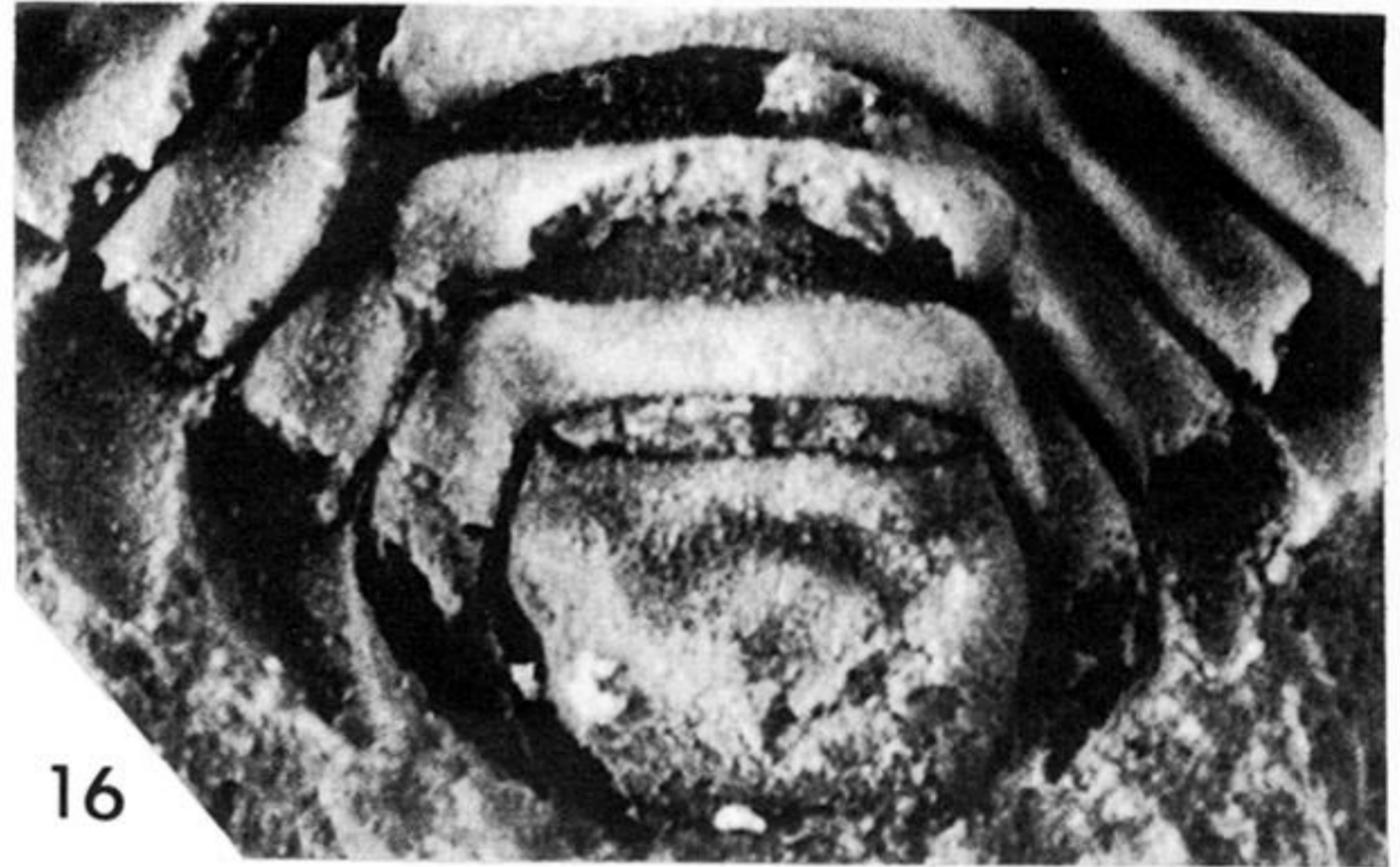
Figures 11 and 12. *Ogygopsis klotzi* (Rominger, 1887), locality and formation as figures 9 and 10. ROM 41876, original of McNamara & Rudkin (1984, figure 9B (printed in reverse)). External mould of axial exoskeleton, respectively, entire (magn. $\times 1$); enlargement showing inverted left (L) and right (R) free cheeks and anterior edge of rostral-hypostomal plate (r) beneath thorax (magn. $\times 2.5$).



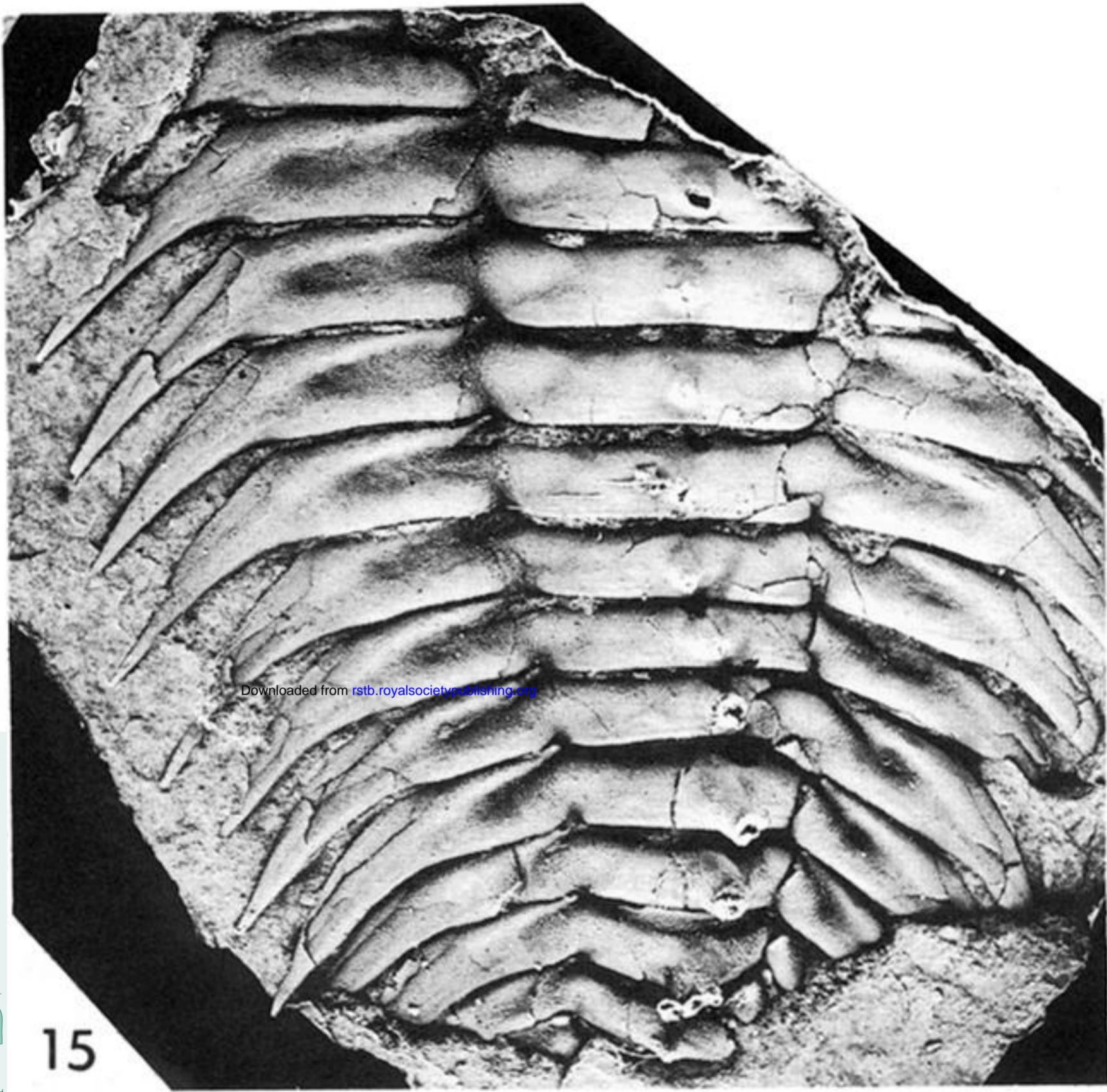
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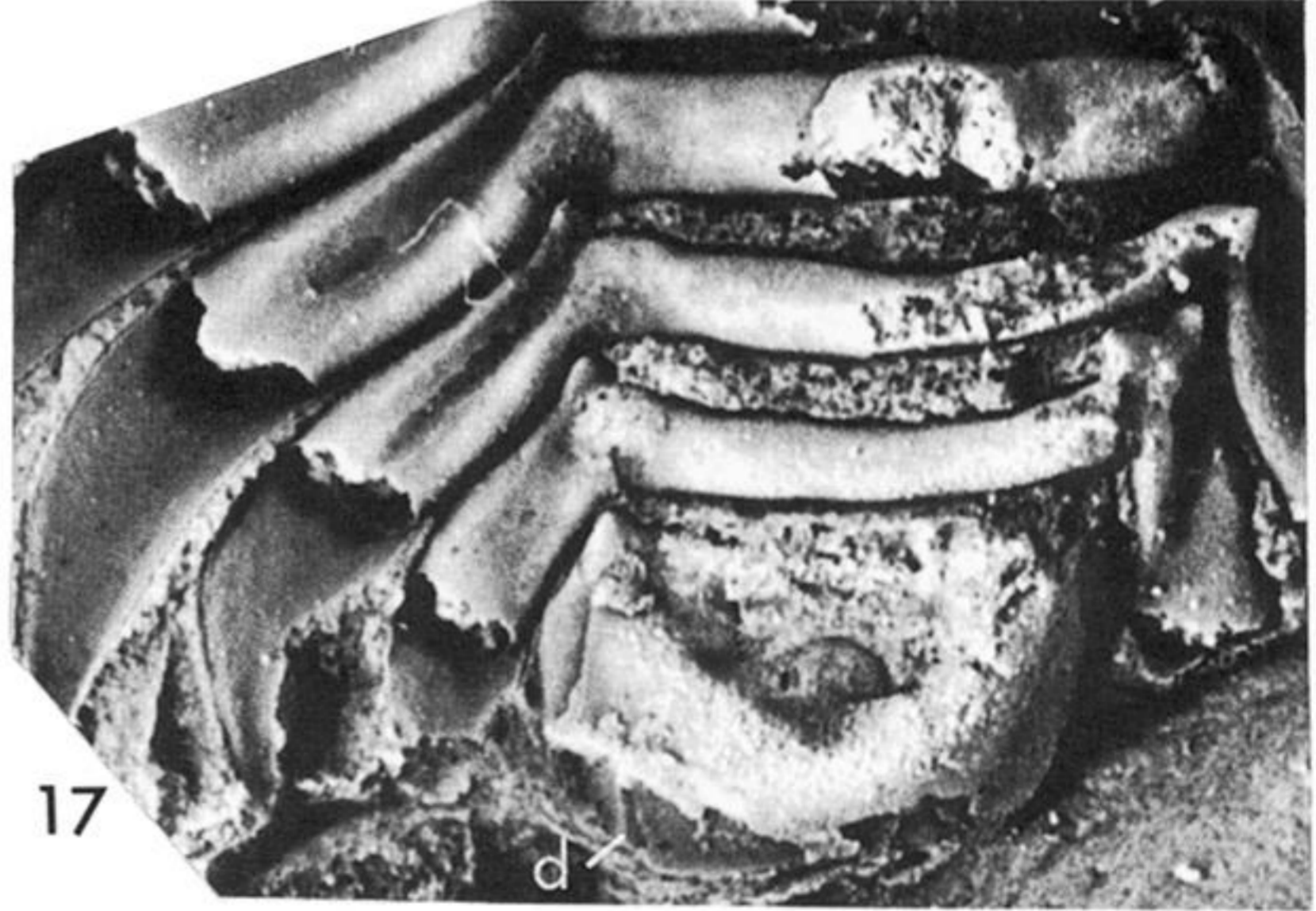
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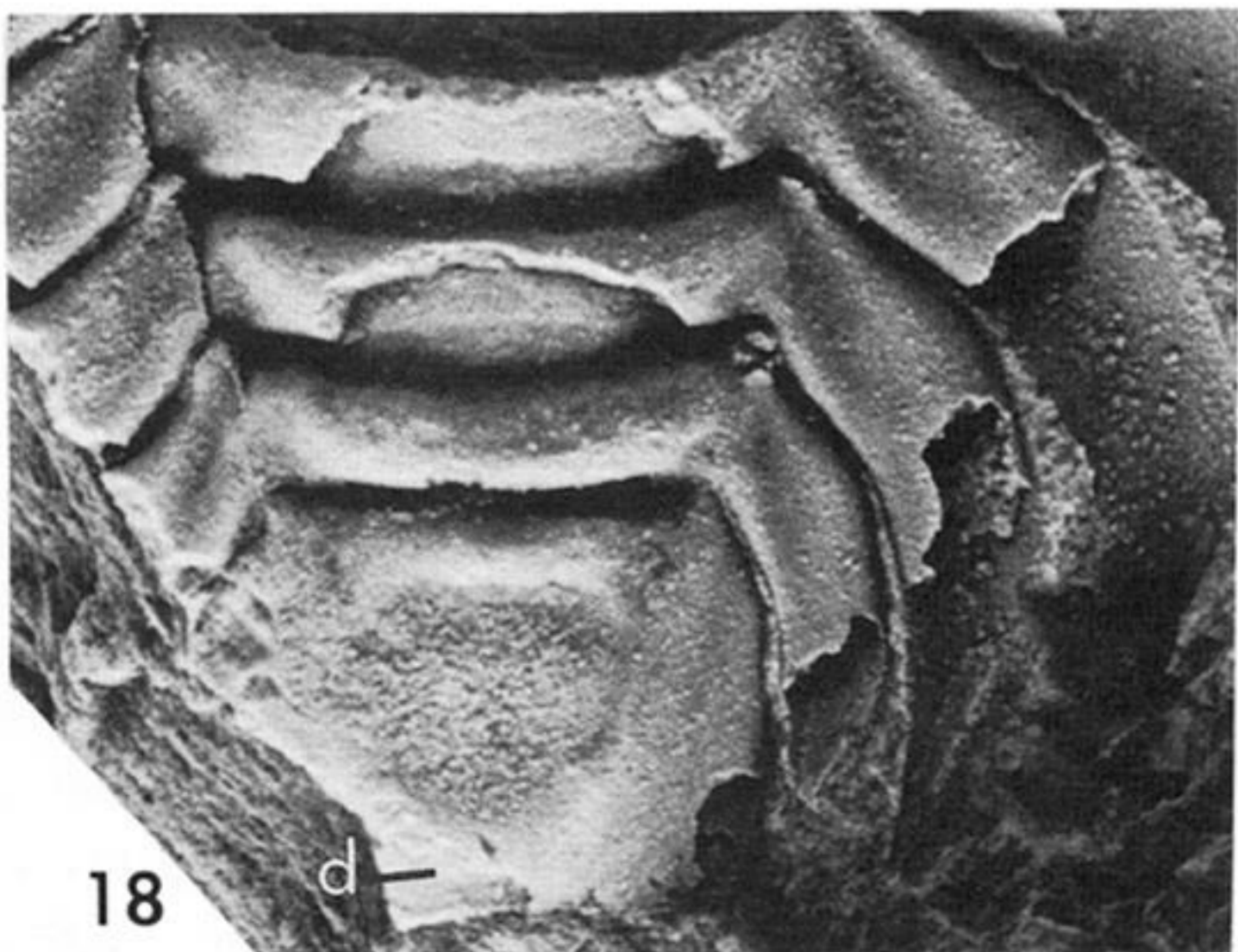
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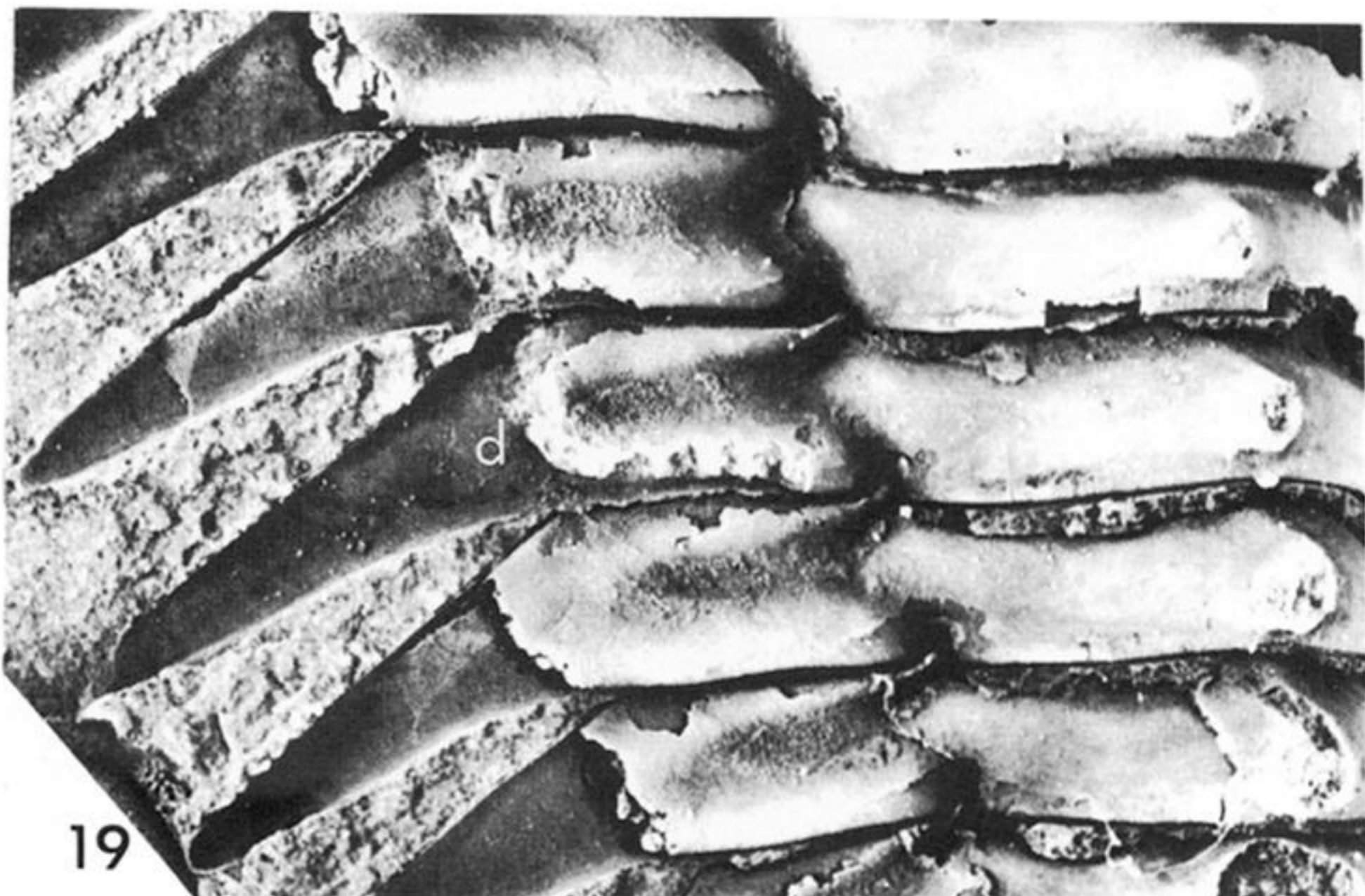
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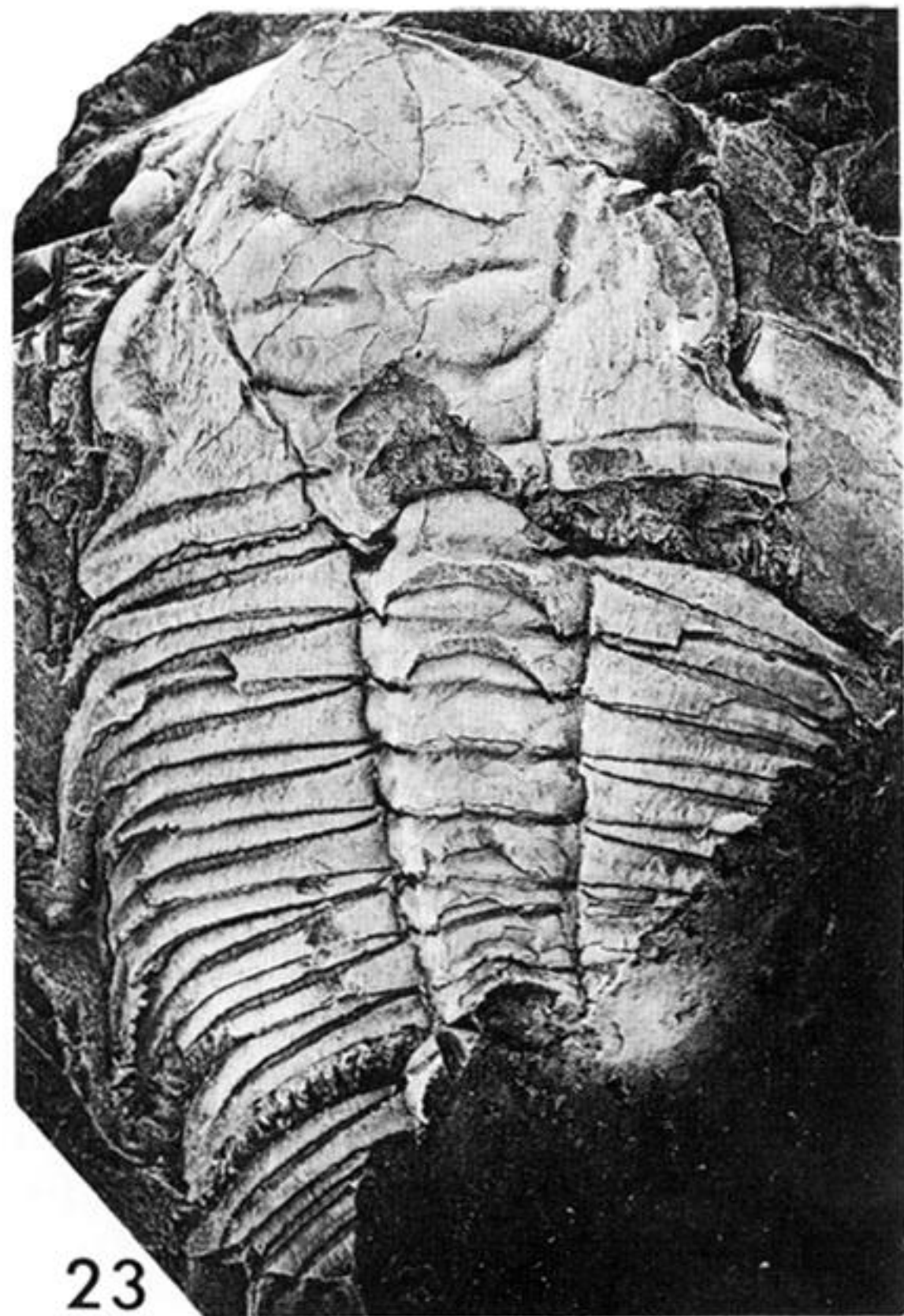


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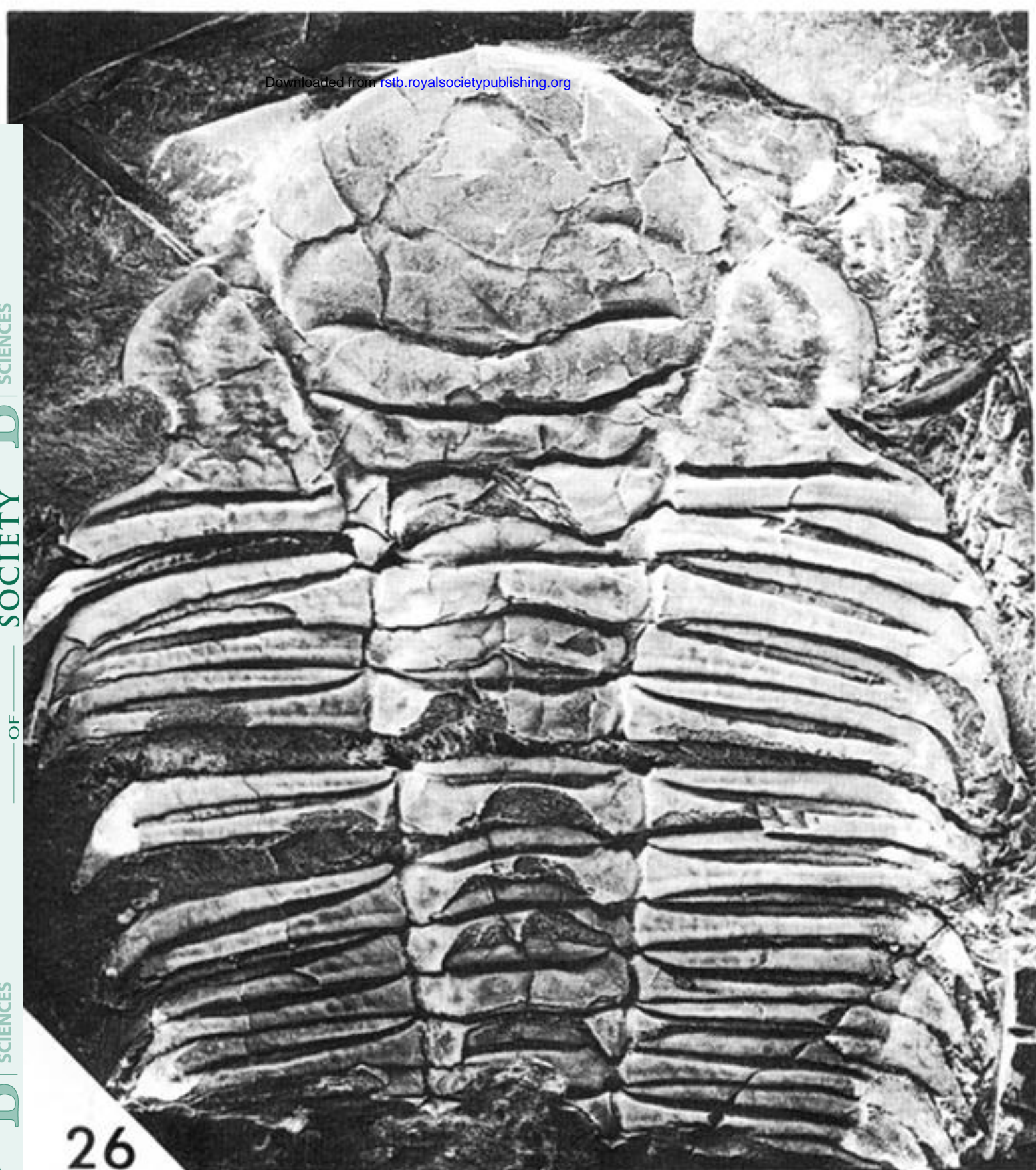
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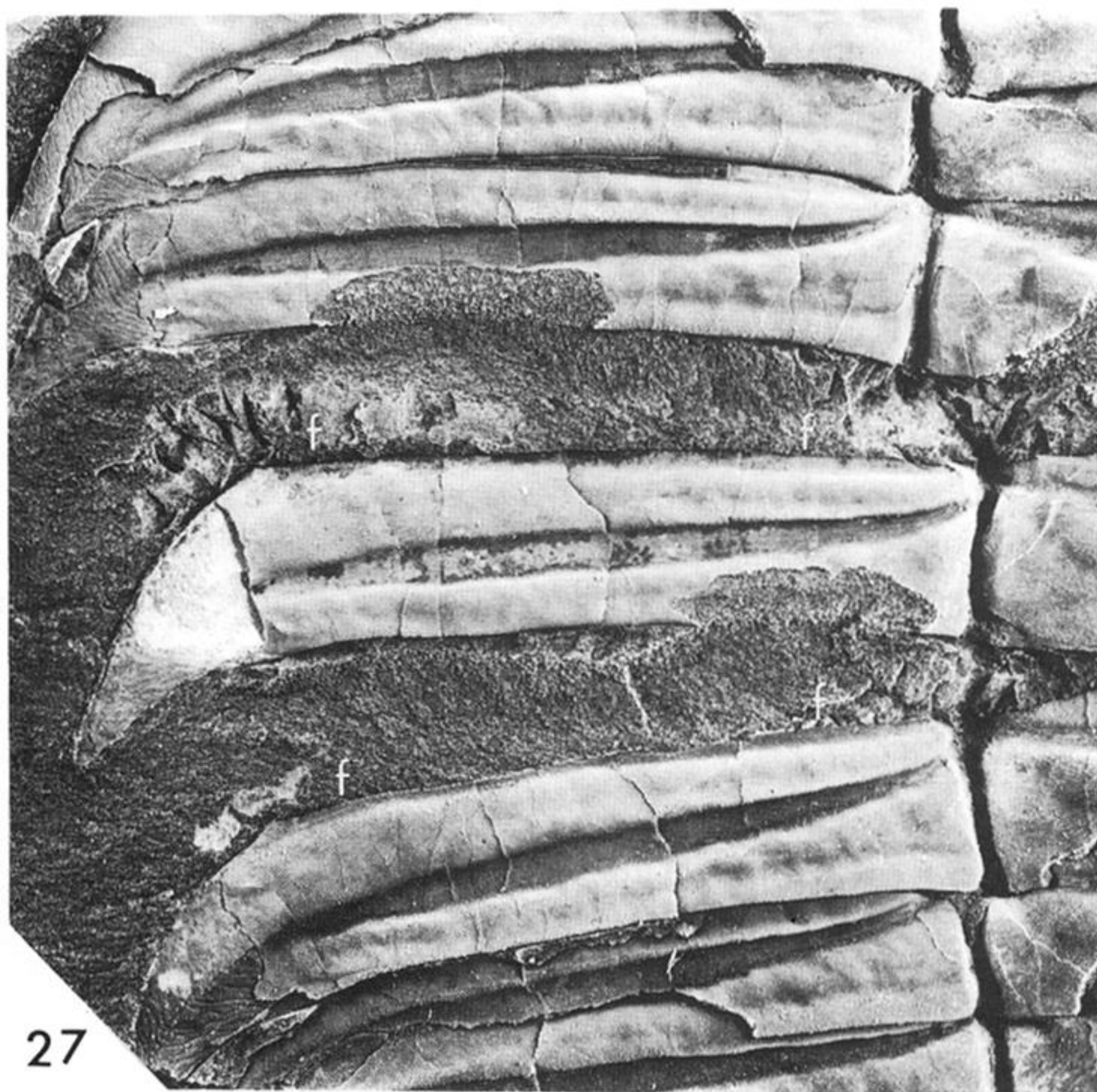
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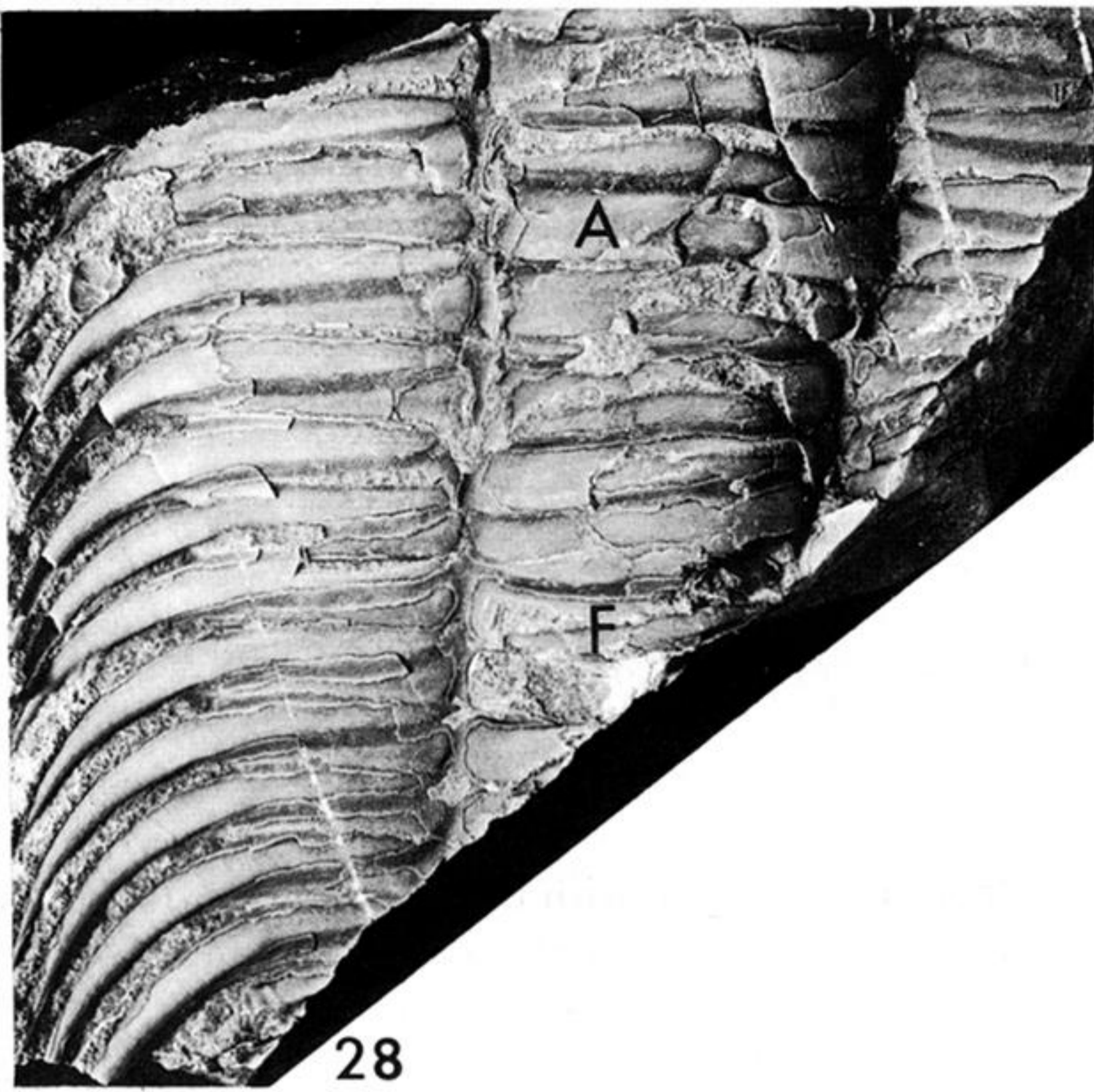


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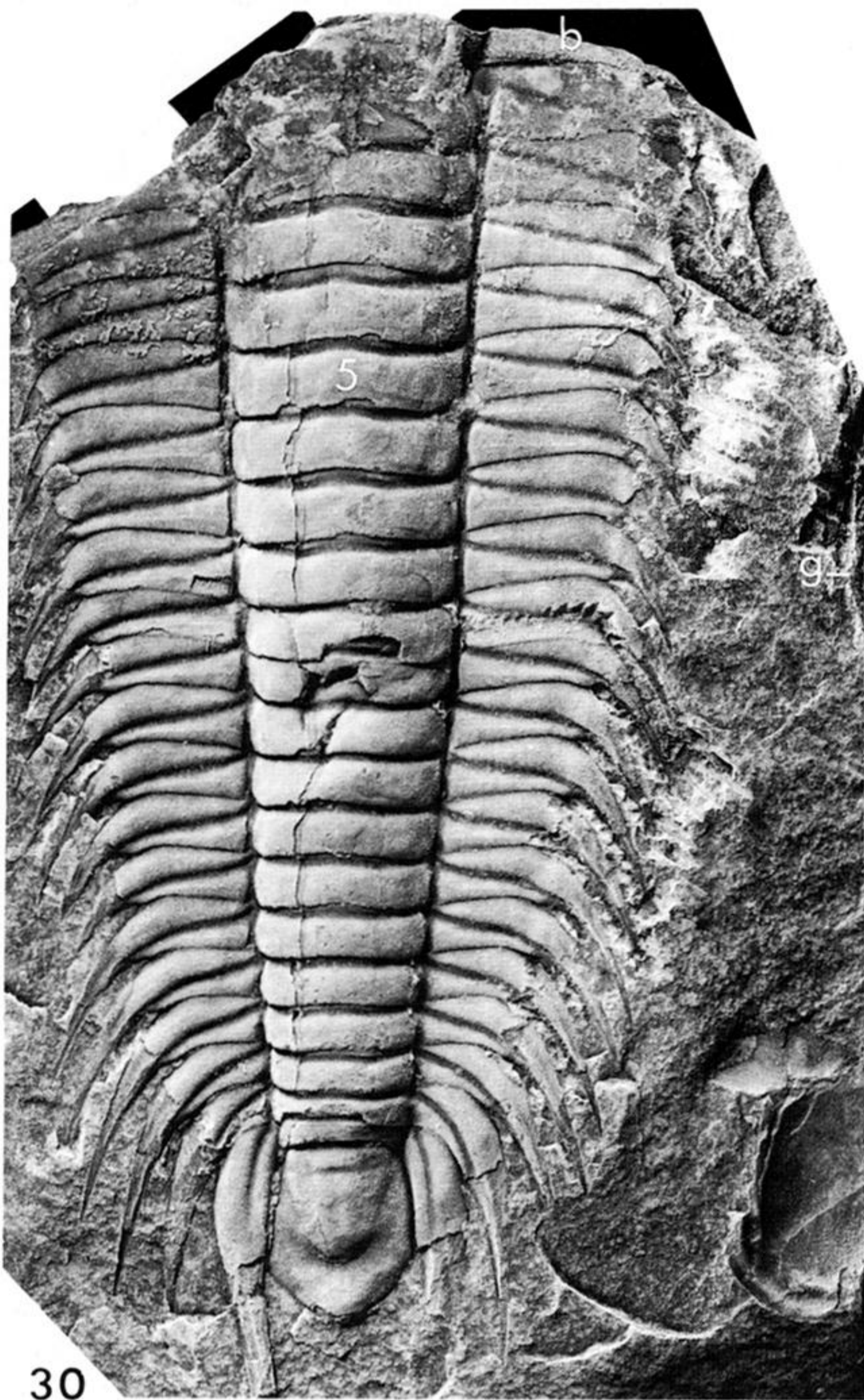


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Figures 22–27. *Paradoxides (Hydrocephalus) carens* (Barrande, 1846). Jince Formation, *Eccaparadoxides pusillus* Zone, Skryje area, Bohemia; Middle Cambrian. 22–24. Internal mould of cranium and portions of the first twelve thoracic segments, oblique posterior, dorsal, left lateral views (magn. $\times 1$). 25. Left side of first nine segments, dorsal view, fifth segment excavated to show doublure, d, including narrow strip exposed below posterior band of pleura, (magn. $\times 4$); SM A 1546. 26 and 27. Internal mould of cranium and portions of the first eleven thoracic segments, SM A 1345. 26. Dorsal view (magn. $\times 1$). 27. Left pleurae of segments 2–8, the fifth and sixth disarticulated and showing the flange f (magn. $\times 4$).

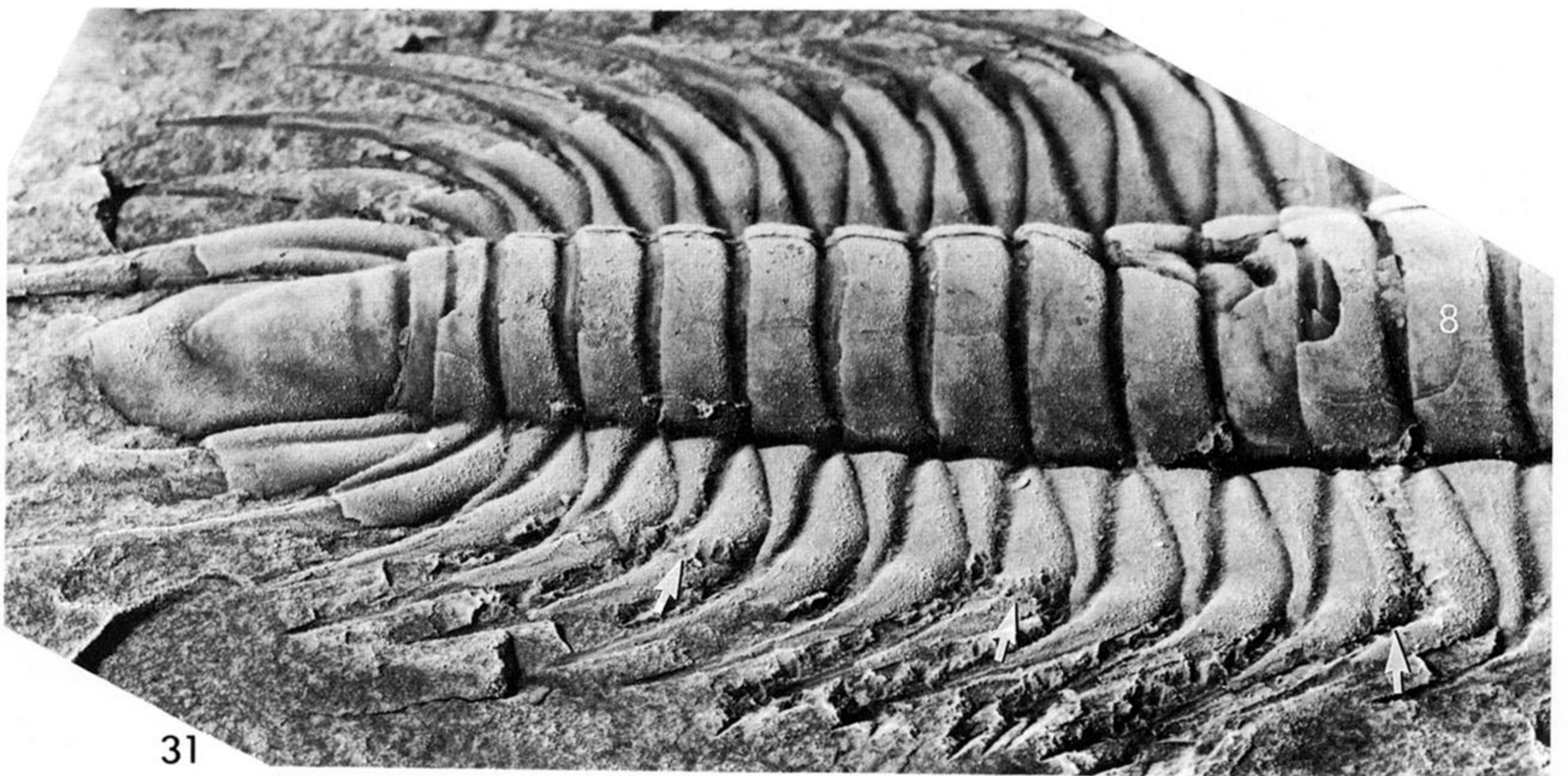


Figures 28 and 29. *Paradoxides davidis* Salter, 1863, Manuels River Formation, 1.5 miles east of Elliot Cove and north of Foster's Point, Random Island, Newfoundland; Middle Cambrian, SM A 105191. 28. Portion of thorax, exfoliated, fragments of exoskeleton adhering in furrows, dorsal view, (magn. $\times 1$). 29. Left pleurae of segments A–F, disarticulation reveals the flanges on segments B to F (arrowed); flange of E overlain distally by posterior band of D, magn. $\times 4$.



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Figures 30 and 31. *Paradoxides gracilis* (Boeck 1827), Jince Beds, Jince, Bohemia; Middle Cambrian. PMO 15098. 26, internal mould of right posterior border (b) of cephalon, thorax and pygidium; g indicates mould of lower surface of genal spine, dorsal view, (magn. $\times 1.5$). 27, right oblique view of portion of thorax and pygidium, (magn. $\times 3$); flange of segment 10 and internal margin of doublure of segments 13 and 16 arrowed.