Anatomy of the Ordovician Trilobite Placoparia

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SUMMARY

A recently discovered specimen of *Placoparia (Placoparia) cambriensis* in shale from Lower Llanvirn rocks of South Wales has the antennae preserved, but more remarkably a partial infilling of the alimentary canal and traces of intersegmental bars and the coxa-body junction. The exoskeleton is reconstructed, including the previously unremarked ridge on the articulating half ring of the thoracic segments and pygidium. Building on earlier ideas and on descriptions of living arthropods, musculature in the extended and fully enrolled positions is suggested, and its operation in enabling the animal's activities.

1. INTRODUCTION

The specimen described herein is the first trilobite from Britain to have the remains of soft parts preserved. These include the antennae projecting forward in front of the exoskeleton, and a filling of a portion of the alimentary canal. What is unique is the preservation of transverse structures, bars made up of several slim rods, situated close to the intersegmental boundaries in the axial region, below the alimentary canal. These may be the remains of tendinous bars to which muscles were attached, bars which have been inferred to be present across the ventral side of the trilobite body, but not previously found preserved in this way. Between the bars are a pair of cylindrical cavities directed vertically downward, which I assume may be the hollow remains of the basal portion of biramous limbs. These features, and the mould of the hypostome below the cephalon, were exposed when the specimen was collected. The right antenna, and the margins of the thoracic exoskeleton, were revealed by subsequent preparation. Further preparation of the soft shale was not attempted, for fear of irreparable damage to features already visible.

Placoparia (Placoparia) cambriensis is a characteristic species from rocks of high Arenig and Llanvirn age in western Europe, and many specimens of the exoskeleton have been described and figured, and a special study made of enrolment in this and allied species. The exoskeleton of *Placoparia* being well known, and now something of the soft parts, I have reviewed earlier ideas on musculature in trilobites and other aspects of anatomy. Biramous limbs like those known in other trilobites are assumed to have been present in *Placoparia*. The nature and arrangement of the musculature, and other features of the anatomy suggested, may well be generally true of other pliomerids, and of other families of trilobites currently placed in the Order Phacopida, all of which had the hypostome firmly attached and braced against the rest of the cephalic exoskeleton. Indeed, more distantly related trilobites which had a convex axial region with transverse furrows, and a peripherally down-curved

pleural region, may have been anatomically similar. Soft parts are not known in any trilobite which had a smooth, unfurrowed exoskeleton, the axial region having a convexity continuous (or nearly so) with that of the pleural region. Speculation on musculature has not been extended to such forms, which may have lacked exoskeletal infolds for muscle attachment. The almost universal ability in trilobites to enrol closely, however, implies at least a general similarity in musculature. The present diagrams of enrolment show that complete closure, aided by co-aptative structures of the exoskeleton, is a position which could have been held only so long as the ventral longitudinal muscles were contracted, and the dorso-ventral muscles extended. It was essentially a temporary position, one that could be held only by a continuous effort. Enrolment appears to have been a protective reaction, whether against attempted predation or in the face of a sudden external change, such as an influx of sediment.

Terminology of the furrows, lobes and occipital ring of the cephalon is explained in figure 7; 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.

2. SYSTEMATIC PALAEONTOLOGY

Family Pliomeridae Raymond, 1913
Placoparia (Placoparia) cambriensis Hicks, 1875
Figures 1–9

Locality and horizon: Haverfordwest district, Dyfed, exact locality not specified, from Lower Llanvirn tuffs and interbedded shales overlying the Llanfallteg Formation, *Didymograptus artus* Biozone (Fortey & Owens 1987, fig. 3). Collected by Mr C. Conolly, who has also obtained disarticulated fragments of *Ormathops llanvirnensis* from the same locality.

Description: Counterpart moulds (figures 1 and 2) in fine-grained shale, distorted by compression oblique-transversely and elongated sagittally. The moulds show portions of the external and internal surfaces of
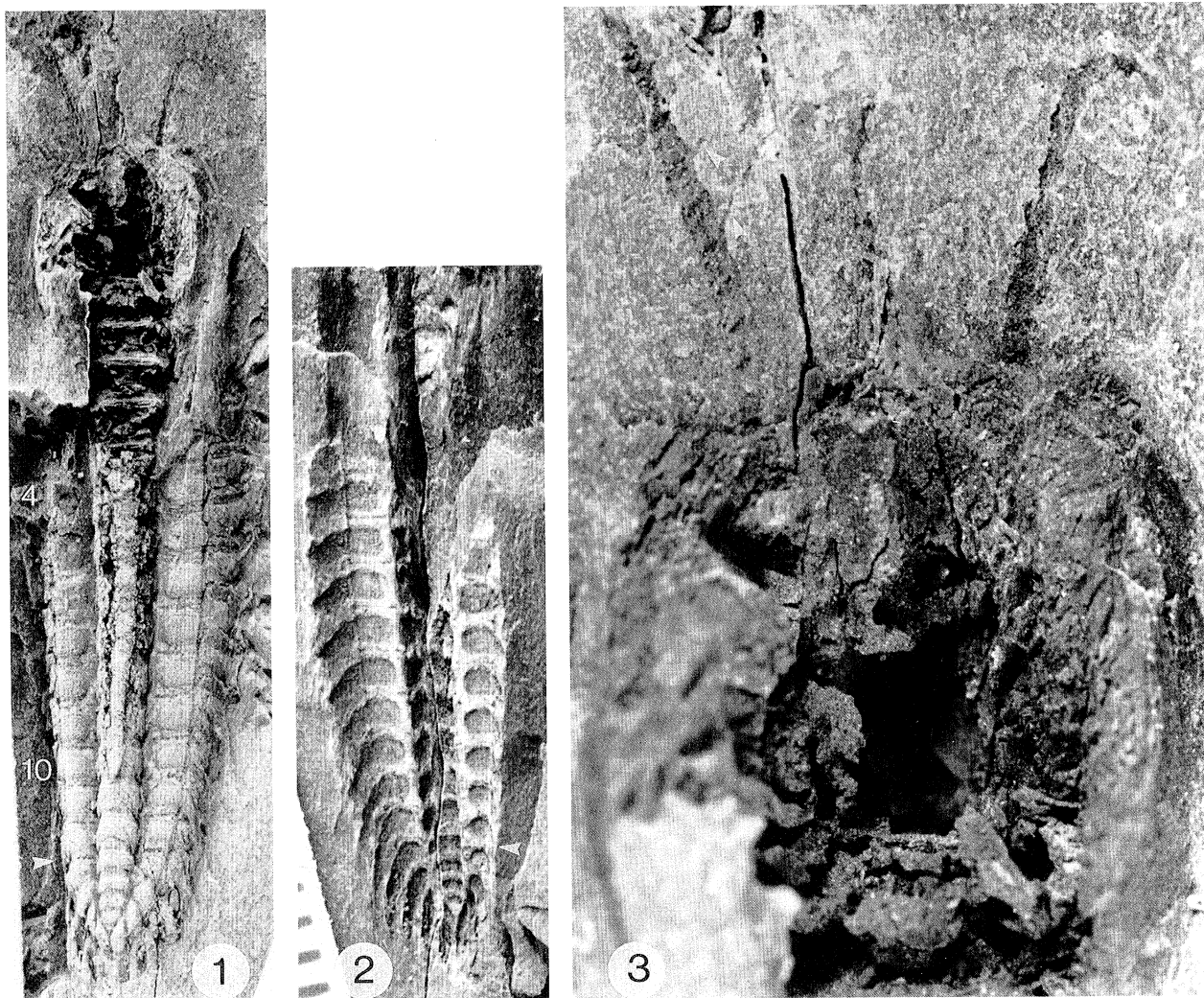
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Figures 1–3. *Placoparia* (*Placoparia*) *cambriensis* Hicks, 1875. NMW 91.46G, *Didymograptus artus* Biozone, Llanvirn, Haverfordwest district, Dyfed. Figures 1 and 2 respectively, internal and external moulds, ×5 (millimetre scale in figure 2). Thoracic segments 4 and 10 numbered; level of anterior margin of pygidium arrowed. Figure 3, anterior portion of internal mould showing antennae with a seta (arrowed) at junction of segments of left antenna, ×18.

thoracic segments 3–12 and the pygidium, and right lateral fragments of segments 1 and 2. These are like those of *P.* (*P.*) *cambriensis* from South Wales (Fortey & Owens 1987, pp. 232–234, fig. 93; Kennedy 1989, pl. 10, fig. 10) and show the four rings and small terminal piece of the pygidial axis. The species is widespread and characteristic of this horizon in western Europe. I have not attempted to prepare the anterior segments or the cheeks of the cephalon (preserved only in the internal mould), fearing that the important features revealed by the way the mould broke in collecting might be damaged. The crests of the axial region of segments 4–10 of this mould (figure 1) are broken away to reveal a tapering, cylindrical median structure that terminates in a rounded tip at the posterior margin of segment 10. This structure, filled with a coarser-grained, darker material than the matrix, is a partial filling of the alimentary canal like those recently described by Šnajdr (1991). In front of segment 4 this filling is broken away (figure 4), to reveal a series of transverse structures, each at the posterior margin of a somite. These somites appear to be those of thoracic segments 1–3, the occipital

segment, and two in front, those of lateral lobes L1 and L2. The transverse structures are preserved as two or three parallel grooves, curved gently ventrally, and are stoutest and widest (tr) beneath the thoracic segments, those of the cephalic segments successively narrower (tr) forward, less robust, and more ventrally situated. These structures appear to be the external moulds of transverse bars, each bar made of a bundle of rods. Between successive transverse bars of the thorax and occipital segment a pair of deep, circular pits is evident, defined on the inner edge by a narrow, raised rim. Similar pits are less clearly preserved between the three anterior transverse bars. These pits are continued downward and outward as vaguely-defined troughs (figure 6). In front of the most anterior, narrowest (tr) transverse structure (at the posterior margin of L2) is a deep cavity, which has a smooth, concave floor and a narrow, lateral groove (figure 6). The left anterior side of the cavity has a semi-cylindrical form, ascending steeply upward and outward. I interpret this antero-lateral structure as the anterior wing of the hypostome, and the axial cavity as floored by the mould of the middle body of
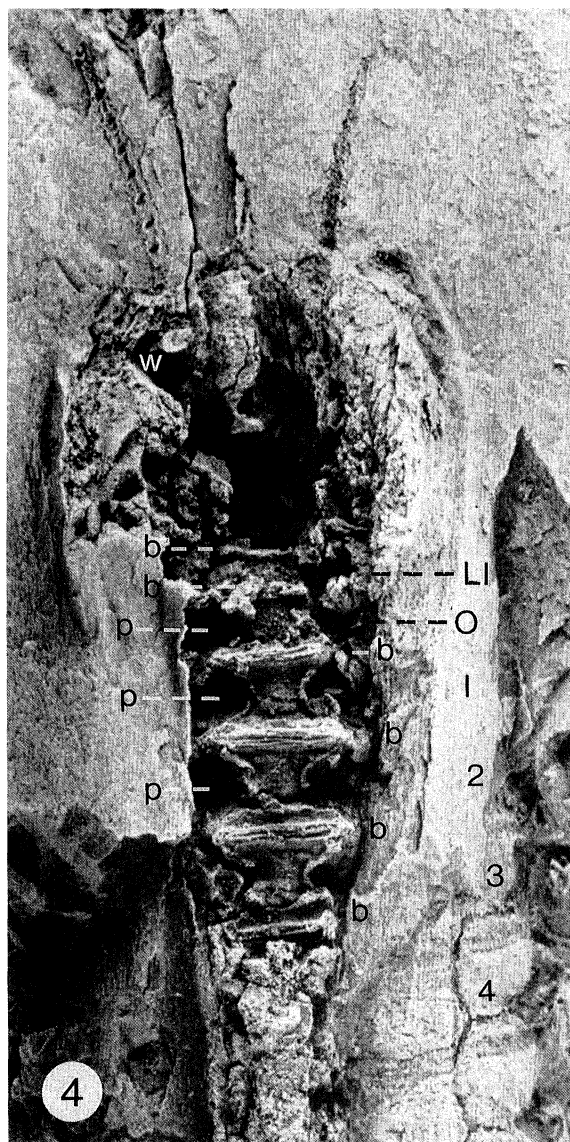
Figure 4. *Placoparia* (*Placoparia*) *cambriensis* Hicks, 1875. NMW 91.46G, original of figures 1–3. Anterior portion of internal mould, × 11, showing moulds of presumed intersegmental bars (b). Right pleural regions of thoracic segments 1–4 numbered, and presumed positions of occipital ring (O) and lateral glabellar lobe L1 indicated. w, anterior wing of hypostome; p, left pit of pair between intersegmental bars.

the hypostome and its lateral and posterior borders. It lies below the anterior portion of the axial region, i.e. the anterior portion of the glabella, slopes downward and backward, and appears to be in place. Part of the filling of this anterior portion of the glabella is preserved on the left side (figure 4), and shows faint inward and slightly backward-directed depressions, possibly the mould of the inner surface of glabellar furrows S2 and S3. In front of the anterior edge of the cephalon a pair of antennae (figures 3 and 4), each proximally about in line with the axial furrow, diverge forward. Both are incomplete distally, the right one curved back. The left antenna (figure 3) shows most clearly the segmental boundaries, directed obliquely as a result of the distortion, and a seta is preserved faintly at two of these junctions.
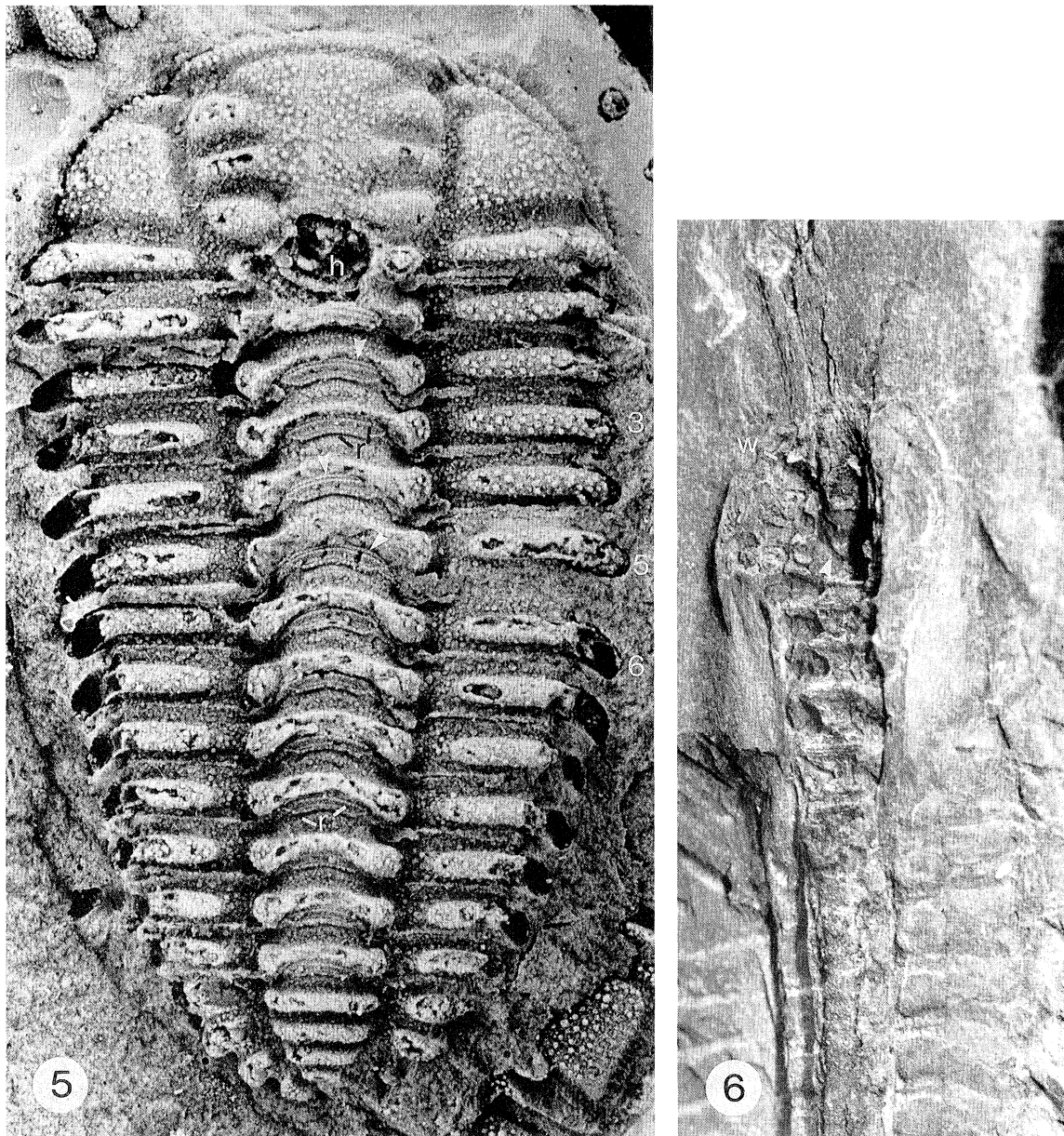
Discussion: The tectonic distortion that has affected the Welsh specimen is evident (compare figures 1 and 2 with figure 5) in the relative narrowing and lengthening of the thorax and pygidium, the enhanced convexity of the axis, and steepness of slope and stronger backward curvature imparted to the outer parts of the pleurae. The distortion is asymmetric, the slope of the axial region and outer portions of the pleurae vertical on the left side, steeply outward on the right side. The cephalon has been similarly distorted, the cavity between glabella and hypostome deepened and elongated. The divisions between segments of the antennae (figure 3) are oblique, not transverse, and the segments themselves may have been elongated. I interpret the transverse structures as the remains of tendinous intersegmental bars, because of their position immediately in front of the boundaries between somites and their situation below the alimentary canal. Each appears to be composed of two or three adjacent rods, and the anterior three are situated at the posterior margins of the three posterior cephalic segments, occipital, lateral lobes 1 and 2. Such bars were assumed to have been present by Campbell (1975a,b, 1977), and were identified in X-ray stereographs by Cisne (1975, 1981). This is the first specimen that appears to show such structures as external moulds. The pair of pits between the outer portions of the bars are another remarkable feature of this specimen. They are in the expected position of the coxa-body junction, and may be the moulds of this most basal portion of the paired, presumably biramous limbs. Because of the possibility of severe damage to the specimen, I have not tried to prepare it to investigate whether any further traces of limbs are preserved.

This chance find is from a new locality on which no detailed information is available. Fortey & Owens (1987, pp. 105, 107) refer to regression of the sea at the end of the Arenig, when the grey shales of the Llanfallteg Formation were deposited, and continuation of these conditions into the early Llanvirn, when volcanogenic sediments were also laid down. They suggest that the formation was deposited in waters of a depth not less than 200 m. This particular carcass was presumably rapidly buried, but the conditions which inhibited decay and led to preservation of soft parts remain mysterious.

3. ANATOMY OF *Placoparia*

(a) *Exoskeleton*

The exoskeleton of figures 7–9 is based on illustrations in Whittard (1958; accepting the synonymy of Dean in Whittard (1967, p. 309), and Fortey & Owens (1987)), Hammann (1971), Henry & Clarkson (1975), and Rabano (1984, 1989). The fossula, rostral plate and hypostome are shown in Whittard, and a cast from an external mould of the hypostome was figured by Rabano (1984, pl. 1, fig. 10). The hypostome in other species (Henry & Clarkson 1975, pl. 1, figs. 11–14) is known in place, and the long anterior wing in *P.* (*P.*). *zippei* (Prantl & Šnajdr 1957, pl. 2, fig.

Figures 5 and 6. *Placoparia (Placoparia) cambriensis* Hicks, 1875. Figure 5, Museum of Comparative Zoology, Harvard University, Cambridge, Mass., 5133a, Šárka Formation (Llanvirn), Osek, near Rokycany, Czechoslovakia, × 5. Internal mould of exoskeleton, left free cheek missing, posterior border of displaced hypostome (h) lies beneath broken occipital ring. Axial rings of segments broken, to reveal the broken edges of the ridge (r) on the articulating half ring of the segment following, and of the pygidium. Close to the anterior edge of this ridge in segments 3, 5 and 6 (numbered), the broken edge of the doublure of the axial ring in front is visible at the tip of the arrow. This portion of the doublure is parallel and close to the anterior slope of the ridge. Figure 6, NMW, 91.46.G, original of figures 1–3 and 4, viewed oblique-dorsally to show anterior wing (w) of hypostome, and the posterolateral portion of the hypostome in the cavity beneath the broken mould of the dorsal exoskeleton, × 7.5. Mould of convex posterolateral border of hypostome arrowed.

8). The hypostome was firmly attached along the hypostomal suture. The wing was braced against the inner surface of the fossula (figure 7), and hence the hypostome was not movable (cf. Whittington 1988), the condition termed conterminant by Fortey & Chatterton (1988). Specimens with the hypostome in place have not been figured in a manner to show the exact attitude in relation to the rest of the cephalon, but the suggestion made here is of an attitude similar to that in other pliomerids (Whittington 1961, text-figs. 1–3, 5), in one of which (pl. 100, fig. 15) the connection of anterior wing and fossula was displayed. The convex anterior border of the cephalon in *Placoparia* curved downward and then inward to form the doublure, the free cheeks separated by the rostral plate. The latter narrowed downward and inward, so that the hypostomal suture traversed the lower, inner edge of the rostral plate and the adjacent margin of the doublure of the free cheek (figure 7). This junction is shown in *P. tournemini* by Henry & Clarkson (1975,

pl. 1, fig. 13), and the rostral plate of *P. cambriensis* in Whittard (1958, text-fig. 6a, d–h).

The thorax of *P. (P.) cambriensis* (figure 5) was of 12 segments, each segment having a convex axial ring and deep axial furrow. The inner portion of the pleura was horizontal, the outer portion a hollow spine, underlain by the doublure and curving steeply down from the fulcrum. The inner portion of the pleura (figure 8*b*) consisted of a broad (exs) outwardly directed, convex ridge, with a lower and much narrower (exs) ridge along the posterior edge. A low strip along the anterior edge of the pleura formed a flange which passed beneath the edge of the ridge on the posterior margin of the segment in front (or the posterior cephalic border). The edges of the flanges thus formed the horizontal hinge line (figure 8*c*) between segments. Henry & Clarkson (1975, p. 88) remarked on the thickness of the exoskeleton in *Placoparia*. The contrast in appearance between internal moulds and casts from external moulds (e.g. Hammann 1971, pl. 1, figs. 1a, 6; pl. 2, figs. 10, 11; Rabano 1989, pl. 26, figs. 3, 11) in the width (exs) of axial rings and pleural ridges, and of furrows, is the result of the thickness of the exoskeleton. The axial ring in the cast is broader (exs) and of more constant width, and the main pleural ridge broader (exs). In the internal mould (figure 5), the axial ring narrows (exs) distally and then expands to a rounded, swollen termination. The articulating furrow in front of it appears broader, and ends distally in a rounded pit, the mould of a low ventral projection, the apodeme. At the posterior edge of the axial furrow there is a pit in the internal mould, the ventrally projecting axial articulating process, which fitted into a socket in the following segment, and lay in the hinge line. In the internal mould (figure 5) the axial rings are broken, so that a mould of a portion of the articulating half ring is revealed. The edges of two, in some cases three, broken layers of exoskeleton are visible. The posterior two edges form a forwardly curved band, the edges uniting distally. I interpret this structure as a forwardly-curving ridge in the articulating half ring (figure 8*b*,*d*) and the edge close in front of it as the broken edge of the steeply descending doublure of the next axial ring in front. The ridge was concealed beneath the unbroken axial ring in front of it when the thorax was horizontally extended, but became visible when the thorax was flexed. The ridge is shown in dorsal view (figure 8*b*), and in lateral view in the sixth segment of the extended thorax (figure 8*d*), and in profile in the enrolled thorax (figure 9*b*). The ridge is visible between the axial rings of flexed segments of *Placoparia* in casts (Hammann 1971, pl. 2, fig. 11; Rabano 1989, pl. 26, fig. 11) and in internal moulds (Horny & Bastl 1970, pl. 15, fig. 3; Hammann 1971, pl. 3, fig. 20; Rabano 1984, pl. 1, figs. 1a, 1b, 3, 6, 7b; Kennedy 1989, pl. 10, fig. 10; pl. 11, fig. 4), and also on the articulating half ring of the pygidium. In extended specimens (figure 5) the doublure of each axial ring lay close to the anterior edge of the ridge in the articulating half ring of the following segment, and matched its curvature. This arrangement supplemented the precise fit between the segments, cephalon
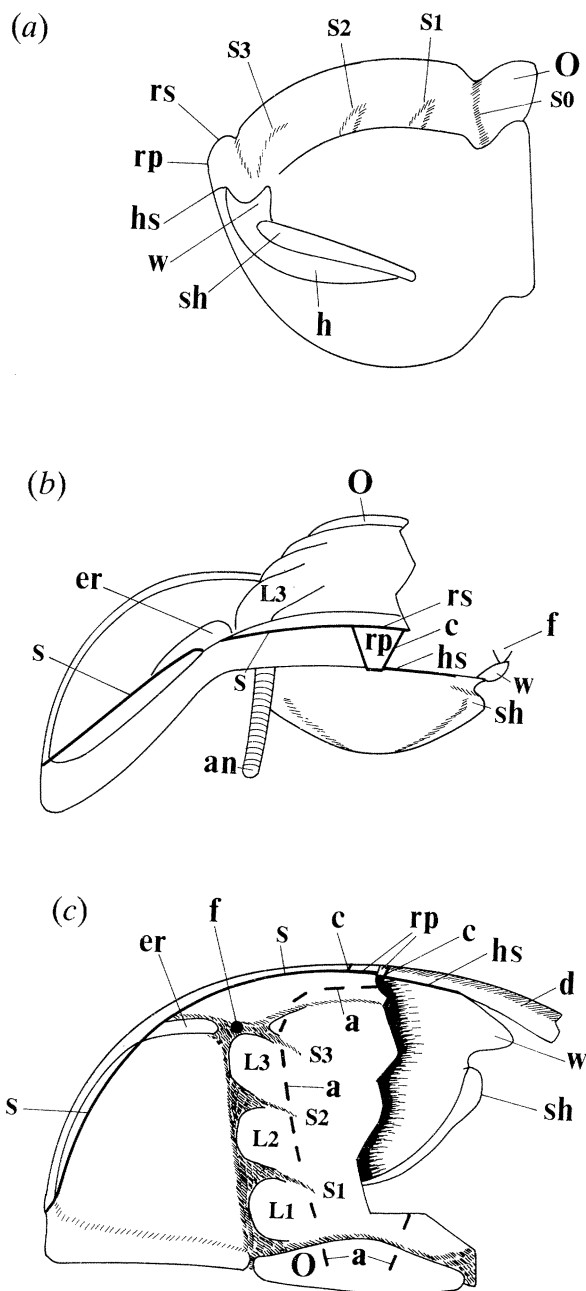

Figure 7. *Placoparia (P.) cambriensis*, reconstruction of the exoskeleton of the cephalon to show the sutures (heavier line) and the attitude of the hypostome (h), braced by the anterior wing (w) against the ventral side of the fossula (f). (*a*) Left lateral view, hypostome shown inside outline of genal region. (*b*) Anterior view, left half of dorsal exoskeleton cut away except for tip of fossula, proximal portion of right antenna (an) shown. (*c*) Dorsal view, right half of dorsal exoskeleton cut away to show doublure (d) and hypostome; dashed line (a), outline of alimentary canal beneath glabella. c, connective suture; er, eye ridge; hs, hypostomal suture; L 1–3, lateral glabellar lobes; O, occipital ring; rp, rostral plate; rs, rostral suture; S 0–3, sulci, occipital furrow SO and lateral glabellar furrows S 1–3. s, facial suture; sh, shoulder of hypostome; w, anterior wing of hypostome.

and pygidium, and appears also to have limited the possible concave-dorsal flexure of the body. The ridge is a different structure from the preannulus of proetids (e.g. Whittington & Campbell 1979, pl. 2, figs. 7, 8,
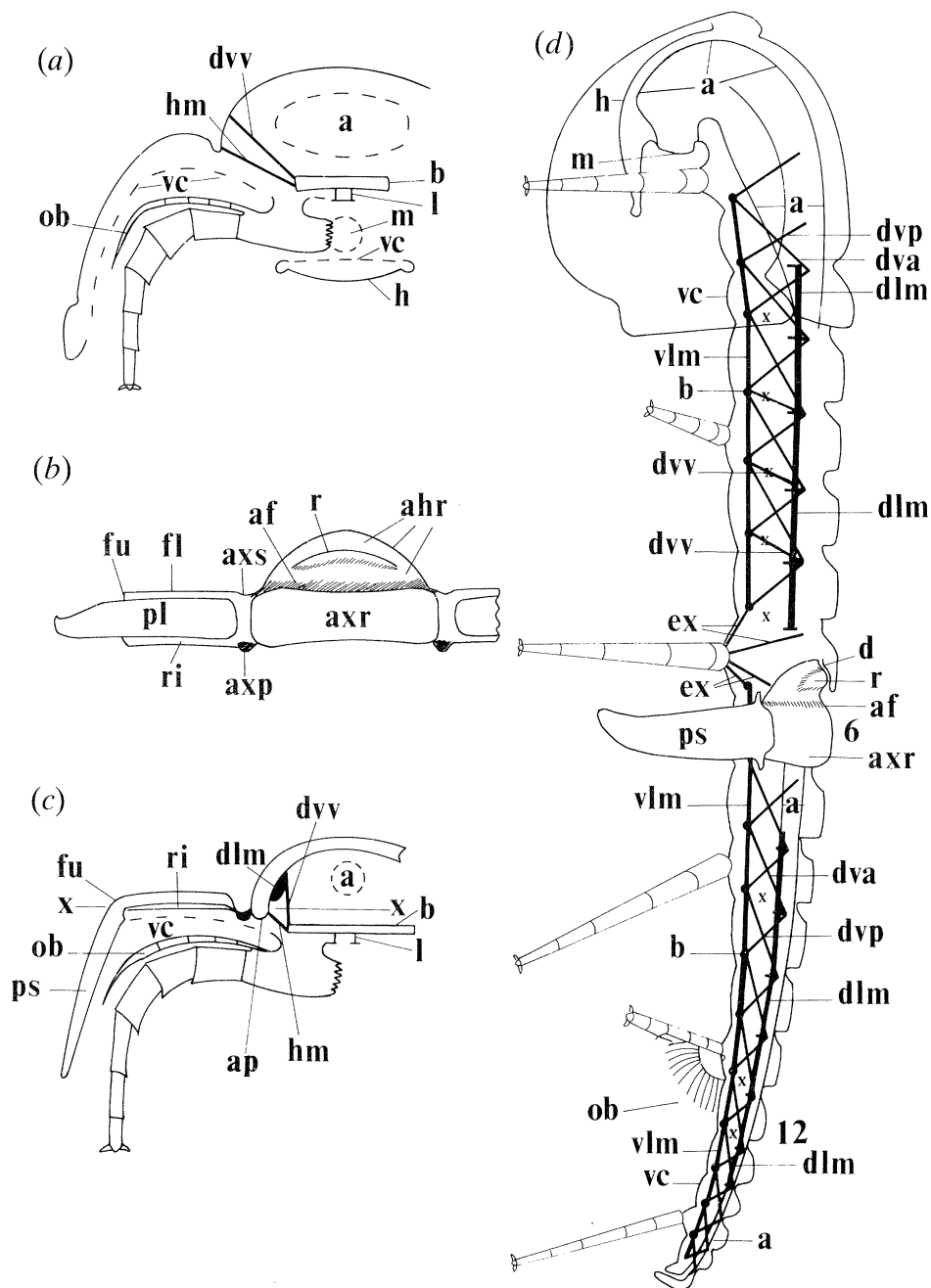
Figure 8. *Placoparia* (*P.*) *cambriensis*, reconstruction of extended body with musculature in heavier lines. (*a,c*) Transverse sections at second glabellar lobe (L2) and sixth thoracic segment, respectively. Left biramous limb shown with inner branch vertical, outer branch (ob) in section. Dashed lines indicate outline of alimentary canal (a), position of mouth (m) in front of anterior limb, and ventral, unmineralized cuticle (vc) which also overlies the hypostome (h). The transverse tendinous bar (b) is linked to the ventral cuticle by ligaments (l). A dorsoventral vertical muscle (dvv) and a horizontal muscle (hm) extend from the glabellar or articulating furrow (af) and the axial furrow or apodeme (ap) to the end of the bar. The dorsal longitudinal muscle (dlm) is shown in section on the left of (*c*), and the hinge line between segments is shown by the line X. (*b*) Dorsal view of sixth thoracic segment, showing ridge (r) in articulating half ring (ahr), the axial ring (axr), the axial articulating socket (axs) and process (axp), the articulating furrow (af), the pleura (pl) with the anterior articulating flange (fl) and posterior ridge (ri), beneath which the flange of the following segment fits. The pleura is bent down at the fulcrum (fu) to form the pleural spine (ps in (*c*)). (*d*) Profile of exoskeleton in left lateral view, broken at segment 6 to show a lateral view of this segment (compare with (*b*)) and the doublure (d) of the axial ring of segment 5. The alimentary canal (a) is shown in the cephalon, and posteriorly from segment 7. The inner branches of limbs I, V, VIII, XI, XIV (with outer branch ob), and XVIII are shown, in the appropriate positions of a gait explained in the text. The dorsal longitudinal (dlm) and ventral longitudinal (vlm) muscles, and tendinous bars (b) are broken between segments 5 and 7, to allow extrinsic limb muscles (ex) of limb VIII to be suggested. The positions of anteriorly descending (dva), vertical (dvv) and posteriorly descending (dvp) dorsoventral muscles are indicated, the vertical muscles only in thoracic segments 2–4. Position of hinge line shown by x.

14, 15; pl. 3, figs. 11, 12), which is a subdivision of the axial ring adjacent to the articulating furrow. Chatterton & Perry (1983, p. 17) have suggested that the function of the preannulus in proetids and other trilobites was to facilitate concave-dorsal flexure of the body. Neither of these structures inhibited convex-dorsal flexure of the body. In complete enrolment of *Placoparia* (Henry & Clarkson 1975; Rabano 1984, pl. 1, fig. 1, 1989, pl. 26, figs. 1, 2) the edges of the thoracic pleural spines were brought into contact, and the tips of the pygidial pleural spines were in contact with the anterior cephalic border.

(b) *Alimentary canal*

A filling of this canal is preserved in the axial region of thoracic segments 4–10 of the present specimen (figure 1). A similar filling was first described in the trinucleid *Deanaspis goldfussi* by Beyrich (1846, pl. 4, fig. 1c) and by Barrande (1852, p. 229, pl. 30, figs. 38 and 39). Their originals, and additional specimens, have recently been described by Šnajdr (1991). These show the filling extending from beneath the glabella to the posterior tip of the pygidium, clavate beneath the glabella and tapering back beneath the axial region of the thorax and pygidium. A narrow, incomplete filling is also illustrated in the thorax and pygidium of *Dalmanitina socialis*. X-ray photographs (Stürmer & Bergström 1971; Cisne 1981) have shown the canal in the thorax and pygidium, and less clearly details of it in the cephalon. The generally accepted view that it expanded beneath the glabella, and was U-shaped, the backward-facing mouth above the hypostome, appears reasonable. It is so reconstructed here (figure 8a,d), with the mouth immediately in front of the coxae of the pair of biramous appendages of somite L2. The most anterior transverse bar preserved appears to belong to this somite, and the assumption is made that there were no more than three pairs of biramous appendages on the cephalon. There then appears to have been adequate space within the capsule enclosed between glabella and hypostome for the anterior portion of the alimentary canal.

(c) *Appendages*

Only the jointed antenna is preserved in the present specimen (figure 3), projecting forward and slightly outward approximately in line with the axial furrow. Extrinsic muscles of the antenna may have been attached to the posterior wall of the inner surface of the fossula, glabellar furrow S3 and the axial furrow. It is portrayed (figure 7b) as directed downward through the lateral notch between anterior wing and shoulder of the hypostome, and curving forward. On enrolment (figure 9b) it would have been curved back immediately inside the border of the cheek.

By analogy with what is known of other trilobites (e.g. Whittington 1975, 1980; Whittington & Almond 1987), 18 pairs of biramous limbs (I to XVIII), of a generalized type are assumed to have been present: three pairs on the cephalon, one pair on each thoracic segment and on the first three pygidial segments. In
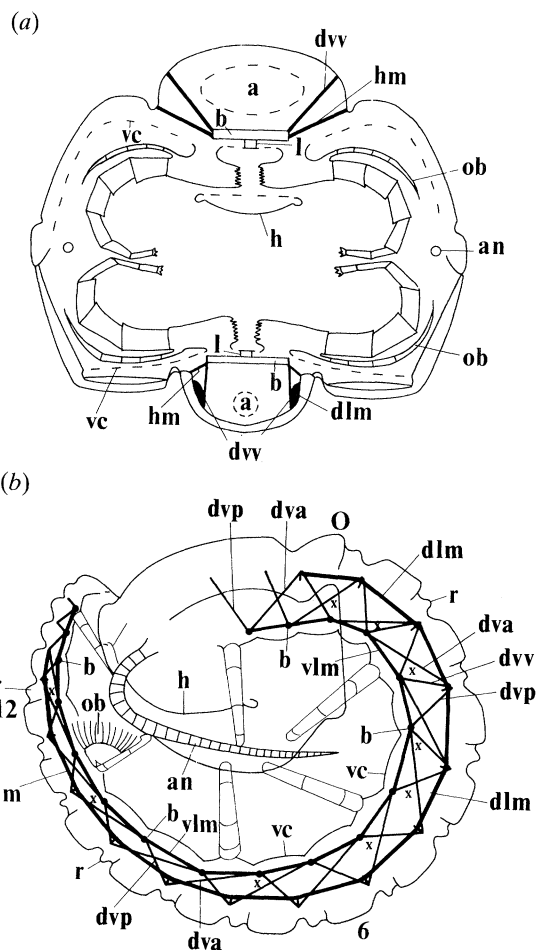

Figure 9. *Placoparia* (*P*). *cambriensis*, reconstruction of body in fully enrolled attitude, to indicate musculature and the manner in which the appendages were accommodated. (*a*) Cross section through glabellar lobe L2 and segment 7 (compare figure 8*a,c*). (*b*) Profile of exoskeleton with antenna (an) in retracted position, limbs and musculature as in figure 8*d*. Position of hinge line indicated by x, lettering as in figure 8.

the cross-sections (figures 8*a,c* and 9*a*) the coxa and inner branch (the walking leg) are shown in a vertical position, and the outer branch, attached to the coxa, is shown in cross-section. This outer branch is modelled on that of the Ordovician cheirurid *Ceraurus* (Størmer 1939), as being the nearest relative of a pliomerid in which limbs are known. In lateral aspect (figure 8*d*) limbs I, V, VIII, XI, XIV and XVIII only are shown, in positions of a generalized gait (Whittington 1980, text-fig. 11b) in which the 18 pairs were participating, eight pairs in each metachronal wave. Only on limb XIV (figures 8*d* and 9*b*) is an outer branch of *Ceraurus* type sketched in, as a reminder that such branches were present on all the biramous limbs.   The filaments are shown directed posteriorly, following Størmer, and not antero-ventrally as suggested by Bergström (1969).

(d) *Musculature*

Speculation on trilobite musculature has a long history (e.g. Beecher 1902; Raymond 1920; Schevill

1936; Størmer 1939; Hupé 1953; Campbell 1975a,b, 1977; Cisne 1975, 1981), and has been greatly influenced by the work of Hessler (1964) and Manton (1977) on living arthropods. Probable attachment areas on the exoskeleton for muscles include smooth areas, infolds, and extensions of the latter as apodemes. Only Cisne has claimed to be able to see, in X-ray stereographs, the remains of muscles and of transverse segmental tendinous bars. In his 1981 reproductions of these photographs it is by no means easy to identify such features, but the presence of the transverse bars, situated below the alimentary canal, appears to be confirmed by the present specimen. Thus the general features of the musculature proposed by earlier authors, and particularly by Cisne and Campbell, is here supported. The position and attachment points of these muscles is shown in simplified form in figures 8 and 9, but not their bulk. As Manton (1977, p. 260) pointed out, enrolment muscles may have been far more massive than the thin strands shown here, for example.

(e) Extension and enrolment of the body

There is general agreement that dorsal longitudinal muscles extended along the axis in parallel sheets on each side of the alimentary canal (figure 8c,d). These may have been attached to the lateral portion of the articulating furrow of each segment of the thorax, to the occipital furrow SO (possibly with strands to glabellar furrows S1 and S2), and to the articulating and one or two inter-ring furrows of the pygidium. Contraction of these muscles (figure 8d), which lay above the hinge-line, maintained the body in an extended position when the animal was walking, resting on the sea bottom, or digging into it with the inner branches of the limbs. Dorsoventral muscles, descending vertical-obliquely from the articulating furrow to the transverse intersegmental tendinous bar, and anteriorly and posteriorly to the adjacent bars, are shown in the pattern observed by Hessler (1964) in *Hutchinsoniella* and other crustaceans. This arrangement is that adopted by Cisne (1975, 1981) and Campbell (1975a, 1977), Cisne suggesting the presence of horizontal muscles attached to the outer end of each bar, and of ligaments connecting the bar to the ventral cuticle (figure 8a,c). These muscles and ligaments aided in maintaining the form of the body in the extended state, and as Hessler (1964, p. 10) pointed out, helped to maintain hydrostatic turgor within the body. Such turgor may have been essential to extend the walking legs when they were lifted off the substrate and swung forward (Whittington 1980, text-fig. 10).

Enrolment of the body was effected by contraction of the ventral longitudinal muscles. Such muscles were considered to have been present by Beecher (1902), in his study of the ventral cuticle of *Triarthrus*. They were shown by Størmer (1939, pl. 11c) and Hupé (1953, fig. 29), attached to intersegmental boundaries of the ventral cuticle. Following the work of Hessler (1964) on crustaceans, and Cisne (1975, 1981) on *Triarthrus*, and the evidence of the present specimen, they are

shown attached to the transverse intersegmental bars (figures 8d and 9b). Figure 9 also suggests how the limbs may have been accommodated: the antennae swung back to lie inside the lateral cephalic border, the inner branches of the limbs relaxed in a flexed position to allow the overlapping outer branches to lie between them and the pleural region. The most anterior intersegmental bar appears to have been that between L2 and L1, the first and second glabellar lobes, and the most posterior perhaps that at the rear of the fourth axial ring of the pygidium. At complete enrolment, when the tips of the pygidial pleurae were in contact with cephalic border (Henry & Clarkson 1975; Rabano 1989, pl. 26, figs. 1 and 2), these muscles were curved through an arc of more than 270°. The ventral pull caused by the contraction of the ventral longitudinal muscles was countered by the dorsoventral muscles, so maintaining the shape of the axial body. Figure 9b shows that the anteriorly descending dorsoventral muscle of thoracic segments 3–12 and the first pygidial segment were markedly extended during enrolment, yet remained dorsal to the hinge-line. The latter crossed the lower portion of the axial body region, and on enrolment this smaller lower portion was compressed. The much greater volume of the portion of the axial body above the hinge-line, however, was expanded during enrolment. The net effect of these changes in volume may have been to lower hydrostatic turgor in the body and so to facilitate enrolment. In extending the body from the fully enrolled position these volume changes would be reversed, the increased hydrostatic turgor aiding the out-rolling. It is also evident that contraction of the anteriorly descending dorsoventral muscles would have aided the dorsal longitudinal muscles to effect extension of the body. Both Størmer (1939, text-fig. 7d) and Hupé (1953, fig. 29) considered that this extension was further aided by the contraction of auxiliary or external dorsal muscles, attached to the anterior edge of each articulating half ring and to the articulating (or occipital) furrow of the segment in front. Campbell (1975a, p. 77; 1975b, pp. 173–174) has argued that such muscles were necessary in *Cryptolithus* and phacopids, and were effective in being situated well above the hinge-line. In the case of *Placoparia* the musculature described above may have been adequate to extend the body without invoking the presence of external dorsal muscles. The internal mould (figure 5) shows that the exoskeleton of the articulating half ring was thin, much thinner than that of the axial ring or pleura. A flexible membrane would presumably have joined the thin anterior edge of the articulating half ring to the equally thin edge of the doublure of the axial (or occipital) ring in front: a membrane which extended as the body was enrolled. I consider it unlikely that external dorsal muscles were also attached to the edge of the half ring.

In *Placoparia* it is suggested that the dorsal longitudinal muscles extended forward to the occipital ring and possibly the first and second glabellar furrows. The present specimen suggests that the most anterior transverse bar in the cephalon may have been that below L2, and hence that ventral longitudinal muscles

did not extend forward beyond this bar. Such an arrangement appears to allow adequate unrestricted space for the expanded anterior portion of the alimentary canal, i.e. the digestive organs (figures 7*c* and 8*d*). In *Triarthrus*, however, Cisne (1975, figs. 5 and 6; 1981, text-fig. 8) claimed the presence of endoskeletal bars beneath L3 and the frontal glabellar lobe, and extended the ventral longitudinal muscles to an attachment at the preglabellar and anterior border furrows. In *Eophacops* (1975*b*, text-fig. 2) and a dalmanitinid (1977, p. 83, text-fig. 26*b,c*) Campbell considered that these muscles must have been attached to the frontal slope of the glabella in order to be effective. In all these cases such an arrangement appears unduly restrictive of space for the digestive tract.

Campbell's studies of *Cryptolithus* (1975*a*) and dalmanitinids (1977) have suggested how musculature may have deviated in particular morphologies from the generalized pattern suggested here. In *Cryptolithus* the thorax is of six segments, and complete enrolment requires a much greater angle of flexure between the cephalon and first thoracic segment than in *Placoparia*. Campbell argued that dorsoventral muscles may have been present only in the posterior two-thirds of the body. Their role was essential, however, in maintaining the form of the axial body against contraction of ventral longitudinal muscles. Hence I doubt that all such muscles were absent in the anterior portion of the body. In dalmanitinids the long, slim apodemes extended some distance into the axial body, and provided muscles attachment areas in a more ventral position than those in *Placoparia*. This affects the position of dorsoventral muscles in relation to the hinge-line, and hence whether or not particular muscles may have aided in enrolment or extension of the body.

(*f*) *Extrinsic limb musculature*

Cisne (1975, figs. 6 and 7; 1981, text-fig. 8) portrayed such muscles in *Triarthrus* as extending to the outer end of the axial ring, the pleural furrow, and the ends of the endoskeletal bars. His restoration of the coxa, and the position of the coxa-body junction, has been questioned by Whittington & Almond (1987, pp. 35–36). In figure 8 the coxa-body junctions are portrayed as relatively close to the midline, in the position of the pair of pits between the intersegmental bars (figure 4). In such a position extrinsic limb muscles may have been attached to the ventral surface of the glabellar furrows, occipital furrow, and the outer ends of the articulating furrow of adjacent segments, and from the ends of the bars, but not to the ventral surface of the pleura.

(*g*) *Cephalic musculature*

As suggested above, it is not thought that in *Placoparia* the dorsal and ventral longitudinal muscles were attached to the frontal slope of the glabella, or to the infold of the preglabellar furrow. This may be true for other trilobites with an attached hypostome and

forwardly expanded glabella. Eldredge (1971) discussed earlier views on cephalic musculature. He concluded that in Phacopina areas on the anterior part of the glabella and the hypostome regarded as for muscle attachment, were for muscles supporting the dorsal cuticle of the hypostome and the digestive tract. It is thought (Whittington 1988) that in Phacopida (including pliomerids) and other groups which had an attached hypostome, it was not movable, so that muscle scars previously associated with such supposed movement (Eldredge 1971, p. 63, text-fig. 7) may also have been for muscles which supported the digestive tract.

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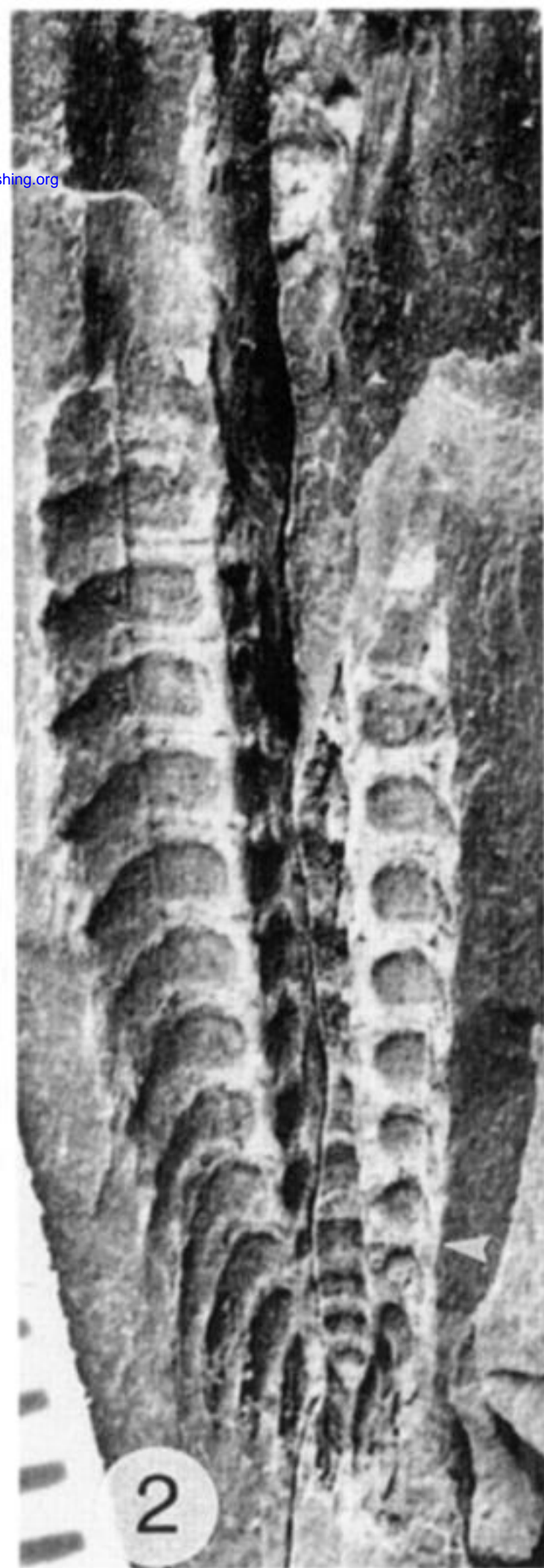
Figures 1–3. *Placoparia* (*Placoparia*) *cambriensis* Hicks, 1875. NMW 91.46G, *Didymograptus artus* Biozone, Llanvirn, Haverfordwest district, Dyfed. Figures 1 and 2 respectively, internal and external moulds, ×5 (millimetre scale in figure 2). Thoracic segments 4 and 10 numbered; level of anterior margin of pygidium arrowed. Figure 3, anterior portion of internal mould showing antennae with a seta (arrowed) at junction of segments of left antenna, ×18.

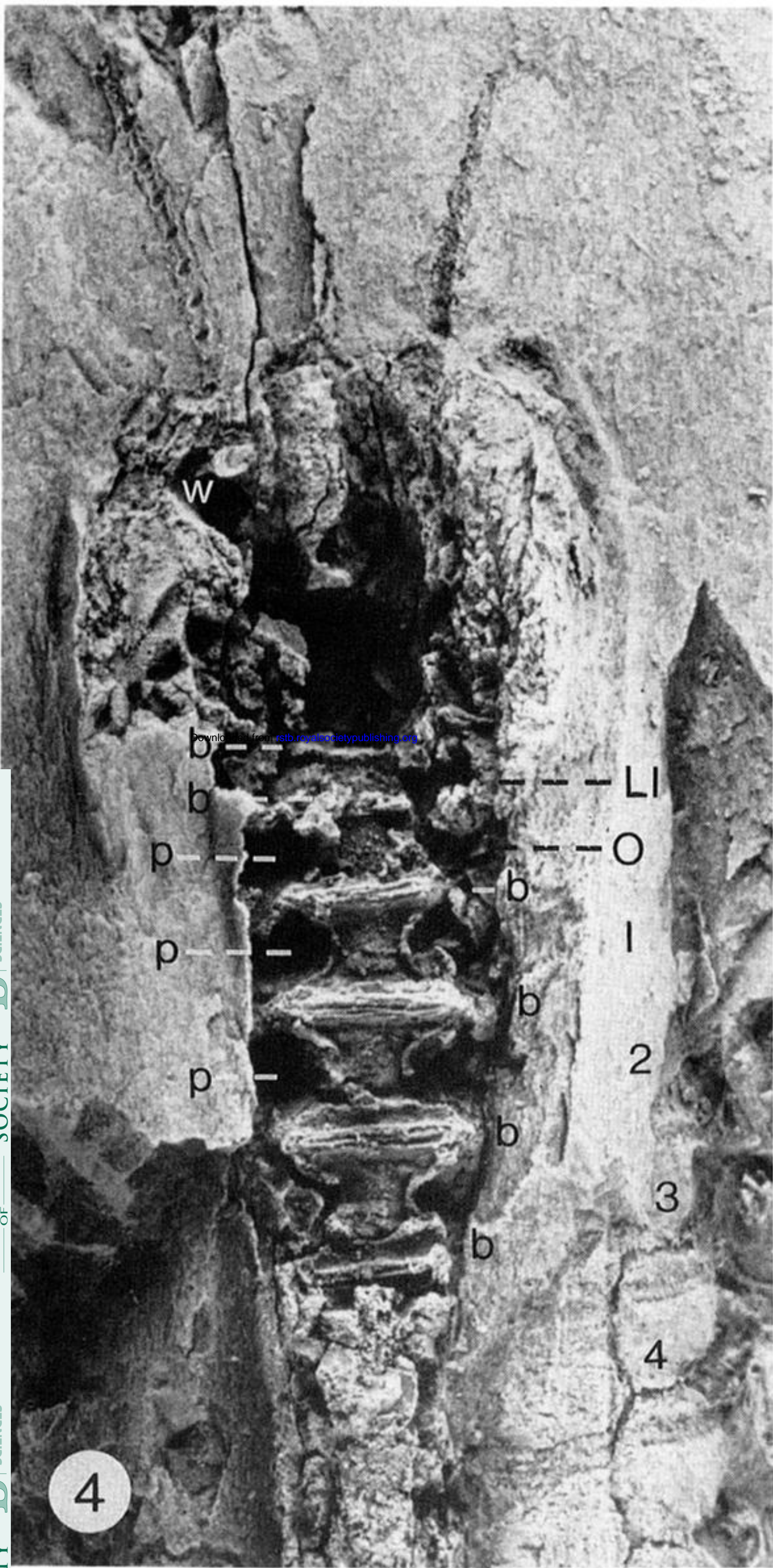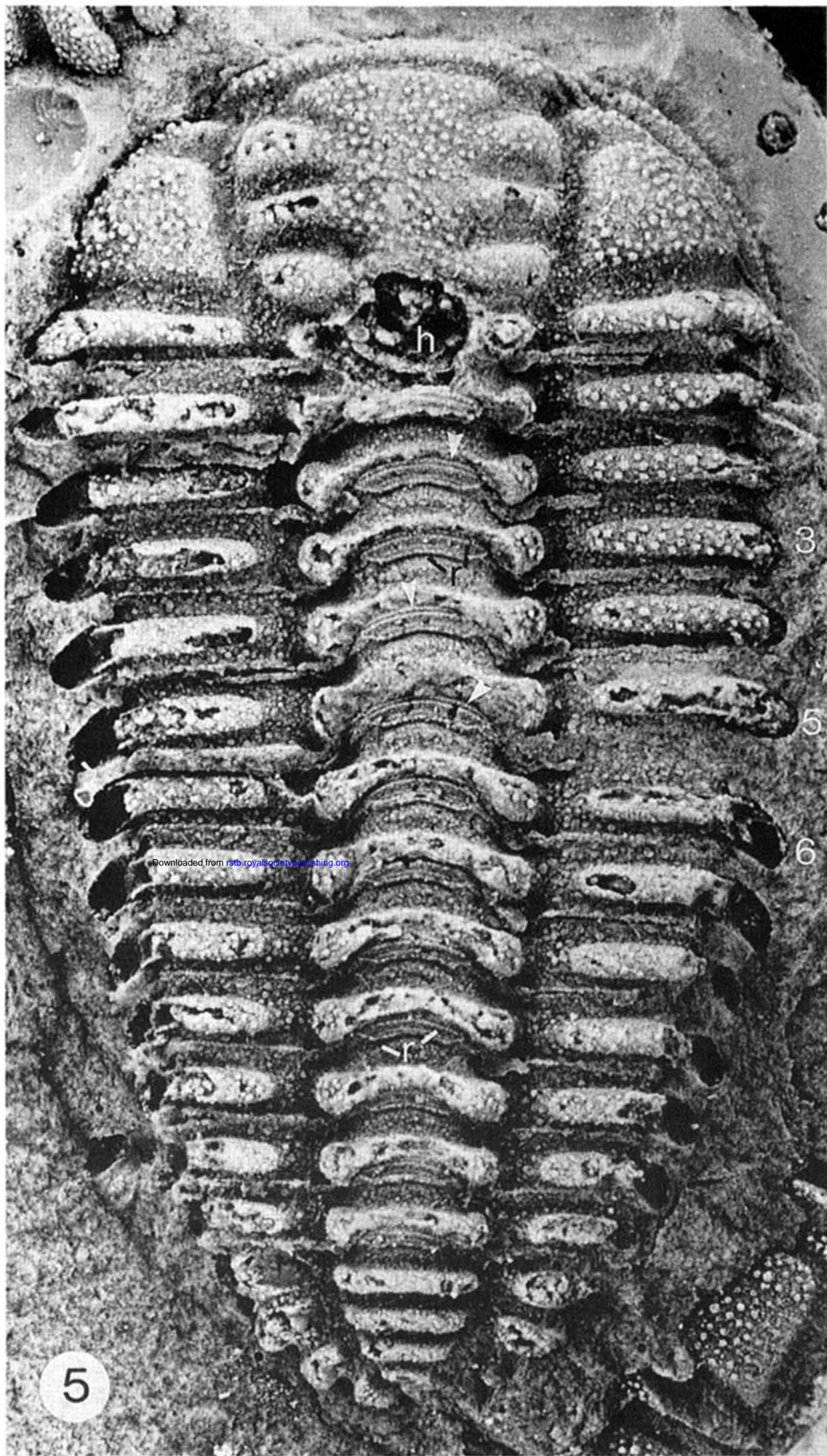Figure 4. *Placoparia* (*Placoparia*) *cambriensis* Hicks, 1875. MW 91.46G, original of figures 1–3. Anterior portion of internal mould, × 11, showing moulds of presumed interseg-mental bars (b). Right pleural regions of thoracic segments 1–4 numbered, and presumed positions of occipital ring (O) and lateral glabellar lobe L1 indicated. w, anterior wing of hypostome; p, left pit of pair between intersegmental bars.

Figures 5 and 6. *Placoparia* (*Placoparia*) *cambriensis* Hicks, 1875. Figure 5, Museum of Comparative Zoology, Harvard University, Cambridge, Mass., 5133a, Šárka Formation (Llanvirn), Osek, near Rokycany, Czechoslovakia, ×5. Internal mould of exoskeleton, left free cheek missing, posterior border of displaced hypostome (h) lies beneath broken occipital ring. Axial rings of segments broken, to reveal the broken edges of the ridge (r) on the articulating half ring of the segment following, and of the pygidium. Close to the anterior edge of this ridge in segments 3, 5 and 6 (numbered), the broken edge of the doublure of the axial ring in front is visible at the tip of the arrow. This portion of the doublure is parallel and close to the anterior slope of the ridge. Figure 6, NMW, 91.46.G, original of figures 1–3 and 4, viewed oblique-dorsally to show anterior wing (w) of hypostome, and the posterolateral portion of the hypostome in the cavity beneath the broken mould of the dorsal exoskeleton, ×7.5. Mould of convex posterolateral border of hypostome arrowed.