

HYPOSTOMES AND VENTRAL CEPHALIC SUTURES IN CAMBRIAN TRILOBITES

by H. B. WHITTINGTON

ABSTRACT. Restorations of the cephala of species of each of eighteen genera show the hypostome and cephalic sutures; new photographs are given of these features in *Holmia*, *Bathynotus*, *Paradoxides*, *Fielaspis*, *Ptychoparia*, *Conocoryphe*, and *Agraulos*. It is considered that probably in all trilobites the tip of the upwardly directed anterior wing of the hypostome was situated close beneath the ridge formed on the internal surface of the cephalon by the axial furrow, in a position immediately in front of where the eye ridge or eye lobe met this furrow. This position of the hypostome may be observed in species in which the hypostome was attached either by a suture to the cephalic doublure, or fused to the rostral plate. In species in which the hypostome was detached from the cephalic doublure it is assumed that it was situated in a morphologically similar position. In forms in which it was attached, the hypostome was thus braced against the dorsal exoskeleton of the cephalon so that movement was not possible; such movement was probably restricted in detached forms. During development the close connection between anterior wing and a particular site in the axial furrow was maintained, hence the hypostome may have been detached in the early stages but attached in the holaspis, or vice versa. Fusion of hypostome to rostral plate in holaspids is known only in Cambrian trilobites. Progressive reduction in transverse width of the rostral plate, culminating in a median suture, is not known in an evolutionary series. Until more is known of the hypostome, cephalic doublure, and ventral sutures in Cambrian trilobites, these features will have only limited value in discriminating familial and higher taxa, compared with their importance in such characterization of post-Cambrian forms; this particularly applies to species having the hypostome detached.

A REVIEW by Rasetti (1952), and the *Treatise* (Harrington in Moore 1959, figs. 42.1-13, 44, 48b-d, g, i) give only ventral (external) views of a limited range of hypostomes of Cambrian trilobites. Hence the convexity of the hypostome, the size and inclination of the anterior wing, and how the hypostome was related to the rest of the cephalic exoskeleton, are not revealed and their significance cannot be appreciated. A limited amount of silicified Cambrian material (that retains the original convexity) has been isolated from the matrix and described, a few entire exoskeletons with the hypostome in place illustrated, and isolated hypostomes recorded and figured. In many of the latter the anterior wing is either hidden in shadow, or has not been exposed from the matrix. The appearance of the dorsal (internal) side of the hypostome is virtually unknown, and there have been only limited attempts to excavate the doublure of the free cheek to show if and where it may have ended at a median or a connective suture. In addition, lateral or anterior views which show the convexity of the cephalon of uncompressed specimens are lacking in many publications. The present review embraces taxa selected to represent major groups (orders and superfamilies of the *Treatise*) of Cambrian trilobites for which information is adequate to provide a reconstruction of the cephalic exoskeleton, and covers a wide range of morphology. Sources are mainly post-1959, supplemented by new investigations (text-fig. 2; Pls. 52-55). The results are summarized in text-figs. 1, 3, 5-20, drawings that show not only dorsal and ventral aspects of the cephalon, but a right lateral view and a sagittal section combined with a right lateral view of the hypostome. The latter also includes a heavy dashed line in the position of the crest of the ridge formed on the inner surface of the cephalon by the axial furrow. This line helps to show how the attitude and position of the hypostome were related to the size and form of the anterior wing, and the position of the axial furrow. It may also be seen that knowledge of the convexity of the exoskeleton is essential to making the reconstruction, and that an estimation may be made of the probability that the

hypostome was attached by a suture to the cephalic doublure, or was detached from it. All the requisite information for such reconstructions may not be known for a single species (preferably the type) of a particular genus. In such cases I have combined information from two or more species into a drawing of an indeterminate species, for which a generalized stratigraphical range is given. The descriptive section deals with the basis for each figure and elements of uncertainty that may obtain. The investigation has shown that in forms in which rostral plate and hypostome were fused, this fused sclerite was firmly braced by the anterior wing of the hypostome against the rest of the cephalic exoskeleton. In species that had the hypostome attached at a hypostomal suture, the anterior wing appears to have fulfilled a similar role. In perhaps the majority of species of Cambrian trilobites, the hypostome was detached from the rest of the exoskeleton and inserted into the un-mineralized ventral integument; muscles linking the anterior wing to the dorsal exoskeleton served to hold it in place. The reasoning lying behind these findings, and their implications, are discussed, together with the relationships between them and those on the hypostomes of post-Cambrian trilobites (Whittington, in press).

FIGURES AND TERMINOLOGY

Text-figs. 1, 3, 5-20, give A, a partial dorsal, B, a partial ventral, and C, a right lateral view of the cephalic exoskeleton; D is a sagittal section of this exoskeleton combined with a right lateral view of the hypostome. Each sagittal section incorporates a gap where it is crossed by a suture, to clarify the position of the suture (no gap is shown where the section follows a median suture). A heavy dashed line indicates the position of the crest of the ridge formed by the axial furrow on the inner surface of the exoskeleton. Scale bars are in millimetres. Certain of these figures are of indeterminate species, being based on more than one species assigned to the genus; the stratigraphical range given is that of species of the genus. Such ranges follow the definitions of Lower, Middle, and Upper Cambrian by Palmer (1977).

Abbreviations used in the plates and text-figures are listed below, and are for terms used earlier (Whittington and Evitt 1954, p. 13; Harrington *et al.* in Moore 1959). An *attached* hypostome was one that was attached to the cephalic doublure and/or the rostral plate at the hypostomal suture, or was fused to the rostral plate; a *detached* hypostome was not so attached, but inserted into the un-mineralized ventral integument of the cephalon. Harrington (in Moore 1959, p. O58) used the term *rostral-hypostomal plate* for the fused rostral plate and hypostome (Henningsmoen 1959, p. 157, proposed 'rostri-hypostomal plate'); in text-figs. 8 and 10, the two portions of this plate are labelled separately.

Abbreviations used. *aw*, anterior wing, subtriangular or rounded extension of anterolateral border of hypostome; *cs*, connective suture, one of pair of sutures that extend from junction of rostral and facial suture to inner margin of cephalic doublure, and hence isolates the rostral plate; *d*, doublure of cephalon; *gr*, genal ridge, the low ridge that runs from the inner, anterior corner of the gena out toward the genal angle; *h*, hypostome, mineralized plate on anterior, ventral surface of cephalon; *hs*, hypostomal suture separating hypostome from anterior cephalic doublure; *imd*, inner margin of cephalic doublure; *mc*, macula, an ovate area situated adjacent to the outer, anterior margin of the posterior lobe of the middle body of the hypostome; *ms*, median suture was directed sagittally and connected dorsal facial and hypostomal sutures; *pa*, panderman opening, a small perforation or notch in posterolateral doublure of cephalon; *pi*, pit in anterior border furrow of cranidium, corresponding pit in doublure; *pr*, perrostral suture in olenelloids traverses ventral cephalic doublure between genal angles and bounds rostral plate; *pw*, posterior wing of hypostome, an extension of the doublure; *rp*, rostral plate, the plate isolated between the rostral and connective sutures, may be bounded along all or part of the posterior edge by the hypostomal suture (in olenelloids isolated from the cephalic doublure by the perrostral suture); *rs*, rostral suture joins distal ends of anterior branches of facial suture and bounds rostral plate anteriorly; *s*, suture, here used for the dorsal facial suture and its extension on to the doublure, or the marginal suture; *wp*, wing process, the rounded or thorn-like process on the inner surface of the anterior wing of the hypostome, that corresponds with a pit in the external surface of the wing.

In the text, the *attitude* of the hypostome refers to the angle at which the external surface was held relative to the horizontal, the posterior margin of the occipital ring having been orientated vertically in the figures. Thus a *downward attitude* refers to a downward and backward slope, an *upward attitude* to an upward and backward slope. In the descriptive section, reference of a genus to a particular family follows the *Treatise* (Moore 1959) unless otherwise noted. In discussing supra-generic relationships the termination '-oid' is given

to a particular generic name to imply a relationship with other genera above the family level, e.g. corynexochoid, ptychoparioid.

SYSTEMATIC DESCRIPTIONS OF HYPOSTOMES AND VENTRAL SUTURES

Family EODISCIDAE Raymond, 1913b

Genus PAGETIA Walcott, 1916

Pagetia ocellata Jell, 1970

Text-fig. 1

Jell (1970; 1975, pp. 50-51) has described the silicified material on which the present drawing is based. Contrary to the views expressed by Jell (1975, p. 22) the hypostome is like that of many other Cambrian trilobites in having a narrow band along the anterior edge bent to incline forward and ventrally, long anterior and shorter posterior wings. As the sagittal section shows, if the tip of the anterior wing was held close beneath the axial furrow immediately in front of the eye ridge, there would have been ample room between hypostome and glabella for the soft parts of the animal. If a flat, crescentic rostral plate were present that extended inward to a position beneath the border furrow, like that described in one agnostid by Hunt (1966), I agree with Jell that the hypostome could not have been joined to it by a hypostomal suture. There would have been a considerable gap between the anterior margin of the hypostome and the inner edge of such a rostral plate, and the downwardly flexed anterior edge of the hypostome makes it unlikely that there was any such junction. *Pagetia* is placed in the family Eodiscidae, accepting the arguments of Jell (1975, pp. 14, 30).

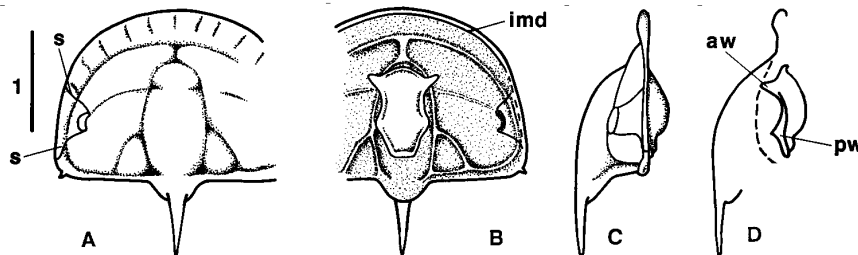
Family HOLMIIDAE Hupé, 1953a

Genus HOLMIA Matthew, 1890

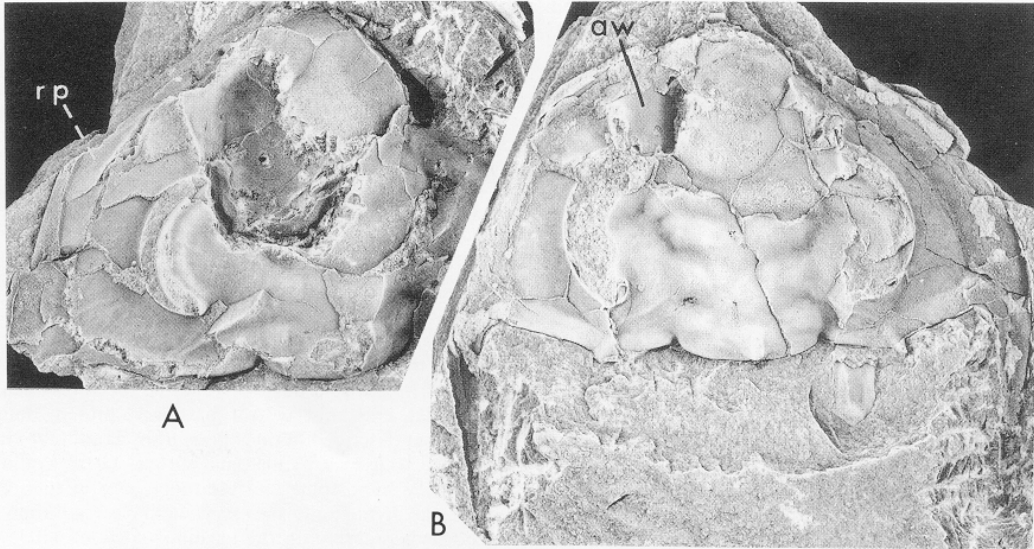
Holmia kjerulfi (Linnarsson, 1871)

Text-figs. 2 and 3

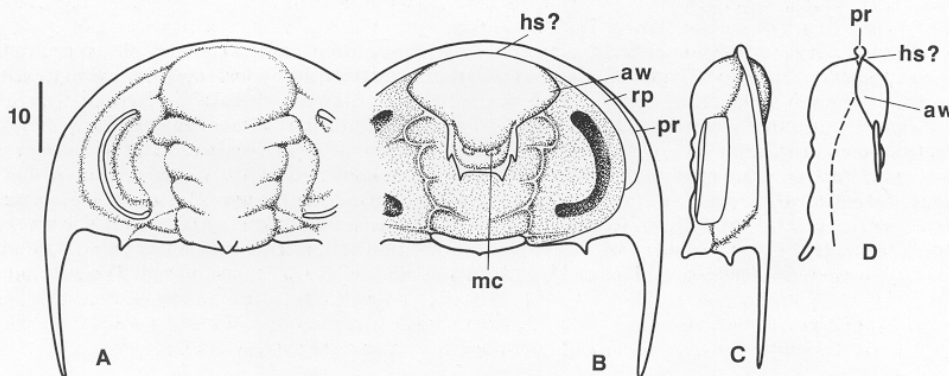
Holm (1887) and Kiaer (1916) described the morphology and ontogeny of this species, the type, from the type locality, and Bergström (1973) and Nikolaisen (1986) have described additional specimens. Two specimens figured here show the cephalon in dorsal aspect, one with part of the left anterior wing of the hypostome exposed (text-fig. 2B); in a second (text-fig. 2A), an external mould of the slightly displaced hypostome has been partially exposed. In the latter specimen a left lateral portion of the external mould of the rostral plate is preserved, and it appears that the anterior wing curved upward free of the rostral plate, so that the extremity lay close beneath the axial furrow in front of the eye ridge (text-fig. 3). Two of the specimens illustrated by Holm (1887, pl. 15, figs. 13 and 14) confirm this shape of the anterior wing, but it is concealed in Holm's (1887, pl. 14, fig. 2) restoration. The form and position of the anterior wing of the hypostome of the related genera *Schmidtellus* and *Wanneria*?, as drawn by Bergström (1973, figs. 12 and 18), were similar.



TEXT-FIG. 1. *Pagetia ocellata* Jell, 1970. Beetle Creek Formation, 1.5-2 miles north of Mount Murray, at approximately 21° 50' south latitude, 139° 58' east longitude, north-western Queensland; early Middle Cambrian. After Jell (1970, 1975). Scale bar in millimetres. See p. 578.

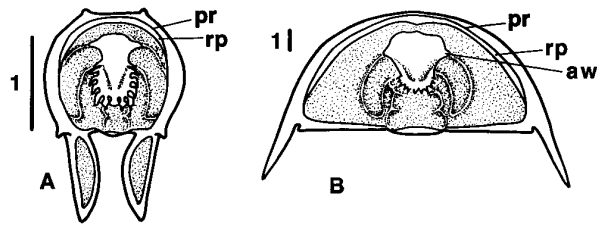


TEXT-FIG. 2. *Holmia kjerulfi* (Linnarsson, 1871). *Holmia* Shale, Tømten, Ringsaker, Norway; Lower Cambrian. A, BMNH It20673, incomplete internal mould of cephalon broken to show portion of rostral plate (rp); glabella excavated to show right side and posterior half of external mould of hypostome, $\times 2$. B, BMNH I150, internal mould of cephalon; glabella broken anteriorly to show anterior wing (aw) of hypostome, $\times 3$.



TEXT-FIG. 3. *Holmia kjerulfi* (Linnarsson, 1871). *Holmia* Shale, Tømten, Ringsaker, Norway; Lower Cambrian. After Holm (1887), Kiaer (1916), and text-fig. 2. Scale bar in millimetres. See p. 578.

Holm (1887, pl. 15, figs. 13 and 14) and Kiaer (1916, pl. 7, fig. 4) figured the hypostome attached to the rostral plate (the 'hypostomal attachments' of Kiaer), and Kiaer considered that no hypostomal suture was present (cf. Resser *in* Stubblefield 1936, fig. 7, p. 422). However, Kiaer noted the 'fine, raised line' between the two sclerites, and figured an isolated hypostome (Kiaer, 1916, pl. 7, fig. 5). Two incomplete hypostomes were figured by Nikolaisen (1986, fig. 1*d, e*), one of which shows the impressed line dividing the hypostome from the narrow (sag. and exs.) median portion of the rostral plate. The occurrence of isolated hypostomes suggests that at particular times during the holaspid period the hypostomal suture may have been functional, at others not; hence the presence of the suture is questioned in text-fig. 3.



TEXT-FIG. 4. *Olenellus gilberti* Meek, 1874. Combined Metals bed, Pioche Shale, Pioche Mining district, Lincoln County, Nevada; Lower Cambrian. A, developmental stage III, ventral view, after Palmer (1957, text-fig. 6, III, a; pl. 19, figs. 2 and 3). B, developmental stage V, ventral view, after Palmer (1957, text-fig. 7, V, e; pl. 19, figs. 16 and 18). Scale bars in millimetres.

The classification of olenelloid trilobites continues to be a matter of debate (e.g. Ahlberg *et al.* 1986); here I have followed Bergström (1973).

Family OLENELLIDAE Vogdes, 1893

Genus OLENELLUS Billings, 1861

Olenellus gilberti Meek, 1874

Text-fig. 4

The development of the cephalon, including the hypostome of *Olenellus* has been revealed by silicified material (Palmer 1957). Palmer suggested that the hypostome may have been attached to the rostral plate along an extremely short (tr.) hypostomal suture. Two of his developmental stages are drawn here (text-fig. 4) with the hypostome placed so that the anterior wing is situated below the anterior margin of the large eye lobe. It is then apparent that a gap separates the bent-down anterior edge of the hypostome from the inner margin of the rostral plate. A small median projection is present on the anterior margin of the hypostome, and the inner margin of the rostral plate has a slight median backward projection; it appears unlikely that these projections were in contact if the hypostome was situated as shown. As growth proceeded the anterior wing of the hypostome became broad and merged with the large, inflated anterior body, so that in isolated specimens the anterior margin of wing and hypostome formed a continuous curve (Walcott 1910, pl. 35, fig. 7; Palmer 1957, pl. 19, fig. 9). In some species a narrow border along this margin may have been down-curved. Attachment in large holaspids of *Olenellus* can only have been at an extremely short (tr.) suture. In *Paedumias* (= *Olenellus*, see Fritz 1972, p. 11), Walcott illustrated (1910, pl. 34, figs. 5-7; cf. Resser and Howell 1938, pl. 9, figs. 6 and 7) a narrow (tr.), presumably mineralized, median strip connecting rostral plate and hypostome. The original of Walcott's fig. 6 is similar in size to that of text-fig. 4B. Such a median strip was evidently present in some species of *Olenellus*, at least in the developmental stages.

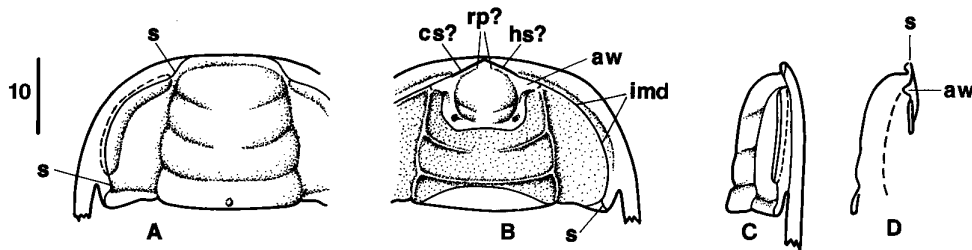
Family BATHYNOTIDAE Hupé, 1953a

Genus BATHYNOTUS Hall, 1860

Bathynotus holopygus (Hall, 1859)

Plate 52; text-fig. 5

A single species of this genus is known from only one locality in the Lower Cambrian of Vermont (Shaw 1955, p. 778). Hall's (1859, pp. 61-62, fig. 3) type specimen was recorded as missing by Resser and Howell (1938, p. 230), but twelve topotype specimens in the US National Museum include those on which Walcott (1886, pp. 191-193, pl. 31, figs. 1 and 1a; 1890, p. 646, pl. 95, figs. 1 and 1a) based his description, and the original of Rasetti's (1952, pl. 1, fig. 5) drawing of the cephalic doublure and hypostome. These and additional specimens are re-figured here as the basis for a reconstruction; the convexity shown in this reconstruction is



TEXT-FIG. 5. *Bathynotus holopygus* (Hall, 1859). Parker Slate, Parker Quarry, Georgia, north-western Vermont; Lower Cambrian. After Plate 52. The eye surface is unknown, the possible form being shown by a dashed line; see text for discussion of queries. Scale bar in millimetres. See p. 578.

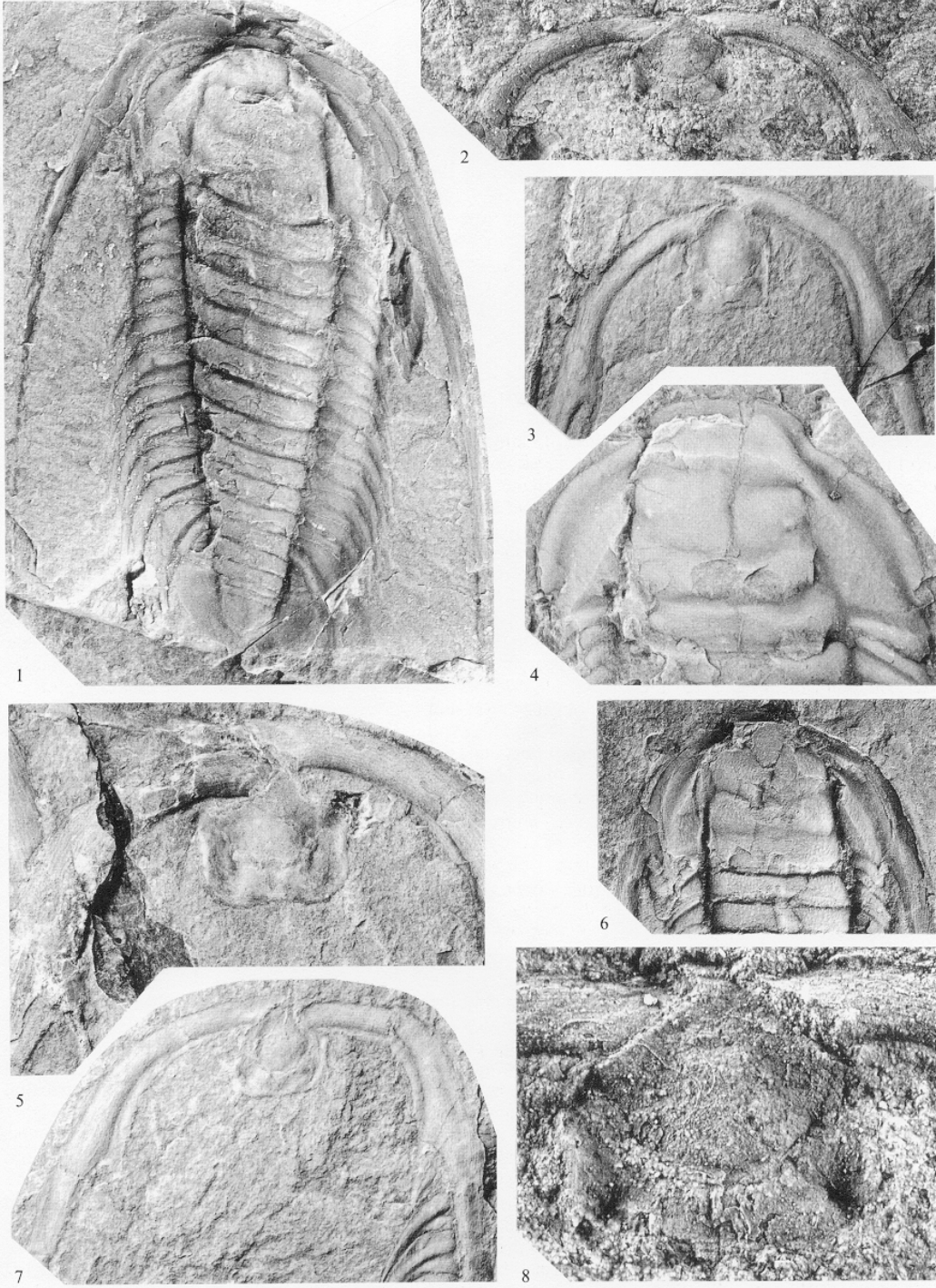
conjectural, since the specimens are partially flattened and distorted, preserved in a dark, iron-stained micaceous shale.

The best-preserved cranidium (Pl. 52, fig. 4) shows the long (exs.), curved, gently convex palpebral lobe, and the anterior branch of the suture directed inward and forward, curving, with the two branches confluent along the anterior margin. The low tubercle on the outer portion of glabella L2 is unique to this specimen; the low median occipital tubercle and granulation on the glabella are better preserved in other specimens. In a cephalon exposed from the dorsal side (Pl. 52, fig. 6) the genal regions are crushed, so that the eye surface is not preserved, hence the dashed outline of its possible form in text-fig. 5. Outside the eye lobe the external surface appears to be preserved, showing a narrow (tr.) librigenal area and a gently convex border, laterally granulose and traversed by terrace lines subparallel to the margin. These lines continued inside the anterior sutural margin of the cranidium and on the long genal spine. Specimens showing an internal mould of the broad cephalic doublure and hypostome (Pl. 52, figs. 2, 3, 5, 7) show the outline and convexity of the doublure, and the convex (ventrally), inner, marginal band that extends from the hypostome to the broadest (tr.) portion of the doublure at the genal angle. Medially this doublure is crossed by the two sections of the hypostomal suture, each directed straight outward and backward from the anterior margin, the angle between the two sections being slightly oblique.

The hypostome was subpentagonal in outline, its length (sag.) about equal to the width (tr.) at the midlength; the example (Pl. 52, fig. 3) used by Rasetti appears to have been elongated by distortion. The triangular, anterior portion of the hypostome lying between the sutures (Pl. 52, fig. 8) was traversed by terrace lines continuous with those on the doublure, directed subparallel to the margin. The middle body of the hypostome was gently convex, externally smooth, and subdivided by a faint, middle furrow. The narrow, convex lateral border, separated by a broad, shallow depression from the middle body, was continued by a less convex posterolateral and posterior border. Terrace lines traverse these borders, and a broader posterolateral area. In this area, inside the convex border, all the specimens show a subcircular depression of varying depth. At the anterolateral angle of the hypostome, adjacent to the convex inner border of the doublure and the anterior end of the lateral border, the hypostomal exoskeleton was bent dorsally and

EXPLANATION OF PLATE 52

Fig. 1-8. *Bathynotus holopygus* (Hall, 1859). Parker Slate, Parker Quarry, Georgia, north-western Vermont; Lower Cambrian. 1, USNM 15409 (255q), internal mould of dorsal exoskeleton, external mould of cephalic doublure and genal spines, dorsal view, $\times 2$; original of Walcott (1886, pl. 31, fig. 1) and of Resser and Howell (1938, pl. 12, fig. 6). 2 and 8, USNM 15409 (255p), ventral views of internal mould of cephalic doublure and hypostome, $\times 2$ and $\times 6$ respectively; original of Walcott (1886, pl. 31, fig. 1a). 3, USNM 419926, internal mould of cephalic doublure and hypostome, ventral view, $\times 2$; original of Rasetti (1952, pl. 1, fig. 5). 4, USNM 15408, internal mould of exoskeleton lacking free cheeks, dorsal view of anterior portion, $\times 2.5$. 5, USNM 419927, internal mould of cephalic doublure and hypostome, ventral view, $\times 3$. 6, USNM 15409 (255o), anterior portion of internal mould of dorsal exoskeleton, dorsal view, $\times 2$. 7, USNM 419928, internal mould of cephalic doublure and hypostome, ventral view, $\times 2$.



WHITTINGTON, *Bathynotus*

extended as the anterior wing. This wing is poorly preserved in all the specimens, but presumably extended upward and outward so that the tip lay close beneath the axial furrow at the anterolateral angle of the glabella. The acute angle between each section of the hypostomal suture and the anterior margin of the doublure shows that the two sections of this suture met at the margin in the median line.

The complete cephalon, though flattened, show that the preglabellar area was short (sag. and exs.). Walcott's original (Pl. 52, fig. 1) combines an internal mould of glabella and fixed cheeks with an external mould of the doublure, and indicates that the inner margin of the doublure lay beneath the anterior slope of the glabella. The preglabellar area of the cranidium (Pl. 52, fig. 4) appears to be of a length (sag. and exs.) such that the confluent anterior sutural branches were situated on the anterior margin of the cephalon. In the reconstruction a triple junction is therefore shown between the confluent dorsal sutures and the two sections of the hypostomal suture. Rasetti (1952, p. 890) suggested that a short (sag.) median suture might intervene between hypostomal and dorsal sutures; but if so it would have been extremely short. He went on to state that there was no rostral plate, nor was the rostral plate fused to the hypostome. However, Harrington (*in* Moore 1959, p. O67), in defining a bathynotid type of sutural pattern, thought that the rostral plate was probably fused with the hypostome, and that the inverted V-shaped suture described here as hypostomal represented a pair of connective sutures diverging backward from the anterior margin of the doublure. The triangular area enclosed by these sutures is traversed by raised terrace lines continuous with those on the adjacent cephalic doublure (Pl. 52, fig. 8). This likeness lends credence to the view that this triangular area represents the rostral plate, which was fused to a hypostome of subrectangular outline, wider (tr.) than long. Text-fig. 5 is labelled with queries because a choice between these conflicting views is hindered by lack of evidence. There is no indication, such as the change in slope in *Paradoxides* (Pl. 53, figs. 1, 3, 4) or *Fieldaspis* (Pl. 54, figs. 1 and 3) between rostral plate and hypostome, of a boundary between the supposed fused sclerites. The gently convex middle body of the hypostome projects into the triangular area enclosed by the suture, and the terrace lines appear to cross this anterior edge of the middle body. For convenience I have referred to the hypostome in the sense of Rasetti (1952), whether or not this sclerite included the rostral plate.

In the originals of Plate 52, figs. 2, 3, 8 and USNM 419925, the free cheeks and hypostome are slightly displaced from one another, but in normal relation to the thorax and pygidium, with the cranidium missing. In the original of Plate 52, fig. 5, free cheeks and hypostome are only slightly displaced from one another, but lie across the pygidium of an articulated thorax and pygidium. In USNM 419928 and 419929, free cheeks and hypostome are slightly displaced from one another, but the entire unit is inverted relative to the rest of the exoskeleton (419929), or to the thorax and pygidium (419928). These specimens are presumably all moults, and suggest that the free cheeks and hypostome were released as a unit, the dorsal facial suture and the articulation between cranidium and thorax being the most important places of opening in ecdysis. Nevertheless, the slight displacements at the two sections of the hypostomal suture show that this suture was functional.

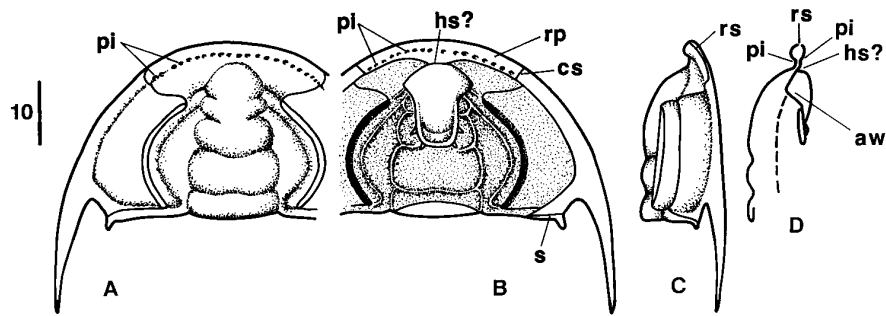
Family REDLICHIIDAE Poulsen, 1927

Genus REDLICHIA Cossman, 1902

Redlichia sp. indet.

Text-fig. 6

The transversely wide rostral plate has a row of pits in the external surface that correspond in position with pits in the border furrow and, as suggested by a photograph in Zhang *et al.* (1980, pl. 20, fig. 9), an extension that narrows posteriorly to the junction with the hypostome. This junction was along the mid-anterior margin of the hypostome; outside it the margin was continuous with that of the anterior wing; the latter curved upward and outward, the tip being close below the axial furrow in front of the eye ridge. This reconstruction is similar to that of Kobayashi and Kato (1951, pl. 5, fig. 6) in showing the anterior wing as a structure distinct from the rostral plate. Schindewolf's (1955, fig. 2) reconstruction was based on an incomplete specimen (Schindewolf and Seilacher 1955, pl. 6, fig. 8) that led him to consider that anterior wing and rostral plate were fused together. I take Öpik's photographs (1958, pl. 5, fig. 1; pl. 6, figs. 4 and 5), together with those of Zhang *et al.* (1980, pl. 14, fig. 3; pl. 20, fig. 9), as evidence of the presence of connective and rostral sutures and of the form of the anterior wing. Öpik (1958, p. 28) showed how the pits in the external surface of the rostral plate and border furrow formed interlocking cones; he considered that the junction between rostral plate and hypostome was fused. Published photographs show both rostral plate and hypostome linked together, and the two plates isolated. The latter may result from breakage, or indicate that a hypostomal



TEXT-FIG. 6. *Redlichia* sp. indet. Lower to Middle Cambrian. After Zhang *et al.* (1980) and Öpik (1958). Scale bar in millimetres. See p. 578.

suture was present; hence the question in text-fig. 6. In the related *Sardoredlichia* Rasetti, 1972, there appears to have been a hypostomal suture, but the interlocking pits of doublure and border are absent. The Chinese material of *Redlichia* appears to have been flattened, so that Öpik's (1958, pl. 3) figures were used to indicate the convexity.

The ventral structures of the emuellids (Pocock 1970) are similar to those of redlichiids, to which they are considered to be related, but the rostral plate is transversely narrower.

Family DOLEROLENIDAE Kobayashi *in* Kobayashi and Kato, 1951

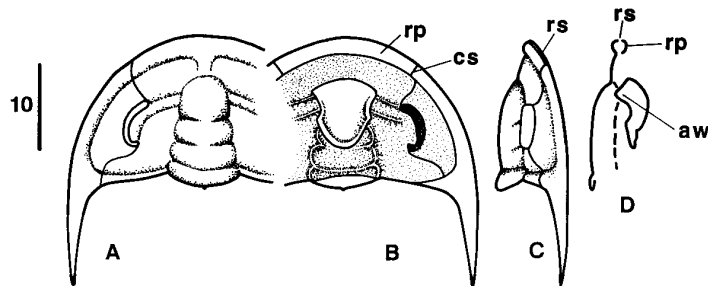
Genus DOLEROLENUS Leanza, 1949

Dolerolenus sp. indet.

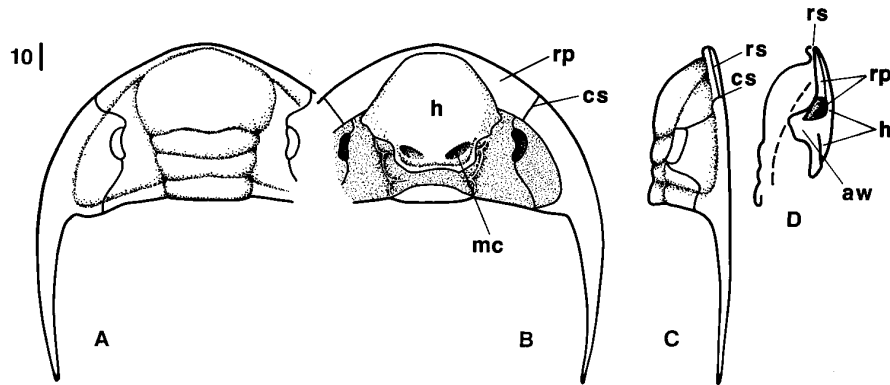
Text-fig. 7

In his description of the type species of the genus, Rasetti (1972, pp. 57–58) figured the isolated rostral plate and the hypostome; Sdzuy (1961, pp. 542–544) described specimens preserved in relief, including the hypostome, of a different species. If the tip of the anterior wing of the hypostome was situated as shown in text-fig. 7, then the hypostome could not have been attached to the wide rostral plate by a suture, but was inserted into the ventral integument to leave a wide gap between them.

A transversely wide rostral plate, the inner edge of which underlies the border furrow, is a character shared by *Dolerolenus* and *Ellipsocephalus* (Šnajdr 1958, fig. 14; pl. 7, fig. 1), but the hypostome of the latter is not known.



TEXT-FIG. 7. *Dolerolenus* sp. indet. Lower Cambrian. After Rasetti (1972) and Sdzuy (1961). Scale bar in millimetres. See p. 578.



TEXT-FIG. 8. *Paradoxides davidis* Salter, 1863. Manuels River Formation, Manuels River, Newfoundland; Middle Cambrian. After Bergström and Levi-Setti (1978, figs. 5 and 7a; pl. 3, fig. 4; pl. 5, figs. 3, 6-8) and Plate 53, figs. 1, 3, 8. Scale bar in millimetres. See p. 578.

Family PARADOXIDIDAE Hawle and Corda, 1847

Genus PARADOXIDES Brongniart, 1822

Paradoxides davidis Salter, 1863

Plate 53, figs. 1-3, 8; text-fig. 8

The dorsal exoskeleton has become well known through the work of Bergström and Levi-Setti (1978), but their illustrations of the fused rostral plate and hypostome show only the proximal portion of the anterior wing. An example from Newfoundland (Pl. 53, figs. 1-3, 8) shows the form and size of the steeply inclined anterior wing, and the rounded margin of the tip. The anterior margin of the wing is separated from the inner side of the gutter-shaped distal portion of the rostral plate. The boundary between rostral plate and hypostome is a shallow furrow that follows the change in slope between the two fused sclerites. The terrace lines (cf. Bergström and Levi-Setti 1978, pl. 3, fig. 4; pl. 5, fig. 7) are continuous across the boundary. Text-fig. 8 shows that the tip of the anterior wing, which lay close to the vertical, inner portion of the rostral plate, must also have been situated close beneath the ventrally projecting axial furrow (cf. Bergström and Levi-Setti 1978, pl. 9, fig. 3, where the same relationship is seen). The convexity of the hypostome and rostral plate is shown here (Pl. 53, figs. 3 and 8) and examples of other species (Sdzuy 1967, pl. 2, fig. 9; Westergård 1936, pl. 3, fig. 1; pl. 6, fig. 4; pl. 9, fig. 3) have been used to suggest the convexity of the cephalon dorsally.

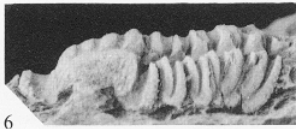
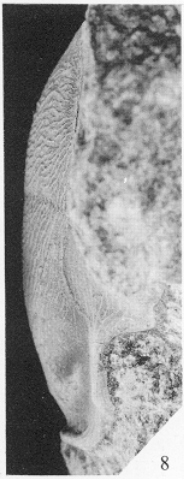
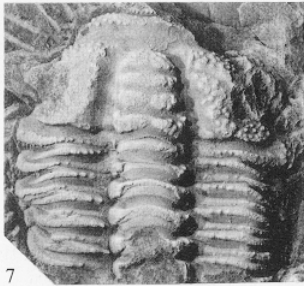
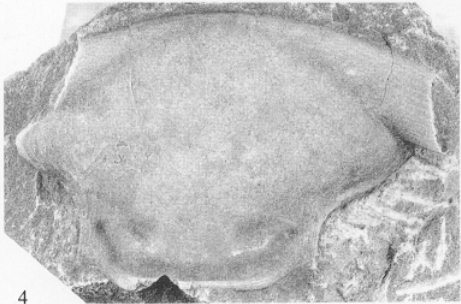
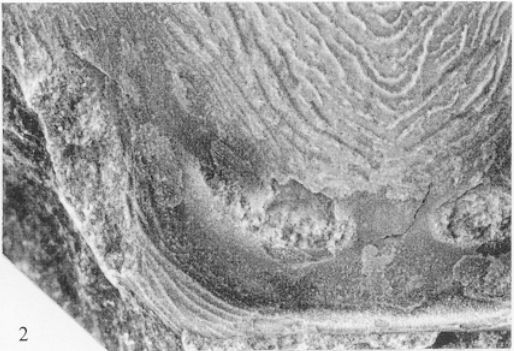
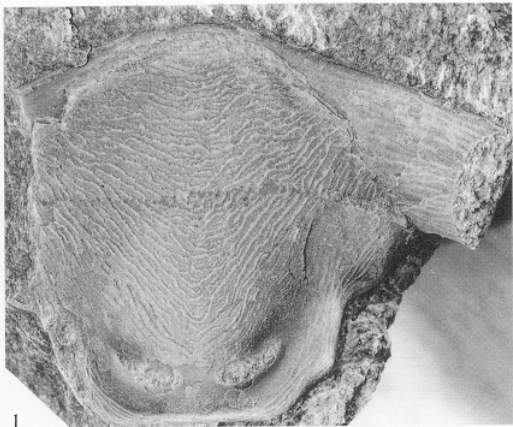
Šnajdr (1958, pp. 102-103; Pl. 53, fig. 4 shows a Bohemian example) regarded the fusion of rostral plate and hypostome as diagnostic of *Paradoxides*, but in other species attributed to this genus by Westergård (1936, p. 33, footnote) a hypostomal suture is developed. Such species are placed in the new genera (or subgenera) proposed by Šnajdr (1958), but how these names are to be used is disputed (cf. Sdzuy 1967,

EXPLANATION OF PLATE 53

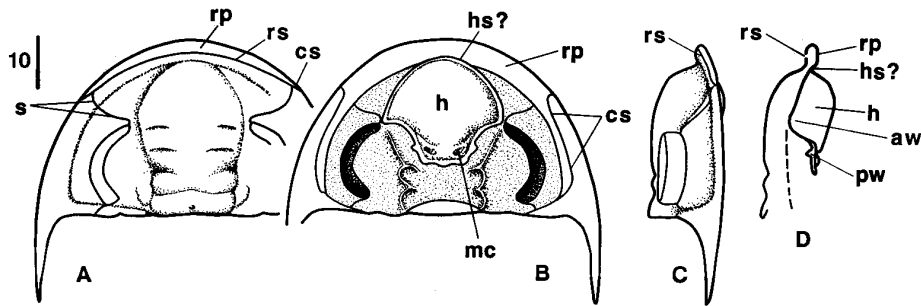
Figs. 1-3, 8. *Paradoxides davidis* Salter, 1863. Manuels River Formation, 1-5 miles east of Elliot Cove and north of Foster's Point, Random Island, Newfoundland; Middle Cambrian. SM A.105203, rostral-hypostomal plate. 1 and 8, ventral and left lateral views, $\times 3$. 2, enlargement of right macula, $\times 7$. 3, oblique view, $\times 5$.

Fig. 4. *Paradoxides gracilis* (Boeck, 1827). Jince Formation, Jince, Czechoslovakia; Middle Cambrian. SM A.49780, internal mould of incomplete rostral-hypostomal plate, ventral view, $\times 3$.

Figs. 5-7. *Sao hirsuta* Barrande, 1846. Skryje Formation, Skryje, Czechoslovakia; Middle Cambrian. SM X.11469, internal mould of cranium and anterior thoracic segments; anterior, left lateral, and dorsal views respectively, $\times 3$.



WHITTINGTON, *Paradoxides*, Sao



TEXT-FIG. 9. *Xystridura* sp. indet. Middle Cambrian. After Öpik (1975) and Palmer and Gatehouse (1972). Scale bar in millimetres. See p. 578.

p. 94; Bergström and Levi-Setti 1978, p. 15; Šnajdr 1985, p. 169). Here I follow Šnajdr's diagnosis of *Paradoxides*.

Family XYSTRIDURIDAE Whitehouse, 1939

Genus XYSTRIDURA Whitehouse, 1936

Xystridura sp. indet.

Text-fig. 9

Öpik (1975) illustrated in detail many species of *Xystridura* (and its subgenera), including the rostral plate and the isolated hypostome (his figs. 8 and 10; pl. 2, figs. 2 and 4; pl. 9, fig. 3; pl. 13, fig. 1; pl. 22, fig. 4; pl. 32, fig. 2), and examples of the two plates in position relative to each other (his pl. 15, fig. 3; pl. 30, fig. 2). Öpik (1975, pp. 35-36) asserted that in *X. (Inosacotes) browni* no hypostomal suture was present in the holaspis, the hypostome being fused to the rostral plate; a hypostomal suture in *Xystridura* is thus shown with question in text-fig. 9. He described the tip of the large anterior wing as braced against the axial furrow, and the much smaller projection of the presumed posterior wing. The anterior margin of the hypostome was bent to slope downward and forward; a small macula was developed. All Öpik's material was flattened, so that the convexity shown in text-fig. 9 is somewhat conjectural, but supported by specimens from Antarctica described by Palmer and Gatehouse (1972, pl. 2, figs. 18, 20, 23, 25). Öpik (1975, pp. 25-26) regarded *Xystridura* as related to *Paradoxides*, remarking on the unusual extension of the rostral plate on to the dorsal surface, and the olenelloid-like extension of the rostral plate rearward. The form of the hypostome supports this view of their relationships.

Family ZACANTHOIDIDAE Swinnerton, 1915

Genus FIELDASPIS Rasetti, 1951

Fieldaspis celer (Walcott, 1917)

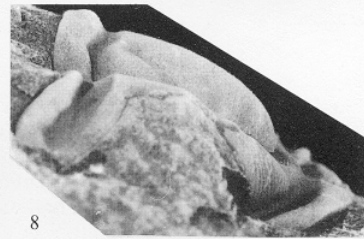
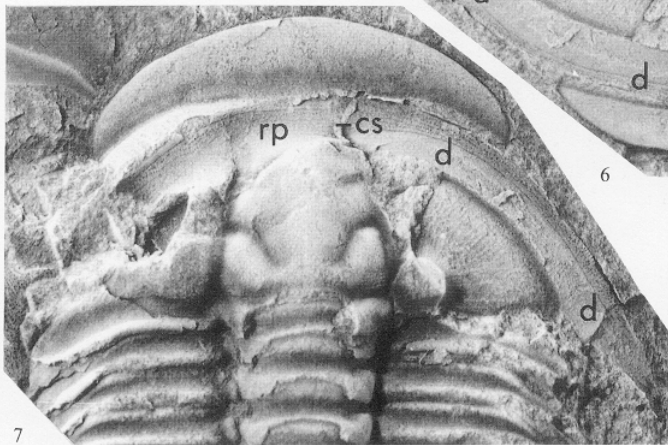
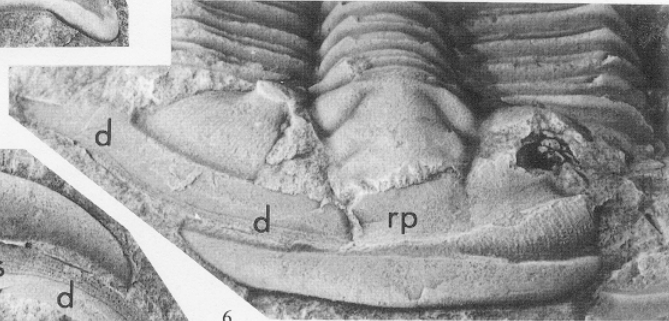
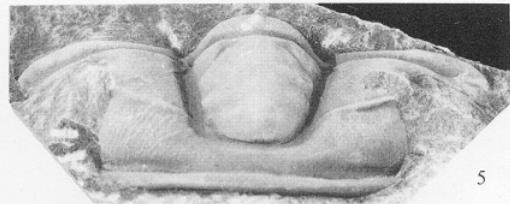
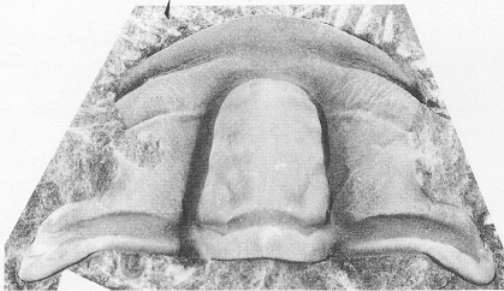
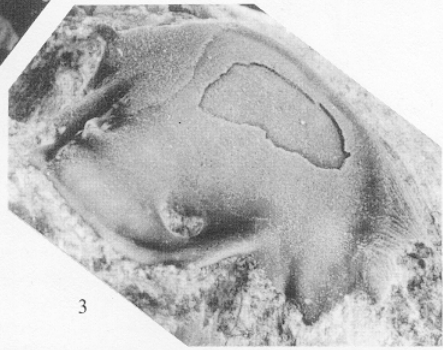
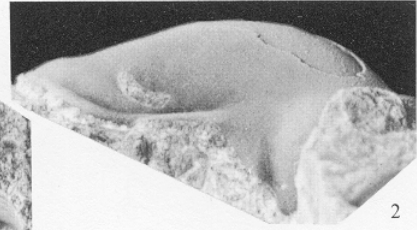
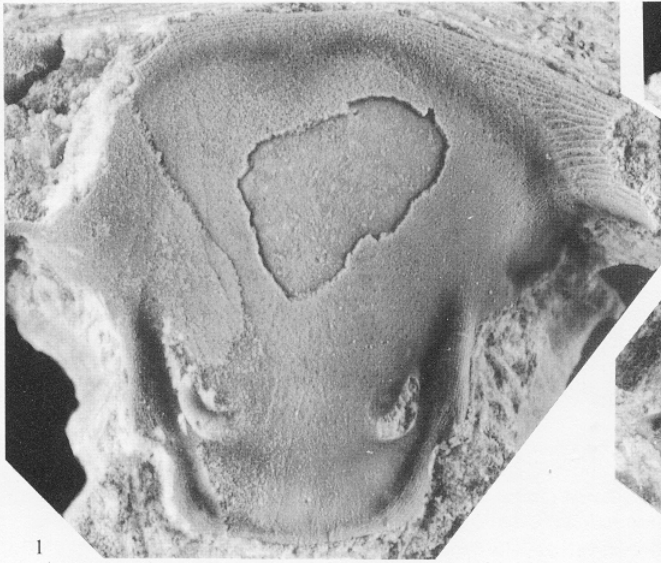
Plate 54, figs. 1-3; text-fig. 10

Rasetti (1957, pp. 957-958, pl. 118, figs. 1-8; text-fig. 4) showed the long, steeply upwardly directed anterior wing of the hypostome. He considered that the anterior wing was part of the rostral plate and hence not

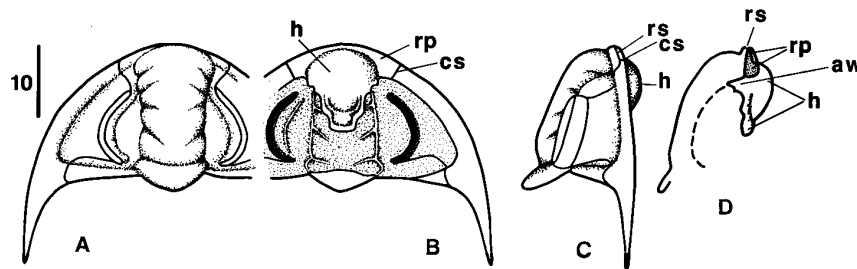
EXPLANATION OF PLATE 54

Figs. 1-3. *Fieldaspis celer* (Walcott, 1917). Mount Whyte Formation, Mount Field, British Columbia, locality W28fg of Rasetti (1957); Middle Cambrian. BMNH It4570, rostral-hypostomal plate. 1, ventral view, $\times 8$. 2 and 3, left lateral and oblique views, $\times 6$.

Figs. 4-8. *Ptychoparia striata* (Emmrich, 1839). Jince Formation, Vinice, near Jince, Czechoslovakia; Middle Cambrian. 4, 5, 8, SM A.51043a, internal mould of cranium, dorsal, anterior, and right lateral views respectively, $\times 3$. 6 and 7, SM A.1574, internal mould, cephalon broken to show displaced external mould of doublure (d), connective suture (cs), and rostral plate (rp), anterior and dorsal views respectively, $\times 3$.



WHITTINGTON, *Fieldaspis*, *Ptychoparia*



TEXT-FIG. 10. *Fieldaspis celer* (Walcott, 1917). Mount Whyte Formation, Mount Field, British Columbia; Middle Cambrian. After Rasetti (1957) and Plate 54, figs. 1-3. Scale bar in millimetres. See p. 578.

homologous with that of other trilobites. A topotype specimen of the rostral-hypostomal plate collected by Rasetti (Pl. 54, figs. 1-3) shows the gutter-shaped lateral portion of the rostral plate to be continuous with a convex, narrower (sag. and exs.) median portion. A shallow furrow at a change in slope indicates the fused boundary between rostral plate and hypostome; a shallow median indentation is present at the anterior margin of the hypostome. The doublure of the free cheek is unknown, but I assume that it was convex and anteriorly similar in form to the lateral portion of the rostral plate. The anterior wing of the hypostome is triangular in outline and the anterior margin straight, with the wing meeting the inner, vertical portion of the rostral plate at almost a right angle. At about half the length of the posterior margin of the wing it is crossed by a short, sharp flexure; the tip of the wing is rounded and there is no pit in the external surface that would indicate the presence of a wing process. Rasetti's text-fig. 4 suggests the presence of such a pit, rather than the flexure. The middle furrow, strongly convex macula, and gently inflated posterior lobe of the middle body are shown by the present specimen. It is slightly smaller, and the middle body is considerably less convex, than Rasetti's example. The present specimen is partially exfoliated (completely so in the mid-region of the anterior lobe of the middle body), but shows the prominent terrace lines on the lateral portion of the rostral plate, and fainter ones on the hypostome. The change in intensity of the terrace lines takes place at the anterior edge of the furrow between rostral plate and hypostome. Between the terrace lines there are minute pits. The structure of the rostral plate in *Fieldaspis* is thus like that in *Paradoxides* (Pl. 53, figs. 1-4, 8; text-fig. 8), and the anterior wing of the hypostome homologous with that of other trilobites. The tip of the wing (text-fig. 10) would have extended up to a point just beneath the axial furrow, immediately in front of where it was met by the eye ridge.

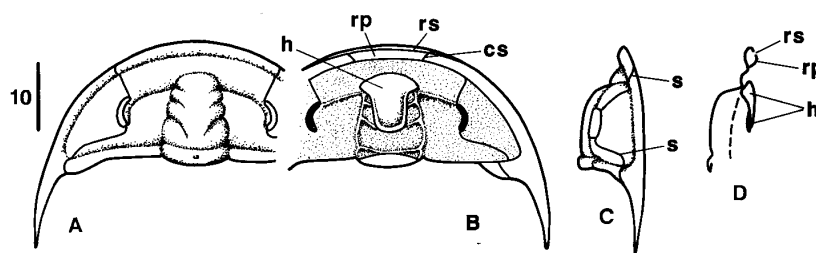
Rasetti (1951, 1957) placed *Fieldaspis* in the Dolichometopidae, but in 1959 (*in* Moore, p. O227) in Zacanthoididae. In the *Treatise* (Moore 1959, p. O217) all trilobites placed in the Order Corynexochida are said to have the rostral plate and hypostome fused. It is by no means certain that this is so (Öpik 1982, pp. 6-7), and in his conception of the corynexochoid family Dolichometopidae Öpik includes the subfamily Horonastinae, which is characterized by having the hypostome and rostral plate as separate sclerites. Here I retain the family assignment of *Fieldaspis* used in the *Treatise*.

Family PTYCHOPARIIDAE Matthew, 1888
Genus PTYCHOPARIA Hawle and Corda, 1847

Ptychoparia striata (Emmrich, 1839)

Plate 54, figs. 4-8; text-fig. 11

Šnajdr (1958, pp. 185-190) figured specimens which showed the doublure of the cephalon, isolated hypostomes, and one hypostome exposed almost in place. Additional specimens (Pl. 54, figs. 4-8) show the doublure of the displaced free cheek, the rostral plate, and the connective suture, and include a cranidium which shows the convexity and that the rostral suture ran along the doublure just inside the anterior margin. The doublure was gently convex, widest (sag. and exs.) anteriorly, with the inner edge underlying the border furrow. It was crossed by the connective suture at a position that lay well outside the projected line of the axial furrow, giving a relatively wide (tr.) rostral plate. The hypostome (Barrande 1852, pl. 14, fig. 3; Šnajdr 1958, pl. 39,



TEXT-FIG. 11. *Ptychoparia striata* (Emmrich, 1839). Jince Formation, Vinice, near Jince, Czechoslovakia; Middle Cambrian. Modified from Šnajdr (1958) and after Plate 54, figs. 4–8. Scale bar in millimetres. See p. 578.

fig. 4; pl. 40, fig. 5) appears to have been moderately convex, and the lateral border well defined. The anterior wing is poorly known, but assuming it was situated beneath the axial furrow immediately in front of the eye ridge (text-fig. 11), there was a considerable gap between the edges of the rostral plate and the hypostome. This accords with Barrande's restoration (1952, pl. 2B, fig. 26) and some specimens of Šnajdr (1958, pl. 39, fig. 7; pl. 40, fig. 3) but not his fig. 40 (in which the hypostome is portrayed as joined to the rostral plate at a hypostomal suture). This type of ventral structure of the cephalon—a wide (tr.) rostral plate, with the hypostome not being attached by a hypostomal suture but inserted into the ventral cuticle some distance behind the rostral plate—has been regarded (Rasetti 1951, p. 140; Öpik 1963, p. 77) as a basic character of ptychoparioids.

Family CONOCORYPHIDAE Angelin, 1854
Genus CONOCORYPHE Hawle and Corda, 1847

Conocoryphe sulzeri (Schlotheim, 1823)

Plate 55, figs. 1, 3, 6, 7; text-fig. 12

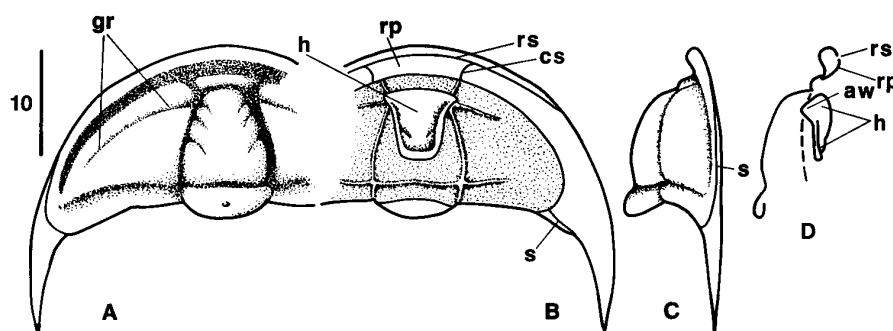
Šnajdr (1958, fig. 32) showed the cephalon of this type species and its doublure in dorsal view. The present cranidium (Pl. 55, figs. 1, 3, 6) shows the course of the suture posterolaterally and, though partially flattened, gives some idea of the convexity; other species illustrated by Sdzuy (1961, pl. 31, fig. 1; 1967, pl. 9, fig. 9) are better in this latter respect. The cephalon (Pl. 55, fig. 7) shows how the anterior doublure, striated with concentric terrace lines, extended some distance horizontally inward before being cut by the rostral suture. The displaced right free cheek shows the steeply upturned, smooth inner portion of the doublure that extended upward under the border furrow to the margin of the gena; it terminates adaxially at the convexly curved connective suture. The rostral plate was similarly shaped, and terminated under the anterior margin of the convex preglabellar field (Šnajdr 1958, pl. 34, fig. 3). The anterior margin and anterior wing of the hypostome (Šnajdr 1958, pl. 34, figs. 4, 8, 9) are not well known, but if it was situated so that the anterior wing lay below the axial furrow immediately in front of the genal ridge, it appears (text-fig. 12) that it was not joined by a hypostomal suture to the rostral plate, but inserted into the ventral integument above and behind the rostral plate. Šnajdr (1958, fig. 32) did not show the hypostome, but this arrangement is similar to that shown (Šnajdr 1958, fig. 35) for the related *Ctenocephalus*, which has a considerably longer (sag.) preglabellar field. Barrande (1852, pl. 2B, fig. 24) interpreted the hypostome of *Conocoryphe* as joined by a hypostomal suture to the rostral plate, but my restoration (that takes account of the convexity of the cephalon) makes this unlikely and accords with the view of Poulsen (*in* Moore 1959, p. Q242).

Family SOLENOPLEURIDAE Angelin, 1854
Genus SAO Barrande, 1846

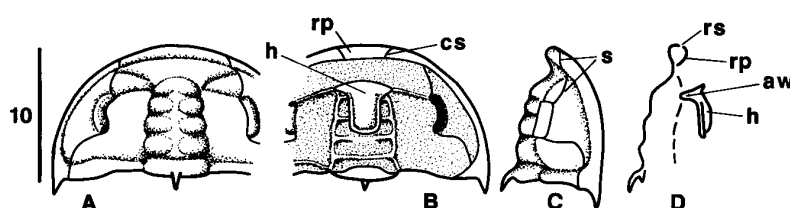
Sao hirsuta Barrande, 1846

Plate 53, figs. 5–7; text-fig. 13

Šnajdr's (1958, pls. 43–45) many illustrations of this type species include two of specimens showing an external mould of the hypostome exposed beneath the broken glabella, and internal moulds of the isolated



TEXT-FIG. 12. *Conocoryphe sulzeri* (Schlotheim, 1823). Jince Formation, Jince, Czechoslovakia; Middle Cambrian. After Šnajdr (1958) and Plate 55, figs. 1, 3, 6, 7. Scale bar in millimetres. See p. 578.

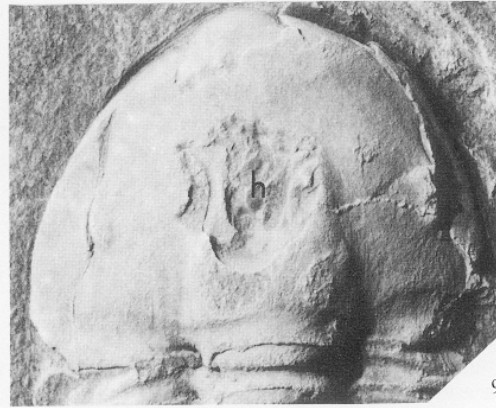
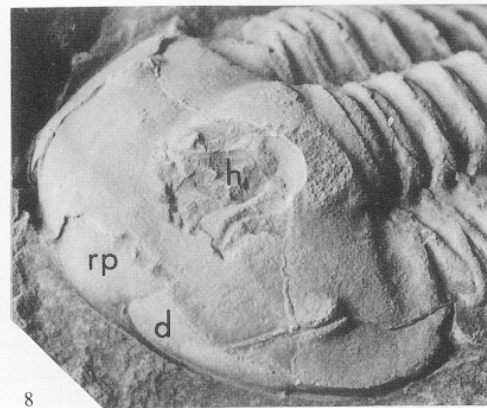
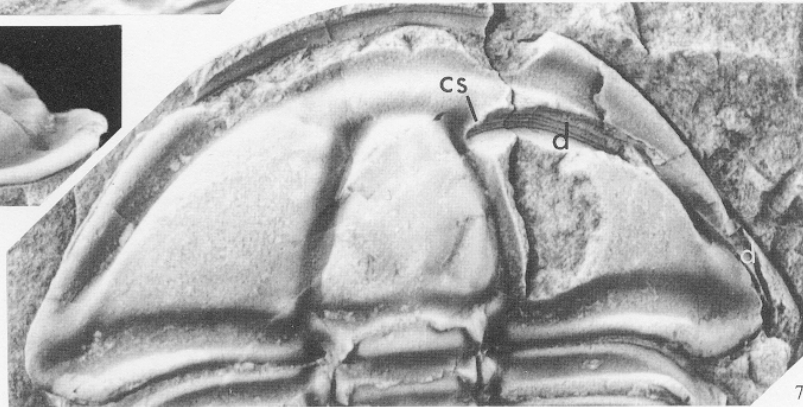
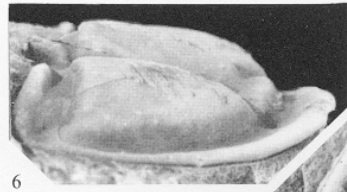
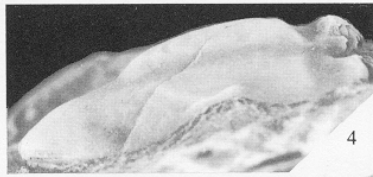
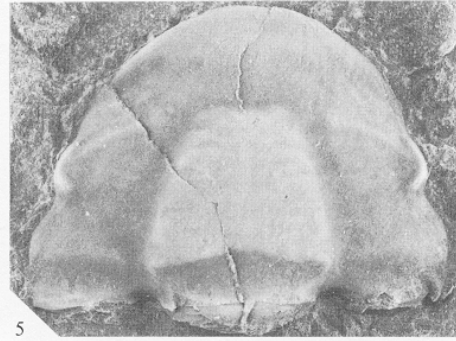
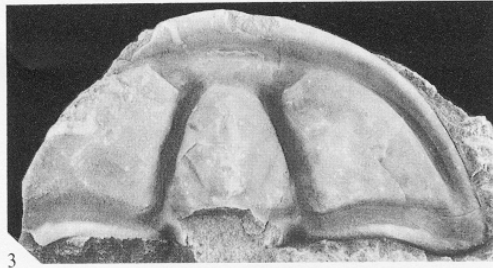
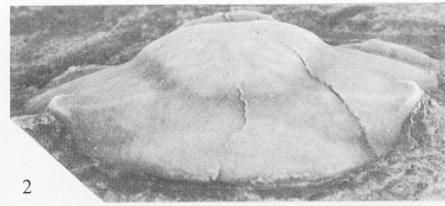


TEXT-FIG. 13. *Sao hirsuta* Barrande, 1846. Skryje Formation, Skryje, Czechoslovakia; Middle Cambrian. After Šnajdr (1958) and Plate 53, figs. 5-7. Small spines and tubercles on external surface omitted. Scale bar in millimetres. See p. 578.

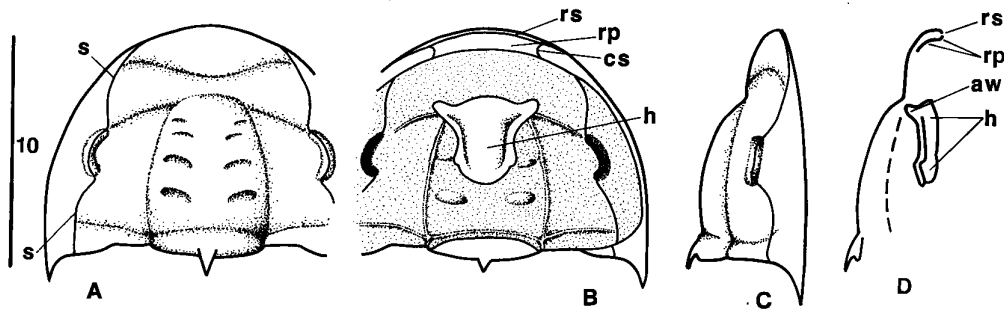
hypostome. The largest isolated hypostome (Šnajdr 1958, pl. 45, fig. 13), a ventral view, gives a suggestion of the convexity and shows the anterior wing and the downward and forward sloping anterior edge of the wing and middle body. The only lateral view of the cephalon is Barrande's (1852, pl. 7, fig. 29), that shows the convexity and the upwardly arched outline of the border that is confirmed by the original of Plates 53, figs. 5-7. An anterolateral view (Whittington 1957a, pl. 115, fig. 22) of a somewhat crushed specimen revealed the external mould of the cephalic doublure and rostral plate. The lateral and anterior borders and doublure together formed a tubular border to the cephalon, with the inner edge of the doublure curving up beneath the outer edge of the border furrow; the curving connective suture crossed the doublure in the projected line of the axial furrow. Šnajdr (1958, fig. 45) did not include the hypostome in his reconstruction, but it seems evident (text-fig. 13) that, because of the convexity and anterior arching of the cephalon, the hypostome was inserted into the ventral integument some distance behind and below the inner edge of the rostral plate.

EXPLANATION OF PLATE 55

- Figs. 1, 3, 6, 7. *Conocoryphe sulzeri* (Schlotheim, 1823). Jince Formation, Jince, Czechoslovakia; Middle Cambrian. 1, 3, 6, SM A.51042, internal mould of cranidium, anterior, dorsal, and right lateral views respectively, $\times 3$. 7, SM X.11477, internal mould, cephalon broken to show doublure (d) anteriorly and laterally, of displaced free cheek (cs, connective suture), dorsal view, $\times 4$.
- Figs. 2, 4, 5, 8, 9. *Agraulos ceticephalus* (Barrande, 1846). Skryje Formation, Skryje, Czechoslovakia; Middle Cambrian. 2, 4, 5, SM X.11475, internal mould of cranidium, anterior, left lateral, and dorsal views respectively, $\times 4-5$. 8 and 9, SM X.11474, internal mould of cephalon broken to show external mould of doublure (d) and rostral plate (rp) separated by the connective suture; glabella excavated to reveal external mould of incomplete hypostome (h); oblique and dorsal views respectively, $\times 7$.



WHITTINGTON, *Conocoryphe*, *Agraulos*



TEXT-FIG. 14. *Agraulos ceticephalus* (Barrande, 1846). Skryje Formation, Skryje, Czechoslovakia; Middle Cambrian. After Plate 55, figs. 2, 4, 5, 8, 9. Scale bar in millimetres. See p. 578.

Family AGRAULIDAE Raymond, 1913a
Genus AGRAULOS Hawle and Corda, 1847

Agraulos ceticephalus (Barrande, 1846)

Plate 55, figs. 2, 4, 5, 8, 9; text-fig. 14

An internal mould of the cephalon and part of the thorax (Pl. 55, figs. 8, 9) has been prepared to show the external mould of an incomplete hypostome below the glabella. The anterior wing has a convex border along the posterior margin, continuous with the lateral border of the middle body; posteriorly this body is convex, sloping almost vertically to the narrow posterior border. Barrande (1852, pl. 10, figs. 12 and 13) illustrated a much smaller example as having a broad, flat posterolateral border; despite the incompleteness, there seems no doubt that in the present example the inflated posterior portion of the middle body had a steep posterior slope and narrow border. Also preserved is an external mould of the cephalic doublure that is narrow and flat adjacent to the outer margin and traversed by concentric terrace lines; a much wider inner portion extended dorsally close beneath the outer slope of the genal region and preglabellar area. The connective suture is curved convexly adaxially, the rostral plate having a narrow (sag.), flat outer portion and a wider inner portion that bulged forward beneath the preglabellar area. An internal mould of a cranidium (Pl. 55, figs. 2, 4, 5) shows that the rostral suture was situated close to the anterior margin of the doublure, and other features, including the faint impressions of glabellar furrows and the eye ridge. Text-fig. 14 shows that the hypostome cannot have been attached by a suture to the rostral plate; Šnajdr (1958, pl. 37, figs. 8 and 13) figured the rostral plate and a poorly preserved hypostome, but did not show the latter in his reconstruction (fig. 37).

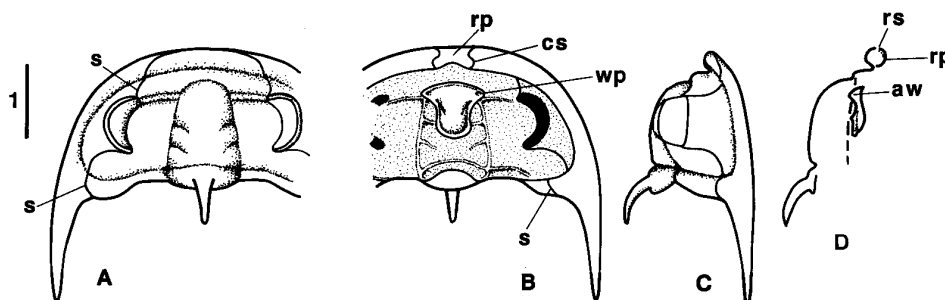
I have followed Henningsmoen (*in* Moore 1959, p. O278) in using the family Agraulidae; Šnajdr (1958) used a broader classification, while Öpik (1961, p. 142) stressed the similarities between *Agraulos* and *Ellipsocephala* (cf. Ahlberg and Bergström 1978, pp. 9-11).

Family MENOMONIIDAE Walcott, 1916
Genus BOLASPIDELLA Resser, 1937

Bolaspidella sp. indet.

Text-fig. 15

The reconstruction is based primarily on silicified material of the type species described by Robison (1964, pp. 552-554, pl. 88, figs. 16-21); other species were described by him (1964, pp. 554-555, pl. 88, figs. 7-15; pl. 89, figs. 1-11, 14-17), and one by Rasetti (1967, pp. 94-96, pl. 13, figs. 17-30). The hypostome is notable in that the pit in the external surface of the anterior wing formed a wing process. The posterior margin of the rostral plate curved convexly forward more strongly than the anterior margin of the hypostome, which bounded the ventrally inclined anterior edge of the hypostome and anterior wing. Robison gave no lateral views of cranidia, but that of Rasetti (1967, pl. 13, fig. 18) suggests how steeply the preglabellar area descended to the border furrow. When a hypostome of appropriate size is placed with the wing process close



TEXT-FIG. 15. *Bolaspidella* sp. indet. Middle to Upper Cambrian (Robison 1976, text-fig. 4). After Robison (1964) and Rasetti (1967). Scale bar in millimetres. See p. 578.

below the axial furrow, immediately in front of the eye ridge, it appears unlikely that the hypostome was attached by a suture to the rostral plate; and the curvature of the opposing edges does not suggest such an attachment.

Family CERATOPYGIDAE Linnarsson, 1869

Genus PROCERATOPYGE Wallerius, 1895

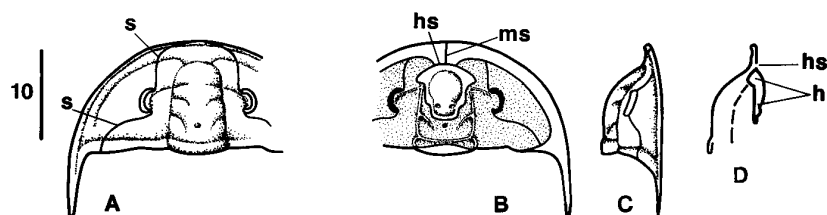
Proceratopyge sp. indet.

Text-fig. 16

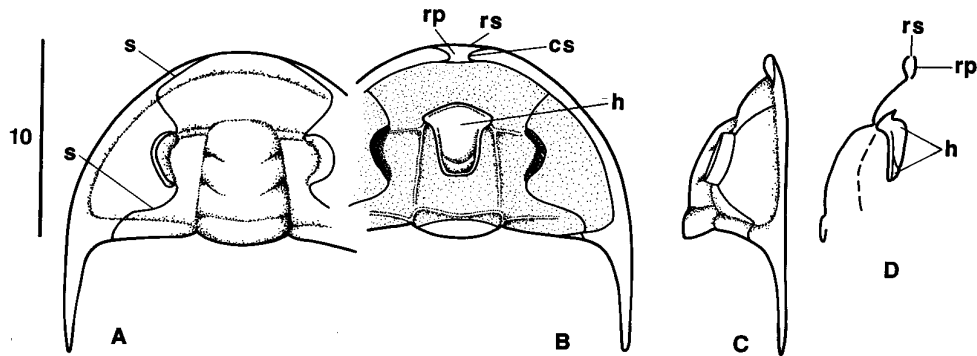
The hypostome of the specimen figured by Rushton (1983, pl. 19, fig. 12; text-fig. 6) is poorly preserved and displaced, but the wide (sag. and exs.) doublure of the cephalon in front of it, and the median suture, are preserved. Text-fig. 16 is based on this specimen, supported by Westergård's (1947, pl. 2, figs. 1-5, 9) figures, and the assumption that the hypostome was like undetermined specimens thought to be of a ceratopygid and figured by Shergold (1980, p. 89, pl. 20, fig. 10; 1982, p. 53, pl. 7, fig. 8). It is also assumed that the hypostome was attached at a hypostomal suture to the backward-projecting doublure. Illustrations by Jago (1987, pl. 26, figs. 3, 5, 6; pl. 27, figs. 7 and 8) support this reconstruction. Species of *Diceratopyge* are like those of *Proceratopyge*, and an example figured recently (Lu and Qian 1983, pl. 10, fig. 12) has a partial external mould of the hypostome exposed beneath the glabella, attached at the suture to the doublure anteriorly, which is crossed by the median suture.

It has been argued (Fortey and Owens in Owens *et al.* 1982, pp. 14-15, pl. 2, figs. *d-f, h-j*; cf. Shergold in Shergold and Sdzuy 1984, pp. 94-95) that *Macropyge* is a ceratopygid, and the form of the hypostome, its attachment to the doublure, and the median suture support this view. An exceptional example of *Macropyge*, showing the cephalic doublure and hypostome, has been figured by Lu and Qian (1983, pl. 13, fig. 3).

Poulsen (in Moore 1959, p. O363) stated that in the ceratopygid *Hysterolenus* the hypostome was probably fused with the rostral plate. This statement may be based on Moberg and Segerberg's (1906, pl. 4, fig. 36) illustration of the hypostome of the type species *H. toernquisti*. I suggest that Moberg and Segerberg were



TEXT-FIG. 16. *Proceratopyge* sp. indet. Late Middle to Upper Cambrian, and Tremadoc. After Rushton (1983) and Westergård (1947). Scale bar in millimetres. See p. 578.



TEXT-FIG. 17. *Aphelaspis* sp. indet. Upper Cambrian (Dresbachian). After Rasetti (1965) and Palmer (1962a, 1965). Scale bar in millimetres. See p. 578.

outlining the anterior border and anterior wings of an incomplete specimen of the hypostome, and not a 'rostral plate', so that Poulsen's supposition is unlikely to be correct.

Family PTEROCEPHALIDAE Kobayashi, 1935

Genus APHELASPIS Resser, 1935

Aphelaspis sp. indet.

Text-fig. 17

The hypostome, free cheek, and probable rostral plate were illustrated by Palmer (1962a, pl. 6, figs. 15-19; 1965, pl. 8, figs. 16, 17, 21, 24); Rasetti's (1965) many illustrations include the type species (pl. 18, figs. 10-20), lateral views of cranidia, and external views of hypostomes. My reconstruction (text-fig. 17) is based on these figures, and when the hypostome is positioned as shown it cannot have been attached by a suture to the rostral plate.

The rostral plate and hypostome of *Cedaria* (Palmer 1962a, pl. 6, figs. 13 and 14), type genus of the Cedariidae, were like those of *Aphelaspis*, with a similar wide gap between the two plates. Middle Cambrian trilobites that had a similar rostral plate, but in which the hypostome is unknown, are *Elrathia* (Robison 1964, pl. 85) and *Modocia* (Robison 1964, pl. 87, figs. 5-19); the rostral plate of the latter has a pointed median projection on the posterior edge.

Family LONCHOCEPHALIDAE Hupé, 1953b

Genus WELLERASPIS Kobayashi, 1935

Welleraspis swartzi (Tasch, 1951)

Text-fig. 18

Rasetti (1954, p. 601, pl. 62, figs. 11-14; text-fig. 1b, c) diagnosed the genus and described the material on which the reconstruction is based. His ventral view of the free cheek shows the course of the connective suture and the genal spine; the hypostome is described as having an angulate anterior outline, and the anterior edge is bent to slope downward and forward. When the tip of the anterior wing is placed as in text-fig. 18 it appears probable that the median, anterior margin of the hypostome may have been joined by a hypostomal suture to the posterior edge of the narrow (tr.) rostral plate.

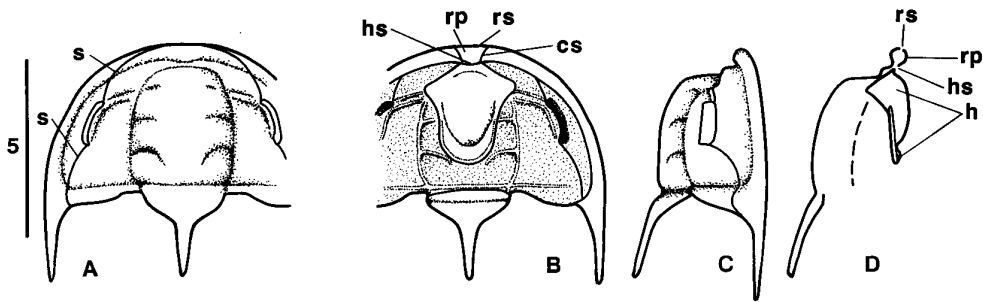
Family OLENIDAE Burmeister, 1843

Genus PARABOLINELLA Brögger, 1882

Parabolinella sp. indet.

Text-fig. 19

Henningsmoen (1957, pp. 135-137, pl. 12, figs. 1-5) described the cranidium, free cheek, and hypostome of the type species, and Ludvigsen (1982, pp. 58-65, figs. 48, 49, 50a-o, q, r) silicified cranidia, free cheeks



TEXT-FIG. 18. *Welleraspis swartzi* (Tasch, 1951). Warrior Limestone, road cut 2.5 miles east of Bedford, Pennsylvania; Upper Cambrian (Dresbachian). After Rasetti (1954). Scale bar in millimetres. See p. 578.

joined by the median, channel-form section of the doublure, and the hypostome of other species. Text-fig. 19 is based on specimens in Ludvigsen's fig. 48, and if the hypostome is placed as shown, it cannot have been connected by a suture to the inner, anterior edge of the doublure. Further, this inner edge of the doublure (Ludvigsen 1982, p. 60) was finely toothed, each tooth connecting with a pit in the anterior border furrow. The anterior lobe of the middle body of the hypostome was convex, with the triangular anterior wing sloping steeply upward; whether or not this wing bore a wing process is not shown by any of the illustrations.

In their diagnosis of Olenidae, Nikolaisen and Henningsmoen (1985, p. 2) stated that the hypostome was not attached by a suture to the cephalic doublure; they considered that in most species connective sutures were absent (cf. Henningsmoen 1957, pp. 90-92). An exception is that Rushton (1983, p. 124, pl. 17, figs. 2 and 3) has recognized the rostral plate in a species of *Olenus*.

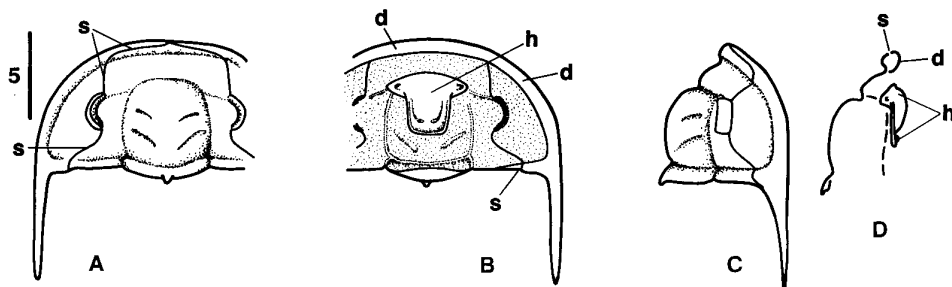
Family EUREKIIDAE Hupé, 1953b

Genus EUREKIA Walcott, 1916

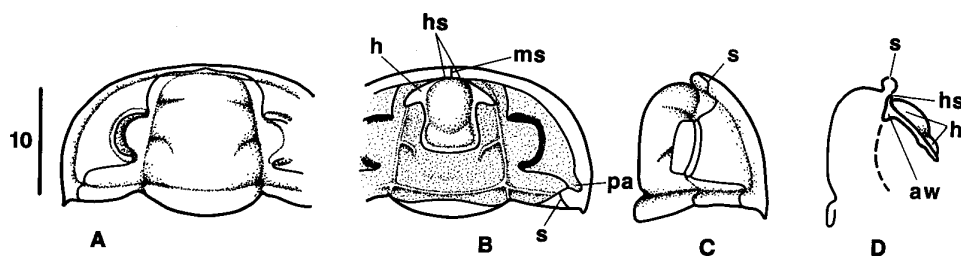
Eurekia ulrichi (Rasetti, 1945)

Text-fig. 20

Taylor (1978) redescribed the type and other species of *Eurekia*, and reconstructed one species showing (without comment) a median suture extending downward from where the two anterior branches met on the outer edge of the border at an oblique angle. The existence of such a suture was not well documented by the specimens, but a silicified specimen illustrated by Ludvigsen (1982, fig. 61g) shows the truncated sutural edge of the doublure of the free cheek. Two other specimens in exterior view (Ludvigsen, 1982, fig. 61h, i) suggest that this suture may be median, and not bounding a narrow (tr.) rostral plate. Text-fig. 20 is based on these and other specimens in Ludvigsen's fig. 61, which includes examples of the hypostome. The anterior edge of



TEXT-FIG. 19. *Parabolinella* sp. indet. Upper Cambrian (Trempealeau and Tremadoc). After Henningsmoen (1957) and Ludvigsen (1982). Scale bar in millimetres. See p. 578.



TEXT-FIG. 20. *Eureka ulrichi* (Rasetti, 1945). Rabbitkettle Formation, Broken Skull River, western District of Mackenzie. Upper Cambrian (Trempealeau). After Ludvigsen (1982). Scale bar in millimetres. See p. 578.

the hypostome is sharply bent to slope ventrally and forward; the anterior wing is small and displays no wing process. In the reconstruction I tentatively show the hypostome as attached for a short distance medially by a suture to the inner edge of the doublure. A steeply downward attitude of the hypostome would have resulted from this attachment and the juxtaposition of the anterior wing and the ridge formed by the axial furrow. The convexity of the cephalon, combined with the strong anterior arch, were sufficient to conceal the hypostome in lateral view (text-fig. 20c) despite the steep attitude.

Taylor (1978, p. 1062) noted a notch in the inner margin of the doublure of the free cheek, close to the genal angle. This notch is clearly visible in Ludvigsen's fig. 61g. Taylor termed it a vincular notch, but it may well be associated with the panderian opening.

DISCUSSION

Relation of hypostome to dorsal exoskeleton

When found in a specimen in what is generally considered to be the original position, the hypostome of Cambrian trilobites is either fused to the rostral plate (Pl. 53, figs. 1, 3, 4; Pl. 54, figs. 1-3) or attached at a hypostomal suture to the anterior cephalic doublure (Pl. 52, figs. 2, 3, 5, 7, 8; text-figs. 3, 6, 9, 16, 18, 20). As shown here, in these and other examples, an anterior wing extended upward and outward from the anterolateral corner of the hypostome. It is considered that the tip of this wing lay immediately beneath the axial furrow at the anterolateral edge of the glabella. The level of the crest of the ridge, formed by the axial furrow on the inner surface of the cephalic exoskeleton, is shown by a heavy dashed line in text-figs. 1D, 3D, 5D-20D. The position and attitude of the hypostome beneath the cephalon shown in these text-figures is determined by the juxtaposition of the tip of the wing and this ridge, and is attached forms by this juxtaposition in combination with the hypostomal suture. The eye ridge, or the anterior end of the palpebral lobe, abuts against the axial furrow immediately behind the tip of the wing, and if an anterior pit is developed in the axial furrow it depresses the axial furrow inward (as a boss) toward the tip of the wing. In species in which neither anterior pit nor eye ridge are evident, the tip of the anterior wing lay in a homologous position, in a transverse line passing in front of the eye lobe. In post-Cambrian trilobites the position of the hypostome is related in the same way to the dorsal exoskeleton, and in particular groups a wing process is developed, the tip of which rested against the boss formed by the anterior pit (Whittington, in press). Similar devices, less prominently developed, are known in a few well-preserved Cambrian specimens. Thus the attached hypostome in trilobites appears to have had a constant relation, via the anterior wing and a particular site in the axial furrow, to the dorsal exoskeleton. Hence the hypostome lay beneath the anterior portion of the glabella.

In a large number of Cambrian, and fewer post-Cambrian, trilobites the hypostome was detached from the inner edge of the anterior cephalic doublure. The morphology of such hypostomes was similar, and a prominent anterior wing developed (Pl. 55, figs. 8 and 9). In this example and others

(Robison 1972, figs. 2*d-f* and 3*a, b*; Palmer 1962*a*, pl. 6, figs. 13 and 15; Šnajdr 1958, pl. 35, fig. 11; pl. 37, fig. 8; pl. 39, fig. 7; pl. 40, fig. 3) the hypostome lies below the anterior portion of the glabella, with the tip of the anterior wing beneath the axial furrow. Such specimens are exoskeletons of whole animals, not moults, and the hypostome presumably was held approximately in its original position by muscles and the ventral integument into a late stage of decay. This assumption, tacitly made by earlier authors, is made here, and implies that in holaspid trilobites in which the hypostome was detached, the anterior wing lay close beneath the axial furrow at a site immediately in front of where the eye ridge abutted against the furrow. This relationship of hypostome to dorsal exoskeleton appears likely to have been universal among trilobites, and text-figs. 1, 7, 11-15, 17, 19 have been drawn accordingly.

My restorations of post-Cambrian trilobites with attached hypostomes (Whittington, in press, figs. 2-10, 12, 17?, 18-26) include two drawings that may appear to cast doubt on the universality of this relationship. That of *Triarthrus* (Whittington, in press, fig. 2) is based on inadequate information; in the pyritized specimens described by Whittington and Almond (1987) the anterior portion of the hypostome is concealed, and the anterior wing therefore unknown. It may well have been larger (compare the olenid *Parabolinella*, text-fig. 19) and have extended beneath the axial furrow anteriorly. In the case of *Remopleurides* (Whittington, in press, fig. 6), the tip of the long, slim wing process reached close not only to the tip of the doublure process, but also to the anterior boss. This boss (Whittington 1959, pl. 2, fig. 25) had a pit at its crest, a feature known in other trilobites that suggests a close connection with the tip of the wing process. The doublure process in *Remopleurides* is an additional, and apparently associated, internal process, while its wing process and anterior boss were like those of other trilobites.

General morphology of Cambrian hypostomes

Many isolated hypostomes from Cambrian rocks have been illustrated, too many to refer to in detail here. In the genera having a detached hypostome (text-figs. 1, 7, 11-15, 17, 19) the outline is subrectangular and elongate sagittally; the anterior wing is a relatively large, dorsally and outwardly directed projection, triangular or elongated in outline. The narrow (sag. and exs.) anterior border of the hypostome is flat, and bent to slope ventrally and forward. The lateral and posterior borders are narrow and convex, with the lateral border projecting moderately or slightly at about two-thirds the length (exs.), so that there is a broad, shallow lateral notch (in ventral view) between anterior wing and projection. Whether or not a posterior wing extended upward from the doublure of this projection (as revealed in *Crassifimbria* by Palmer 1958, pl. 25, figs. 12 and 14) is not known because of the rarity of specimens showing the internal aspect of the hypostome. The middle body is convex, with a depression dividing a larger anterior lobe from the smaller (and in some cases strongly convex) posterior lobe. In attached forms in which the glabella expanded forward (text-figs. 3, 8-10) the anterior lobe is wide and merges into the large triangular anterior wing. The lateral border is short (exs.), with a slight posterior projection; in oblique view (Pl. 53, fig. 3; Pl. 54, fig. 3) there is a rounded lateral notch between anterior wing and projection. Wide lateral and posterior borders are developed in such Upper Cambrian genera as *Dikelocephalus* (Ulrich and Resser 1930, pl. 10, figs. 1 and 2), *Palaeodotes* (Öpik 1967, fig. 129; pl. 50, fig. 3), and *Polycyrtaspis* (Öpik 1967, p. 384; pl. 9, fig. 4), and in the upper Middle Cambrian *Iranoleesia* and *Chelidonocephalus* (Wittke 1984, pl. 1, fig. 5; pl. 3, fig. 4). In *Polycyrtaspis*, Öpik noted a deep pit in the anterior wing distally—presumably the external expression of a wing process.

The anterior wing of Cambrian hypostomes has been so poorly illustrated that any generalization about presence or absence of a wing process is questionable. There is no evidence of the wing process in the form of a pit in the exterior surface at the tip of the anterior wing in *Pagetia* (Jell 1975, pl. 28, figs. 1 and 2), *Holmia* (text-fig. 2), *Olenellus* (Palmer 1957, pl. 19, fig. 9), *Redlichia* (text-fig. 6), *Dolerolenus* (text-fig. 7), *Paradoxides* (Pl. 53, fig. 3), *Xystridura* (Öpik 1975, pl. 2, fig. 2; pl. 13, fig. 1), or *Eokaolishania* (Wittke 1984, pl. 6, figs. 5 and 10). In *Fieldaspsis* (Pl. 54, figs. 2 and 3) a fold in the anterior wing formed a ridge on the inner surface that may have acted as a wing process; the exact form of the anterior wing of the hypostome of other corynexochoids is

unknown. Silicified material has revealed a low wing process in *Crassifimbria* (Palmer 1958, p. 162, pl. 25, figs. 12–14), but in other genera which had the hypostome detached in the holaspid stage (text-figs. 11–14, 17) no wing process is known; however, silicified material of *Bolaspidea* (text-fig. 15) reveals such a process. In *Parabolinella* (text-fig. 19) the presence of a wing process is uncertain, and it was absent in *Eureka* (Ludvigsen 1982, fig. 61o–q).

The macula is visible in many Cambrian hypostomes and takes the form of an elongate raised area adjacent to the posterior edge of the middle furrow, on the crescentic posterior lobe of the middle body. Lindström (1901, p. 64, pl. 5, figs. 33 and 34) noted that the macula of a species of *Paradoxides* was elongated, with a broken area along the crest, which he suggested was originally covered by a 'thinner membrane'. In *P. davidis* the macula is similar, and though the right one is partly exfoliated in the figured specimen (Pl. 53, figs. 1 and 2), it appears that the crest bore closely spaced, circular depressions that had a central mound. In *Fieldaspis* (Pl. 54, fig. 1) the prominent right macula appears smooth externally, but may bear minute tubercles along the crest.

Relation of hypostome to cephalic doublure, connective and median sutures

Text-figs. 1, 7, 11–15, 17, 19 show that in more than half the holaspid species of genera chosen for illustration the hypostome was detached. This condition contrasts with that prevailing in post-Cambrian trilobites in which fewer genera (Whittington, in press, figs. 1, 11, 14) have the hypostome detached. In *Pagetia* (text-fig. 1) there may have been a crescentic ventral plate, like that known in one species of agnostid (Hunt 1966); in the latter there were no connective sutures. In *Parabolinella* (text-fig. 19), as in other olenid genera, the doublure was not crossed by connective sutures, but in one olenid species such sutures have been described. In the other genera (text-figs. 7, 11–15, 17) connective sutures isolate a rostral plate; in *Dolerolenus* (text-fig. 7) this plate is wide (tr.), but is less so in the other examples. *Ptychoparia* (text-fig. 11) has a moderately wide rostral plate; this character, and the detached hypostome, were regarded by Öpik (1963, p. 77) as important features of a superfamily or other taxa of higher rank centred on *Ptychoparia*. The 'ptychopariid type' of ventral sutures as defined by Harrington (*in* Moore 1959, p. O67, fig. 48e) is highly misleading. Whether the presence of a rostral plate, and a detached hypostome, should be regarded as cardinal features of any ptychoparioid group, is a matter for consideration.

In *Paradoxides* (Pl. 53, figs. 1, 3, 8) and *Fieldaspis* (Pl. 54, figs. 1–3) the hypostome and rostral plate are fused into a single sclerite, the rostral-hypostomal plate. The evidence for fusion is that specimens of the two plates are not found separately, but invariably fused, with a change in slope marking the boundary between them, across which terrace lines may run continuously. The same evidence is seen in species of genera of corynexochoids related to *Fieldaspis* (e.g. Rasetti 1948; Palmer and Halley 1979), and Moore (*in* Moore 1959, p. O217) regarded this fusion as an ordinal character. Included in this order were the oryctocephalids; more recent work (Chernysheva 1962, pl. 6, fig. 1; Shergold 1969, pl. 1, fig. 4; Lu and Qian 1983, pl. 3, fig. 7) has provided excellent examples that support Rasetti's drawing (1952, pl. 1, fig. 1) of the cephalic doublure, including the rostral plate with the hypostome fused to it. The two components of the plate are separated only by a change in slope, ill-defined medially, and have not been found to occur separately. Shergold (1969, pl. 2, fig. 4) also showed the anterior wing of the hypostome, which must have extended up close beneath the axial furrow immediately in front of the eye ridge.

A hypostomal suture was present in trilobites of widely differing morphology. The evidence for such a suture having been functional includes the occurrence of rostral plate and hypostome in isolation, and possession by the hypostome of a well-defined anterior margin appropriately shaped to fit against the margin of the cephalic doublure. In the cases of *Holmia* (text-fig. 3), *Redlichia* (text-fig. 6), and *Xystridura* (text-fig. 9) I have questioned the existence of a functional hypostomal suture because specimens are known that show rostral plate and hypostome linked together, with an impressed line at the junction. Such specimens have been considered (Stubblefield 1936, p. 413; Harrington *in* Moore 1959, p. O66, fig. 44a, b) to indicate that the suture was in a state of symphysis, and was not functional in ecdysis. However, in species of each of these genera isolated hypostomes have been figured which appear to cast doubt on this interpretation. It may be that

an isolated hypostome was entombed as a part of a completely dissociated, moulted exoskeleton, whereas when found in place in a complete exoskeleton, the specimen is of a dead, whole animal entombed between moults. That is, the hypostomal suture was functional only at ecdysis, the hypostome having been attached to the rostral plate by the closed suture between moults. Such an argument may be applicable to the originals of text-fig. 2, for example, but apparently not to the *Redlichia* figured by Öpik (1958, pl. 4, fig. 2). He argued that this specimen was a moult that had the cranidium displaced, but rostral plate and hypostome linked to each other and to the free cheeks. A parallel case is that of the specimens of *Bathynotus* described above that were also presumably moults. In these the cranidium may be displaced, but the hypostome and free cheeks were separated as a unit from the rest of the exoskeleton, and may be the right way up or inverted in relation to it. Yet there is clearly a slight displacement between free cheeks and hypostome, indicating a functional hypostomal suture that was not apparently a primary line of separation at ecdysis. It appears likely that slightly greater disturbance of the moult would have resulted in greater separation of parts and the occurrence of an isolated hypostome. The taphonomy of trilobite exoskeletons needs further study, and claims that particular sutures were in a state of symphysis need re-examination.

Isolated hypostomes of olenelloids other than *Holmia* have been figured (Palmer 1957; Poulsen 1958, pl. 7, figs. 8 and 9; Fritz 1972, pl. 3, figs. 11 and 12; pl. 14, fig. 14), which also show the large anterior wing and the evenly curved anterior margin; whether the holaspide hypostome was detached, or a short (tr.) hypostomal suture was functional, is not known. In such redlichioids as *Sardoredlichia* (Rasetti 1972), and in emuellids (Pocock 1970), the evidence for a functional hypostomal suture is that cited above, as it is for the originals of text-figs. 16, 18, and 20, and more post-Cambrian trilobites. The queries in text-fig. 5 of *Bathynotus* relate to interpretation, not function. If the hypostome is regarded as inserted into the doublure at an inverted V-shaped hypostomal suture, it is an arrangement without parallel. If the hypostome was fused with the rostral plate, and the inverted V-shaped sutures are connective, a broadly triangular rostral plate having the apex anteriorly directed is otherwise unknown.

A median suture crossing the doublure, to which the hypostome was joined at the hypostomal suture, is present in various late Middle and Upper Cambrian trilobites. Specimens of *Dikelocephalus* (Ulrich and Resser 1930, pl. 10, fig. 2; pl. 14, figs. 3 and 4; pl. 15, figs. 2 and 9) offer ambivalent evidence on the presence or absence of a median suture, but the presence of such a suture has been cited (Ludvigsen and Westrop 1983, p. 28) as characteristic of Dikelocephalacea, a superfamily that is regarded as including saukiids and ptychaspidids. The evidence for a median suture in saukiids is not compelling (even in silicified specimens described by Ludvigsen 1982, fig. 58*a-j*), but is more satisfactory in ptychaspidids (Ludvigsen 1982, figs. 58*k-p*, 59, 60*a-k*; Ludvigsen and Westrop 1986, fig. 4*F*). The hypostome of *Dikelocephalus* (e.g. Ulrich and Resser 1930, pl. 10, figs. 2 and 3; pl. 11, fig. 4) is transversely rectangular in outline, with broad lateral and posterior borders; that of saukiids is poorly known, and the 'hypostome' attributed to the ptychaspidid *Kathleenella* (Ludvigsen 1982, p. 92, figs. 31, 59*o-r*, 60*d, e*) is not a hypostome (R. Ludvigsen, pers. comm. 25 March 1987). In *Eurekia* (text-fig. 20) the evidence for the ventral structure of the cephalon is adequate; relationships of the eurekiids are considered (Ludvigsen and Westrop 1983, p. 28) uncertain. Another group having a median suture is represented by *Proceratopyge* (text-fig. 16). A median suture is known in the Upper Cambrian genera *Theodenisia* (Rasetti 1954, fig. 3*a*), *Leiocoryphe*, *Plethometopus*, and *Stenopilus* (Rasetti 1959, p. 385), as well as *Housia* (Rasetti 1952, p. 892); in none of these is the hypostome known.

Attitude of hypostome, relation to mouth, and possible movement

In the holaspide of species of genera in which the hypostome was not attached to the cephalic doublure (text-figs. 1, 7, 11–15, 17, 19) each restoration assumes that the tip of the anterior wing lay close beneath the axial furrow, and that an approximately horizontal attitude of the hypostome was reasonable. In *Pagetia* (text-fig. 1) the hypostome projected below the plane in which the lateral margins of the cephalon lay, but in others the convexity of the cephalon (text-figs. 15 and

17) and the upward anterior arch (text-figs. 13 and 19) kept the hypostome above this level. Attachment at the hypostomal suture in *Holmia* (text-fig. 3) and *Xystridura* (text-fig. 9), and the tip of the anterior wing lying close to the ridge formed by the axial furrow, implies that the hypostome would have been held firmly in a horizontal attitude. Symphysis of the hypostomal suture would have contributed to this firmness. The convexity of the middle body of the hypostome of both these genera was such that it was partially visible in the lateral view of the cephalon. In *Redlichia* (text-fig. 6) the rostral plate was held firmly in place by the device of the interlocking pits, and the hypostome attached to it in a horizontal attitude, with the tip of the anterior wing close against the axial furrow. Symphysis at the hypostomal suture would have contributed to holding the hypostome in place. Fusion of rostral plate and hypostome (text-figs. 8 and 10), and a close fit at the rostral and connective sutures, meant that the hypostome was held horizontally with the tip of the anterior wing close against the ridge formed by the axial furrow. This arrangement seems devised to hold the hypostome rigid, the close-fitting rostral and connective sutures being at right angles to one another. Whether the sutures in *Bathynotus* (text-fig. 5) are regarded as connective or hypostomal, a close fit along them, combined with the position of the anterior wing, would have braced the hypostome rigidly. The hypostomes of *Kootenia* and *Olenoides* (Whittington 1975, pp. 121–122, 135) were fused with the rostral plate, and in *Olenoides* there was a wing process that probably lay close to the boss formed by the anterior pit (Whittington 1975, fig. 25). These devices, if closely linked, helped to hold the hypostome firmly in position. The furrow in the long anterior wing of *Fieldaspsis* (Pl. 54, figs. 2 and 3) may have formed a ridge on the inner surface, that lay against the ridge formed by the axial furrow (no anterior pit is developed) and functioned in the same way. In *Welleraspis* (text-fig. 18) and *Eurekaia* (text-fig. 20) anterior wings and presumed attachment held the hypostome firmly, the attitude being steeply downward in the latter. In *Proceratopyge* (text-fig. 16) the ventral aspect recalls that of asaphids (Whittington, in press, figs. 3 and 4), though in contrast the attachment was along a relatively short (tr.) hypostomal suture that lay almost in one plane, and there was a relatively large anterior wing that braced the hypostome. The different ventral structures found in this wide range of taxa having an attached hypostome all appear to have braced the hypostome rigidly against the rest of the cephalic exoskeleton.

An anterior pit in the axial furrow has rarely been described in holaspid Cambrian trilobites. Such a pit is regarded as characteristic of dorypygids (Poulsen in Moore 1959, p. O217), and Öpik (1982) observed them in some dolichometopids. Apparently an anterior boss, which lay close to a wing process and aided in bracing the hypostome firmly against the rest of the exoskeleton, was not as widespread and important a device in Cambrian as in post-Cambrian trilobites (Whittington, in press). I consider, however, that in Cambrian trilobites the function of the anterior wing was to brace the hypostome, though it may have lacked this particular device. The presence in some species of a wing process, but not apparently an anterior boss, suggests that the latter was developed subsequently as a complementary structure.

I have reviewed (Whittington, in press) the evidence for believing that the backward-facing mouth of the trilobite lay above and just behind the posterior margin of the hypostome. Restorations of *Olenoides* (Whittington 1975) and *Triarthrus* (Whittington and Almond 1987) suggest that firm bracing of the hypostome may have aligned the mouth axially with the coxal gnathobases that brought food forward along the ventral mid-line. In species of genera in which the hypostome was detached, it was less firmly so aligned, but the position and manner of any link between the anterior wing and dorsal exoskeleton would have been important in positioning the mouth. Possible movements of the hypostome—vibratory or swinging up and down—have long been discussed (Stubblefield 1936, p. 410; Whittington, in press). In species in which the hypostome was fused to the rostral plate, as in *Paradoxides* and *Fieldaspsis* (text-figs. 8 and 10), such movements would have been impossible if there was a close fit at the rostral and connective sutures; the anterior wing braced the hypostome firmly. In species that appear to have had a hypostomal suture (text-figs. 3, 6, 16, 18, 20), movement up and down about this suture would have required extension and contraction of muscles at the tips of the wings. A rocking motion of the hypostome about the

tips of the wings would have required a membrane along the hypostomal suture capable of extension and contraction. Silicified material representing many families of post-Cambrian trilobites has shown that there was a close fit along the hypostomal suture at flat faces that cut across the thickness of the exoskeleton (Whittington, in press), and movement of the types mentioned above at such sutures appears unlikely. If the fit at the hypostomal suture was similarly close in Cambrian species, any movement of the hypostome appears to have been equally unlikely, and the anterior wing would have served to brace the hypostome against the rest of the exoskeleton. More exact knowledge of the nature of the attachment at the hypostomal suture in Cambrian trilobites may clarify this question of possible movement. In genera in which the hypostome was detached, the nature and amount of any movement would have depended on arrangement of muscles and flexibility of the integument.

Evolution of hypostome and ventral cephalic sutures in Cambrian and post-Cambrian trilobites

This review and that on post-Cambrian hypostomes (Whittington, in press) has shown the basic, conservative similarity of all trilobite hypostomes—the convex, subdivided middle body with the macula; the presence of anterior, and probably posterior wings; the lateral notch; and convex lateral and posterior borders. The wing process is present in the Lower Cambrian *Crassifimbria* (Palmer 1958), but not linked in the holaspis to an anterior boss. The wing process is most widely developed in post-Cambrian forms; in cheirurids, encrinurids, pliomerids, and calymenids it is associated with a prominent anterior boss to form a device that assisted in bracing the hypostome firmly. This device is not confined to these groups but appears, for example, in some proetids and some lichids. The lateral notch in Cambrian hypostomes was wide (exs.) and shallow, extending between anterior wing and projection of the lateral border, in contrast to the deep, narrow notch and conspicuous shoulder in the post-Cambrian cheirurids and their allies. It appears probable that the antenna passed through this notch as it curved downward and forward (Whittington, in press). Wide lateral and posterior borders have been described in the hypostome of a small number of late Middle and Upper Cambrian genera, the posterior border in *Palaeodotes* (Öpik 1967, pl. 50, fig. 3) having a median notch. Similar features occur more commonly in various post-Cambrian trilobites such as asaphids, remopleuridids, and lichids. The rhynchos, a raised median area on the middle body of the hypostome, related to enrolment, is only known in post-Cambrian trilobites. It appears from the present drawings that the attitude of the hypostome in most Cambrian trilobites was approximately horizontal; a steep downward attitude is suggested for the late Cambrian *Eureka*; an upward attitude is not known. After the Cambrian, groups in which the hypostome was detached are fewer, and were much reduced in the Upper Palaeozoic; fusion of rostral plate and hypostome is not known. Broadly, evolution of the hypostome is in the direction of attachment, and of the development of more diverse special structures and attitudes in post-Cambrian forms that are characteristic of particular families, and may reflect particular habits and adaptations. These special structures include elongation of the anterior wing and elaboration of the wing process and distal tip of the wing, structures that aided in bracing the hypostome in a particular attitude against the rest of the cephalic exoskeleton.

Studies on the ontogeny of trilobites (Whittington 1957b; Palmer 1957, 1958, 1962b; Chatterton 1980) have revealed the relatively large, spinose hypostome as typical of protaspides. In *Sao* (Whittington 1957b, fig. 6g), *Crassifimbria* (Palmer 1958, pl. 26, figs. 5 and 6), and *Bathyriscus* (Robison 1967) the hypostome was attached, and fused to the rostral plate in *Bathyriscus*; a shallow anterior pit was developed. Attached hypostomes (in one asaphid fused with the rostral plate in its earliest stages: Tripp and Evitt 1986) are characteristic of protaspides of some post-Cambrian trilobites; in such examples the glabella extended far forward, close to the anterior margin. During development, the hypostome in *Sao* (text-fig. 13), *Crassifimbria* (Palmer 1958, p. 162), and *Aphelaspis* (text-fig. 17; Palmer 1962b, fig. 2a) became detached, as the convexity of the cephalon and the length (sag.) of the preglabellar field increased and the hypostome retained its relation to the glabella and position of the anterior pit (the pit disappears). In *Bathyriscus* and many post-Cambrian trilobites such detachment did not occur, the preglabellar field being short

(sag.) or absent. It is possible that heterochrony (Robison 1967; McNamara 1986) was one of many factors in lines of evolution that led, for example, to retention of the fused rostral plate and hypostome in the holaspid stages. The relationship between length of preglabellar field, cephalic convexity, and detachment of the hypostome is illustrated in the ontogeny of *Olenellus* (text-fig. 4). The hypostome appears not to have been attached during known developmental stages, when a preglabellar field is present. If the developmental stages of *Holmia* (text-fig. 3) were similar, attachment of the hypostome may have taken place in step with anterior expansion of the glabella to bring it in contact with the doublure of the anterior border.

It has been suggested (Stubblefield 1936, p. 410, fig. 2; Hupé 1954, p. 15, fig. 9; Robison 1964, p. 520; Öpik 1967, p. 214) that an evolutionary trend may have led to the reduction in width (tr.) of the rostral plate, resulting in the median suture. Diagrams illustrating this view are a morphological, not a phylogenetic, series (as Stubblefield pointed out) and Palmer's diagram (1960, fig. 8), referred to by Robison and Öpik, was not presented as illustrating an evolutionary trend. It showed a median suture crossing the doublure in *Housia* and a relatively narrow (tr.) rostral plate in *Prehousia*. Neither Palmer's illustrations of species of these genera (1960, pl. 7, figs. 1-19; 1965, pl. 12, figs. 1-11, 16-26; pl. 13, figs. 1-18) nor earlier work offer clear evidence for his diagram; Rasetti (1952, p. 892) referred to specimens giving evidence of a median suture in *Housia*. The hypostome of neither genus is known. I conclude that Palmer's diagram (1960, fig. 8) needs substantiation, but that in any event it was not intended to show an evolutionary lineage; no such lineage appears to have been demonstrated. Thus the origin of the median suture, and whether it took place more than once, appears to be unknown. Various late Middle and Upper Cambrian trilobites having such a suture have been mentioned above, and two in which the hypostome is known are illustrated (text-figs. 16 and 20). These various trilobites may not be closely related, but until we know more of ventral sutures and hypostomes relationships will remain uncertain. It might be expected, for example, that *Richardsonella* and its allies, if they are remopleuridids, would have a median suture. However, in a specimen from Alaska (Palmer 1968, pl. 14, fig. 8) no suture crosses the doublure.

The hypostome and supra-generic relationships

Text-figs. 1, 3, 5-20 reflect the limitations of knowledge, and suggest that, in contrast to hypostomes of post-Cambrian trilobites, those of the Cambrian are not so readily distinctive of family groups. The olenelloid hypostome (text-figs. 2 and 3) may prove to be distinctive, as may that of *Paradoxides* (Pl. 53, figs. 1-4) and its allies, although it was fused with the rostral plate in species of *Paradoxides* (in the restricted sense of Šnajdr 1958). The *Feldaspis* (Pl. 54, figs. 1-3) type of rostral-hypostomal plate is readily recognizable, and may prove of value in determining family relationships within the corynexochoids. Öpik (1982, p. 7) included within dolichometopids (which he regarded as corynexochoids) a subfamily in which rostral plate and hypostome were not fused. Supposed symphysis of the hypostomal suture or the rostral-hypostomal plate do not appear to be characters of high taxonomic rank.

The detached hypostomes of various genera (text-figs. 1, 7, 11-15, 17, 19) do not exhibit distinctive features, but the morphology of other parts of the exoskeleton shows that some clearly belong to different family groups (e.g. *Pagetia*, *Dolerolenus*, *Parabolinella*). The lack of distinctive features in the hypostome is reflected in many publications on Cambrian trilobites in which unassigned, or doubtfully assigned, isolated hypostomes are described. Detachment in the holaspid results from a variety of factors, including width (sag. and exs.) and form of the doublure, length of preglabellar field, and convexity of the cephalon, and this single character cannot be taken as characteristic of any particular group. Thus to suggest (Rasetti 1952, p. 894) that trilobites with a detached hypostome be referred to as 'the ptychopariid type' may be misleading, and the definition of this 'type' given by Harrington (*in* Moore 1959, p. O67) is too general to be useful. The difficulties in defining the ptychoparioid type of trilobite are notorious, and are well illustrated by Palmer's (1958) description of *Crassifimbria*. This genus is regarded as a ptychoparioid (*in* Moore 1959) in agreement with Palmer, who noted (1958, p. 159) the similarity to *Agraulos* (text-fig. 14). As Öpik

(1961, p. 143) pointed out, the cephalon of *Crassifimbria* was far more like that of *Agraulos* than it was like *Ptychoparia* (text-fig. 11), and it might be regarded as an ellipsocephalid, and hence transferred to the redlichoid group.

Acknowledgements. Helpful comments on earlier drafts by Sir James Stubblefield, FRS, Dr R. A. Fortey, and Dr C. P. Hughes are gratefully acknowledged, as are those by anonymous reviewers. Dr R. A. Fortey loaned to me specimens from the British Museum (Natural History) (BMNH), Dr R. B. Rickards material in the Sedgwick Museum, University of Cambridge (SM); Dr J. E. Almond kindly examined and photographed the type specimens of *Bathynotus* in the US National Museum of Natural History (USNM), and Mr F. J. Collier loaned additional specimens. I am indebted to Mrs Sandra Last for preparing the typescript, to Miss Sheila Ripper for drawing the figures from my sketches, and to the Leverhulme Trust for their support. This is Cambridge Earth Sciences Publication no. 1020.

REFERENCES

- AHLBERG, P. and BERGSTRÖM, J. 1978. Lower Cambrian ptychopariid trilobites from Scandinavia. *Sver. geol. Unders. Ca* **49**, 1-40.
- and JOHANSSON, J. 1986. Lower Cambrian olenellid trilobites from the Baltic faunal province. *Geol. För. Stockh. Förh.* **108**, 39-56.
- ANGELIN, N. P. 1854. *Palaeontologia Scandinavica*, 92 pp. Lund.
- BARRANDE, J. 1846. *Notice préliminaire sur le Système Silurien et les trilobites de Bohême*, vi+97 pp. Leipsic.
- 1852. *Système Silurien du centre de la Bohême. Ière partie. Recherches paléontologiques*, Vol. I. *Crustacés, Trilobites*, xxx+935 pp., 51 pls. Prague and Paris.
- BERGSTRÖM, J. 1973. Classification of olenellid trilobites and some Balto-Scandian Species. *Norsk geol. Tidsskr.* **53**, 283-314.
- and LEVI-SETTI, R. 1978. Phenotypic variation in the Middle Cambrian trilobite *Paradoxides davidis* Salter at Manuels, southeast Newfoundland. *Geol. Palaeont.* **12**, 1-40.
- BILLINGS, E. 1861. On some new or little-known species of Lower Silurian fossils from the Potsdam Group (Primordial zone). *Geol. Surv. Canada, Palaeozoic Fossils*, **1**, 1-24.
- BOECK, C. 1827. Notitser til laeren om trilobiterna. *Magazin Naturv. Christ.* **8**, **1**, 11-44.
- BRÖGGER, W. C. 1882. *Die Silurischen étagen 2 und 3 im Kristianiagebeit und auf Eker*, 376 pp. Kristiania [Oslo].
- BRONGNIART, A. In BRONGNIART, A. and DESMAREST, A. G. 1822. *Histoire naturelle des Crustacés fossiles*, 154 pp. Paris.
- BURMEISTER, H. 1843. *Die organisation der trilobiten*, xii+148 pp. Berlin.
- CHATTERTON, B. D. E. 1980. Ontogenetic studies of Middle Ordovician trilobites from the Esbataottine Formation, Mackenzie Mountains, Canada. *Palaeontographica*, **A171**, 1-74.
- CHERNYSHEVA, N. E. 1962. Cambrian trilobites of the family Oryctocephalidae. In Problemy neftegazonosti Sovetskoi Arktiki. Paleontologiya i biostratigrafiya. 3. *Trudy nauchno-issled. Inst. Geol. Arkt.* **127**, 3-64.
- COSSMAN, M. 1902. Rectifications de la nomenclature. *Revue crit. Paléozool.* **16**, 52.
- EMMRICH, H. F. 1839. *De trilobitis*, 56 pp. Berolini, Berlin.
- FRTZ, W. H. 1972. Lower Cambrian trilobites from the Sekwi Formation type section, Mackenzie Mountains, northwestern Canada. *Bull. geol. Surv. Can.* **212**, 1-58.
- HALL, J. 1859. Contributions to the palaeontology of New York. *12th Ann. Rep. NY St. Cab. nat. Hist.*, pp. 7-64.
- 1860. *13th Ann. Rep. NY St. Cab. nat. Hist.*, p. 118.
- HAWLE, I. and CORDA, A. J. C. 1847. *Prodrom einer Monographie der böhmischen trilobiten*, 176 pp. Prague.
- HENNINGSMOEN, G. 1957. The trilobite family Olenidae. *Skr. norske Vidensk-Akad. mat. nat. Kl.* **1957**, **1**, 1-303.
- 1959. Rare Tremadocian trilobites from Norway. *Norsk geol. Tidsskr.* **39**, 153-173.
- HOLM, G. 1887. Om *Olenellus kjerulfi* Linrs. *Geol. För. Stockh. Förh.* **9**, 493-522.
- HUNT, A. S. 1966. Submarginal suture and ventral plate of an agnostid trilobite. *J. Paleont.* **40**, 1238-1240.
- HUPÉ, P. 1953a. Contribution à l'étude du Cambrien inférieur et du PréCambrien III de l'Anti-Atlas Marocain. *Notes Mém. Serv. géol. Maroc*, **103**, 1-402.
- 1953b. Classe des trilobites. In PIVETEAU, J. (ed.). *Traité de Paléontologie*, **3**, 44-246. Masson, Paris.

- HUPÉ, P. 1954. Classification des trilobites. *Annls Paléont.* **39**, 59-168.
- JAGO, J. B. 1987. Idamean (Late Cambrian) trilobites from the Denison Range, south-west Tasmania. *Palaeontology*, **30**, 207-231.
- JELL, P. A. 1970. *Pagetia ocellata*, a new Cambrian trilobite from northwestern Queensland. *Mem. Qd Mus.* **15**, 303-313.
- 1975. Australian Middle Cambrian eodiscoids, with a review of the Superfamily. *Palaeontographica*, **A150**, 1-97.
- KIAER, J. 1916. The Lower Cambrian *Holmia* fauna at Tømten in Norway. *Skr. norske Vidensk-Akad. mat. nat. Kl.* **10**, 1-140.
- KOBAYASHI, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. *Palaeontology*. Pt. III. *J. Fac. Sci. Tokyo Univ. (Sect. 2)*, **4**, 49-344.
- and KATO, F. 1951. On the ontogeny and the ventral morphology of *Redlichia chinensis* with description of *Alutella nakamurai* new gen. and sp. *Ibid.* **8**, 99-143.
- LEANZA, A. F. 1949. *Olenopsis* Ameghino 1889 (un Reodor) versus *Olenopsis* Bornemann 1891 (un trilobite). *Revta Asoc. geol. argent.* **4**, 1.
- LINDSTRÖM, G. 1901. Researches on the visual organs of the trilobites. *K. svenska VetenskAkad. Handl.* **34**, 1-86.
- LINNARSSON, J. G. O. 1869. Om vestergötlands Cambriska och Siluriska aflagringar. *Ibid.* **8**, 1-89.
- 1871. Om några försteningar från sveriges och Norges 'primordialzon'. *Ofvers. K. VetenskAkad. Förh. Stockh.* 1871, 789-796.
- LU YAN-HAO, and QIAN YI-YUAN. 1983. Cambro-Ordovician trilobites from eastern Guizhou. *Palaeont. cathayana*, **1**, 1-105.
- LUDVIGSEN, R. 1982. Upper Cambrian and Lower Ordovician trilobite biostratigraphy of the Rabbitkettle Formation, western District of Mackenzie. *Contr. Life Sci. Div. R. Ont. Mus.* **134**, 1-188.
- and WESTROP, S. R. 1983. Franconian trilobites of New York State. *Mem. NY St. Mus.* **23**, 1-82.
- 1986. Classification of the Late Cambrian trilobite *Idiomesus* Raymond. *Can. J. Earth Sci.* **23**, 300-307.
- MCNAMARA, K. J. 1986. The role of heterochrony in the evolution of Cambrian trilobites. *Biol. Rev.* **61**, 121-156.
- MATTHEW, G. F. 1888. Illustrations of the fauna of the St John Group. No. 4. Pt. 1. Description of a new species of *Paradoxides* (*Paradoxides regina*). Pt. 2. The smaller trilobites with eyes (Ptychoparidae and Ellipsocephalidae). *Proc. Trans. R. Soc. Can.* **5** (sect. 4), 115-166.
- 1890. On Cambrian organisms in Acadia. *Ibid.* **7** (sect. 4), 135-162.
- MEEK, F. B. 1874. Preliminary report upon invertebrate fossils. In WHITE, C. A. (ed.). *US geol. geogr. Surv., W. 100th Meridian*, Report, pp. 5-27.
- MOBERG, J. C. and SEGERBERG, C. O. 1906. Bidrag till kännedomen om Ceratopygeregionen. *Lunds Univ. Arsskr.* NF **2**, **2**, 1-113.
- MOORE, R. C. (ed.). 1959. *Treatise on invertebrate paleontology. Part O. Arthropoda 1*, xix + O1-560. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.
- NIKOLAISEN, F. 1986. Olenellid trilobites from the uppermost Lower Cambrian Evjevik Limestone at Tømten in Ringsaker, Norway. *Norsk geol. Tidsskr.* **66**, 305-309.
- and HENNINGSMOEN, G. 1985. Upper Cambrian and lower Tremadoc olenid trilobites from the Digermul peninsula, Finnmark, northern Norway. *Norg. geol. Unders.* **400**, 1-49.
- ÖPIK, A. A. 1958. The Cambrian trilobite *Redlichia*: organization and generic concept. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **42**, 1-50.
- 1961. The geology and palaeontology of the headwaters of the Burke River, Queensland. *Ibid.* **53**, 1-249.
- 1963. Early Upper Cambrian fossils from Queensland. *Ibid.* **64**, 1-107.
- 1967. The Mindyallan fauna of north-western Queensland. *Ibid.* **74** (1), 1-104, (2) 1-167.
- 1975. Templetonian and Ordian xystridurid trilobites of Australia. *Ibid.* **121**, 1-184.
- 1982. Dolichometopid trilobites of Queensland, Northern Territory, and New South Wales. *Ibid.* **175**, 1-85.
- OWENS, R. M., FORTEY, R. A., COPE, J. C. W., RUSHTON, A. W. A. and BASSETT, M. G. 1982. Tremadoc faunas from the Carmarthen district, South Wales. *Geol. Mag.* **119**, 1-38.
- PALMER, A. R. 1957. Ontogenetic development of two olenellid trilobites. *J. Paleont.* **31**, 105-128.
- 1958. Morphology and ontogeny of a Lower Cambrian ptychoparioid trilobite from Nevada. *Ibid.* **32**, 154-170.

- 1960. Trilobites of the Upper Cambrian Dunderberg Shale, Eureka District, Nevada. *Prof. Pap. US geol. Surv.* **334-C**, 53–109.
- 1962a. *Glyptagnostus* and associated trilobites in the United States. *Ibid.* **374-F**, 1–49.
- 1962b. Comparative ontogeny of some opisthoparian, gonatoparian, and proparian Upper Cambrian trilobites. *J. Paleont.* **36**, 87–96.
- 1965. Trilobites from the Late Cambrian pteroccephaliid biomere in the Great Basin, United States. *Prof. Pap. US geol. Surv.* **493**, 1–105.
- 1968. Cambrian trilobites of east-central Alaska. *Ibid.* **559-B**, 1–115.
- 1977. Biostratigraphy of the Cambrian System—a progress report. *Ann. Rev. Earth Planet. Sci.* **5**, 13–33.
- and GATEHOUSE, C. G. 1972. Early and Middle Cambrian trilobites from Antarctica. *Prof. Pap. US geol. Surv.* **456-D**, 1–36.
- and HALLEY, R. B. 1979. Physical stratigraphy and trilobite biostratigraphy of the Carrara Formation (Lower and Middle Cambrian) in the southern Great Basin. *Ibid.* **1047**, i–v, 1–131.
- POCOCK, K. J. 1970. The Emuellidae, a new family of trilobites from the Lower Cambrian of South Australia. *Palaeontology*, **13**, 522–562.
- POULSEN, C. 1927. The Cambrian, Ozarkian and Canadian faunas of northwest Greenland. *Meddr Grønland*, **70**, 237–343.
- 1958. Contribution to the palaeontology of the Lower Cambrian Wulff River Formation. *Ibid.* **162**, 1–24.
- RASETTI, F. 1945. New Upper Cambrian trilobites from the Lévis Conglomerate. *J. Paleont.* **19**, 462–478.
- 1948. Middle Cambrian trilobites from the conglomerates of Quebec. *Ibid.* **22**, 315–339.
- 1951. Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smithson. misc. Collns.* **116**, 1–270.
- 1952. Ventral cephalic sutures in Cambrian trilobites. *Am. J. Sci.* **250**, 885–898.
- 1954. Phylogeny of the Cambrian trilobite family Catillicephalidae and the ontogeny of *Welleraspis*. *J. Paleont.* **28**, 599–612.
- 1957. Additional fossils from the Middle Cambrian Mt. Whyte Formation of the Canadian Rocky Mountains. *Ibid.* **31**, 955–972.
- 1959. Trempealeauian trilobites from the Conococheague, Frederick and Grove limestones of the central Appalachians. *Ibid.* **33**, 375–398.
- 1965. Upper Cambrian trilobite faunas of northeastern Tennessee. *Smithson. misc. Collns.* **148**, 1–127.
- 1967. Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. *Ibid.* **152**, 1–111.
- 1972. Cambrian trilobite faunas of Sardinia. *Atti Accad. naz. Lincei Memorie*, Ser. 8, Sec. IIa, **11**, 1–100.
- RAYMOND, P. E. 1913a. A revision of the species which have been referred to the genus *Bathyrurus*. *Bull. Victoria meml Mus. geol. Surv. Can.* **1**, 51–69.
- 1913b. On the genera of the Eodiscidae. *Ottawa Nat.* **27**, 101–106.
- RESSER, C. E. 1935. Nomenclature of some Cambrian trilobites. *Smithson. misc. Collns.* **93**, 1–46.
- 1937. Third contribution to nomenclature of Cambrian trilobites. *Ibid.* **95**, 1–29.
- and HOWELL, B. F. 1938. Lower Cambrian *Olenellus* zone of the Appalachians. *Bull. geol. Soc. Am.* **49**, 195–248.
- ROBISON, R. A. 1964. Late Middle Cambrian faunas from western Utah. *J. Paleont.* **38**, 510–566.
- 1967. Ontogeny of *Bathyriscus fimbriatus* and its bearing on affinities of corynexochid trilobites. *Ibid.* **41**, 213–221.
- 1972. Hypostoma of agnostid trilobites. *Lethaia*, **5**, 239–248.
- 1976. Middle Cambrian trilobite biostratigraphy of the Great Basin. *Geology Stud. Brigham Young Univ.* **23**, 93–109.
- RUSHTON, A. W. A. 1983. Trilobites from the Upper Cambrian *Olenus* zone in central England. In BRIGGS, D. E. G. and LANE, P. D. (eds.). Trilobites and other early arthropods: papers in honour of Professor H. B. Whittington, F.R.S. *Spec. Pap. Palaeont.* **30**, 107–139, pls. 14–19.
- SALTER, J. W. 1863. On the discovery of *Paradoxides* in Britain. *Q. Jl geol. Soc. Lond.* **19**, 274–277.
- SCHINDEWOLF, O. H. 1955. Über Hypostom und gesichtsacht bei *Redlichia* (Trilob.). *Neues Jb. Geol. Paläont. Mh.* **1955**, 130–136.
- and SEILACHER, A. 1955. Beiträge zur kenntnis des Kambriums in der Salt Range (Pakistan). *Abh. math.-naturw. Kl. Akad. Wiss. Lit.* **1955** (10), 1–90.

- SCHLOTHEIM, E. F. 1823. *Nachtrage zur Petrefactenkunde* II, 114 pp. Gotha.
- SDZUY, K. 1961. Das Kambrium Spaniens. Pt. II: trilobiten. *Abh. math.-naturw. Kl. Akad. Wiss. Lit.* 1961 (7, 8), 501-693.
- 1967. Trilobites del Cambrico Medio de Asturias. *Trab. Geol. Fac. cienc. Univ. Oviedo*, 1, 77-133.
- SHAW, A. B. 1955. Paleontology of northwestern Vermont. V. The Lower Cambrian fauna. *J. Paleont.* 29, 775-805.
- SHERGOLD, J. H. 1969. Oryctocephalidae (Trilobita: Middle Cambrian) of Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* 104, 1-66.
- 1980. Late Cambrian trilobites from the Chatsworth Limestone, western Queensland. *Ibid.* 186, 1-111.
- 1982. Idamean (Late Cambrian) trilobites, Burke River Structural belt, western Queensland. *Ibid.* 187, 1-69.
- and SDZUY, K. 1984. Cambrian and early Tremadocian trilobites from Sultan Dag, central Turkey. *Senckenberg. leth.* 65, 51-135.
- ŠNAJDR, M. 1958. The trilobites of the Middle Cambrian of Bohemia. *Rozpr. ústřed. Úst. geol.* 24, 1-230.
- 1985. Two new paradoxid trilobites from the Jince Formation (Middle Cambrian, Czechoslovakia). *Věst. ústř. Úst. geol.* 61, 169-174.
- STUBBLEFIELD, C. J. 1936. Cephalic sutures and their bearing on current classifications of trilobites. *Biol. Rev.* 11, 407-440.
- SWINNERTON, H. H. 1915. Suggestions for a revised classification of trilobites. *Geol. Mag.* NS (Dec. 6), 2, 487-496, 538-545.
- TASCH, P. 1951. Fauna and paleoecology of the Upper Cambrian Warrior Formation of central Pennsylvania. *J. Paleont.* 25, 275-306.
- TAYLOR, M. E. 1978. Type species of the Late Cambrian trilobite *Eurekaia* Walcott, 1916. *Ibid.* 52, 1054-1064.
- TRIPP, R. P. and EVITT, W. R. 1986. Silicified trilobites of the family Asaphidae from the Middle Ordovician of Virginia. *Palaeontology*, 29, 705-724.
- ULRICH, E. O. and RESSER, C. E. 1930. The Cambrian of the upper Mississippi valley. I, Trilobita: Dikelocephalinae and Osceolinae. *Bull. publ. Mus. Milwaukee*, 121, 1-122.
- VOGDEN, A. W. 1893. Bibliography of the Palaeozoic Crustacea. *Occ. Pap. Calif. Acad. Sci.* 4, 1-412.
- WALCOTT, C. D. 1886. Second contribution to the studies on the Cambrian faunas of North America. *Bull. US geol. Surv.* 30, 1-369.
- 1890. The fauna of the Lower Cambrian or *Olenellus* zone. *Rep. Dir. U.S. geol. Surv.* 10, 1-774.
- 1910. *Olenellus* and other genera of the Mesonacidae. *Smithson. misc. Collns.* 53, 231-422.
- 1916. Cambrian geology and paleontology. III. No. 5. Cambrian trilobites. *Ibid.* 64, 303-456.
- 1917. Fauna of the Mount Whyte Formation. *Ibid.* 67, 61-114.
- WALLERIUS, I. D. 1895. *Undersökningar öfver zonen med Agnostus laevigatus i Vestergötland*, 72 pp. Lund.
- WESTERGÅRD, A. H. 1936. *Paradoxides oelandicus* beds of Öland. *Sver. geol. Unders. Avh.*, Ser. C, 394, 1-66.
- 1947. Supplementary notes on the Upper Cambrian trilobites of Sweden. *Ibid.* 489, 1-34.
- WHITEHOUSE, F. W. 1936. The Cambrian faunas of north-eastern Australia. Parts 1, 2. *Mem. Qd Mus.* 11, 59-112.
- 1939. The Cambrian faunas of north-eastern Australia. Part 3: the polymerid trilobites. *Ibid.* 179-282.
- WHITTINGTON, H. B. 1957a. Ontogeny of *Elliptocephala*, *Paradoxides*, *Sao*, *Blainia* and *Triarthrus* (Trilobita). *J. Paleont.* 31, 934-946.
- 1957b. The ontogeny of trilobites. *Biol. Rev.* 32, 421-469.
- 1959. Silicified Middle Ordovician trilobites. Remopleurididae, Trinucleidae, Raphiophoridae, Endymionidae. *Bull. Mus. comp. Zool. Harv.* 121, 371-496.
- 1975. Trilobites with appendages from the Middle Cambrian Burgess Shale, British Columbia. *Fossils Strata*, 4, 97-136.
- In press. Hypostomes of post-Cambrian trilobites. *New Mex. Bur. Mines Miner. Resour.*
- and ALMOND, J. E. 1987. Appendages and habits of the Upper Ordovician trilobite *Triarthrus eatoni*. *Phil. Trans. R. Soc.* B317, 1-46.
- and EVITT, W. R. 1954. Silicified Middle Ordovician trilobites. *Mem. geol. Soc. Am.* 59, 1-137.
- WITTKÉ, H. W. 1984. Middle and Upper Cambrian trilobites from Iran: their taxonomy, stratigraphy and significance for provincialism. *Palaeontographica*, A183, 91-161.

ZHANG WENTANG, LU YANHAO, ZHU ZAOLING, QIAN YIYUAN, LIN HUANLING, ZHOU ZHIYI, ZHANG SENGUI and YUAN JINLIANG. 1980. Cambrian trilobite faunas of southwestern China. *Palaeont. sin.* **159** (New Series B 16), 1-497.

Typescript received 11 May 1987

Revised typescript received 14 September 1987

H. B. WHITTINGTON
Sedgwick Museum
Department of Earth Sciences
Downing Street
Cambridge CB2 3EQ
England