

BURLINGIIDS: SMALL PROPARIAN CAMBRIAN TRILOBITES OF ENIGMATIC ORIGIN

by H. B. WHITTINGTON

ABSTRACT. The original, and additional, specimens of *Burlingia hectori* are described from Canada and Sweden, *B. laevis* being considered synonymous with *B. hectori*. Westergaard's original material of *Schmalenseeia amphionura* and *S. acutangula* is redescribed, two cranidia included with the latter being segregated as *S. jagoi* sp. nov. No burlingioid exoskeleton exceeds a length of 13 mm, most being less than half this size. The eye lobe was close to the glabella, the two branches of the facial suture directed outward and forward. A large rostral plate beneath the frontal area is described, the incomplete hypostome is outlined in one specimen; the condition may have been conterminant. The exoskeleton was non-fulcrate, the sclerites separate but apparently flexure between them limited, lacking border and pleural furrows; lateral and posterior doublure unknown. The pygidium of *B. hectori* was narrow and short; in species of *Schmalenseeia* the pygidium incorporated more segments, those of the thorax having been fewer. Burlingiids were world-wide in distribution, and occur in outer shelf to slope facies. They may belong with those trilobites in which the conterminant condition of the hypostome was retained throughout growth.

THE relatively small size of burlingiids, and their unusual facial suture, have presented intriguing problems since they were discovered early in this century. They are Cambrian in age, yet the suture was of a type that Beecher (1897) thought arose in the post-Cambrian. Were the small specimens the remains of immature individuals, or was this their maximum size? This study of new and old material shows that the distinctiveness of burlingiids lies not only in their size and peculiar suture, but in that they had an unusual rostral plate and a thorax which lacked a horizontal hinge-line and the facet, i.e. was non-fulcrate (for definition and discussion of this term see Whittington 1990, p. 28). Known specimens are all relatively small in size, and the exoskeleton thin; their distribution was world-wide in outer shelf margin or slope facies.

In 1981, I described the disarticulated type material of *Schmalenseeia amphionura*, and complete exoskeletons from Newfoundland. Since then, eighteen specimens of *Burlingia hectori*, the first found since Walcott's original lot of three, were obtained by a party from the Royal Ontario Museum, Toronto, Canada. A generous invitation from Mr David M. Rudkin to study them, and the loan of new and old material of *Burlingia* and *Schmalenseeia* from Sweden, has enabled this re-assessment of the morphology of species of both genera to be made from the best-preserved and most complete examples so far known.

MORPHOLOGY, MODE OF LIFE AND AFFINITIES

Exoskeleton. The broken edges of the specimens in limestone (Pl. 3, fig. 6; Pl. 4, figs 1, 4), and the similarity between internal mould and cast from external mould (Whittington 1981, pl. 2), show the thinness of the exoskeleton. Crumpling of both limestone and shale specimens is further evidence of this thinness. The exoskeleton was non-fulcrate (Pl. 1, fig. 3; Pl. 3, fig. 4), curving downward with increasing steepness, outward from the change in slope at the axial furrow. Impressed furrows – axial, pleural or border – are lacking. Within the axial region, occipital and glabellar furrows were shallowly impressed or absent, articulating and inter-ring furrows barely impressed. Only in the

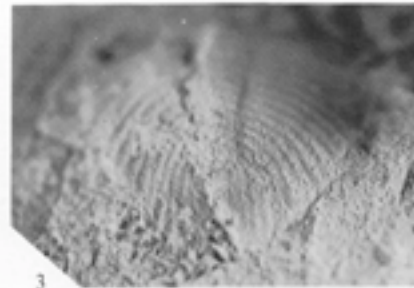
Newfoundland material of *S. amphionura* (Pl. 3, fig. 5) do glabellar furrows appear moderately impressed, and the articulating furrows have a deep pit which formed an apodeme on the inner surface. In my earlier study of *S. amphionura* (Whittington 1981, p. 598) I saw no evidence of the articulating half ring, and argued that the exoskeleton may have been a rigid shield, possibly having had sutures between the segments. The broken posterior edges of the cephalon and thoracic segments in the present specimens (Pl. 3, fig. 6; Pl. 4, figs 1, 4, 6) reveal the short (sag.), raised articulating half ring, and the ridge along the anterior edge of the pleura. In Canadian specimens of *B. hectori* (Pl. 1, fig. 4; Pl. 2, fig. 1) the forwardly-convex arc impressed into the axial ring may result from the underlying doublure of the ring, and half ring of the segment following. The disarticulation and telescoping of individual specimens (Pl. 3, figs 3, 6; Pl. 4, figs 1, 6) indicate that the segments were separate from one another and from cephalon and thorax. In particular Canadian specimens of *B. hectori* (Pl. 1, fig. 1) the first thoracic segment is pushed beneath the anterior edge of the cephalon, while other entire specimens (Pl. 2, fig. 3) show no displacement of segments. The Swedish examples (Pl. 2, fig. 2; Pl. 3, fig. 1) of this species show such displacement. This evidence, from specimens preserved in different ways, leads me to withdraw my argument and conclude that the burlingioid exoskeleton was not a rigid shield, but of separate, articulated sclerites. No facet is present in any species, nor any articulating process or socket; the ridge along the anterior margin of the pleura acted as an articulating flange beneath the turned-up edge of the sclerite in front. In *B. hectori* the ridge died out abaxially, and this may have allowed the distal portions of the pleurae to slip one below the other, and some limited convex-upward flexure of the exoskeleton. In the two species of *Schmalenseeia* considered here (Pl. 3, figs 2-4; Pl. 4, figs 1-6), the ridge extends to the margin of the pleura, and this morphology suggests that convex-upward flexure was limited. Some limited concave-upward flexure may have been possible in all three species. No even partly enrolled example is known. Most unusual is the lack of any evidence of a doublure in the lateral cheek area, thorax, or pygidium. The distal edge of the exoskeleton is ill-defined and irregular in almost all specimens, an exception being the low marginal ridge visible on a small specimen of *S. amphionura* (Pl. 3, figs 2-3). Evidence is described below for the presence of a rostral plate (Text-fig. 1) beneath the frontal area of the cranium in species of both genera. The outline of a hypostome is preserved in one Swedish specimen (Pl. 2, fig. 2), the anterior margin not defined. Hence whether or not the hypostome was linked by a suture to the rostral plate (the conterminant condition of Fortey and Chatterton 1988) is uncertain. Because the rostral plate extends back to the line of the preglabellar furrow, such attachment may seem probable, but remains to be confirmed. The boss on the anterior of the fixed cheek in *S. amphionura* (Pl. 3, figs 3, 5) appears to lie above the posterolateral corner of the rostral plate, and where the tip of the anterior wing of the hypostome may have been. Whether this boss had any association with attachment of the hypostome is uncertain; the boss is an unusual feature.

Size. Moberg (1903, p. 96) regarded *Schmalenseeia amphionura* as 'one of our smallest trilobites'. The length (exs., measured between the level of the median edge of the cephalon and that of the tip

EXPLANATION OF PLATE I

Figs 1-5. *Burlingia hectori* Walcott, 1908. Middle Cambrian, Stephen Formation; British Columbia, Canada. 1, USNM 53418, lectotype; arrow on left (pointing backward) indicates anterior margin of first thoracic segment, arrow on right (pointing forward) position of posterior margin of cephalon; thoracic segments 5 and 14 are numbered; dorsal view; $\times 15$. 2-3, USNM 53419b; incomplete exoskeleton; dorsal and postero-dorsal views; $\times 10$. 4, ROM 48463; thoracic segments 5 and 15 are numbered; arrow points to notch in posterior margin of pygidium; frontal area of cranium removed to expose rostral plate (r); complete exoskeleton; $\times 15$. 5, USNM 53419a; axial region broken away; beneath frontal area of cranium rostral plate (r) is exposed; posterior margin arrowed on left side; incomplete and poorly preserved exoskeleton; $\times 15$.

PLATE I



WHITTINGTON, *Burlingia*

of the most posterior pleura) ranges from 2.8 to 5.0 mm. That of the older *S. acutangula* is about 4 mm, and specimens of *Burlingia hectori* from British Columbia, Canada, are all between 5 and 6 mm in length, except one of 8 mm. Among burlingiids only Westergaard's type of *B. laevis* (Pl. 2, fig. 2) exceeds 10 mm in length. I have not included small size in the diagnosis of burlingiids because of the difficulty of giving meaning to such a characterization. Specimens of holaspid Agnostina (e.g. Robison 1984; 1988) range in length from 3–10 mm, and small holaspides of other trilobites (e.g. Whittington 1957, p. 444) lie within or below this range. Burlingiids are small only in relation to larger holaspides of certain other trilobites.

Geographical distribution. In relation to Cambrian geography (e.g. Scotese and McKerrow 1990, fig. 4) burlingiids are known from marginal, outer shelf sites of Laurentia, Baltica, Siberia (Lazarenko 1960; Soloviev 1969) and peripheral Gondwana (Avalonia (Rushton 1978), Tasmania (Jago 1972), South China). The occurrences of *Burlingia* and *Schmalenseeia* in South China are in the slope biofacies (W. T. Chang, pers. comm.) – in dark muddy limestones or fine-grained shales. Oil shales in Siberia yielded *B. obscura* Soloviev, 1969. In Canada and China (Chang 1988, p. 55) *Burlingia* occurs with *Oryctocephalus*, a genus which Fritz (1990, p. 108) noted is not found in shallow water strata in North America. The Siberian species is accompanied by other oryctocephalids. I agreed (1981, p. 599) with Jago (1972, p. 233) in suggesting, in part because of the supposedly rigid, thin exoskeleton, that the mode of life of *S. amphionura* was probably planktonic. Neither the morphology of burlingiids, nor their wide distribution, provides compelling evidence for this view.

Origin and relationships. Stubblefield (1936, p. 429) discussed burlingiids, norwoodiids and eodiscids as Cambrian trilobites having a proparian suture, no complete exoskeleton being more than 12 mm long. This size he regarded as considerably below the dimensions of an adult trilobite, and suggested that such forms either were immature, or were mature forms that had arisen by paedomorphosis. Fortey and Owens (1990) reviewed the operation of this latter process in trilobites, and point to one evolutionary trend, miniaturization, as occurring throughout the Palaeozoic. The species which portray this trend are not named, but are characterized as having a mature size of a few millimetres. They are considered to have different origins, but to be comparable adaptations. I assume that burlingiids are included among the families they plot (figure 5.5), and since I reviewed (1981) the problem of origins of new groups of trilobites, one new fact has emerged. This is that the smallest protaspid stage of the Middle Cambrian ptychopariid *Spencella* sp. had a proparian suture (Fortey and Chatterton 1988, text-fig. 10. 8a–b; based on their plate 17, figs 7, 9–10; the names *Spencella?* and *Bathyriscus?* having been transposed in the explanation of the plate, as B. D. E. Chatterton informs me (pers. comm.)). In the largest protaspid stage (Fortey and Chatterton 1988, text-fig. 10. 7a–b; pl. 17, figs 16–19) the suture was opisthoparian, and in both stages the hypostome was conterminant. The further development of ptychoparioids has been reviewed by Fortey (1990, p. 546, text-fig 9), laying stress on how during the early meraspid period the hypostome became natant. Little is known of development in early Middle Cambrian trilobites, and an immature stage –

EXPLANATION OF PLATE 2

Figs 1–4. *Burlingia hectori* Walcott, 1980. 1, 3–4, Middle Cambrian, Stephen Formation; British Columbia, Canada; 2, *Eccaparadoxides oelandicus* zone, early Middle Cambrian; Öland, Sweden. 1, ROM 48449; posterior margin of cephalon arrowed (pointing backward) on right, overlies first thoracic segment; segments 5 and 14 are numbered; notched posterior margin of pygidium arrowed; $\times 15$. 2, SGU 6246, holotype of *B. laevis* Westergaard, 1936 (original of his pl. 12, fig. 9); external mould, outline of hypostome impressed on anterior portion of glabella; $\times 8$. 3, ROM 48450; exoskeleton; notched posterior margin of pygidium arrowed; $\times 15$. 4, ROM 48454; crumpled, incomplete exoskeleton; external mould of rostral plate (r) exposed beneath frontal area of cranium, showing groove along anterior margin; $\times 15$.



WHITTINGTON, *Burlingia*

a small meraspis, for example – resembling a burlingiid is not known. The oldest species of burlingiids, *Burlingia hectori*, *B. obscura* Soloviev, 1969, and *Schmalenseeia acutangula*, appeared at about the same time in the early Middle Cambrian. They have many characters in common, which suggest a relationship between them, their morphology (Text-fig. 1) being quite different from that of any contemporary group. Distinctive of *S. acutangula* (Pl. 4, figs 1–6) is the incorporation of many more segments into a larger pygidium, apparently retaining the notched posterior outline which is lost in the younger *S. amphionura*.

Henningsmoen (1951, p. 194) tentatively placed the Burlingiidae in the Ptychoparioids, a suggestion followed by Poulsen (*in* Moore 1959, p. 293). Bergström (1973, pp. 18, 40) noted some of the peculiar characters of the thorax, considering that enrolment was not possible, and hence (presumably) allied burlingiids with redlichioids. Fortey's (1990) discussion of trilobite classification stressed the importance of early stages in ontogeny and of the attachment (or otherwise) of the hypostome. The apparent presence of a large rostral plate in burlingiids suggests that the hypostomal condition may have been conterminant. If so, burlingiids may be trilobites exhibiting the primary conterminant condition (Fortey 1990, p. 540), that is, the conterminant condition is presumably retained throughout growth. Among such Cambrian trilobites are Redlichiida, Corynexochida, Leiostegioidea, Damselloidea, and Odontopleurida. Relationships within this group have yet to be resolved, and what little is known of ontogeny does not suggest whence burlingiids may have been derived.

SYSTEMATIC PALAEOLOGY

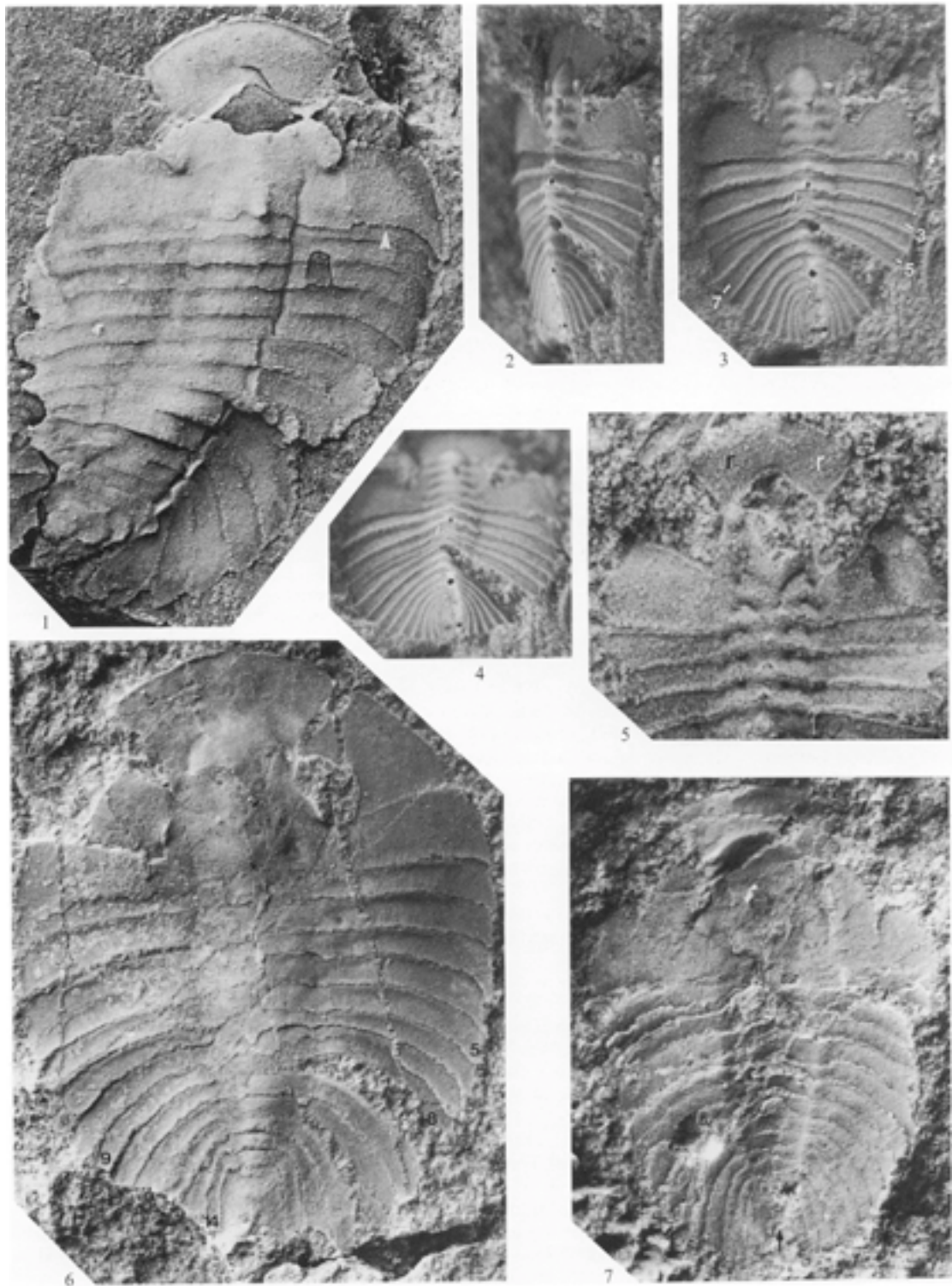
Family BURLINGIIDAE Walcott, 1908

Diagnosis. Exoskeleton suboval in outline, gently convex; axial region gently convex, axial furrow a change in slope, not impressed; pleural region non-fulcrate, doublure apparently absent, except for broad (tr.) rostral plate beneath relatively long (sag.) frontal area; condition of hypostome uncertain. Eye lobe close to anterior half of glabella, both branches of facial suture directed outward and forward. Narrow, low, anterior and anterolateral cephalic border. Pleurae directed progressively more strongly backward, no pleural furrow, no facet, ridge along anterior edge of each pleura fitted beneath raised posterior edge of cephalon or pleura; no axial or other articulating processes and sockets.

Distribution. Middle and early Upper Cambrian, worldwide.

EXPLANATION OF PLATE 3

- Figs 1, 6–7. *Burlingia hectori* Walcott, 1908. Middle Cambrian, *Eccaparadoxides oelandicus* zone; Sweden. 1, SGU 6245; original of Westergaard (1936, pl. 12, fig. 8); Öland; thin exoskeletal layer partly broken and weathered on the left side; irregular, broken posterior margin of cephalon (arrowed) overlying first thoracic segment; dorsal view; $\times 9$. 6–7. M. J. Collins collection, Jämtland. 6, thoracic segments disarticulated and partly telescoped; segments 5, 8, 9 and 14 numbered; dorsal view; $\times 15$. 7, exoskeleton exposed from ventral side; notch in posterior margin of pygidium arrowed; $\times 15$.
- Figs 2–5. *Schmalenseeia amphionura* Moberg, 1903. early Upper Cambrian. 2–4, SGU 134; original of Westergaard (1922, pl. 1, fig. 19); Skogsby, Öland, Sweden; latex cast from external mould; oblique right lateral, dorsal and postero-dorsal views; thorax partly disarticulated; segments 3, 5 and 7 numbered; $\times 18$. 5, SM A 104876; original of Whittington (1981, pl. 2, fig. 3); basal Elliot Cove Group, beds with *Agnostus pisiformis*; Little Ridge, east shore of Chapel Arm, 2.4 km south of McLeod Point, Trinity Bay, eastern Newfoundland, Canada; internal mould of incomplete cephalon and four thoracic segments; anterior portion of glabella and frontal area broken away to show rostral plate (r); arrow points to boss on fixed cheek beside anterior glabellar lobe; $\times 22.5$.



WHITTINGTON, *Burlingia*, *Schmalenseeia*

Genus BURLINGIA Walcott, 1908

Type species. By monotypy; *B. hectori* Walcott, 1908, from the early Middle Cambrian, Stephen Formation, of Mt Stephen, British Columbia, Canada.

Diagnosis. Glabella tapering slightly forward, rounded anteriorly, median occipital node, occipital and glabellar furrows either absent, or in rare specimens S0, S1 and S2 present as shallow lateral depressions. Eye lobe of length (sag.) more than one-third that of glabella. Thorax of 14 (rarely 15) segments in the type species, last pair of pleurae directed exsagittally, flanking the narrow (tr.), parallel-sided pygidium, which has the short axis poorly defined, two pairs of backward-directed pleurae behind it, posterior margin deeply notched; length (exs.) of pygidium less than that of posterior thoracic pleurae.

Distribution. British Columbia, Canada; Sweden; northern Siberia; Guizhou province, China.

Stratigraphical range. Early Middle Cambrian.

Burlingia hectori Walcott, 1908

Plates 1–2; Plate 3, figures 1, 6–7; Text-figure 1

Lectotype (selected by Rasetti 1951, p. 138). USNM 53418, flattened exoskeleton, original of Walcott 1908, pl. 1, fig. 8.

Paratypes. USNM 53419a–b, two specimens, figured herein, from Walcott's collection.

Other material. ROM 48449–48467, complete and incomplete exoskeletons, crumpled and flattened.

Locality and horizon. Locality S8D of Rasetti (1951, p. 128), equivalent to USNM locality 14S, southwest flank of Mt Stephen, 1.5 miles east 30° south of Field station. ROM locality EST (NTS 82N8, UTM 377933) approximately 350 m. NE of locality S8D, at about 1981 m altitude, Mt Stephen, collected in 1982 and 1984. Early Middle Cambrian, *Ogygopsis klotzi* faunule (Rasetti 1951, p. 101) at base of *Bathyriscus* – *Elrathina* zone, Stephen Formation (Fritz 1971, fig. 6; 1990, fig. 1). All the specimens are on the brown, weathered surfaces of pieces of the dark grey shale; none has been split from unweathered shale, so no counterparts are available. On the surface of occasional pieces (USNM 53419b, ROM 48454, 48458) are entire exoskeletons, or scattered parts of varying size, of *Oryctocephalus reynoldsi* Reed, 1899. Reed illustrated his new species by a drawing; additional specimens have been figured by Rasetti (1951) and Shergold (1969).

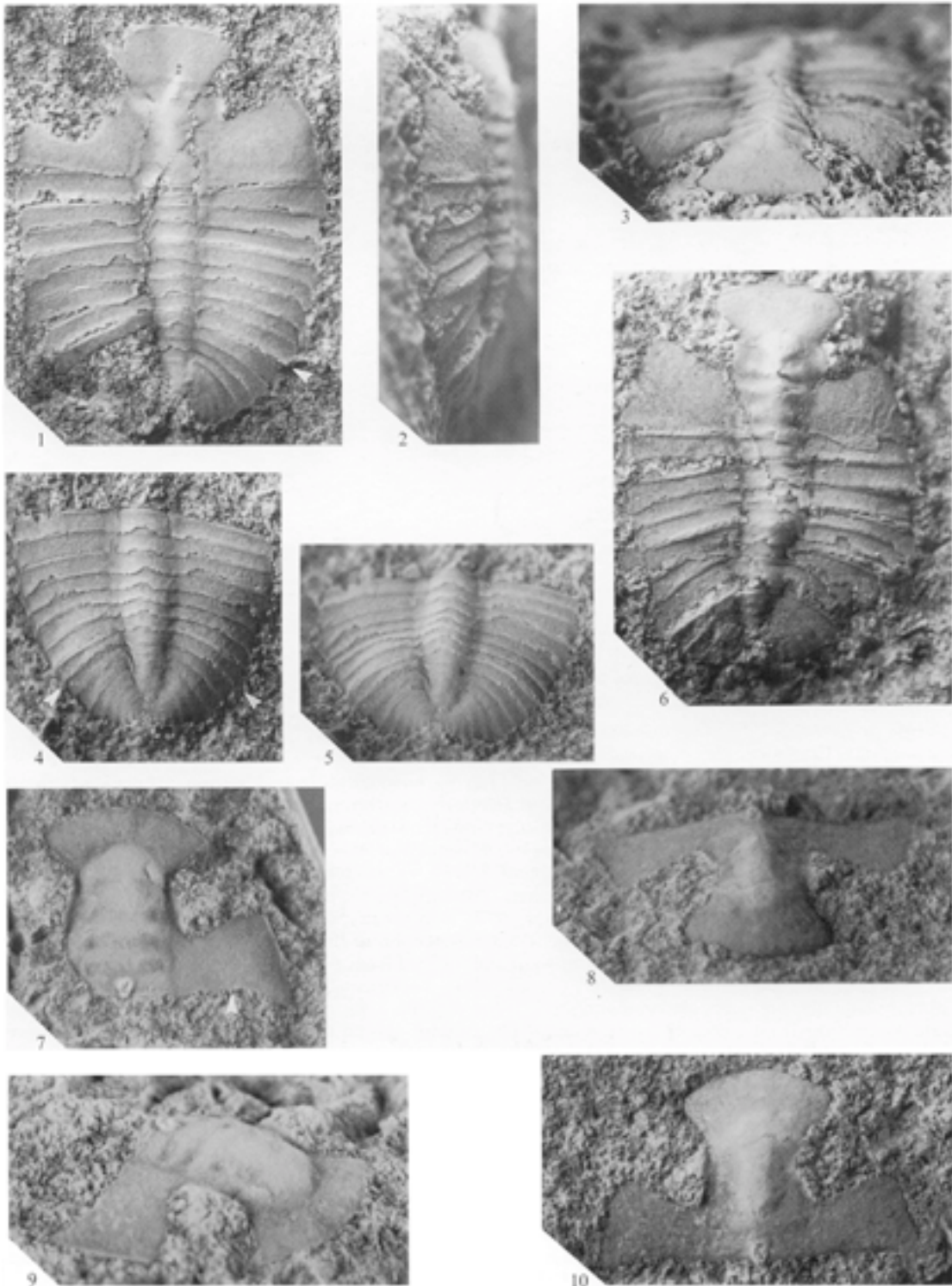
Description. Exoskeleton oval in outline, axial region of low convexity, shallow axial furrow, maximum width (tr.) at about midlength of exoskeleton, and about 0.7 of length to tip 13th thoracic pleura. Genal and pleural

EXPLANATION OF PLATE 4

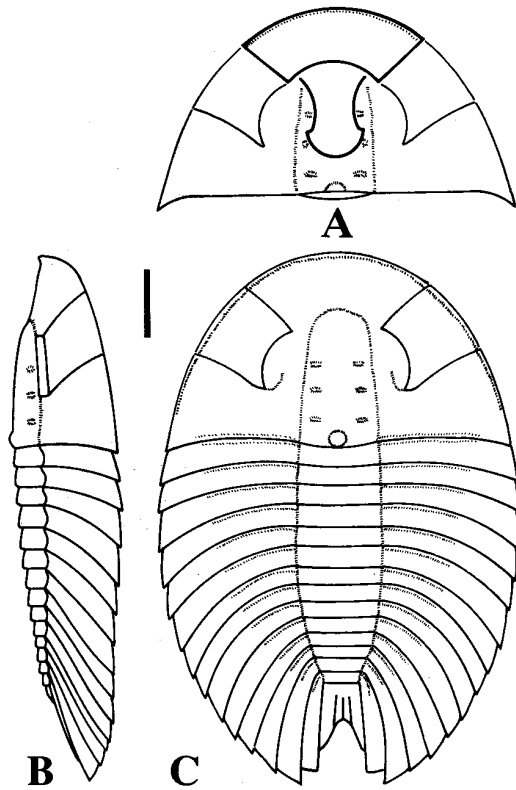
Figs 1–6. *Schmalenseeia acutangula* Westergaard, 1948. early Middle Cambrian; Scania, Sweden. 1, SGU 6354, holotype; incomplete exoskeleton; original of Westergaard (1948, pl. 1, fig. 2); arrow indicates division between thorax and pygidium; dorsal view; $\times 15$. 2–3, 6, SGU 6353; incomplete exoskeleton; original of Westergaard (1948, pl. 1, fig. 3); left lateral, anterior and dorsal views; $\times 15$. 4–5, SGU 6355; thorax and pygidium; original of Westergaard (1948, pl. 1, fig. 4); arrow indicates division between them; dorsal and postero-dorsal views; $\times 15$.

Figs 7–10. *Schmalenseeia jagoi* sp. nov. early Middle Cambrian; Scania, Sweden. 7, 9, SGU 6357, holotype; original of Westergaard (1948, pl. 1, fig. 6); incomplete exfoliated cranidium; arrow indicates broken posterior margin of cheek; dorsal and oblique right lateral views; $\times 12$. 8, 10, SGU 6356; original of Westergaard (1948, pl. 1, fig. 5); exfoliated cranidium; antero-dorsal and dorsal views; $\times 15$.

PLATE 4



WHITTINGTON, *Schmalenseeia*



TEXT-FIG. 1. *Burlingia hectori* Walcott, 1908. Restoration of exoskeleton, based on Canadian and Swedish specimens. A, ventral view of cephalon, rostral plate and hypostome (incomplete anteriorly) in heavier outline; doublure not known elsewhere, except that of occipital ring. B-C, right lateral and dorsal views. Scale bar represents 1 mm, for largest Canadian specimen known, for the Swedish material it is three-fifths of this length.

regions (Pl. 1, figs 2-3) curved downward from axial furrow, no inner horizontal portion or fulcrum. Glabella widest at base, tapers gently forward and rounded anteriorly, length (sag.) about two-thirds that of cephalon; low median occipital node visible in most specimens; faint lateral depressions (Pl. 1, fig. 4) of occipital furrow, S1 and S2 may be visible, and a suggestion in some individuals of S3. Genal region slopes gently downward, outward and forward, to a narrow, wire-like border (Pl. 1, fig. 1), which is best developed anteriorly, appearing to die out laterally without reaching the genal angle. Posterior margin transverse proximally, distally curving slightly back to an acute genal angle, not prolonged by a spine; no posterior border or border furrow, but posterior edge upturned. Curved eye lobe close to anterior portion of glabella, posterior end in transverse line with S1. Branches of facial suture directed outward and forward from eye lobe, anterior straight and at about 45° to sagittal line, posterior at about 70°, curved slightly back distally. No specimen shows evidence of a doublure laterally, but occasional specimens (Pl. 1, figs 4-5; Pl. 2, fig. 4) show what appears to be a ventral plate beneath the frontal area of the cranium. The anterior margin of the plate coincides with the dorsal cephalic margin, but has a groove along the margin (mould of a ventrally projecting ridge). The lateral margin of the plate appears to be a straight line, lying beneath the course of the anterior branch of the suture. The posterior margin coincides medially with the anterior margin of the glabella, laterally it is directed out to a position outside the anterior end of the eye lobe. In the figured specimens the plate lies at a level below that of the free cheeks; this and the distinct posterior and lateral edges suggest that this structure is a ventral plate and not part of the crumpled dorsal exoskeleton. It is regarded as an unusual rostral plate, not separated laterally from the doublure of the cheek by a connective suture, there being no sign of the presence of such a doublure.

Thorax of 14 segments (Pl. 1, fig. 1; Pl. 2, figs 1, 3), in occasional specimens 15 (Pl. 1, fig. 4). Axial region tapers gradually behind sixth ring; rings with transverse posterior margin, rarely (Pl. 1, fig. 4; Pl. 2, fig. 1) the forwardly-curved arc impressed into the ring indicates the presence of the doublure. Axial furrow shallow,

ill-defined. In relatively broader specimens (Pl. 2, fig. 1) the inner half of first pleura is directed transversely, outer portion curving gently back to falcate tip. The inner, transverse portion of the pleura is reduced in width (tr.) in successive pleurae and is gone by about the eighth pleura. In relatively narrower specimens (Pl. 2, fig. 3) there is no transverse inner portion of the pleura. The outer portions of the pleurae curve progressively more strongly posteriorly, and the 14th pair are directed exsagittally beside the pygidium. The tips of the pleurae are backwardly pointed. Anterior edge of each pleura a raised ridge proximally, which fades away distally. Posterior edge of each pleura bent up to overlie ridge of succeeding pleura. Between these transverse marginal ridges the faintly concave pleura is not impressed by a pleural furrow. No specimen shows any evidence of a pleural doublure, the tip being ill-defined.

Pygidium (Pl. 1, fig. 4) narrow (tr.), parallel-sided, axial region not convex, faint parallel lines suggesting a division into two pairs of backwardly directed pleurae, the inner pair shorter so that the posterior outline is deeply notched. The posterior thoracic pleurae extend well beyond the pygidial pleurae.

Discussion. All the specimens from Canada are internal moulds, flattened or crumpled, except for one incomplete example which appears to show the original convexity (Pl. 1, figs 2–3). Reference has been made to relatively broader and narrower specimens (Pl. 2, figs 1, 3), probably the result of tectonic distortion. The restoration (Text-fig. 1) is a compromise between these two types of flattened specimens, and the single example showing the convexity. The crumpling, and the indefinite ragged margins of the exoskeleton laterally, suggest that the cuticle was thin. In no specimen is there any breakage at the lateral margin of cephalon or thorax to reveal the mould of a doublure. The presence of the apparently ventral and relatively large rostral plate, beneath the frontal area of the cranidium, is therefore most unusual. Its seemingly definite shape and posterior margin suggest that it is real, and if the cuticle of the plate was thin, and lay close to the dorsal exoskeleton, it was presumably rarely exposed. Two specimens from Canada (Pl. 1, figs 1, 4) show a slightly more convex median portion of the axial region, about half the width of the axis. It extends almost the length of the thorax in the lectotype, being evident only posteriorly in the other specimen. I suggest that this convexity may be the impression in the thin axial exoskeleton of a partial filling of the alimentary canal.

The originals of Westergaard's (1936) *Burlingia laevis* (Pl. 2, fig. 2; Pl. 3, fig. 1) are also early Middle Cambrian in age, from the *Eccaparadoxides oelandicus* zone (*E. pinus* subzone) of Öland, Sweden. They are differently preserved, and the holotype is about twice the size of all but one of the Canadian specimens. It is an external mould in fine-grained shale, and has the outline of the hypostome preserved on the glabella by a narrow, low ridge. The lateral margin is a curve concave abaxially, the posterior portion wider, semicircular in outline; the anterior margin is not outlined, and the sagittal line of the hypostome is only slightly displaced from that of the dorsal exoskeleton. Thus the hypostome appears to be almost in position beneath the anterior portion of the glabella, but no rostral plate is visible, only what are taken to be the anterior branches of the suture crossing the frontal area of the cephalon. The right free cheek is displaced inwards, the left apparently in place. Hence whether this hypostome was natant, or whether it was conterminant, i.e. attached by a hypostomal suture to the rostral plate seen in the Canadian specimens, is uncertain. The second specimen (Pl. 3, fig. 1) in shale has a thin, light coloured layer adhering to it, presumably a replacement of the original exoskeleton. The right genal region has the lateral border extending to the genal angle; the latter appears acute because the posterior margin is broken and incomplete. Both examples have 14 thoracic segments, the holotype showing the low axis of the pygidium divided by 4 inter-ring furrows, the post-axial region ill-defined posteriorly. One additional specimen (RS Ar 46253) from the same locality, counterpart moulds of a telescoped exoskeleton, is smaller than the holotype and shows the notched posterior margin of the pygidium.

A small block of limestone was collected by Mr M. J. Collins in 1968 from Kloxasen, Jämtland, Sweden (stop 9 of Thorslund and Jaanusson 1960, p. 47). It contains five specimens of *Burlingia* (those referred to by Bergström 1973, p. 18), a cranidium of *Eccaparadoxides* cf. *oelandicus*, and *Ellipsocephalus polytomus*, and is of early Middle Cambrian age. In two of the specimens of *Burlingia*, the exoskeleton is exposed from the dorsal side, in the other three from the ventral. The two best (Pl. 3, figs 6–7) are of similar size to the Canadian specimens, and have 14 thoracic

segments and the narrow, elongate pygidium with the deep posterior notch. Some of the original convexity is retained, and the overlap of the posterior edge of each pleura (and the cephalon), upon the ridge of the following pleura is clearly shown. Some displacement and telescoping of segments has occurred, and the ragged edges of the thin thoracic exoskeleton are well displayed. The rostral plate may be pressed against the dorsal exoskeleton in the specimen exposed from the ventral side, but the evidence is equivocal. The axial furrow is shallow, with no posterior pit in the thoracic segments suggestive of an axial articulating process and socket, nor any evidence of fulcrum, fulcral articulating devices, or of doublure in the thorax or pygidium.

Westergaard (1936, pl. 32) remarked on the lack of glabellar furrows, the outline of the thorax, and the larger size as distinctive of his species, but acknowledged the close similarity to *B. hectori*. Comparisons between specimens of similar size show no distinctive differences. Some Canadian specimens (e.g. Pl. 2, figs 1, 3) show little or nothing of glabellar furrows. The appearance of there being a genal spine on the right side of the original of Plate 3, figure 1, is in part because the posterior edge of the right cheek is irregularly broken, the first thoracic segment pushed beneath it. Other specimens (Pl. 3, figs 6–7) show only a small point at the genal angle. I regard the Canadian and Swedish specimens as probably representing one species.

The species *Burlingia obscura* Soloviev, 1969, was described from incomplete, crumpled and partly disarticulated specimens in oil shale, from the northern region of the Siberian platform, Anabar river basin, Amgan Stage, Kuonamsk horizon, *Oryctocephalops frischenfeldi* zone, of early Middle Cambrian age. Soloviev's reconstruction (1969, pl. 2, fig. 3) of an exoskeleton c. 8 mm in length shows 12 thoracic segments, the last pair of pleurae directed outward at about 35° to the sagittal line, beside a bilobed pygidium. The latter has a short (sag.) undivided axis, and the pleural region lacks furrows. Soloviev questioned the number of thoracic segments, but regarded the pygidium as characteristic of his species. One photograph (Soloviev 1969, pl. 1, fig. 10), however, shows the posterior portion of the thorax with pleurae directed progressively more strongly backward, and almost exsagittally posteriorly, much as in *B. hectori*. In the diagnosis of *Burlingia*, I have cited the characters of the better-known type species, rather than those of the apparently distinctive Siberian species.

A single example of *B. ovata* Zhou and Yuan, in Chang *et al.* 1980 (p. 380, fig. 105; pl. 110, fig. 1) is from the early Middle Cambrian Kaili Formation, eastern Guizhou province, southwest China (Chang 1988, p. 55). It appears similar to *B. hectori*, and is smaller than the Canadian examples.

Genus SCHMALENSEEIA Moberg, 1903

Type species. By monotypy; *S. amphionura* Moberg, 1903, from the earliest Upper Cambrian, zone of *Agnostus pisiformis* of Sweden.

Diagnosis. Glabella with SO, S1–3 developed as moderately deep lateral depressions; in the Swedish species thorax of 7 or 8 segments, pygidium with 7 or 8 pairs of fused pleurae, posterior pair directed back behind axis.

Distribution. Early Middle Cambrian in Sweden, in the late Middle Cambrian of eastern Guizhou, China, and Tasmania, Australia, and in the early Upper Cambrian of Newfoundland, England, Sweden and Siberia.

Schmalenseeia amphionura Moberg, 1903

Plate 3, figures 2–5

Diagnosis. Glabella tapering forward to rounded, blunt, frontal glabellar lobe, sagittal ridge on preglabellar field, prominent boss adjacent to axial furrow, beside frontal glabellar lobe, branches of facial suture lie on sutural ridge. Median node on occipital ring, each of the seven thoracic segments, and the anterior axial rings of the pygidium.

Discussion. The original type material from the early Upper Cambrian *Agnostus pisiformis* zone of Öland, Sweden, and flattened and crumpled specimens from the same horizon in Newfoundland, have been described (Whittington 1981). Additional pieces of dark grey, fine-grained limestone from the type locality in Öland in the SGU collections contain many fragmentary cranidia and pygidia. The external mould of a small exoskeleton, original of Westergaard (1922, p. 119), from Skogsby, Öland, has the thorax partly telescoped and the pygidium broken sagittally, but shows the original convexity. The axial furrow is not impressed, but is a change in slope, the pleural region inclined downward and outward, more steeply distally (not flattened distally as my 1981, fig. 1, restoration implies). The irregularly broken posterior edge of cephalon and segments is upturned to overlie the short (sag.), convex articulating half ring and ridge along the anterior margin of each pleura. A low, narrow ridge appears to be present along the outer edge of each pleura; there is no evidence of any doublure. Between the marginal ridges the pleura is flat, lacking a pleural furrow.

Both internal and external mould are present in the Newfoundland material, and one of the former (Pl. 3, fig. 5) shows a ventral plate in front of the glabella. The lateral margin of the plate appears to coincide with the course of the anterior branch of the facial suture, and the median portion of the posterior margin with the preglabellar furrow. Distally this posterior margin is directed outward and backward to a point below the boss in the fixed cheek, and appears to lie below it in the internal mould. On this slim evidence I suggest that a rostral plate like that in *Burlingia* may have been present in *Schmalenseeia*.

Specimens of *Schmalenseeia* which resemble *S. amphionura* in having the median preglabellar ridge, the boss on the fixed cheek beside the frontal glabellar lobe, well-defined glabellar furrows, and in the form of the thoracic segments and pygidium, have been described from the early Upper Cambrian of northern Siberia (*S. spinulosa* Lazarenko, 1960) and central England (Rushton 1978). Similar specimens of uppermost Middle Cambrian age include those named *S. gostinensis* Jago, 1972, from Tasmania, *S. sinensis* Yang, 1978, an exoskeleton from eastern Guizhou, and two species based on isolated cranidia and pygidium from eastern China (Ju, in Qui *et al.*, 1983). Relationship between these forms is indicated by the characters they have in common, distinctions between them being based on minor characters such as axial tubercles or spines on the glabella (Rushton 1978, p. 274), or the continuation of the preglabellar ridge on to the frontal glabellar lobe (Jago 1972, p. 233). Better material is needed to clarify specific distinctions.

Schmalenseeia acutangula Westergaard, 1948

Plate 4, figures 1–6

Holotype. SGU 6354, incomplete exoskeleton, by original designation of Westergaard 1948, pl. 1, fig. 2, from a block of dark grey limestone, Gislövshammar, south-east coast of Scania, Sweden.

Other material. SGU 6353, incomplete exoskeleton, original of Westergaard 1948, pl. 1, fig. 3; SGU 6355, thorax and pygidium, original of same, pl. 1, fig. 4, locality and horizon as holotype. SGU, further unnumbered pieces from Gislövshammar, and one from a boring in Jämtland, Sweden.

Horizon. *Tomagnostus fissus* and *Acidusus atavus* zone, *Paradoxides paradoxissimus* beds, early Middle Cambrian.

Diagnosis. Differs from *S. amphionura* in lacking sagittal preglabellar ridge and boss beside frontal glabellar lobe, outer portion of occipital furrow and S1–3 less deeply impressed; eight thoracic segments, no median axial node, interpleural ribs of pygidium less prominent posteriorly.

Discussion. In outline and convexity of the exoskeleton this species is similar to *S. amphionura*. The narrow, raised cephalic border is present on the frontal area, and may be present laterally. The upturned palpebral lobe is close to the glabella, and extends from opposite the frontal glabellar lobe to opposite L3; the course of the facial sutures similar in the two species, but there is no evidence

of a sutural ridge in *S. acutangula*. The genal angle appears to be almost a right angle, and is not prolonged backward in a blunt point or spine. Thoracic segments are like those of *S. amphionura*, and show the short (sag.), raised articulating half ring, the anterior marginal ridge of the pleura, and upturned posterior edge. The thin exoskeleton is broken and irregular along this posterior edge, the distal edge also broken and shows no evidence of a marginal ridge, nor of a facet. In the original of Plate 4, figures 4 and 5, there appears to be an eighth pair of pleurae in the pygidium, faintly defined, behind the tip of the axis. These pleurae appear to have been the shortest, the seventh, sixth and fifth extended successively farther backward, so that the outline of the pygidium was indented by a notch behind the axis.

Schmalenseeia jagoi sp. nov.

Plate 4, figures 7–10

Holotype. SGU 6357, internal mould of incomplete cranium, original of Westergaard 1948, pl. 1, fig. 6, from a block of dark limestone, Brantevik, south-east coast of Scania, Sweden.

Other material. SGU 6356, internal mould of cranium, original of Westergaard 1948, pl. 1, fig. 5, same locality as holotype. Unnumbered pieces of similar limestone from Gislövshammar, south-east coast of Scania, Sweden, containing fragmentary internal moulds of crania.

Horizon. *Tomagnostus fissus* and *Acidusus atavus* zones, *Paradoxides paradoxissimus* beds, early Middle Cambrian.

Diagnosis. Cranium with facial sutures of *Schmalenseeia* type, differs from *S. acutangula* in that glabella at base is one-third (rather than one-fifth) width (tr.) of cranium at posterior margin; palpebral lobe adjacent to axial furrow and longer (exs.), posterior end opposite L2 and consequently postocular area of cheek relatively shorter (exs.); prominent median occipital node. In larger crania outer end of occipital furrow and S1–3 each a shallow, subcircular pit inside axial furrow.

Discussion. Jago (1972, p. 233) first recognized the distinctive characters of this cranium, and the new species is named in his honour. Additional material from the same locality and horizon as those figured, includes two external and five internal moulds of crania, poorly preserved and crumpled. Only the largest of these shows glabellar furrows like those in the holotype, other lacking such depressions; all show the median occipital tubercle. In the original of Plate 4, figs 8 and 10, and a smaller, unfigured cranium, the posterior margin appears complete, and the genal angle scarcely prolonged. The posterior margin of the cheek in the holotype (Pl. 4, figs 7, 9) is ragged and broken, and the appearance of an acutely angulate genal angle on the right side may be because of this breakage. Westergaard (1948, p. 4) regarded an acute genal angle as characteristic of his species, presumably because of this specimen, but I omit this character as of doubtful validity.

The glabellar furrows of the larger cranium, position of the eye lobe, course of the sutures, and lack of the posterior border, combine to suggest retaining this species in *Schmalenseeia*, although the thorax and pygidium are unknown. Jago's view that this species, and *acutangula*, be removed from *Schmalenseeia* is not accepted.

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REFERENCES

- BEECHER, C. E. 1897. Outline of a natural classification of the trilobites. *American Journal of Science, Series 4*, **3**, 89–106, 181–207.
- BERGSTRÖM, J. 1973. Organisation, life and systematics of trilobites. *Fossils and Strata*, **2**, 1–69, pls 1–6.
- CHANG, WEN-TANG 1988. The Cambrian System in Eastern Asia, correlation chart and explanatory notes. *International Union of Geological Sciences, Publication*, **24**, 1–81, 4 charts.
- (ZHANG WENTANG), ZHANG SENGUI, LIN HUANLING, ZHU ZHAOLING, QIAN YIYUAN, ZHOU ZHIYI, YUAN JINLIANG and LU YANHAO. 1980. Cambrian trilobite faunas of southwestern China. *Palaeontologica Sinica (new series B)*, **16**, 1–497, pls 1–134. [In Chinese].
- FORTEY, R. A. 1990. Ontogeny, hypostome attachment and trilobite classification. *Palaeontology*, **33**, 529–576.
- and CHATTERTON, B. D. E. 1988. Classification of the trilobite suborder Asaphina. *Palaeontology*, **31**, 165–222.
- and OWENS, R. M. 1990. Trilobites. 121–142. In McNAMARA, K. J. (ed.). *Evolutionary trends*. Belhaven Press, London, xviii + 368 pp.
- FRITZ, W. H. 1971. Geological setting of the Burgess Shale. *Proceedings of the North American Paleontological Convention, September 1969, Part I, Extraordinary Fossils*, Allen Press, Lawrence, Kansas, 1155–1170.
- 1990. Comments: in defense of the escarpment near the Burgess Shale fossil locality. *Geoscience Canada*, **17**, 106–110.
- HENNINGSMOEN, G. 1951. Remarks on the classification of trilobites. *Norsk geologisk Tidsskrift*, **29**, 174–217.
- JAGO, J. B. 1972. Two new Cambrian trilobites from Tasmania. *Palaeontology*, **15**, 226–237.
- LAZARENKO, N. P. 1960. In KRYSKOV, L. N., LAZARENKO, N. P., OGIENKO, L. V., and CHERNYSHEVA, N. E. 211–255, pls 50–53, in MARKOVSY, B. P. (ed.) [*New species of prehistoric plants and invertebrates of the U.S.S.R., part 2*] VSEGEI, Moscow. [In Russian].
- MOBERG, J. C. 1903. *Schmalenseeia amphionura*, en ny trilobit-type. *Geologiska Föreningens i Stockholm Förhandlingar*, **25**, 93–102.
- MOORE, R. C. (ed.). 1959. *Treatise on invertebrate paleontology. Part O. Arthropoda 1*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, xix + 560 pp.
- QIU, H. A., LU, Y. H., ZHU, Z. L., BI, D. C., LIN, T. R., ZHOU, Z. R., ZHANG, Q. Z., QIAN, Y. Y., JU, T. Y., HAN, N. R. and WEI, X. 1983 [*Palaeontological atlas of East China, I, Early Palaeozoic*]. Geological Publishing House, Beijing, ix + 657 pp, 176 pls. [In Chinese].
- RASETTI, F. 1951. Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smithsonian Miscellaneous Collections*, **116**, 1–277, pls 1–34.
- REED, F. R. C. 1899. Woodwardian Museum Notes: a new trilobite from Mount Stephen, Field, B.C. *Geological Magazine, New Series, Decade 4*, **6**, 358–361.
- ROBISON, R. A. 1984. Cambrian Agnostida of North American and Greenland. Part 1, Ptychagnostidae. *University of Kansas, Paleontological Contributions*, **109**, 1–59.
- 1988. Trilobites of the Hom Dal Formation (late Middle Cambrian), central North Greenland. *Meddelelser om Grønland, Geoscience*, **20**, 23–103.
- RUSHTON, A. W. A. 1978. Fossils from the Middle–Upper Cambrian Transition in the Nuneaton District. *Palaeontology*, **21**, 245–283.
- SCOTESE, C. R. and MCKERROW, S. W. 1990. Revised World maps and introduction. 1–21. In MCKERROW, S. W. and SCOTESE, C. R. (eds). *Palaeozoic palaeogeography and biogeography. Memoirs of the Geological Society, London*, **12**, 435 pp.
- SHERGOLD, J. H. 1969. Oryctocephalidae (Trilobita: Middle Cambrian) of Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia*, **104**, 1–66, pls 1–12.
- SOLOVIEV, I. A. 1969. [Discovery of representatives of the genus *Burlingia* Walcott in the Amgan Stage of Northern Siberia]. *Uchenye Zapiski nauchno-issledovatel'skikh Institutov Geologicheskogo Arktika*, **26**, 9–12, pls 1–2. [In Russian].
- STUBBLEFIELD, C. J. 1936. Cephalic sutures and their bearing on current classifications of trilobites. *Biological Reviews*, **11**, 407–440.
- THORSLUND, P. and JAANUSSON, V. 1960. The Cambrian, Ordovician and Silurian in Västergötland, Närke, Dalarna and Jemtland, central Sweden. *International Geological Congress, XXIst Session, Norden 1960, Excursions A23 and C18*, 51 pp.

- WALCOTT, C. D. 1908. Cambrian trilobites. *Smithsonian Miscellaneous Collections*, **53**, 13–52.
- WESTERGAARD, A. H. 1922. Sveriges Olenidskiffer. *Sveriges Geologiska Undersökning, Series C*, **18**, 1–205, pls 1–16.
- 1936. *Paradoxides oelandicus* beds of Öland. *Sveriges Geologiska Undersökning, Series C*, **394**, 1–66, pls 1–12.
- 1948. Non-agnostidean trilobites of the Middle Cambrian of Sweden. *Sveriges Geologiska Undersökning, Ser. C*, **498**, 1–32, pls 1–4.
- WHITTINGTON, H. B. 1957. The ontogeny of trilobites. *Biological Reviews*, **32**, 421–469.
- 1981. Paedomorphosis and cryptogenesis in trilobites. *Geological Magazine*, **119**, 591–602.
- 1990. Articulation and exuviation in Cambrian trilobites. *Philosophical Transactions of the Royal Society of London, Series B*, **329**, 27–46.
- YANG JIA-LU. 1978. [Middle and Upper Cambrian trilobites of western Hunan and eastern Guizhou]. *Professional Papers of Stratigraphy and Palaeontology*, **4**, 1–82, pls 1–13. Geological Publishing House, Peking, China. [In Chinese].

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H. B. WHITTINGTON
Sedgwick Museum
Department of Earth Sciences
University of Cambridge
Cambridge CB2 3EQ, UK