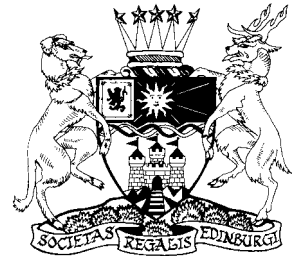


The age of the Middle Cambrian ‘*Paradoxides forchhammeri* Grit’ of the Wrekin district, Shropshire, England

A. W. A. Rushton and V. Berg-Madsen

ABSTRACT: The fossiliferous bed in the Upper Comley Sandstone, described by Cobbold & Pocock (in 1934) as the ‘*Paradoxides forchhammeri* Grit’ and correlated by them with the Andrarum Limestone of the late Middle Cambrian (*P. forchhammeri* Stage) in Scandinavia, is shown to be a shallow-water development of the older *punctuosus* Zone (medial Middle Cambrian, *P. paradoxissimus* Stage). It is here re-named the ‘Rushton Brook Bed’. The trilobite fauna, formerly considered comparable with that of the Andrarum Limestone, is reviewed and found taxonomically distinct, the supposed similarities being attributable to facial and preservational factors.

KEY WORDS: correlation, facies, trilobites.



The ‘*Paradoxides forchhammeri* Grit’ in the Middle Cambrian of Shropshire is notable for its unusually diverse shelly fauna (Cobbold & Pocock 1934, p. 390), more diverse than any other bed described from the Middle Cambrian of Britain. Cobbold & Pocock listed about thirty taxa, including seven of hyoliths and about 20 of trilobites, and correlated the unit with the *Paradoxides forchhammeri* Stage of Scandinavia. Since then, not only has the biostratigraphy been revised (Westergård 1946, 1953; Mens *et al.* 1987, 1990), but the trilobite ranges have been more firmly established both in Scandinavia and in Britain. However, it appears that everywhere else in Britain equivalents of the lower part of the *P. forchhammeri* Stage are represented by a hiatus induced by a marine regression. Therefore, confirmation of the presence of a *P. forchhammeri* fauna would, by suggesting that local tectonic subsidence had overridden the effects of eustatic regression, add a new phase to the long-continued movements along the Church Stretton Fault Complex (Cobbold 1927; Smith & Rushton 1993, fig. 2). This, and the need to verify the biostratigraphical age of the associated faunas, makes a review of the trilobites from the ‘*Paradoxides forchhammeri* Grit’ necessary. Cobbold & Pocock also recognised Scandinavian affinities in the hyolith fauna, but most of their taxa were described as specifically or subspecifically distinct, and the question arises whether these differences are connected with a difference in age rather than, or as well as, other factors such as biofacies and depositional environment.

1. Stratigraphical setting

The Cambrian rocks of Shropshire occur along the Church Stretton Fault Complex and crop out in two main areas: the Comley area near Caer Caradoc and the Rushton area W of the Wrekin (Fig. 1). Knowledge of the Comley area is the more complete because, although the rocks are not well exposed, Cobbold (1927) made numerous excavations that provided sufficient information to piece together the stratigraphical succession (Greig *et al.* 1968, p. 93). By assiduously collecting and describing the faunas, Cobbold (1921) was able

to make the Cambrian of the Comley area an important biostratigraphical standard of reference, especially for shallower-water facies.

When Cobbold & Pocock (1934) described the Cambrian of the Rushton area they made fewer excavations. Nevertheless, they found many similarities with the Comley succession, especially in the lower parts, and identified certain differences in the higher Middle Cambrian, as discussed below (and see Table 1).

The ‘*Paradoxides forchhammeri* Grit’ is exposed at only one locality, in the left bank of the eastern tributary (or ‘Rushton branch’) of Dryton Brook, 800 m SW of the cross-roads at Rushton [National Grid reference SJ 5995 0769]. Here Cobbold & Pocock (1934, p. 316, locality 9; ‘Loc. 9’ in Fig. 1C herein) described a section showing less than 1 m of sandy micaceous shales (the ‘*Liostracus bruno* Shale’), overlain by a bed of pebbly sandstone 0.3 m thick, followed by 1 m of grits and sandy shales, all dipping at up to 18° to the S. The basal grit bed is calcareous in places and contains pebbles and abundant rounded quartz grains. Locally it is highly fossiliferous, and many of the fossils, notably the larger trilobites, were already in fragmentary condition when deposited. Deposition appears to have been in high-energy conditions, probably in fairly shallow, well-oxygenated water. The exposure is now rather degraded and a visit by the authors in 1991 did not reveal further substantial fossiliferous blocks. A sample of about 1.5 kg was later disaggregated in 10% acetic acid, but yielded few microfossils.

Cobbold & Pocock (1934, pl. 38) mapped the ‘*Paradoxides forchhammeri* Grit’ as lying close to the top of the Upper Comley Sandstone, and at a trench about 400 m to the W [their locality 10 at SJ 5963 0760], they inferred that the shales overlying the gritty beds there lay higher in the Middle Cambrian succession (Fig. 1C). The fauna from locality 10 was considered to be of the latest Middle Cambrian age and referable to the *Lejopyge laevigata* Zone, though the few fossils found (in the British Geological Survey collection and re-examined by Adrian Rushton) are too small and fragmentary to be identified with certainty.

In view of our conclusion that the ‘*Paradoxides forchhammeri* Grit’ neither contains *Paradoxides forchhammeri*, nor can be correlated with the *Paradoxides forchhammeri* Stage in

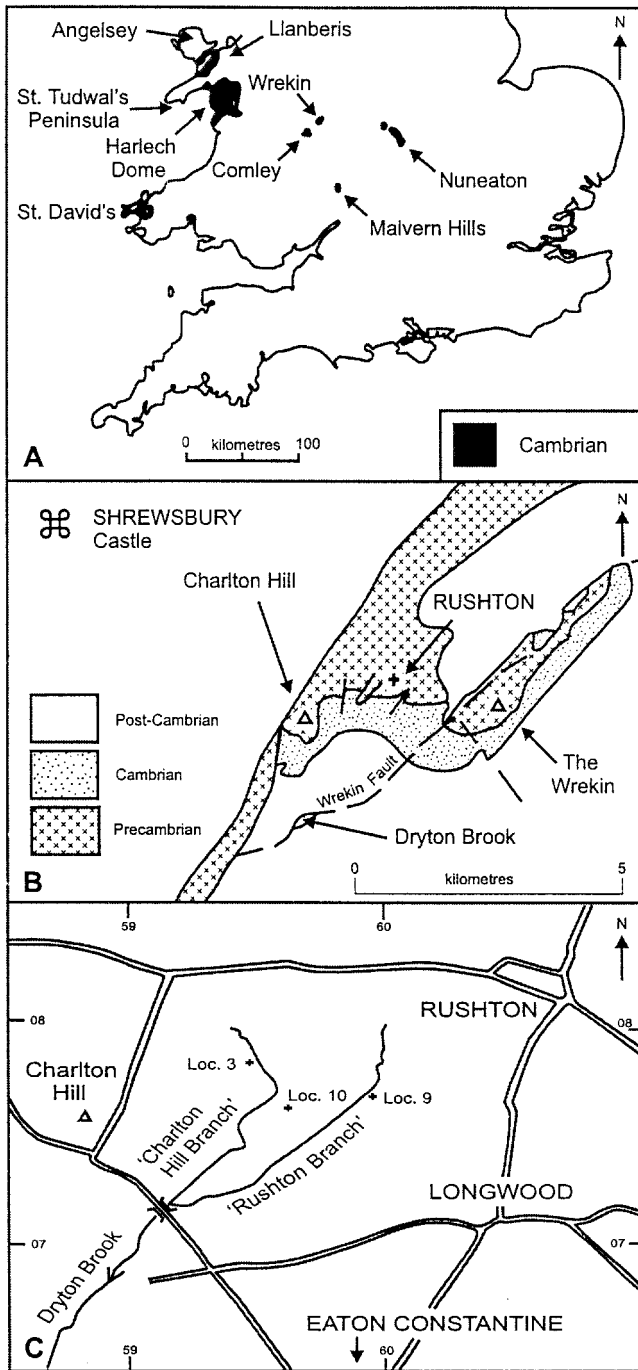


Figure 1 (A) Cambrian outcrops in England and Wales. (B) Sketch map of the Cambrian outcrops in the Wrekin area, Shropshire (from Cobbold & Pocock 1934, fig. 1). (C) Localities around Rushton, SE of Shrewsbury, the locality numbers being those of Cobbold & Pocock 1934, pl. 1; the 'Paradoxides forchhammeri Grit' (= Rushton Brook Bed) is exposed at Loc. 9; the numbers at the margin refer to the National Grid in the square SJ.

other ways, we here recommend that the calcareous sandstones known as 'the *Paradoxides forchhammeri* Grit' be re-named the **Rushton Brook Bed** of the Upper Comley Sandstone. The type locality is at Cobbold & Pocock's Locality 9 in the Rushton branch of Dryton Brook.

2. The *Paradoxides forchhammeri* Stage

2.1. Scandinavia

The highest Middle Cambrian in Scandinavia is referred to the

Paradoxides forchhammeri Stage and in Westergård's (1946, 1953) synthesis is divided into three zones, named in ascending order the *Ptychagnostus* (*Triplagnostus*) *lundgreni*-*Goniagnostus nathorsti* Zone (C1), *Solenopleura brachymetopa* Zone (C2) and *Lejopyge laevigata* Zone (C3).

The *lundgreni*-*nathorsti* Zone is now excluded from the *forchhammeri* Stage: Henningsmoen (1956) recommended against the use of *Triplagnostus lundgreni* as a zone fossil because of its long range, and that name has since been omitted by most authors. Henningsmoen regarded the *nathorsti* Zone as the topmost zone of the *Paradoxides paradoxissimus* Stage in Norway because of the general similarities in the faunas, and Berg-Madsen (1985a) argued that the *nathorsti* Zone has no utility within the East European Platform as all agnostid species within the zone range down into the *Ptychagnostus punctuosus* Zone or up into the *Solenopleura brachymetopa* Zone; furthermore no polymerid trilobites were recorded from the *nathorsti* Zone (Westergård 1953; Berg-Madsen 1985a). In fact, when Westergård (1944) earlier discussed the presence of a *Triplagnostus lundgreni* Zone, he noted that it was recognisable, if at all, only in Scania, southern Sweden. It therefore appears that the *nathorsti* Zone can be regarded as no more than a local sub-zone in Scania, and is not distinguishable elsewhere in Scandinavia. In the revision of the Cambrian biostratigraphical standard for the East European Platform (including Scandinavia) by Mens *et al.* (1987, 1990), strata formerly assigned to the *nathorsti* Zone (C1) are included in the *punctuosus* Zone (as in Norway), and Westergård's system of zonal letters and numbers is abandoned. It should be added that Mens *et al.* also suppressed the *Hypagnostus parvifrons* Zone (B3), referring strata of that zone to the *Ptychagnostus atavus* Zone (B2). It is nevertheless useful to recognise the *parvifrons* Zone (or Subzone) in some regions to indicate local ranges of trilobite species more precisely.

In Scania, the *brachymetopa* Zone is represented by the Andrarum Limestone and the underlying Hyolithes Limestone; these are separated by 0.12 m of unfossiliferous black shale but contain the same trilobite taxa and a rich hyolith fauna. In most parts of southern Sweden, equivalent strata are either absent, or else the succession from the *punctuosus* Zone up to the *laevigata* Zone or the lower part of the overlying Upper Cambrian *pisiiformis* Zone is represented by the Exporrecta Conglomerate (named after its rich content of the brachiopod *Oligomys exporrecta*). The latter unit is absent in Bornholm and Scania. The boundary between the *P. paradoxissimus* and *P. forchhammeri* stages is recognisable only in westernmost Västergötland (Hunneberg), in a bed of bituminous limestone. In Norway the Andrarum Limestone is not developed, though a considerable part of the *forchhammeri* fauna occurs in calcareous concretions within the shale sequence at Krekling (Brøgger 1878) and elements of it are reported at Ritland, near Stavanger (Bruton & Harper 2000).

According to Nielsen (1996) the Andrarum Limestone represents deposition in a deeper part of the Baltic Shelf Sea during a rapid marine regression, and the Exporrecta Conglomerate is the result of erosion in the more marginal areas. In intermediate areas, as on Bornholm, the Andrarum Limestone is present but there the lower part of the underlying Hyolithes Limestone is referable to the *punctuosus* Zone.

The Andrarum Limestone is primarily a precipitated limestone (Buchardt & Nielsen 1985) and represents a relatively well-oxygenated biofacies, quite different from that of the agnostid-rich black shales of the underlying *punctuosus* and overlying *laevigata* zones. The Andrarum Limestone contains large non-agnostid trilobites, inarticulate brachiopods, a few hyolith taxa and a rich and very distinct microfauna of molluscs, echinoderms and bradoriids.

Table 1 A comparison of the Middle Cambrian succession in the Comley area (from Cobbold 1921) and the Rushton area (Cobbold & Pocock 1934).

U.C. (part)	Comley Area			Rushton Area	
		Shoot-Rough Road Shales	Ca	' <i>Orusia</i> Shales'	
	(disconformity)			(presumed disconformity)	
MIDDLE CAMBRIAN	Upper Comley Sandstone	Shoot-Rough Road Flags	Bc Bb5	' <i>Billingsella</i> Beds' ' <i>Paradoxides davidis</i> Flags'	' <i>Agnostus laevigatus</i> Shale' ' <i>Paradoxides forchhammeri</i> Grit' ' <i>Liostracus bruno</i> Shale'
		Shoot-Rough Road sandstone	Bb4	' <i>Paradoxides rugulosus</i> Sandstone'	
		(not explored)	Bb3)		(unexposed interval)
		Hill House Shale	Bb2		' <i>Paradoxides hicksi</i> fauna'
		Hill House Grit	Bb1	' <i>Paradoxides intermedius</i> Grit'	' <i>Paradoxides bohemicus salopiensis</i> fauna'
		Hill House Flags	Ba3	' <i>Dorypyge lakei</i> Flags'	
		Quarry Ridge Shales	Ba2		
		Quarry Ridge Grit	Ba1	' <i>Paradoxides groomi</i> Grit'	' <i>Paradoxides groomi</i> Grit'
	(unconformity)				
L.C.					

In contrast, the *Hyalolithes* Limestone is a diagenetic limestone formed in more dysaerobic conditions. It is rich in agnostids with a few *hyoliths*, but brachiopods and microfaunas are scarce. Non-agnostid trilobites such as *Paradoxides davidis* Salter, indicative of the *punctuosus* Zone, are known only from the lower part of the bed on Bornholm (Grönwall 1902; Westergård 1953). Fossils are less common in the sub- and superjacent strata, though most groups are represented in the black shales (Berg-Madsen 1985b).

2.2. Great Britain

In Britain the *brachymetopa* Zone is known to be absent in the Nuneaton area, central England (Rushton 1978, p. 248), and is probably absent in the Harlech Dome of N Wales also (Allen *et al.* 1981, p. 307). In S Wales the *brachymetopa* Zone is not proved, but strata above the *punctuosus* Zone are said to yield *Paradoxides* and '*Billingsella*' (possibly = *Oligomys*) that may well correspond partly to the *Paradoxides forchhammeri* Stage (Rushton 1974, p. 90). Young *et al.* (1994) showed that in the sequence on St Tudwal's Peninsula, W of the Harlech Dome, no Middle Cambrian strata above the base of the *punctuosus* Zone are preserved. However, calcareous conglomeratic beds at the base of the Maentwrog Formation contain blocks with trilobites of the *brachymetopa* Zone that are inferred to have been derived from a late Middle Cambrian limestone unit not otherwise known in N Wales (Young *et al.* 1994, p. 345). The *brachymetopa* zonal age is confirmed by microfaunas in the conglomerate whose preservation suggests *in situ* erosion and re-deposition rather than transport from other areas. Thus the conglomerate may represent a local very condensed sequence, not unlike the Exporrecta Conglomerate in Sweden (Berg-Madsen & Bassett, unpublished research).

In the Comley area of Shropshire the nearest equivalent of the *forchhammeri* Stage lies in the upper two metres of the Shoot Rough Road Flags, the *Billingsella* Beds (Bc) of Cobbold (1921, p. 373), in the highest part of the Upper Comley Group (see Greig *et al.* 1968, pp. 93, 97). These strata overlie

beds (Bb5) with *Paradoxides davidis* that are referred to the *punctuosus* Zone (Table 1).

3. Fauna of the Rushton Brook Bed

The fossils in the Rushton Brook Bed are abundant and well preserved, but commonly fragmentary. The fossiliferous blocks collected by J. Pringle and S. W. Hester of the Geological Survey were broken up by Cobbold, who identified and labelled the fossils he thus revealed. He did his best to develop the fossils, no easy task in such a hard quartzitic sandstone, but many fossils sustained damage during collection or development. Cobbold illustrated most of the fauna with drawings: he was an accomplished draughtsman and many of his earlier drawings were good, but in Cobbold & Pocock (1934) some, such as those of *Agaso*, are not altogether lifelike. Therefore, we here offer photographs to supplement the published drawings.

Nearly all the material is in the collections of the British Geological Survey, Keyworth, and their registration numbers are prefixed GSM. One block collected by K. P. Oakley is in the Natural History Museum, London (no. PG 4206).

Cobbold & Pocock (1934, p. 390) listed three species of brachiopods and on p. 327 added *Lingulella* cf. *ferruginea* Salter. Of these, '*Acrotreta*' *sagittalis* (Davidson) and *Micromitra pusilla* (Linnarsson) are doubtfully assigned and have a long recorded range; their specimens of *Oligomys* [*Billingsella*] *exporrecta* (Linnarsson) are fragmentary and equally doubtful. No firm biostratigraphical conclusions could be drawn from the brachiopods. The one bradoriid, *Dielymella?* *corpulenta* Cobbold, was assigned by Williams & Siveter (1998) to *Anabariochilina*, but is too fragmentary to be identified or exploited stratigraphically. Examination of the diverse and well-preserved *hyolith* fauna, now under revision, shows that the restricted distribution of Scandinavian species observed by Berg-Madsen & Malinky (1999) applies equally to the fauna of the Rushton Brook Bed. Although there are some genera

in common that indicate limited faunal exchange between the regions, none of the species known from either the *P. paradoxissimus* or *P. forchhammeri* stages of Scandinavia is present at Rushton Brook (Berg-Madsen unpublished research).

The residue of the dissolved sample mentioned above contains one specimen of *A. corpulenta* and one other unidentifiable bradoriid, fragments of lingulate brachiopods and some problematical tubiform fossils. A few minute hyolith conchs and juvenile opercula are to be discussed in connection with the revision of the hyolith fauna.

3.1. Trilobite fauna

The trilobite fauna listed by Cobbold & Pocock (1934, p. 390) includes agnostids, paradoxidids, a supposed agraulid, a *Dorypyge*, and several taxa referred to *Solenopleura* and '*Liostracus*' of Angelin, 1854. Our interpretations are shown in Table 2.

The commonest agnostid is *Hypagnostus* (Fig. 2a–d, g–i). Having examined Westergård's (1946, pl. 5, figs 2–4) material of the subspecies *H. parvifrons mammillatus* (Brøgger), we refer all but one or two of the specimens from the Rushton Brook Bed to the same taxon. This is in agreement with Samson *et al.* (1990, p. 1466), who elevated *mammillatus* to specific rank and placed Cobbold & Pocock's (1934, pl. 44, figs 13–19) figured specimens of *Agnostus parvifrons* in their synonymy of *Hypagnostus mammillatus*. Although Peng & Robison (2000, p. 61) placed Cobbold & Pocock's specimens in their synonymy of *H. parvifrons*, Prof. Robison informs us (*in litt.*, 2001) that this was inadvertent, and that the specimens are better placed in *H. mammillatus*. We confirm the identification of *Cotalagnostus lens* (Grönwall) and use cephalic and pygidial features to restrict the identification to *C. lens lens* (Fig. 2e–f, j–k). The pygidia that Cobbold assigned to *Agnostus rotundus* Grönwall (Cobbold & Pocock 1934, pl. 44, figs 1, 2) are also assigned to *C. lens*. The cephalon that Cobbold assigned to *Agnostus lundgreni* Tullberg (Cobbold & Pocock 1934, pl. 44, fig. 20) differs from small cephalons that occur on blocks with Westergård's figured specimens (1946, pl. 10, figs.

23–25; pl. 11, figs 1–2), especially in having a blunter anterior glabellar lobe (see Robison 1984, fig. 28.5); the specimen (Fig. 2n, o) agrees more closely with *Ptychagnostus hybridus* (Brøgger), as indicated by Robison (1984, p. 51). Although this species was placed by Laurie (1988) in *Onymagnostus* and by Robison (1994, p. 49) in *Lejopyge*, Westrop *et al.* (1996) have transferred it to *Ptychagnostus* s.l. The pygidium that Cobbold & Pocock (1934, pl. 44, fig. 7) assigned to *Agnostus lens* (Fig. 2p–q) is here referred with doubt to *Lejopyge elegans* (Tullberg), as figured by Westergård (1946, pl. 10, fig. 19).

The paradoxidids are fragmentary and cannot be identified securely. Cobbold & Pocock identified some of the fragments as *P. forchhammeri* Angelin, but Lake (1935, p. 223) pointed out differences from that species and doubted the identification. One fairly complete but small pygidium (Fig. 3g) differs from many other bispinose paradoxidid pygidia, which tend to have a longer pleural area behind the axis (e.g. Dean 1982, fig. 23, and Sdzuy 1961, p. 21, figs 3–9). Most similar is the pygidium of comparable size described by Cobbold (1911, pl. 24, fig. 18), which differs in having a lateral ridge to the pleural field and a slightly shallower posterior embayment. That specimen is from the part of the Shoot Rough Road Flags (Bb5) of Comley that yielded *Paradoxides davidis* (Table 1).

The specimens identified as *Agraulos robustus* Cobbold (*in* Cobbold & Pocock 1934, p. 376, pl. 43, figs 6–9) differ from typical *Agraulos* in the shape of the glabella, convexity of the preglabellar field and obliquity of the eye-ridges (Fig. 3a–d). In these and other features they are more like *Lonchocephalus peregrinus* Wallerius (1930), which Westergård (1953, p. 30, pl. 7, figs 9–10) assigned questionably to *Parasolenopleura*. We believe *P.?* *peregrina* is a senior synonym of *A. robustus*.

The long-ranging and widely distributed genus *Dorypyge* is represented by the endemic species *D. rushtonensis* Cobbold (Fig. 3e–f).

Of the five species assigned to '*Liostracus*' of Angelin (1854, *non* Mörch, 1852) one, '*L. dubius* Cobbold (1911), was originally described from the Bb5 horizon (with *Paradoxides davidis*)

Table 2 The trilobite fauna of the '*Paradoxides forchhammeri* Grit' listed by Cobbold & Pocock (1934, p. 390), with the present identifications shown on the right

Cobbold & Pocock 1934	Herein
<i>Agnostus lens</i> Grönwall	<i>Cotalagnostus lens lens</i> (Grönwall)
<i>A. lens</i> [one figured pygidium]	<i>Lejopyge elegans</i> (Tullberg)
<i>A. lundgreni</i> Tullberg	<i>Ptychagnostus hybridus</i> (Brøgger)
<i>A. parvifrons</i> Linnarsson	<i>Hypagnostus mammillatus</i> (Brøgger)
<i>A. rotundus</i> Grönwall	<i>Cotalagnostus lens?</i> (Grönwall)
<i>Agraulos robustus</i> Cobbold	<i>Parasolenopleura? peregrina</i> (Wallerius)
<i>Paradoxides forchhammeri</i> Angelin	<i>Paradoxides</i> sp. indet.
<i>P.</i> sp. indet. A	<i>P.</i> (s.l.) sp.
<i>P.</i> sp. indet. B	<i>P.</i> (s.l.) sp. indet.
<i>Liostracus dubius</i> Cobbold	genus? <i>dubium</i>
<i>L. bruno</i> Cobbold	<i>Agaso bruno</i> (Cobbold)
<i>L.</i> sp. indet. [pygidium]	pygidium no. 1 [<i>Agaso?</i>]
<i>Liostracus (Agaso) rushtonensis</i> Cobbold	<i>Agaso rushtonensis</i>
<i>L. (A.) pringlei</i> Cobbold	<i>A. rushtonensis</i>
<i>L. (A.) pococki</i> Cobbold	<i>A. rushtonensis</i>
<i>L. (A.)</i> sp. [pygidium]	pygidium no. 2
<i>Solenopleura angustiora</i> Cobbold	<i>Elrathia? angustiora</i> (Cobbold)
<i>S. applanata</i> (Salter)	<i>Solenopleura</i> (s.l.) cf. <i>applanata</i> (Hicks)
<i>S.?</i> sp. indet.	<i>S.</i> aff. <i>brachymetopa</i> [juvenile]
<i>S. brachymetopa</i> (Angelin)	<i>S.</i> aff. <i>conifrons</i> Westergård
<i>S.</i> cf. <i>brachymetopa</i>	<i>S.</i> cf. <i>nuntia</i> Grönwall
<i>S. brachymetopa nuntia</i> Grönwall	<i>S.</i> sp. indet.
<i>S.</i> cf. <i>bucculenta</i> Grönwall	<i>S.</i> sp. indet.
<i>Dorypyge rushtonensis</i> Cobbold	<i>Dorypyge rushtonensis</i> Cobbold

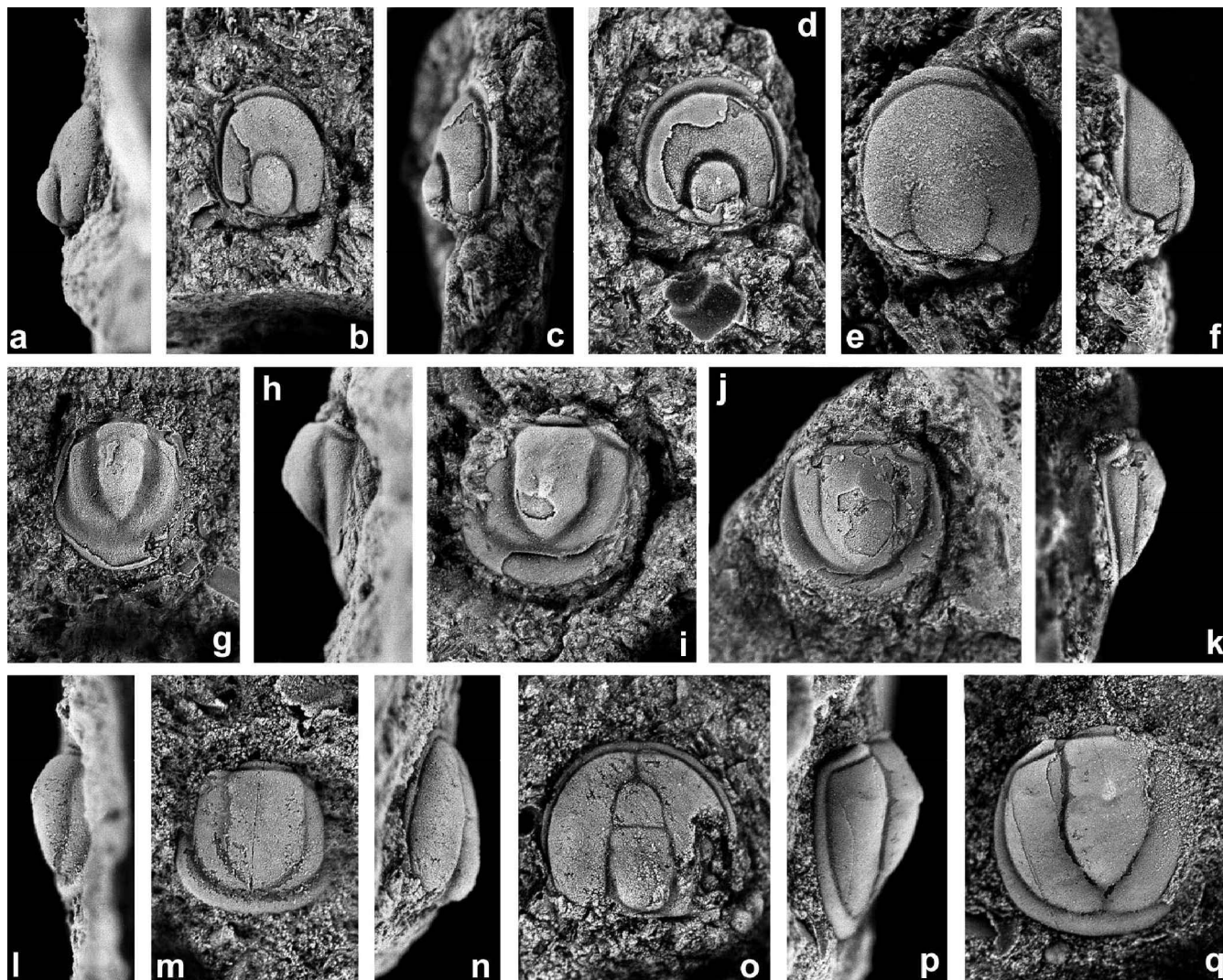


Figure 2 Agnostid trilobites from the Rushton Brook Bed. Specimens retain the exoskeleton except where indicated.

(a–d, g–i) *Hypagnostus mammillatus* (Brøgger): (a–d) side and top views of cephalon GSM 51750 (no. 15) and 51748, all $\times 10$; (g–i) pygidia GSM 51752 (internal mould), and side and top view of 51750 (no. 16), all $\times 8$.

(e–f, j–k) *Cotalagnostus lens lens* (Grönwall): (e–f) top and side views of cephalon GSM 51739, $\times 10$; (j–k) top and side views of pygidium GSM 105454, $\times 8$.

(l–m) *Hypagnostus?* side and top views of latex cast of external mould of pygidium GSM 51740D, $\times 8$.

(n–o) *Ptychagnostus hybridus* (Brøgger): side and top views of cephalon GSM 51754, $\times 10$.

(p–q) *Lejopyge elegans* (Tullberg): side and top views of latex cast of external mould of pygidium GSM 51741, $\times 8$.

in the Comley area (see Table 1), and later recorded from the Comley Breccia Bed (with '*Paradoxides intermedius* Cobbold'), which is equivalent to the Bb1 horizon (Cobbold 1913). The other four are, so far as known, endemic to the Rushton area. '*L. bruno* Cobbold is known from the beds underlying the *P. forchhammeri* Grit, where it is associated with *Paradoxides paradoxissimus* (Wahlenberg) (= *P. tessini* in Lake 1935, p. 208). The other three species are all assigned to Cobbold's subgenus *Liostracus* (*Agaso*). This is treated here as a genus and briefly revised and illustrated below (Fig. 6).

The six fragmentary taxa that Cobbold & Pocock assigned to *Solenopleura* (Fig. 5) are discussed below under that name, which we take in a wide sense. In summary, the specimen that Cobbold & Pocock assigned to *S. applanata* is closely comparable with that species, whereas the specimens attributed to *Solenopleura* cf. *bucculenta*, *S. brachymetopa* and the subspecies *nuntia* are all rejected from those taxa. The juvenile '*Solenopleura?* sp.' of Cobbold & Pocock (1934, pl. 43, fig. 3) has wide fixigenae, somewhat like *S. brachymetopa*. *Solenopleura*

angustiora Cobbold is here referred to *Elrathia* and is closely comparable to *Peregrinaspis subtilis* Buchholz (1997).

3.2. The age of the fauna

In assessing the biostratigraphical age of the Rushton Brook Bed, the greatest reliance is placed on the agnostids. These have a fairly continuous record in the Middle Cambrian of Scandinavia and their ranges are therefore considered more reliable than those of other genera, such as the solenopleurids; the latter appear to be controlled by facies and occur chiefly in the relatively oxygenated environments of the Andrarum Limestone and Exporrecta Conglomerate. The paradoxidids might also be considered reliable, but none of the specimens is identifiable. See Figure 4.

The agnostids range up to the *punctuosus* Zone and, if the identification of *Ptychagnostus hybridus* is accepted, this is the only zone in which the ranges of the four taxa identified overlap. None is known to extend to the *brachymetopa* Zone (Fig. 4). The ranges of the non-agnostid trilobites are less

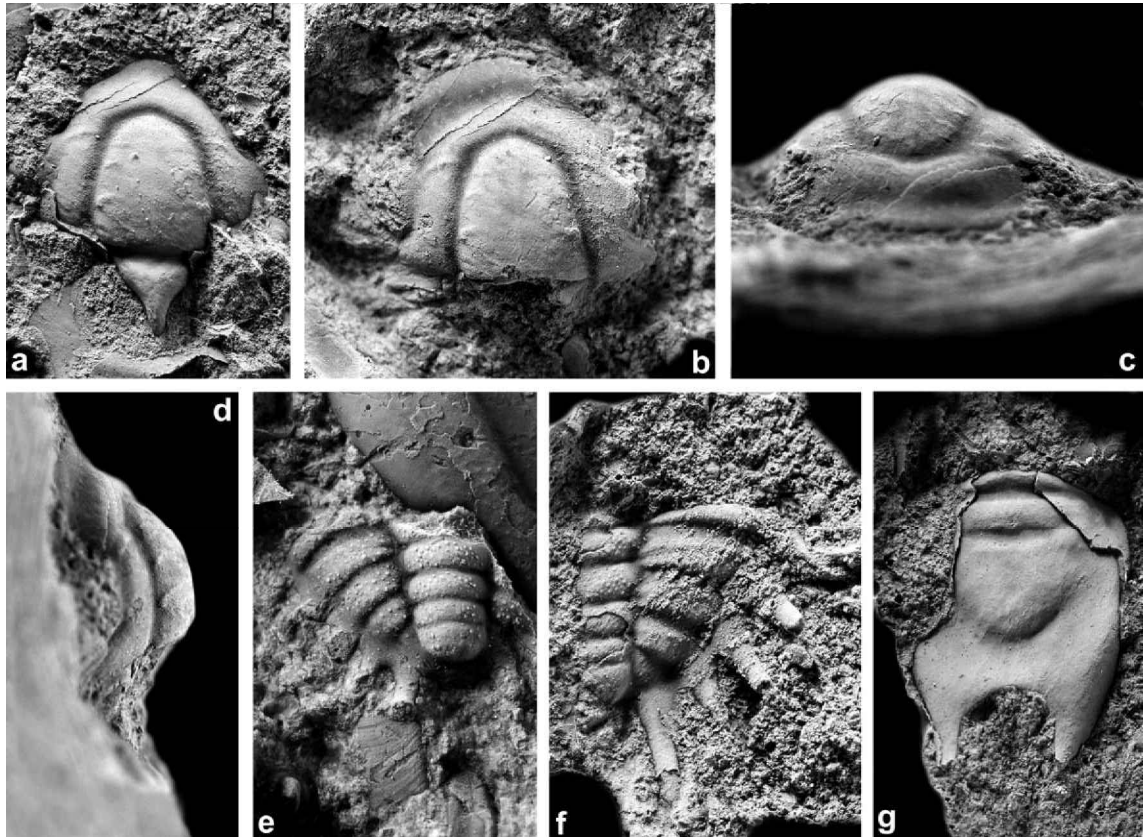


Figure 3 (a–d) *Parasolenopleura? peregrina* (Wallerius), figured Cobbold & Pocock 1934, pl. 43, fig. 6, as holotype of *Agraulos robustus* Cobbold: (a) latex cast of intaglio showing the inner surface of cranidium, which therefore simulates an internal mould, GSM 51725 counterpart, $\times 6$; (b–d) top, front and side views of natural internal mould, GSM 51725, all $\times 6$; (e, f) *Dorypyge rushtonensis* Cobbold, pygidia: (e) paratype GSM 51708; (f) latex cast of counterpart of holotype, GSM 51706, both $\times 6$. (g). *Paradoxides* sp. indet. A of Cobbold & Pocock (1934, p. 349); latex cast of intaglio showing the internal surface of pygidium, GSM 51786, $\times 6$.

MIDDLE CAMBRIAN (part) Stages and zones of Scandinavia and the East European Platform modified after Mens <i>et al.</i> 1990	<i>Paradoxides paradoxissimus</i>			<i>Paradoxides forchhammeri</i>		
	<i>Ptychagnostus gibbus</i>	<i>Pt. atavus</i>		<i>Ptychagnostus punctuosus</i>	<i>Solenopleura brachymetopa</i>	<i>Lejopyge laevigata</i>
		<i>Tomagnostus fissus</i>	<i>Hypagnostus parvifrons</i>			
<i>Cotalagnostus lens lens</i> (Grönwall)						
<i>Hypagnostus mammillatus</i> (Brøgger)						
<i>Ptychagnostus hybridus</i> (Brøgger)						
<i>Lejopyge elegans</i> (Tullberg)						
<i>Parasolenopleura? peregrina</i> (Wallerius)						
<i>Solenopleura? applanata</i> (Hicks)						
<i>Solenopleura conifrons</i> Westergård						
<i>Solenopleura brachymetopa</i> (Angelin)?						
<i>Elrathia? angustiora</i> (Cobbold)						
' <i>Liostracus</i> ' <i>dubius</i> Cobbold						

Figure 4 The zonal ranges of taxa in the Rushton Brook Bed, as inferred from the occurrences of the same or similar taxa in other areas; the ranges of species whose identification is less certain are shown with dashed lines.

well known: '*Liostracus dubius* was originally described from beds with *Paradoxides davidis* which elsewhere is typical of the *punctuosus* Zone, but '*L. dubius* is also recorded from lower levels. Westergård's specimens of *Parasolenopleura? peregrina* were recorded from the *punctuosus* Zone, whilst Bruton & Harper (2000) described a comparable form from strata at Ritland, Norway, that they assigned to the *brachymetopa* Zone. In contrast, *Solenopleura applanata* is confined to levels below the *punctuosus* Zone, the upward extension of its range shown by Thomas *et al.* (1984) being dependent only on the one variant specimen from the '*forchhammeri* fauna of Shropshire. Two other *Solenopleura* species, *S. cf. brachymetopa* (juv.) and *S. aff. conifrons*, are both under open nomenclature and therefore of less certain stratigraphical significance, though they are comparable with species from the *brachymetopa* Zone of Sweden.

We conclude that the '*Paradoxides forchhammeri* fauna' of Shropshire is most probably a shallow-water development of the *Ptychagnostus punctuosus* Zone. Its Scandinavian equivalents are the lower part of the Hyolithes Limestone of Bornholm, Denmark, and a bituminous stinkstone bed representing the same zone at Hunneberg, Västergötland, Sweden. Some of the taxa resemble those in the fauna from Ritland that Bruton & Harper (2000) correlated with the *brachymetopa* Zone, namely *Parasolenopleura? peregrina* and a *Solenopleura cf. bucculenta* with an elevated glabella (discussed below). It seems to us that the Ritland fauna may, like that of the Rushton Brook Bed, possibly be an earlier development of a shallow-water oxygenated facies than the Andrarum Limestone. The only agnostid at Ritland, *Peronopsis fallax* (Linnarsson), is typical of the *paradoxissimus* Stage; their *Anomocare cf. leave* (Angelin) is not typical of the Andrarum species as it has a shorter preglabellar field; and the ranges of the non-trilobitic taxa recorded are either long or not definitively known. If it is accepted that the Ritland fauna may possibly be older than the *forchhammeri* Stage, the quartzite bed that overlies the Ritland fauna may represent the Andrarum regression.

4. Palaeontological notes

Genus *Solenopleura* Angelin, 1854

We follow Westergård (1953) and Chernysheva (1980) in taking a wide view of this genus. Taylor & Rushton (1972) showed that the type species is *S. holometopa* (Angelin), not *S. canaliculata* (Angelin) as some had previously supposed, and others have accepted this (Chernysheva 1980; Babcock 1994; Geyer 1998). We follow Šnajdr (1958, p. 197) in regarding *S. holometopa* as congeneric with *Jincella prantli* Růžička, and hence treat *Solenopleura* as a senior synonym of *Jincella*. Geyer (1998) took a much more restricted view of *Solenopleura*, restricting it to *S. holometopa*. He accepted *Jincella* Šnajdr, 1957, *Erratojincella* Rudolph, 1994 (with *S. brachymetopa* (Angelin) as type species), *Foveatella* Rudolph, 1994 (with *S. bucculenta* Grönwall as type species), and proposed the new genus *Gonzaloia* with *S. canaliculata* as type species. Although Geyer gave diagnoses for some of these genera, most of the criteria he used to distinguish them, such as the width and convexity of the fixigenae or length of the preglabellar field, are unquantified and not at present objectively applicable. Furthermore, in view of the very variable characters of certain well-studied Cambrian trilobites, to try and define genera by a mosaic of such characters is unlikely to provide an enduring taxonomy. For example, Hughes (1991, 1994) has demonstrated that the morphological plasticity of the Upper Cambrian trilobite

Dikelocephalus is such that thirty supposed species were placed in synonymy; and Blaker & Peel (1997, p. 124) illustrated one population of their Lower Cambrian *Ptychoparella* sp. 'A' which is so variable that extreme examples would, if found in isolation, be placed in different genera. We consider that more needs to be known about intraspecific variability before generic categories can be drawn reliably.

Aside from this general consideration, some of Geyer's (1998) conclusions are unjustifiable: on p. 390 he indicates that *Solenopleura conifrons* Westergård is congeneric with *S. canaliculata*, whereas on p. 391 he states that *Gonzaloia* is a monotypic genus proposed to accommodate *Solenopleura canaliculata* only. In our opinion *S. conifrons* can be placed in *Solenopleura*. Geyer stated that there is 'no difficulty' in distinguishing between *Solenopleura* and typical species of *Jincella*, and gave eight features in differentiation. However, a comparison of the figures of the type-species of the two genera given by Westergård (1953, pl. 4) and Šnajdr (1958, pl. 41) does not bear this out: some criteria show no evident differences between the two species and other criteria, such as those concerned with convexity, are not shown by the figures of *Jincella*, making comparison of the figures impossible. Geyer may be correct to say that the palpebral lobe lies in a more forward position in *S. holometopa* than in *J. prantli*, but the difference (by about 3% of the cephalic length) is slight and there is overlap between the two taxa. Our conclusion is that a generic distinction between the type species of *Solenopleura* and *Jincella* has yet to be demonstrated, and for that reason we take a wide view of *Solenopleura*.

Of the *Solenopleura* species described by Cobbold (*in* Cobbold & Pocock 1934, p. 362), the specimen described as *Solenopleura applanata* (Salter) [*recte* (Hicks)] (Fig. 5d–f) is close to that species, differing only slightly in having the interocular fixigenae a little narrower than in material from Wales and the Nuneaton district (Lake 1931). This difference may, however, be due to the distorted and flattened condition of the specimens from Wales and Nuneaton. Morphologically it differs very little from the type of *Solenopleuranuntia* Grönwall, 1902 (refigured here in Fig. 5l, o, p), though the glabella is more tapered. The clearest distinction lies in the coarser granulation of *S. cf. applanata*.

The specimen that Cobbold & Pocock (1934) figured as *S. brachymetopa nuntia* (Fig. 5a–c; their pl. 43, fig. 2) has the glabella more tapered and more sharply rounded in front than the type of *nuntia* (Fig. 5p). It differs from *S. holometopa* in which the glabella is wider and the granulation is sparser. It is more like *S. conifrons* Westergård (1953, pl. 4, fig. 10), but has slightly narrower interocular fixigenae, the eyes lie a little farther back and the preglabellar field appears to have been shorter.

The specimen assigned by Cobbold to *Solenopleura cf. bucculenta* Grönwall (Fig. 5g, h) differs from that species because the glabella is not sunk between the fixigenae. The present specimen lacks the fovea or pit seen in front of the glabella in many specimens of *S. bucculenta* (Babcock 1994, figs 6a, 7), and which is taken as an autapomorphy for the genus *Foveatella* Rudolph, despite the lack of a fovea in some specimens (Westergård 1953, pl. 3, fig. 2a). Bruton & Harper (2000, fig. 4G) identified a specimen as *S. bucculenta* even though the glabella is raised above the fixigenae, as in Cobbold & Pocock's specimen.

Solenopleura angustiora Cobbold (*in* Cobbold & Pocock 1934, p. 363, pl. 43, fig. 4) is excluded from *Solenopleura* on account of its divergent preocular sutures and flatter anterior border (Fig. 7a–c). It is provisionally assigned to the well-known North American genus *Elrathia* Walcott because it resembles closely some of the smaller-eyed species such as

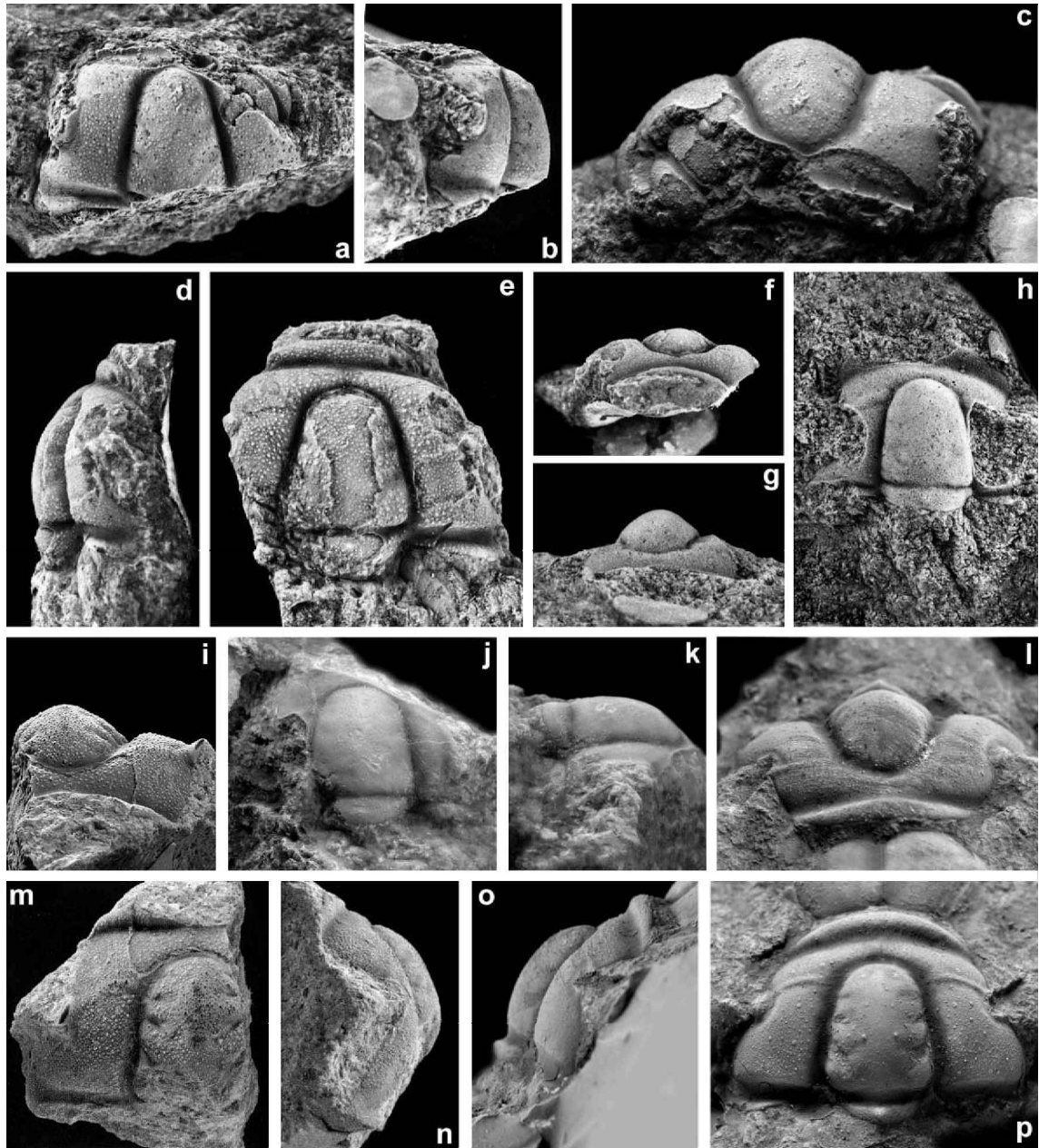


Figure 5 Cranidia of *Solenopleura* s.l.

(a–c) *Solenopleura* aff. *conifrons* Westergård, top, left side and front views, GSM 51723, a–b $\times 3$, c $\times 4$.

(d–f) *Solenopleura* cf. *applanata* (Hicks), side, top and front views, GSM 51722, all $\times 4$.

(g, h) *Solenopleura* sp.: front and top views of internal mould described by Cobbold & Pocock 1934, p. 366, pl. 42, fig. 18, as *Solenopleura* cf. *bucculenta* Grönwall, GSM 51720, $\times 4$.

(i, m, n) *Solenopleura* cf. *nuntia* Grönwall, front, top and side views, GSM 105455, all $\times 3$.

(j, k) '*Liostracus*' *dubius* Cobbold: top and side view of fragmentary cranium, figured Cobbold & Pocock 1934, pl. 43, fig. 14, GSM 51731, $\times 6$.

(l, o, p) *Solenopleura nuntia* Grönwall: front, side and top views of a cast of the figured specimen (Grönwall 1902, pl. 4, fig. 14), all $\times 4$, Geological Museum, University of Copenhagen MGUH 189.

E. kingii (Meek) and *E. marjumi* Robison (as figured by Robison 1964, pl. 85), in which the palpebral lobe is about a quarter of the cranidial length. The preglabellar field is, however, a little shorter in *S. angustiora*, and in this resembles the longer-eyed species *E. gaspensis* Rasetti (1963, pl. 69, figs 1–7) and *E. grazierensis* Rasetti (1965a, pl. 119, figs 21–24). Only the cranidium is known with certainty, but the generic assignment is considered justified on morphological grounds. Associated librigenae (Fig. 6i) recall those of *Elrathia* and may belong to *Elrathia*? *angustiora*, but the contour of the facial suture suggests that they are more likely to be those of *Agaso rushtonensis*. We note the close resemblance of *E.*? *angustiora*

to *Peregrinaspis subtilis* Buchholz (1997, p. 197, pl. 15, fig. 2), from a drift block (Geschiebe) of Exporrecta Conglomerate on the isle of Rügen, N Germany, and suspect they are synonymous.

Genus *Agaso* Cobbold, in Cobbold & Pocock, 1934

The type species is *Liostracus (Agaso) rushtonensis* Cobbold (Cobbold & Pocock 1934, p. 359). In common with other authors of the time, Cobbold (1911, 1913) used the genus *Liostracus* of Angelin for certain ptychoparioid trilobites that resemble *Solenopleura* (s.l.) but have weak glabellar furrows,

or none, and are not conspicuously granulose. Westergård (1953, p. 21) discussed *Liostracus* Angelin, 1854 (a junior homonym of *Liostracus* Mörch, 1852) and distributed the Swedish species among such genera as *Andrarina* (type species *Liostracus costatus* Angelin) and *Parasolenopleura* Westergård (type species *L. aculeatus* Angelin). In those genera the glabella is well marked and is generally elevated above the fixigenae. In *Agaso* the glabella is scarcely distinguishable on the external surface of the cranidium, but on the internal surface it is marked by a distinct, though shallow, axial furrow. Cobbold regarded *Agaso* as a '*Liostracus*' in which the dorsal features are obsolescent, although the flat anterior border differs from the convex border of many species now assigned to *Parasolenopleura*. Other parts of the exoskeleton are not known with

certainty, but a librigena and two pygidia are tentatively assigned here.

Agaso shows considerable similarity to *Glossocoryphus* Deiss, 1939 (p. 91, pl. 15, figs 13–17, 20–24). The differences in the cranidium are not very significant, being mainly proportional. In *Glossocoryphus* the glabella is less effaced externally, the frontal area is longer, the fixigenae narrower and the eyes more backwardly placed. *Agaso* has a more sharply defined frontal border. The pygidia of *Glossocoryphus* are better furrowed than that assigned to *Agaso* and have a relatively broad axis, and the librigena of *G. cliffensis* Deiss (1939, pl. 15, fig. 17) is much broader in proportion than that assigned to *Agaso* (Fig. 6i). The effaced genus *Koldiniella* Sivov is also similar, especially the type species *K. mitella* Sivov as figured

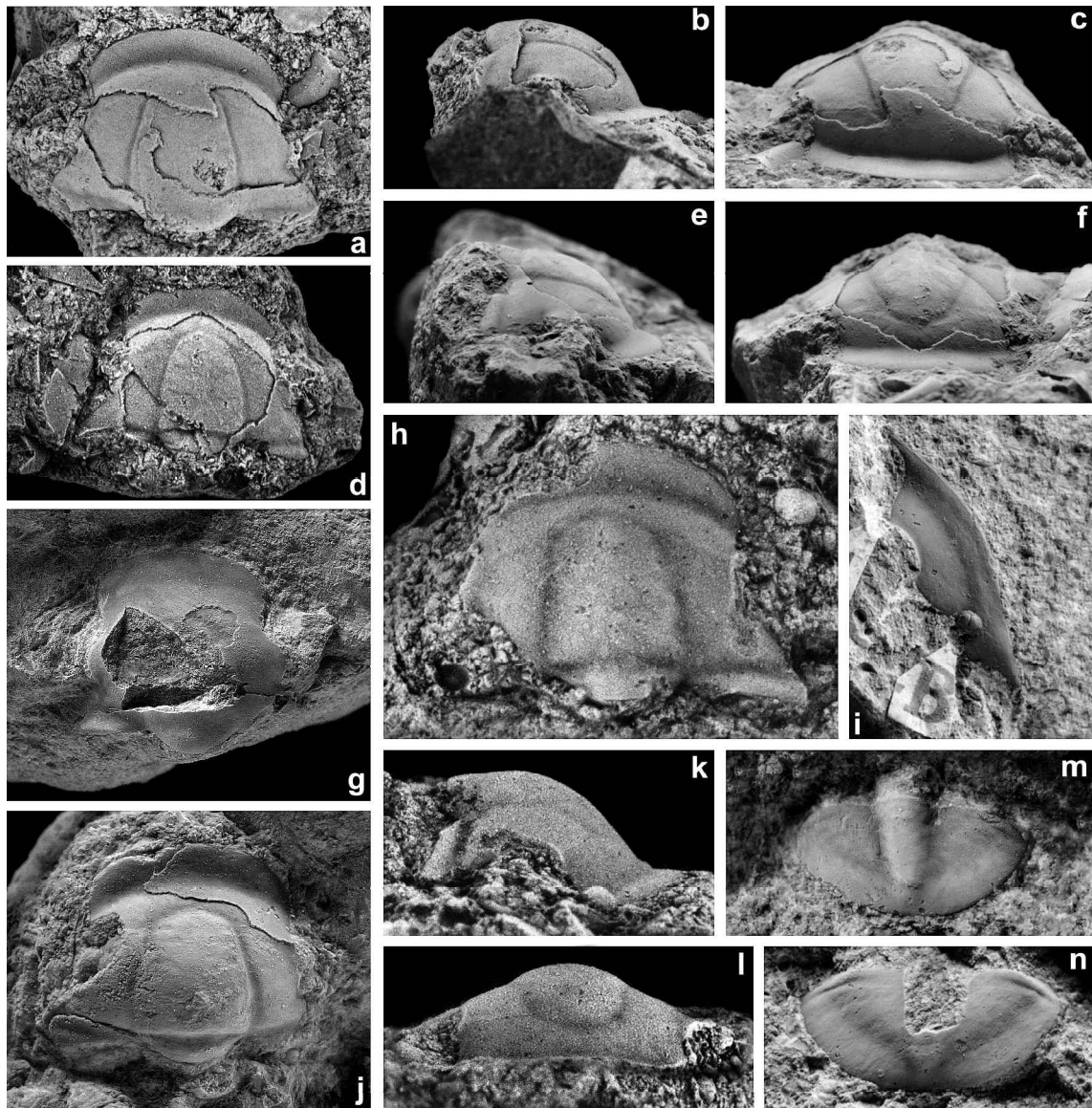


Figure 6 (a–g, i?, m?, n?) *Agaso rushtonensis* Cobbold (in Cobbold & Pocock 1934, p. 359): (a–c) holotype cranidium, partly exfoliated, top, side and front views, $\times 3$; figured by Cobbold & Pocock 1934, pl. 45, fig. 3 (though cited on p. 359 as fig. 2); specimen no. GSM 51764 (cited in error as 51763 in Cobbold & Pocock); (d–f) top, side and front views of larger cranidium, partly exfoliated, $\times 2$, GSM 51762, holotype of *Liostracus (Agaso) pringlei* Cobbold; (g) broken cranidium showing course of facial suture, holotype of *Liostracus (Agaso) pococki* Cobbold; figured by Cobbold & Pocock 1934, pl. 45, fig. 2 (though cited on p. 360 as fig. 3), GSM 51763 (cited in error as 51764), $\times 3$. (i) librigena attributed to *A. rushtonensis*, GSM 105456, $\times 3$; (m, n) 'pygidium no. 1', attributed here to *Agaso rushtonensis* Cobbold, GSM 51733, $\times 6$, and GSM 51732, $\times 3$; figured by Cobbold & Pocock 1934, pl. 4, figs 15, 16, as 'pygidia associated with *Solenopleura* and *Liostracus*'. (h, j–l) *Agaso bruno* (Cobbold): (h, k, l) top, side and front views of holotype cranidium, exoskeleton preserved, GSM 51794, $\times 6$ (figured Cobbold & Pocock 1934, pl. 43, fig. 10); (j) paratype cranidium, partly exfoliated, GSM 51728, $\times 5$ (figured Cobbold & Pocock 1934, pl. 43, fig. 11).

by Kushan (1973) and Fortey & Rushton (1976). *K. mitella* is more effaced, such that the glabella and occipital furrow cannot be seen, even in internal moulds (Fortey & Rushton 1976, pl. 10, fig. 6), but the lateral extent of the occipital ring can be discerned and shows that the fixigenae of *K. mitella* (like other *Koldiniella* species) are narrower than in *Agaso*. In *K. convexa* Lazarenko (1960, pl. 1) the glabella is outlined faintly and ends well behind the anterior border furrow (contrary to what was inferred for *K. mitella* by Fortey & Rushton 1976, p. 332), and in this, and in features of the elongate pygidium, it resembles genera of the Asaphiscidae. Compared with *K. convexa*, the palpebral lobes in *Agaso* lie farther forward and the fixigenae are wider.

Agaso resembles the asaphiscid genus *Maryvillia* Walcott, the type species of which, *M. arion* Walcott, shows the same sort of effacement of the cranidium and has a similar glabellar outline, pregabellar field and frontal border (Rasetti 1956, 1965b). However, the occipital furrow in *Agaso*, as seen in internal moulds, is quite conventional, whereas in *Maryvillia* it appears to be placed unusually far back (Rasetti 1965b, pl. 9, fig. 22). Study of specimens of *Maryvillia arion* in the Rasetti Collection (Natural History Museum) suggests that the occipital furrow is not expressed in that species and that the furrow observed in internal moulds at the back of the occipital ring more probably relates to the articulation with the anterior thoracic segment. In *Maryvillia* (and in the related genus *Blountia*) the postocular fixigenae are swept back distally so that the distal tips lie well behind the occipital ring (Rasetti 1965b, pl. 9, fig. 23), whereas in *Agaso* the posterior edges of the fixigenae are fairly transverse. Species of the asaphiscid *Blountia* (*Mindycrusta*) described by Öpik (1967, p. 234) have the palpebral lobes placed farther forward than in *Agaso*, the glabella less effaced and narrower interocular fixigenae.

Cobbold described three species of *Agaso*, *A. rushtonensis*, *A. pringlei* and *A. pococki*, all based only on cranidia. They all have a flat anterior border and an evenly convex cranidium in which the glabella scarcely shows any independent convexity (Fig. 6). The holotype of *A. rushtonensis* (Fig. 6a–c) shows the obsolescence on the external mould both of the axial furrow anteriorly and the occipital furrow posteriorly. The holotype of *A. pringlei* (Fig. 6d–f) shows that on the internal mould the front of the glabella is rounded and the occipital furrow well marked. Cobbold discussed differences between these taxa, but they are slight and seen in few specimens; we consider that they are likely to be due to intraspecific variation. The holotype of *A. pococki* (Fig. 6g) is damaged, and although Cobbold's drawing (Cobbold & Pocock 1934, pl. 45, fig. 2a) suggests that the occipital furrow was visible on the external mould, it differs little from the type species in this feature. Cobbold & Pocock (1934, pl. 45, fig. 2a) figured a faint occipital node in *A. pococki* but it is scarcely discernible on the specimen (Fig. 6g).

We suggest that Cobbold's *Liostracus bruno* (Fig. 6h, j–l) is also referable to *Agaso*. Features of the external surface are less effaced than in *A. rushtonensis* and the glabella is less tapered, and the glabellar front is blunter than in *A. pringlei* (Fig. 6d), but in the flat frontal border and other respects *L. bruno* resembles *Agaso rushtonensis*.

Cobbold (*in* Cobbold & Pocock, 1934, p. 358) assigned a transverse type of pygidium with faint pleural furrows and a broad border (Fig. 6m, n, = 'pygidium no. 1' in Table 2) to '*Liostracus* (?) sp. indet.' It does not resemble the pygidia referred to species of *Parasolenopleura*. The axis extends back beyond the border furrow, and in this it resembles pygidia of *Koldiniella mitella*, whose length are about half of their width. The pygidium of Asaphiscids such as *Asaphiscus* and *Maryvillia*

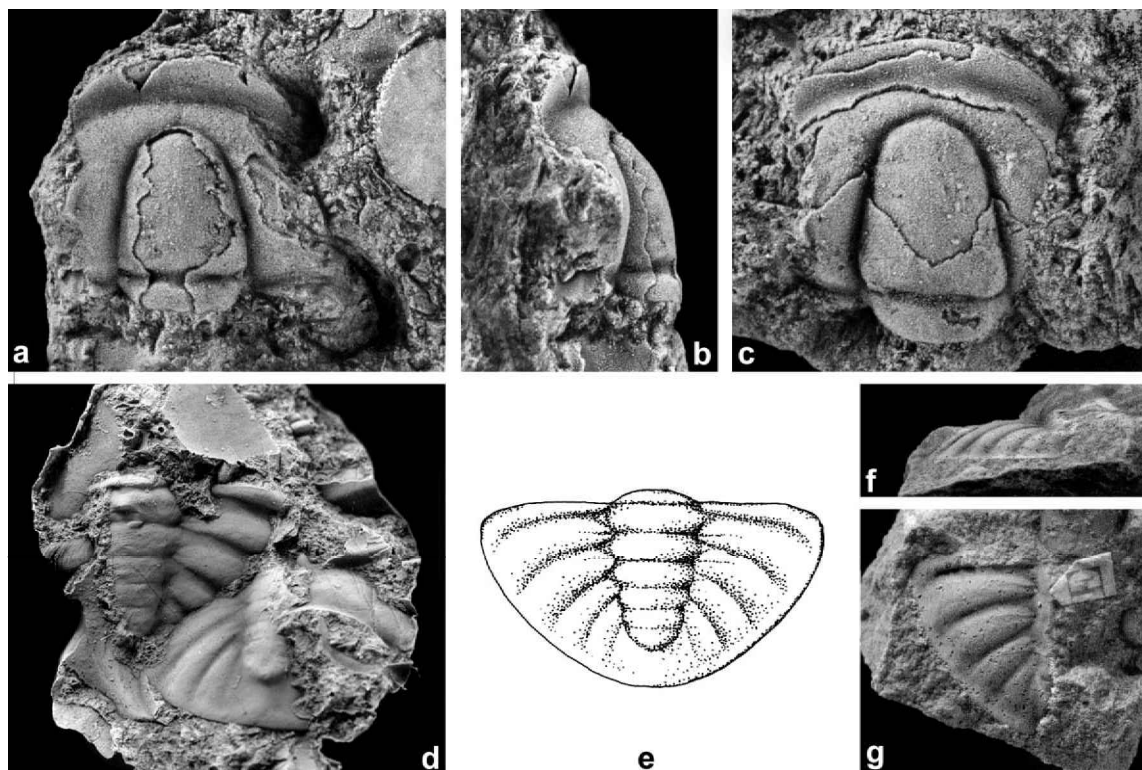


Figure 7 (a–c) *Elrathia? angustiora* (Cobbold), all $\times 6$: (a–b) top and side views of holotype cranidium, glabella exfoliated, GSM 51792 (figured Cobbold & Pocock, pl. 43, fig. 4); (c) paratype, partly exfoliated, GSM 52865. (d–g) 'pygidium no. 2' (genus uncertain): (d) two fragmentary pygidia that Cobbold & Pocock (pl. 45, figs 4–6) doubtfully attributed to *Agaso*, latex cast of external moulds, GSM 51765, $\times 4$; (e) reconstruction based on figs d and g; (f, g) fragment showing the pleural field, rear and top view, GSM 105457, $\times 2$.

are generally similar but are more elongate, the length being about two-thirds or three-quarters of the width, with a multi-segmented axis (Rasetti 1965b, pl. 9, figs 24–26).

Another kind of unassigned pygidium ('pygidium no. 2' in Table 2) that occurs with *Agaso* has five or six axial rings, five pleural furrows that extend almost to the margin, and no border (Fig. 7d–g). This was the form that Cobbold (in Cobbold & Pocock 1934, p. 361) assigned to *Agaso*, though with reserve. Its relatively large size reminded him of the pygidium of *Asaphiscus*, but it has stronger pleural furrows than those of such Asaphiscidae as *Asaphiscus*, *Blountia* and *Maryvillia*, and differs from them in lacking a broad border. We regard its relationships as uncertain.

5. Conclusions

The '*Paradoxides forchhammeri* Grit' of the Wrekin district (Cobbold & Pocock 1934) is here renamed the 'Rushton Brook Bed'. It does not contain a fauna distinctive of the Scandinavian *P. forchhammeri* Stage.

The superficial resemblance of the fauna to that of the Andrarum Limestone of Sweden, based on the variety of *Solenopleura* spp. and the presence of some supposedly similar hyoliths, etc., is considered to be a function of the shallow, oxygenated biofacies.

The trilobite fauna is correlated with the *punctuosus* Zone in the Scandinavian *paradoxissimus* Stage.

The trilobite *Liostracrus (Agaso)* Cobbold in Cobbold & Pocock, 1934, is revised and regarded as a member of the Asaphiscidae. It is potentially to be regarded as a senior synonym of *Glossocoryphus* Deiss, 1939.

6. Acknowledgements

We thank Mr S. P. Tunnicliff (formerly the Curator, British Geological Survey) who made available most of the material studied. We examined other specimens furnished by C. Åkermann (Swedish Geological Survey), Dr C. Franzén (Swedish Museum of Natural History) and P. Jeffrey (Natural History Museum, London). M. Elmgaard (Geological Museum, Copenhagen University) kindly supplied the cast of the type of *Solenopleura nuntia* (Fig. 5l, o, p). The photographs are by Mrs K. Bryant (National Museum of Wales) and Mr H. Taylor (Natural History Museum). Part of the costs of this work were met by a grant from the Royal Society to Dr Berg-Madsen, who also thanks the National Museum of Wales for support. We thank Drs S. G. Molyneux and M. Williams for their helpful comments on the typescript, and Professor R. A. Robison and Dr T. P. Fletcher for their constructive reviews.

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MS received 16 February 2001. Accepted for publication 23 July 2001.