FOSSILS FROM THE MIDDLE-UPPER CAMBRIAN TRANSITION IN THE NUNEATON DISTRICT

by A. W. A. RUSHTON

ABSTRACT. In Britain the Middle-Upper Cambrian transition is fossiliferous only in the Nuneaton district. The *Lejopyge laevigata* Zone (Middle Cambrian) is recognized by a sparse fauna, chiefly of agnostid trilobites of Scandinavian character. The *Agnostus pisiformis* Zone (Upper Cambrian) contains Scandinavian agnostids and bradoriid Crustacea and also agnostids known from North America and Siberia, and rare polymerid trilobites akin to forms from Asia, Australia, and the U.S.A. *Cristagnostus papilio* gen. et sp. nov. and *Modocia anglica* sp. nov. are described.

IN the Cambrian successions in Scandinavia, which furnish a biostratigraphical standard for much of the Cambrian in Europe and eastern Canada, the boundary between the Middle Cambrian and Upper Cambrian is taken between the *Lejopyge laevigata* Zone and *Agnostus pisiformis* Zone. In Sweden Westergård (1944; 1946; 1947; 1953) adopted the following zones and listed the fossils, especially trilobites, from each:

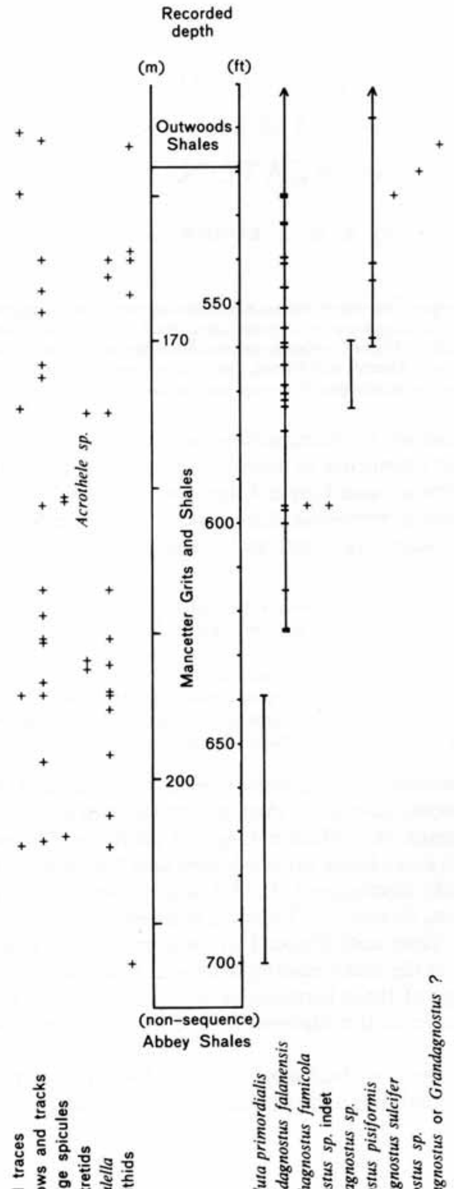
Upper Cambrian (lower part)	*Olenus* Zone (six subzones) *A. pisiformis* Zone
Middle Cambrian (upper part) = *Paradoxides forchhammeri* zonal group	*L. laevigata* Zone *Solenopleura brachymetopa* Zone *Ptychagnostus lundgreni–P.* (*Goniagnostus*) *nathorsti* Zone

Daily and Jago (1975) discussed the distribution of *L. laevigata* and the correlation of the Middle-Upper Cambrian boundary throughout the world.

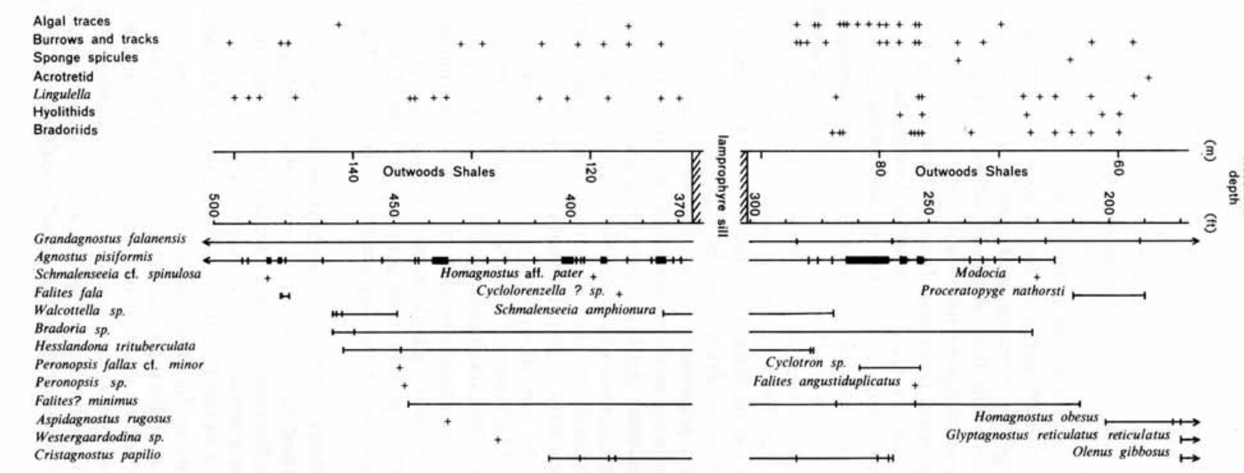
In most areas of Britain the Middle-Upper Cambrian boundary cannot be identified, the *A. pisiformis* Zone being unrecognized and the higher Middle Cambrian zones being only doubtfully represented (Taylor and Rushton 1972, pp. 9, 18). In the Nuneaton district, however, Taylor and Rushton showed that the *L. laevigata* Zone is present in the Mancetter Grits and Shales Formation and the *A. pisiformis* Zone is present in the lower 91 m of the conformably overlying Outwoods Shales Formation; they described the geology of these formations, deriving much of their information, and nearly all their fossils, from the Merevale No. 3 Borehole (op. cit., pp. 7, 10, 104; pl. 4).

Text-figs. 1 and 2 show the distribution of fossils in Merevale No. 3 Borehole, with species on the right of each column and the occurrence of undifferentiated taxa on the left.

[Palaeontology, Vol. 21, Part 2, 1978, pp. 245–283, pls. 24–26.]



TEXT-FIG. 1. Distribution of fossils in the *Lejopyge laevigata* Zone in Merevale No. 3 Borehole. Occurrence of undifferentiated taxa on the left, ranges of species on the right.



TEXT-FIG. 2. Distribution of fossils in the *Agnostus pisiformis* Zone in Merevale No. 3 Borehole. Occurrence of undifferentiated taxa on the left, ranges of species on the right. *Proceratopyge nathorsti* and *Modocia* [= *M. anglica*] were collected at Purley Quarry; their stratigraphical position is plotted on the assumption that the incoming of *Olenus gibbosus* and *Glyptagnostus reticulatus* is at the same level in the Quarry as in the Borehole.

CORRELATION OF THE FAUNAS

Lejopyge laevigata Zone

Westergård (1946; 1953) listed up to twelve species of polymerid trilobites and about twenty of agnostids from the *laevigata* Zone in Sweden, whereas the borehole yielded no polymerids and only eight species of agnostids (text-fig. 1*a*). Most of the forms present in the borehole are comparable with Swedish species, though the commonest form, *Grandagnostus falanensis*, is not recorded from the *laevigata* Zone in Sweden and the *Innitagnostus* species present resembles the Swedish *I. neglectus* (Westergård) less than it does some other species of the genus. However, *Ptychagnostus* (*Goniagnostus*) *fumicola* is known elsewhere only from Australia where it ranges from the '*laevigata* III' Zone to the *torosa-janitrix* Zone which Öpik (1967, p. 91) regarded as a Middle–Upper Cambrian passage zone. Daily and Jago (1975) have argued that this passage zone lies within the European *laevigata* Zone and below the Middle–Upper Cambrian boundary. Incidentally, a consequence of this revision of the correlation is to restore Öpik's 'Upper Cambrian' species of *Hypagnostus*, *Grandagnostus*, *Lejopyge*, *Ptychagnostus* (*Goniagnostus*), and *Olenoides* to the Middle Cambrian.

In Merevale No. 3 Borehole the *laevigata* Zone is estimated to be 55 m thick. The base is taken down to the base of the Mancetter Formation because *Svealuta primordialis* occurs almost at the base of the formation. Daily and Jago (1975, p. 540) suggested that the *brachymetopa* Zone might be indicated in the borehole but as I can find no confirmation that *S. primordialis* occurs below the *laevigata* Zone, I retain here the correlation originally proposed by Taylor and Rushton (1972, p. 8).

The erosional break between the Mancetter Grits and Shales and the underlying Abbey Shales indicates a regression at about the horizon of the *brachymetopa* Zone which in Sweden corresponds to the Andrarum Limestone and the Exporrecta Conglomerate (Martinsson 1974, p. 250). Furthermore, the *laevigata* Zone represents a transgression and marks the start of a new cycle of sedimentation in various areas of Sweden (summarized by Martinsson 1974), Newfoundland (Poulsen and Anderson 1975, discussed below), and Britain (Taylor and Rushton 1972, p. 9); it may be noted that poorly preserved agnostids indicative of the Middle Cambrian have been collected from near the base of the Maentwrog Beds (lower '*Lingula* Flags') in the Harlech Dome, North Wales (Rushton 1976, p. 115), thus showing that the '*Lingula* Flags' cycle of sedimentation commenced before the beginning of the Upper Cambrian in North Wales.

A comparable break occurs in Newfoundland. At localities in Manuels River and on Random Island, Poulsen and Anderson (1975) reported a lithological change between beds of the Manuels River Formation with a *Paradoxides davidis* fauna and the base of the overlying Elliott Cove Formation (or Group). They found fossils of the *laevigata* Zone within the basal 4 m of the Elliott Cove Formation at Random Island and the basal 1·5 m at Manuels River. In those places the *brachymetopa* Zone is absent; but half-way between them, at Highland Cove, Hutchinson (1962) found a '*Paradoxides forchhammeri* Zone' fauna which Poulsen and Anderson (1975, p. 2068) referred to the lower part of the *brachymetopa* Zone. However, there is insufficient palaeontological evidence to support this correlation, as Poulsen and Anderson (p. 2068) suggest: e.g. Hutchinson's '*Peronopsis* cf. *quadrata*' has a pygidial collar (1962, pl. 5, figs. 6, 7) and thus differs from the Swedish *P. quadrata* (Tullberg) from the *brachymetopa* Zone; furthermore, Hutchinson's fauna includes *Ptychagnostus hybridus* (Brögger) and *Pt. punctuosus* (Angelin), both of which are indicative of lower zones. Therefore the *brachymetopa* Zone is not yet proved in Newfoundland and may be altogether absent.

Hutchinson (1962, p. 27) recognized the *pisiformis* Zone above the base of the Elliott Cove Formation at Random Island, Manuels River, and Trinity Bay, but he thought that beds representing the *laevigata* Zone were absent or unfossiliferous in Newfoundland (1962, pp. 24, 27). However, three of his specimens of *Oidalagnostus* cf. *trispinifer* Westergård (Hutchinson 1962, pl. 7, figs. 17–19), though poorly preserved, seem identical to Westergård's species and thus indicate the *laevigata* Zone: they came from 16·5 m above the base of the Elliott Cove Formation in the Manuels River section. Hutchinson's fourth specimen of *O.* cf. *trispinifer* (1962, pl. 7, fig. 20), which evidently led him not to identify his material with *O. trispinifer* (s.s.), came from the same locality but from a higher level, 21·0 m above the base of the Formation; it is referable to *Cristagnostus papilio* sp. nov. and if it represents the *pisiformis* Zone, as in England, the base of the *pisiformis* Zone in the Manuels River section lies between 16·5 m and 21·0 m above the base of the Elliott Cove Formation. At Manuels River both *A. pisiformis* and *Grandagnostus* '*bairdi*' (= *falanensis*) range above and below these occurrences.

Agnostus pisiformis Zone

The fauna of the *pisiformis* Zone is more varied and cosmopolitan in character at Nuneaton than in Sweden where the facies was very favourable to *Agnostus pisiformis* but almost excluded other trilobites. The different environments indicated by the various mudstones of the Outwoods Shales seem to have allowed a wider variety of forms to make a sporadic appearance in the Nuneaton area. Of the species found there (text-fig. 2), some of the bradoriids and four of the trilobite species (*A. pisiformis*, *G. falanensis*, *Schmalenseeia amphionura*, and *Proceratopyge nathorsti*) occur in the *pisiformis* Zone in Sweden.

The *pisiformis* Zone is estimated to be 58 m thick in Merevale No. 3 Borehole. The base of the zone is taken at a depth of 485 ft 0 in. (147·83 m) where *Schmalenseeia* cf. *spinulosa* occurs with several specimens of *A. pisiformis* and a juvenile *Aedotes*? *S. spinulosa* was described from the *pisiformis* Zone in northern Siberia and is the lowest fossil in the borehole which can be taken to indicate the *pisiformis* Zone.

Of the other species present, *C. papilio* is known from the presumed *pisiformis* Zone at Manuels River in Newfoundland, as mentioned above. *Homagnostus* aff. *pater* is known (as '*Proagnostus bulbus*') at Cedar Bluff, Alabama, U.S.A., from beds assigned by Resser (1938, p. 33) to the *Cedaria* Zone, which was considered by Daily and Jago (1975, p. 542) to span the *laevigata–pisiformis* zonal boundary. *Aspidagnostus rugosus* occurs at Cedar Bluff, and also in Nevada, in beds overlying those with *Glyptagnostus stolidotus* Öpik and which therefore lie near or at the top of the *pisiformis* Zone. *A. rugosus* occurs at about the same horizon in northern Siberia (Datsenko *et al.* 1968, atlas, pp. 38, 39) and in the Altay Mountains (Poletaeva and Romanenko 1970, p. 72). *Modocia anglica* is referred to a genus known from several strata around the Middle–Upper Cambrian boundary in North America. *Cyclolorenzella* sp. is likewise referred to a genus known from around the Middle–Upper Cambrian boundary in China and especially from the Kushan Formation which Daily and Jago (1975, p. 543) considered to span this boundary.

The base of the overlying *Olenus* Zone is taken at 200 ft 8 in. (61·16 m) in Merevale No. 3 Borehole where the lowest specimen of *H. obesus* (Belt) occurs; another specimen was found at 189 ft 8 in. (57·81 m) and several at 182 ft 0 in. (55·47 m), just below the lowest *G. reticulatus* (Angelin) and *O. gibbosus* (Wahlenberg) at 180 ft 4 in. (54·96 m).

PALAEOENVIRONMENT

The Mancetter and Outwoods formations are thought to have been deposited in quiet offshore conditions of no great depth. They consist mainly of pale-grey to dark-grey laminated and unlaminated mudstones. Some of the pale beds are much burrowed (Taylor and Rushton 1972, pp. 7, 10), and these beds contain no body fossils apart from occasional inarticulate brachiopods (Pl. 26, figs. 18, 19), and never contain traces of algae. They represent comparatively well-aerated bottom conditions.

Some of the trilobites were found in dark unlaminated mudstones: most of these are represented by isolated specimens, many of which appear to represent exuvia (Henningsmoen 1975), e.g. *Grandagnostus falanensis*, *Cristagnostus papilio*, *Cyclolorenzella* sp., and *Modocia anglica*. Hyolithids occur sporadically in this type of mudstone (Pl. 26, figs. 16, 17). The dark laminated mudstones include horizons with abundant algal traces (Taylor and Rushton 1972, pl. 6, figs. 1, 2) and a general absence of bioturbation. These represent phases with little detrital sedimentation; the bottom conditions were deoxygenated and therefore unsuitable for grazing or burrowing benthos. The layers with algae sometimes also have crowds of *Agnostus pisiformis* (at higher levels *H. obesus* and *Olenus* spp. occur in this facies), together with small bradoriids (mainly juveniles), rare *Schmalenseeia*, and *Protospongia*-like sponges. Of these forms, the agnostids and *Schmalenseeia* may have been pelagic (Robison 1972; Jago 1972, p. 233) and therefore not affected by the bottom conditions; Henningsmoen (1957, pp. 79–82) and Fortey (1975) postulated that olenids were adapted to living in poorly oxygenated conditions. The mode of life of the bradoriids and sponges is not known, but *Protospongia* is found articulated in low-energy environments (including graptolitic facies) of Middle Cambrian to Arenig age, and it seems likely that it was adapted to such environments.

Palmer (1972) showed that, in the Cambrian, north-west Europe formed part of the 'shelf-margin—open ocean' palaeogeographic region and probably lay at high latitudes. Elements of the faunas of this region are comparatively widespread and are thought to have inhabited cool water, shallow at the poles but deeper in low latitudes (cf. Cook and Taylor 1975). Occasional agnostids from the Nuneaton district which were not previously recorded from Europe but were known from near the edge of the 'restricted shelf' regions (Palmer 1972) of the U.S.A., Siberia, and Australia probably migrated along belts of cooler water. The present research adds some polymerids exotic to Europe to the Swedish record of *Drepanura eremita* Westergård (1947)—*Aedotes*?, *Cyclolorenzella*, *Modocia*: these are related to forms from 'restricted shelf' regions (Palmer 1972) but were able to penetrate the barrier (of cold water according to Cook and Taylor 1975) which prevented most of the shelf region trilobites from migrating more widely.

SYSTEMATIC DESCRIPTIONS

The terminology for trilobites is generally that of Moore (1959). 'Glabella' refers to the pre-occipital part of the cephalic axis. The classification generally follows that of Moore (1959) except where superseded by Öpik (1967), whose treatment of Agnostida is followed here.

AGNOSTID TRILOBITES

Family AGNOSTIDAE McCoy, 1849

Subfamily QUADRAGNOSTINAE Howell, 1937

Peronopsis Hawle and Corda, 1847

Peronopsis fallax (Linnarsson, 1869) *minor* (Brögger, 1878)

Plate 24, fig. 1

1878 *Agnostus fallax* Linnarsson var. 3 *minor*; Brögger, p. 65, table opposite p. 34.
1946 *Peronopsis fallax minor* (Brögger, 1878); Westergård, p. 38, pl. 3, figs. 3–7.
1972 *Peronopsis* sp.; Taylor and Rushton, p. 19, pl. 4 [borehole record].
1976 *Peronopsis fallax* cf. *minor* (Brögger, 1878); Fortey and Rushton, p. 327, pl. 12, fig. 15.

Material. Internal mould of one specimen 6·0 mm long, BDA 1781.

Remarks. The cephalon agrees with the specimen in Westergård's plate 3, fig. 4, except that the anterior glabellar lobe is a little longer; the posterior glabellar lobe has a node slightly in front of its mid-length instead of at its mid-point; and there appears to be a very faint depression in front of the glabella, though in the specimen this is slightly emphasized by damage during preparation. It is doubtful if these slight differences are significant. The anterior glabellar lobe is longer and the basal lobes shorter than in the early Upper Cambrian form from Iran described by Fortey and Rushton (1976, pl. 12, figs. 1–14) as *P. fallax* aff. *minor*.

The pygidium of *P. f. minor* is variable. The rounded posterior to the axis of the present specimen resembles Westergård's fig. 6 but the axis reaches nearly, though not quite, to the marginal furrow, as in his fig. 7. The present specimen differs from all Westergård's figured specimens because the lateral edges of the pygidium do not diverge towards the posterolateral spines, but this may be due to compaction of the mudstone matrix of the Nuneaton specimen. *P.* [*Homagnostus*] *incerta* (Robison, 1964, p. 531, pl. 82, figs. 16, 17, 19, 20) has a wider glabella and a shorter, wider anterior glabellar lobe than the present specimen; the pygidial axis is fully half the width of the pygidium (less than half in the present specimen), and reaches to the marginal furrow; the border is considerably wider and the marginal spines are larger.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depth 448 ft 6 in. (136·70 m). *P. f. minor* occurs in the *Solenopleura brachymetopa* Zone in Scandinavia.

Peronopsis sp.

Plate 24, fig. 2

1972 *Peronopsis*? sp.; Taylor and Rushton, p. 19, pl. 4 [borehole record].

Material. External mould of one specimen 12·2 mm long, BDA 1776.

Description. Cephalon as long as wide, weakly convex. Glabella with individual convexity, surrounded by shallow axial furrow, two-thirds as long as cephalon.

Anterior lobe rounded in front, half as long as posterior lobe, quarter the cephalic width. Posterior lobe widens backwards to one-third of the cephalic width, rounded behind. Small median node at anterior quarter of posterior glabellar lobe. Basal lobes small, triangular, not well preserved. Cheeks confluent anteriorly. Border furrow narrow, border narrower than one-tenth of the cephalic length.

Thoracic axis not effaced.

Pygidium as long as wide, weakly convex. Axial furrows obscure but anterior ends are just visible, more than half pygidial width apart, dying out about one-third of the pygidial length from the anterior margin. Very faint furrows marking off the anterior lobes of the pygidial axis extend inwards from the axial furrows at about one-fifth of the pygidial length from the front. Elongate median node at anterior one-third of pygidial length. Border furrow marking off flat border about as wide as one-eighth of the pygidial length, and about twice as wide as the cephalic border. No marginal spine seen. Surface smooth.

Remarks. The present specimen, though not sufficiently well preserved to serve as a monotype of a new species, is clearly distinct from described species of *Peronopsis* in having the axial furrows distinct on the cephalon but nearly effaced on the pygidium. In the main stock of effaced peronopsids—*Hypagnostus* and *Cotalagnostus*—the glabella is effaced anteriorly and the pygidial axis is clearly outlined. It is unusual for an agnostid to have the cephalon less effaced than the pygidium, though such a condition might be claimed for *Delagnostus dilemma* Öpik (1961, p. 88) which, however, differs from the present form because it has no distinct pygidial border and the glabella is not clearly outlined anteriorly.

The present species differs from species of *Peronopsella* Sdzuy, 1967 because the

---

EXPLANATION OF PLATE 24

Except where stated otherwise the specimens are in the collection of the Institute of Geological Sciences, London, and are internal moulds. All were whitened with ammonium chloride. Specimens marked M3 are from Merevale No. 3 Borehole; localities of other specimens are given more fully. Photographs by Mr. J. Evans.

Fig. 1. *Peronopsis fallax minor* (Brögger). BDA 1781, ×6. M3, 448 ft 6 in. (136·70 m).

Fig. 2. *Peronopsis* sp. BDA 1776 latex cast, ×4. M3, 447 ft 5 in. (136·37 m).

Figs. 3, 4. *Hypagnostus sulcifer* (Wallerius), ×6. M3, 525 ft 3 in. (160·40 m). 3, GSM 103278. 4, fragment of pygidium showing axial lobes. GSM 103280, latex cast.

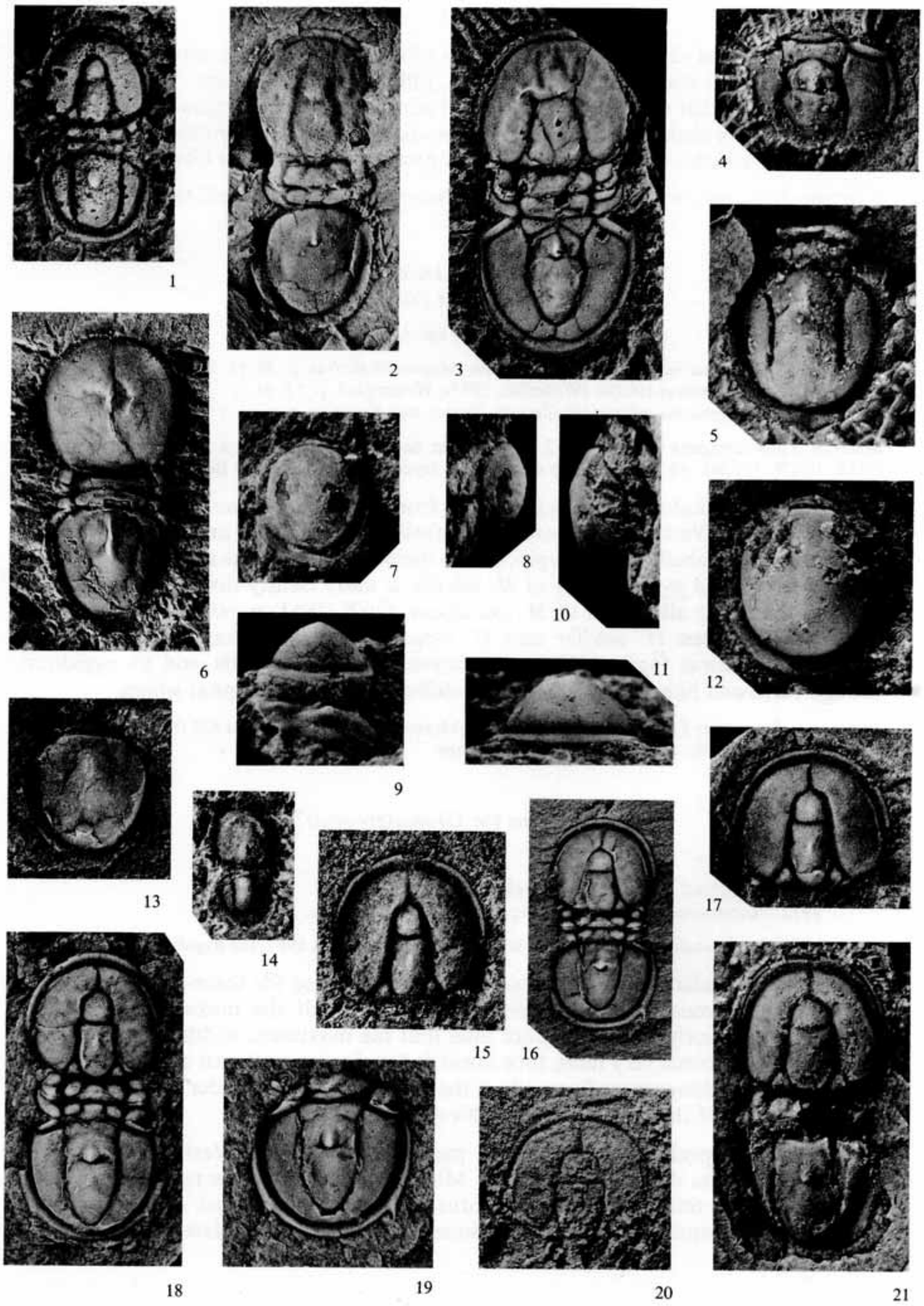
Fig. 5. *Hypagnostus* or *Grandagnostus*? sp. BDA 1967 latex, ×6. M3, 514 ft 4 in. (156·77 m).

Figs. 6–14. *Grandagnostus falanensis* (Westergård). 6, BDA 2257, ×6. M3, 624 ft 6 in. (190·35 m). 7–9, top, side, and back views of pygidium, holotype of *Phalacroma bairdi* Hutchinson (1962, pl. 11, fig. 9*b* only, not fig. 9*a*); 9 shows a valve of *Walcottella* in the foreground. Geological Survey of Canada 13055, ×6. Elliott Cove Formation, Manuels River, South-eastern Newfoundland. 10–12, holotype, side, back, and top views. Sveriges Geologiska Undersökning, figured Westergård 1947, pl. 1, fig. 14, ×7. *Agnostus pisiformis* Zone, Djupadalen, Västergötland, Sweden. 13, pygidium, BDA 2210, ×6. M3, 599 ft 8 in. (182·78 m). 14, juvenile form BDA 2205, ×12. M3, 597 ft 0 in. (181·97 m).

Figs. 15–19. *Agnostus pisiformis pisiformis* (Wahlenberg), M3. BDA 1632, 400 ft 7 in. (122·10 m); BDA 1699 latex, 427 ft 11 in. (130·43 m); BDA 1415, 271 ft 6 in. (82·75 m); BDA 1398 latex, 268 ft 4 in. (81·79 m); BDA 1417 latex, 271 ft 8 in. (82·80 m). All ×6.

Fig. 20. *Innitagnostus* sp. Flattened cephalon, BDA 2094, ×12. M3, 558 ft 6 in. (170·23 m).

Fig. 21. *Agnostus* sp. BDA 1984, ×6. M3, 520 ft 0 in. (158·50 m).



RUSHTON, Cambrian trilobites

glabella is outlined all round. Two species in which the cephalon is imperfectly known, *P. spinata* (Illing) and *P. definita* (Howell), differ from the species described above because the pygidial margin bears a pair of comparatively large spines and the axial furrows are more distinct anteriorly. (It is improbable that the present form is related to *Peronopsella* which is based on a close-knit group of mid-Middle Cambrian species.)

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depth 447 ft 5 in. (136·37 m).

Hypagnostus Jaekel, 1909
Hypagnostus sulcifer (Wallerius, 1895)

Plate 24, figs. 3, 4

1895 *Agnostus exsculptus* Angelin forma *sulcifera* Wallerius, p. 38, pl. 1, fig. 1*a*, *b*.
1946 *Hypagnostus sulcifer* (Wallerius, 1895); Westergård, p. 52, pl. 6, figs. 7–17.
1972 *Hypagnostus sulcifer* (Wallerius); Taylor and Rushton, p. 9, pl. 4 [borehole record].

Material. Three complete specimens, 9·2 mm, 7·8 mm, and 4·8 mm long, and a fragmentary pygidium; GSM 103278–103282; all from a single slickensided layer in Merevale No. 3 Borehole.

Remarks. The cephalon of *H. sulcifer* differs from those of *H. exsculptus* (Angelin) and *H. scrobiculatus* Westergård because the glabella tapers slightly and is clearly limited anteriorly. The glabella of *H. sulcifer*, unlike the other species, has at most a very weak median node. The pygidial axis of *H. sulcifer* is more clearly divided by transverse furrows than that attributed to *H. exsculptus*. Öpik (1961, p. 60) has discussed the differences between *H. sulcifer* and *H. hippalus*; the latter has a quite different pygidium. *H. durus* Öpik, 1967 has a shorter, truncate glabella and its pygidium, though furrowed like that of *H. sulcifer*, differs in having marginal spines.

Occurrence. Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole, at 525 ft 3 in. (160·40 m). In Sweden it occurs in the upper part of the same zone.

Hypagnostus (or *Grandagnostus*)? sp.

Plate 24, fig. 5

cf. 1946 '*Agnostus*' sp. No. 8; Westergård, p. 99, pl. 16, fig. 21.
1972 '*Ciceragnostus*'-like pygidium; Taylor and Rushton, p. 18.

Material. External mould of one pygidium with part of thorax, BDA 1967; the pygidium is 4·4 mm long.

Description. Pygidial length equal to width. Axis outlined for three-fifths of pygidial length, for the most part parallel-sided, less than half the maximum width, but expanding anteriorly to a little more than half the maximum width. Posteriorly the axial furrows become very faint, turn inwards but do not meet, nor do they reach the border furrow. Elongate median node at the anterior quarter. Border flat, broad (more than one-tenth of the length and breadth of the pygidium).

Remarks. This specimen resembles the pygidia described by Westergård (1946) as '*Ciceragnostus*' (as discussed below the Middle Cambrian forms related to *A. cicer* Tullberg may be referred to *Grandagnostus* but not *Ciceragnostus*). Although Taylor and Rushton compared the present specimen with Westergård's plate 16, fig. 6, it has a lower convexity and a wider border, and is nearer to '*Agnostus*' sp. No. 8 in his plate 16, fig. 21. It differs from that form because the axis widens somewhat towards the articulating half-ring and the axial furrows extend a little further back and tend to turn in towards the mid-line posteriorly. In these respects it agrees better with the pygidia illustrated by Westergård as '*Agnostus*' sp. No. 4 (1946, pl. 16, figs. 13–17), which Öpik (1961) suggested might belong to a *Hypagnostus* species; those forms, however, have a narrower axis than the present specimen. Without knowledge of the cephalon the generic reference remains uncertain.

A comparable pygidium occurs in equivalents of the *pisiformis* Zone at Cherry Creek and McGill, Nevada (Palmer 1962, pl. 1, figs. 32, 33), but in that form the width increases towards the articulating margin and the axial furrows are relatively shorter and further apart.

Occurrence. Merevale No. 3 Borehole, at depth 514 ft 4 in. (156·77 m), 1 m above the base of the Outwoods Formation as recognized in that borehole, *laevigata* Zone or possibly *pisiformis* Zone. The pygidium '*Agnostus*' sp. No. 8 of Westergård is from the *laevigata* Zone, upper part, in Sweden.

Grandagnostus Howell, 1935*a*

Remarks. The type species *G. vermontensis* Howell (1935*a*) is poorly known but the genus was framed with *A. glandiformis* Angelin (Westergård 1946, pl. 15, figs. 3–17; pl. 16, figs. 1, 2) also in mind (Howell 1935*a*, p. 221). Öpik (1961, p. 54) and Jago (1976, p. 144) have discussed the genus. *Grandagnostus*, as interpreted here, includes effaced agnostids with a broad border on the pygidium but none on the cephalon; they are probably peronopsids representing the end of the sequence *Peronopsis–Hypagnostus–Cotalagnostus–Grandagnostus*. Basal glabella lobes may be present or absent. The pygidial axis may be effaced or partly developed and is long, as shown by vestigial axial furrows or by the terminal axial node. Species referred to the genus include *A. bituberculatus* Angelin and *A. cicer* Tullberg (Westergård 1946), *Ciceragnostus*? *falanensis* Westergård, 1947, *Phoidagnostus angustiformis* Pokrovskaya, 1958, *Phalacroma maja* Pokrovskaya, 1958 [? *pars*], *G. velaevis* Öpik, 1961, *Phalacroma bairdi* Hutchinson, 1962, and *Grandagnostus* sp. of Jago (1976). Species with a cephalic border and broad pygidial border were grouped in *Valenagnostus* Jago, 1976 (p. 142), with *V. marginatus* (Brögger) as type species.

Öpik (1967, pp. 76, 82) showed that neither of the genera *Phalacroma* Hawle and Corda, 1847, nor *Phoidagnostus* Whitehouse, 1936, can be used for these agnostids. He also showed (1961, p. 53) that *A. cicer* should not be placed in *Ciceragnostus* Kobayashi, 1937. Juveniles of *G. falanensis* described below resemble *A. cicer* and also *Hypagnostus*, showing that they were descended from the peronopsid stock. Accordingly *Grandagnostus* is extended here to include forms in which part of the pygidial axis is distinctly outlined in full-grown specimens, as in *A. cicer*. *G. bituberculatus* has a pygidium typical of *Grandagnostus* but the cephalon has distinct basal glabellar lobes, the presence of which led Öpik (1961, p. 54) to refer it to *Phalagnostus* Howell, 1955 (type species *Battus nudus* Beyrich). In *Phalagnostus*, however, the axis is not effaced but is large and subcircular, and the 'border' is composed of the flanks with or without the border. Rasetti (1967, p. 38; also Jago 1976, p. 146) tentatively proposed this interpretation because the anterior border furrow, instead of delimiting the anterolateral border, crosses the border-like structure. Having examined Bohemian and British material of *Phalagnostus* I agree with Rasetti and consider that the ontogenetic development of the pygidium (Šnajdr 1958, p. 79) also confirms this interpretation. Other species of *Phalagnostus* include *A. eskriggei* Hicks, *A. nudus scanicus* Tullberg, *P. prantli* Šnajdr, *Phalacroma calvum* Pokrovskaya, and *A. n. ovalis* Illing; the last named is the type species of *Phalacromina* Kobayashi (1962, p. 29), which is therefore a junior subjective synonym of *Phalagnostus*. Some unnamed pygidia (Westergård 1946, pl. 16, fig. 3; Hutchinson 1962, pl. 12, fig. 1; Rasetti 1967, pl. 10, figs. 22–26) have a comparable structure but the corresponding cephala have not been recognized.

Peratagnostus Öpik (1967, p. 86) can be distinguished from *Grandagnostus* because the pygidial border is narrower, its width posteriorly being less than one-tenth of the length of the pygidium; the axis is narrow and ends well short of the posterior border in described species (Palmer 1968, p. 26).

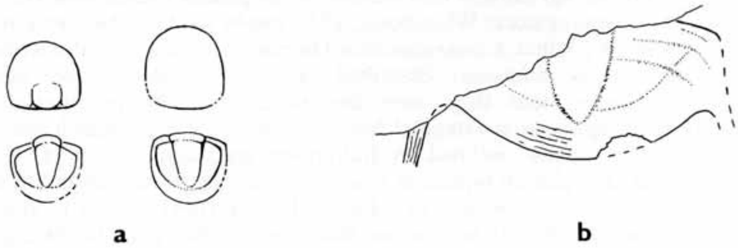
Grandagnostus falanensis (Westergård, 1947)

Plate 24, figs. 6–14; text-fig. 3*a*

1947 *Ciceragnostus*? *falanensis* n. sp.; Westergård, p. 7, pl. 1, fig. 14.
1962 *Phalacroma bairdi* n. sp.; Hutchinson, p. 90, pl. 11, figs. 9–11.
1972 *Grandagnostus bairdi* (Hutchinson); Taylor and Rushton, pp. 8, 18, 20, text-fig. 4 [recorded].
1975 *Lejopyge laevigata* (Dalman, 1828); Poulsen and Anderson [*pars*], p. 2076, pl. 2, figs. 1?, 4?, 7, 8.

Material. About forty specimens from the Mancetter Formation in Merevale No. 3 Borehole, including BDA 1986–1987, 1995–1997, 2004–2006, 2014–2015, 2017, 2019–2020, 2029–2033, 2038–2039, 2041–2042, 2051–2052, 2067–2068, 2097, 2106, 2124, 2137, 2139–2142, 2148–2149, 2172–2175, 2191–2195, 2197–2198, 2205–2210, 2242–2243, 2257–2266. A few specimens from the upper part of the *pisiformis* Zone in the Outwoods Formation in the borehole (e.g. BDA 1188, 1205–1206, 1222, 1314–1315) and several from a similar horizon at Purley Quarry (RU 2180–2209). Many specimens from the *Olenus* Zone. Most of the specimens are more or less flattened or crushed.

Description. Cephalon domed, usually a little longer than wide. A trace of the basal lobes and posterolateral borders seen in some specimens but no lateral or anterior



a **b**

TEXT-FIG. 3. *a*, *Grandagnostus falanensis* (Westergård), two meraspides of degree 1, showing pygidial axis and part of glabella. Both on BDA 983, × 16. *Olenus* Zone, Merevale No. 3 Borehole, 168 ft 0 in. (51·21 m). *b*, *Proceratopyge nathorsti* Westergård. Fragmentary pygidium RU 122, × 8. Locality as for Plate 26, fig. 4.

border. Small node just behind mid-length of cephalon occasionally seen. Some internal moulds show a thin groove extending just within and roughly parallel to the lateral and frontal edges of the cephalon; it is not always preserved quite symmetrical in relation to the sagittal line. It is not a border furrow but represents the inner edge of the cephalic doublure.

Thorax with smooth axial region, thoracic recess present; anterior segment with short (tr.) pleurae, posterior segment with long, forwardly curved pleurae. Pygidium slightly longer than wide (but length equal to breadth in flattened material), convex, slightly carinate in the anterior half. Faint median node may be visible between a quarter and one-third of the length from front. Border widening slightly posteriorly where it attains about one-ninth of the total length; in life the border sloped down a little but as preserved in shale it lies flat or may even be bent upwards slightly. Moulds of the underside of the border show thin grooves subparallel to the margin and indicate a structure of the doublure which is not interpretable in shale-preserved material.

Fully grown specimens have cephalic and pygidial shields generally from 4·0 to 4·5 mm long and wide, but occasionally reach larger sizes. Meraspid specimens of degree 1 with a cephalic length less than 0·75 mm long show the posterior glabellar lobe faintly outlined all round, most weakly anteriorly (text-fig. 3*a*); it is half or less of the cephalic length, not truncate anteriorly, parallel-sided and two-fifths the width of the cephalon, and has a faint node anterior to its mid-length. There is no cephalic border. The meraspid pygidial axis tapers and reaches to, or nearly to, the posterior border furrow. The border behind the axis is proportionally wider than in the adult, about one-fifth of the pygidial length.

Remarks. The present form agrees with the Westergård's monotype of *C. falanensis* (Pl. 24, figs. 10–12) in proportions and in lateral and posterior profile. Smaller specimens resemble the holotype of *G. bairdi* (Pl. 24, figs. 7–9) which is thought to be a younger growth-stage of the same species and has a more evenly vaulted lateral profile. The present form differs from *G. bituberculatus* because it has no median anterior ridge on the cephalon and the basal lobes become effaced in ontogeny. *G. glandiformis* reaches much greater sizes and its pygidium is not carinate. Comparison with Pokrovskaya's species is inconclusive but the pygidium of *Phoidagnostus angustiformis* (1958, pl. 3, fig. 15) resembles *G. falanensis*. *G.? maja* (1958, pl. 4, figs. 9–12) has a narrower thoracic axis and the holotype at least (fig. 10) has a narrower pygidial border. *G. velaevis* has a subquadrate cephalon, a distinct terminal pygidial node, and the pygidial border is wider posteriorly than in *G. falanensis*.

Poulsen and Anderson (1975, p. 2076) suggested that the specimens described above might be referable to *L. laevigata* (Dalman); but no specimens have a cephalic border, and the thoracic axis and pygidial border are too wide for that species. Having examined Scandinavian material of *L. laevigata* preserved in shale and limestone I consider that some at least of Poulsen and Anderson's specimens (1975, pl. 2, figs. 1–9) are wrongly determined: the thoracic axis in their figs. 1 and 7 and the pygidial border in their figs. 7 and 8 are too wide compared with Westergård's (1946) figures. Nor do Poulsen and Anderson's specimens show the posterior of the glabella and front of the pygidial axis, both of which are persistent features in *L. laevigata* (although less so in

L. calva Robison 1964, pl. 83, figs. 1–4), and clearly preserved even when the specimens are flattened in shale.

Occurrence. Mancetter and Outwoods Formations, *laevigata*, *pisiformis*, and *Olenus* Zones. Common at some horizons. In Sweden only one specimen has been found (*pisiformis* Zone). Newfoundland (*laevigata*, *pisiformis*, and *Olenus* zones).

Subfamily AGNOSTINAE McCoy, 1849
Agnostus Brongniart, 1822
Agnostus pisiformis pisiformis (Wahlenberg, 1818)

Plate 24, figs. 15–19

1757 *Entomolithus paradoxus γ pisiformis* Linnaeus, p. 121.
1768 *Entomolithus paradoxus γ pisiformis* Linnaeus, pp. 160–161.
1818 *Entomostracites pisiformis*, Wahlenberg, p. 42, pl. 1, fig. 5.
1958 *Agnostus* (*Agnostus*) *pisiformis* Linnaeus, 1757; Henningsmoen, p. 181, pl. 5, figs. 1–12 [synonymy].
1962 *Agnostus pisiformis* (Linnaeus); Hutchinson, p. 86, pl. 12, figs. 2–6.
1972 *Agnostus pisiformis* (Linnaeus); Taylor and Rushton, pp. 18, 19, pl. 4 [borehole record].

Material. Hundreds of specimens preserved in shale from the Merevale No. 3 Borehole.

Remarks. Some writers have attributed the specific name *pisiformis* to Linnaeus on the strength of the 1757 reference above, which, however, does not make the name available since it predates the 10th edition of *Systema Naturae* (1758); the name does not appear in the latter work, nor in Linnaeus's paper on trilobites (1759). The entry in vol. 3 (Regnum Lapidarum) of the 12th edition of *Systema Naturae* (1768) was ruled invalid in 1954 by I.C.Z.N. Opinion 298. The earliest valid reference seems to be that of Wahlenberg, to whom the species was correctly attributed in Moore 1959, p. O172.

Specimens with rugose cheeks occur (Pl. 24, fig. 18) but as nearly all the specimens are flattened in shale (Pl. 24, fig. 15 is an exception) it is impossible to determine the proportion of such forms. The subspecies *A. pisiformis spiniger* (Dalman) and *subsulcatus* Westergård (1946, pl. 13, figs. 15, 16 and pl. 16, figs. 4, 5, respectively) were not recognized.

Occurrence. In Merevale No. 3 Borehole: fragmentary and poorly preserved specimens probably referable to this species occur sporadically in the Mancetter Formation from 559 ft 7 in. (170·56 m) to the top of the formation; better-preserved specimens occur in the Outwoods Formation from 485 ft 0 in. (147·83 m) to 215 ft 2 in. (65·58 m), being especially abundant towards the top. *L. laevigata* and *A. pisiformis* zones. Scandinavia (same horizons). East maritime Canada (*pisiformis* Zone; also in *laevigata* Zone, judging from the information given by Hutchinson 1962, p. 127, etc.). Siberia (*A. pisiformis–Homagnostus fecundus* Zone; Ivshin and Pokrovskaya 1968). Related subspecies occur in the Mindyallan Stage in Queensland, Australia (Öpik 1967, pp. 96, 98).

Agnostus sp.

Plate 24, fig. 21

1972 cf. *Agnostoglossa*?; Taylor and Rushton, p. 9, pl. 4 [borehole record].

Material. One external mould of a complete specimen about 8·5 mm long, BDA 1984.

Remarks. The present specimen resembles some species of *Agnostus* with weak lateral furrows on the pygidial axis, including specimens referred to *A. pisiformis* itself

(Westergård 1946, pl. 13, fig. 11). The cephalon resembles that of *A. pisiformis* (Henningsmoen 1958, pl. 5, fig. 1) but the pygidial axis extends further back towards the border-furrow, is more expanded and rounded behind, and has less distinct lateral furrows than is general in *A. pisiformis*; the pygidial flanks are narrower and the border is broader. It differs from *A. exsulatus* Poulsen (1960, pl. 1, figs. 3, 4) which has a wider cephalon and a shorter and narrower glabella; the pygidium of *A. exsulatus* appears to have a narrower border. *A. artilimbatus* Öpik (1967, pl. 57, figs. 10, 11) has narrower borders and a shorter anterior glabellar lobe. The associated pygidium has a weaker median axial node and also has a terminal axial node (Öpik 1967, p. 97, text-fig. 22).

Species of *Agnostoglossa* Öpik (1967, p. 145) are similar to the present form but differ because there is no preglabellar median furrow, either in the type species *A. bassa* Öpik or in *A. simplexiformis* (Rozova) as figured by Lazarenko and Nikiforov (1968, pl. 2, figs. 1–4).

Occurrence. Uppermost part of the Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole, depth 520 ft 0 in. (158·50 m).

Homagnostus Howell, 1935*c* (May)

Remarks. The type species, *Homagnostus obesus* (Belt), is a small agnostid characterized by a relatively long and broad pygidial axis on which the anterior pair of lateral furrows curves inwards and forwards to meet the articular furrow which is of agnostoid type; there is a strong median tubercle extending across the second pair of lateral furrows on to the posterior axial lobe which is rounded behind and does not bear a terminal node. The cephalon has a preglabellar median furrow and a narrow border.

Compared with *Agnostus pisiformis* the shape and furrowing of the pygidial axis are the chief distinguishing features, but *A. pater* Westergård, which has a comparatively smaller axis than *H. obesus*, represents a transitional form.

Forms closely related to *H. obesus* may have the preglabellar median furrow obsolete, for example *H. o. laevis* Westergård (1947) and *H. tumidosus* (Hall and Whitfield) (Palmer 1960, pl. 4, figs. 1, 2). These forms in turn resemble *Rudagnostus* Lermontova, 1951 and *Micragnostus* Howell, 1935*b* (April) which both have a relatively smaller pygidial axis than *H. obesus* and lack a preglabellar median furrow. *Micragnostus* has been treated as a subgenus of *Geragnostus* Howell but the glabella in the type species of *Geragnostus* (*A. sidenbladhi* Linnarsson) is quite distinct (Tjernvik 1956, fig. 27) and the genera are probably unrelated.

For the present I follow Palmer's definition of *Homagnostus* (1960, p. 62) and treat it as a separate genus but its limits are difficult to define exactly as it grades into *Agnostus* and *Micragnostus*, the latter having priority over *Homagnostus*.

Homagnostus aff. *pater* (Westergård, 1930)

Plate 25, fig. 3

aff. 1930 *Agnostus pisiformis pater* subsp. nov.; Westergård *in* Holm and Westergård, p. 9, pl. 1, fig. 1?; pl. 4, figs. 9, 10.
1938 *Proagnostus bulbus* Butts; Resser, p. 48 [*pars*], pl. 10, fig. 21 only.
1972 cf. *Homagnostus obesus* (Belt); Taylor and Rushton, p. 19, pl. 4 [borehole record].

Material. One complete external mould 4·4 mm long from Merevale No. 3 Borehole, BDA 1604. Resser's specimen, U.S. National Museum 94867, was kindly loaned by Mr. F. C. Collier.

Remarks. The present specimens resemble *H. pater* (Westergård, 1946, pl. 13, figs. 4–6) from the Andrarum Limestone of Sweden but differ because the pygidial axis is longer and wider; it is nearly half the width of the pygidium and extends back to a transverse line between the bases of the marginal spines, whereas in *H. pater* the axis is about two-fifths the pygidial width, the axis does not extend as far as the marginal spines, and the tubercle on the second axial lobe does not bulge back so strongly. The present form may be distinguished from *H. obesus* (Belt) because the cephalic and pygidial borders are somewhat wider, the posterior glabellar lobe has an elongate (not rounded) median node, the anterior pair of furrows on the pygidial axis curve forwards but do not meet the articulating furrow so distinctly, and because the pygidial axis only just reaches the level of the marginal spines, whereas in a specimen of *H. obesus* of comparable size (Pl. 25, fig. 4) the axis extends further back.

Resser's specimen (1938, pl. 10, fig. 21) agrees with BDA 1604, except that the pygidial axis is slightly broader in proportion; Resser's figure, which is otherwise representative, does not show the left-hand marginal spine which is preserved on the pygidium.

The present form cannot be referred to *P. bulbus* Butts. This binomen was used by Butts (1926, pl. 9, figs. 11, 12) for two specimens he figured but did not describe, one a *Peronopsis*-like pygidium and the other a complete flattened specimen referred by Öpik (1967, pp. 112, 147) to his genus *Agnostascus*. Resser (1938, pl. 10, fig. 17) figured Butts's *Agnostascus*-like specimen and a second complete specimen preserved in chert (fig. 21) which he mistakenly referred to as the 'holotype', even though Butts made no reference to it; the chert-preserved specimen, which is referred to here as *Homagnostus* aff. *pater* is not even available for selection as lectotype of *P. bulbus*. It is evident that the name *Proagnostus bulbus* is available from 1926 (I.C.Z.N. Art. 11) but that the generic concept depends on which of Butts's two specimens is chosen as lectotype; and that *Proagnostus* is no threat to the validity of *Homagnostus* (Öpik 1967, p. 112) but, according to the choice of lectotype, is potentially a synonym of *Peronopsis* (or whatever genus Butts's fig. 11 represents), or a senior subjective synonym of *Agnostascus*.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depth 393 ft 10 in. (120·04 m). Resser's specimen is from a chert nodule from the Nolichucky Formation, *Cedaria* Zone, of Cedar Bluff, Alabama. Poletaeva and Romanenko (1970, pp. 72, 73) recorded '*Homagnostus bulbus*' from the basal Upper Cambrian of the Altay Mountains, Siberia, but it is not known if their species corresponds to *H.* aff. *pater*.

Innitagnostus Öpik, 1967
Innitagnostus sp.

Plate 24, fig. 20

1972 *Innitagnostus* cf. *neglectus* (Westergård); Taylor and Rushton, p. 9, pl. 4 [borehole record].

Material. A flattened cephalon about 1·8 mm long, BDA 2094. A small pygidium 1·3 mm long (BDA 2153–2154, counterparts) is referred doubtfully to the genus.

Remarks. The cephalon differs from that of *I. neglectus* (Westergård, 1946, pl. 13, fig. 1) because the anterior glabellar lobe is more truncate in front and the lateral furrows are more sharply cut. It appears to have a stronger preglabellar median furrow than *I. innitens* Öpik (1967, pl. 58, fig. 2). Although the present form has weakly scrobiculate cheeks and a small median indentation in the front of the anterior glabellar lobe it cannot be compared closely with *I. tchatertensis* (Kryskov *in* Borovikov and Kryskov 1963, pl. 1, figs. 13, 14) in which these features are strongly developed, together with a pair of distinctive arcuate scrobicules opposite the front of the glabella. The present form compares most closely with cephala assigned to the variable species *I. inexpectans* (Kobayashi) by Öpik (1963, pl. 2, fig. 13; 1967, pl. 63, fig. 2).

The pygidium appears to conform to those of *Innitagnostus* species but the pygidial axis differs from that of *I. inexpectans* in being somewhat pointed posteriorly. It is too small and too badly preserved at the front of the axis to be compared with other species.

Occurrence. Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole, the cephalon at a depth of 558 ft 6 in. (170·23 m) and the pygidium at 574 ft 0 in. (174·96 m). *Innitagnostus* species have been described from the upper part of the *laevigata* Zone to the lower part of the *Olenus* Zone.

Subfamily PTYCHAGNOSTINAE Kobayashi, 1939
Ptychagnostus Jaekel, 1909

Öpik (1961, p. 76) discussed *Ptychagnostus* and its relationship with *Goniagnostus* Howell, 1935*c* which he treated as a subgenus.

Ptychagnostus (*Goniagnostus*) *fumicola* Öpik, 1961

Plate 25, figs. 1, 2

1961 *Ptychagnostus (Goniagnostus) fumicola* sp. nov.; Öpik, p. 81, pl. 20, figs. 14–17; text-figs. 28, 29, *non* pl. 21, fig. 2.
1967 *Ptychagnostus (Goniagnostus) fumicola* Öpik, 1961; Öpik, p. 91, pl. 57, figs. 1, 2.
1972 *Ptychagnostus (Goniagnostus) fumicola* Öpik; Taylor and Rushton, p. 9, pl. 4 [borehole record as '*Ptychagnostus* cf. *fumicola*'].
1975 *Ptychagnostus (Goniagnostus) fumicola* Öpik; Daily and Jago, p. 540.

Material. One cephalic fragment and one pygidium approximately 3 mm long, BDA 2199, 2201.

Remarks. The cephalic fragment shows only a triangular anterior glabellar lobe, as long as wide, a short lateral lobe behind this, and some radiating marginal scrobiculae. The pygidium agrees most closely with that in Öpik's (1967) plate 57, fig. 2, in the proportions of the divisions of the axis; the specimen in his plate 57, fig. 1 has a shorter terminal portion, and in the holotype (Öpik 1961, pl. 20, fig. 14) the two anterior portions, taken together, are shorter whilst the third portion is longer. The presence of a post-axial longitudinal furrow cannot be established. The external mould of the pygidium shows the base of a marginal spine.

Amongst strongly granulose species of *Ptychagnostus* the present form differs from *P.* (*P.*) *punctuosus* (Angelin) and *P.* (*P.*) *aculeatus* (Angelin) (see Westergård 1946) and *Ptychagnostus* (*P.*) *akanthodes* Robison, 1964, because the posterior part of the pygidium is separated off as in *P.* (*Goniagnostus*) species; furthermore, the pygidial margin has a pair of spines, unlike *punctuosus* and *aculeatus*.

P. aff. *fumicola* (Öpik 1967, p. 91) and *P. nodibundus* Öpik, 1967 (p. 92) are both more closely related but the former has a finer sculpture on the pygidium and the latter has coarser granulation.

Occurrence. Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole at 595 ft 10 in. (181·61 m). Steamboat Sandstone and Mungerebar Limestone, Queensland, Australia (*laevigata* Zone and *torosa-janitrix* Zone).

Family DIPLAGNOSTIDAE Whitehouse, 1936

According to Öpik (1967, p. 81) the Diplagnostidae includes the subfamilies Ammagnostinae, Glyptagnostinae, Pseudagnostinae, Tomagnostinae, Diplagnostinae, Oidalagnostinae, and a few forms not referable to any of these subfamilies. The first four subfamilies need not be considered further here.

Cristagnostus papilio sp. nov., described below, is a modified axiolobate form (Öpik 1967, p. 58) and resembles the Oidalagnostinae (Öpik 1967, p. 134) in having the anterior part of the pygidial axis triannulated and the posterior part of the axis expanded; but it differs in lacking scrobiculae on the flanks and a depression in the pygidial collar. It cannot be referred to the Oidalagnostinae as construed by Öpik, but equally the modified pygidial axis seems inappropriate for the Diplagnostinae. *Cristagnostus* is not, therefore, referred to a subfamily.

Cristagnostus gen. nov.

Name. Cristatus, Latin, crested, and *agnostus*; referring to the longitudinal axial ridge and the pygidial 'crest' or collar.

Type species. Cristagnostus papilio sp. nov.

Other species. Linguagnostus? *reconditus* Poletaeva and Romanenko.

Diagnosis. Diplagnostidae with semi-elliptical cephalon, glabellar rear rounded; anterior part of the pygidial axis short, distinct, divided into three pairs of lateral lobes; this part traversed for its full length by a median ridge which has a pair of knobs side by

---

EXPLANATION OF PLATE 25

Figs. 1, 2. *Ptychagnostus* (*Goniagnostus*) *fumicola* Öpik, × 12. 1, fragmentary cephalon, BDA 2199 latex. 2, pygidium, BDA 2201. M3, 595 ft 10 in. (181·61 m).

Fig. 3. *Homagnostus* aff. *pater* (Westergård). BDA 1604 latex, × 8. M3, 393 ft 10 in. (120·04 m).

Fig. 4. *Homagnostus obesus* (Belt). TE6 latex, × 8. Trench opposite Old Wharfe Inn, Chilvers Coton, near Nuneaton (SP 3623 9050). Outwoods Formation, *Olenus* Zone.

Figs. 5–13. *Cristagnostus papilio* gen. et sp. nov. 5, holotype, BDA 1320 latex, × 6. M3, 261 ft 6 in. (79·71 m). 6, oblique view of pygidium of holotype, showing posterior median spine (right-hand end of figure), × 20. 7, BDA 1318, × 6. M3, 261 ft 5 in. (79·68 m). 8, 9, small cephala, BDA 1588, 389 ft 6 in. (118·72 m), BDA 1349, 264 ft 7 in. (80·64 m), × 12. M3. 10, BDA 1322 latex, × 6. M3, 261 ft 6 in. (79·71 m). 11, Birmingham University BU 529, × 6. Dumped shale south-west of Cemetery, Hartshill, 4 km north-west of Nuneaton (SP 3241 9408). Coll. Dr. I. Strachan. 12, small pygidium, same exuvia as 8, BDA 1588 latex, × 12. M3. 13, largest pygidium, BDA 1312 latex, × 6. M3, 260 ft 0 in. (79·25 m).

Fig. 14. *Aspidagnostus rugosus* Palmer. BDA 1720, × 12. M3, 435 ft 2 in. (132·64 m).

Figs. 15, 17, 18. *Schmalenseeia amphionura* Moberg. 15, fragmentary thorax and pygidium, BDA 1533, × 12. M3, 374 ft 6 in. (114·15 m). 17, lectotype cranidium, Paleontological Institute, Lund, LO 1660T latex, × 12. Original figured Moberg 1903, pl. 4, fig. 1, Köpingsklint, Borgholm, Öland, Sweden. 18, glabella, BDA 1464, × 25. M3, 277 ft 0 in. (84·43 m).

Fig. 16. *Schmalenseeia* cf. *spinulosa* Lazarenko. Cranidium, BDA 1891, × 14. M3, 485 ft 0 in. (147·83 m).

RUSHTON, Cambrian trilobites

side at its anterior end. Posterior part of axis expanded but obscurely delimited. Pygidial flanks not scrobiculate. Pygidial collar sinuous, uninterrupted, pygidial margin with median notch and median spine.

Remarks. Genera related to the Diplagnostinae and Oidalagnostinae include several species in which the cephala vary little but the pygidia show very diverse features. Genera have been distinguished by combinations of characters such as the development and lobation of the pygidial axis, the presence of scrobicules on the flanks, the presence and development of a pygidial collar, and the development of a median spine on the margin. Most of these features are apt to vary: scrobiculation is present in *Tasagnostus compani* Jago but absent in *T. debori* (Jago 1976, pp. 164, 166); the pygidial collar is present in *Linguagnostus kjerulfi* (Brögger) but absent in *L. groenwalli* Kobayashi (Westergård 1946, pl. 8, figs. 30, 32); and the median spine, though absent in typical forms, may be present in some *Oedorhachis* and *Dolichagnostus* (Öpik 1967, pp. 128, 132). Therefore the genera are most clearly distinguished by the features of the pygidial axis.

In *Cristagnostus* the anterior end of the pygidial axis is comparable with that of *Oidalagnostus* and *Tasagnostus* (Jago 1976, pp. 160–161) but the median ridge differs in being uninterrupted by a cross-furrow. The posterior part of the axis is less well defined and the pygidial collar lies further forward than in those genera. *Cristagnostus* lacks the scrobiculate flanks and the low swellings on either side of the axis in *Oidalagnostus*. The known *Oidalagnostus* species—*O. trispinifer* Westergård 1946, pl. 9, figs. 4–7; *O. personatus* Öpik 1967, pl. 54, figs. 7–9; *O. tienshanicus* Lu (Lu *et al.* 1974, pl. 1, figs. 5–7)—form a well-defined group, so I prefer not to extend it by referring the new form to *Oidalagnostus*.

The semi-elliptical cephalon and advanced pygidial collar of *Cristagnostus* recall those of *Ovalagnostus changi* (Lu *et al.* 1974, pl. 1, fig. 8); but *Ovalagnostus* resembles *Tasagnostus* rather than *Cristagnostus* in the development of the posterior part of the pygidial axis and in the interrupted ridge on the anterior part of the pygidial axis.

The pygidial collar and uninterrupted median ridge of *Cristagnostus* resembles those of *L. kjerulfi* (although the ridge of *Cristagnostus* differs in bearing two knobs at its anterior end). The posterior part of the axis in *Linguagnostus* is, however, small and triangular, indicating an axiolobate structure. I prefer to restrict *Linguagnostus* to axiolobate forms allied to *Diplagnostus* rather than extend it to include the modified axiolobate *Cristagnostus*. No *Linguagnostus* has a median spine on the pygidial margin. The axis of *Plurinodus discretus* Öpik (1967, p. 170, text-fig. 51) is comparable to that of *C. papilio*, but the median ridge is shorter and the furrow behind the axis is not so deep; *P. discretus* has no pygidial collar nor a notched margin. There is some resemblance between the pygidial axial structure of *C. papilio* and the Ordovician form *Galbagnostus galba* (Billings), as figured by Whittington (1965, pl. 4).

The two species referred to *Cristagnostus* are united by two peculiar features: the paired knobs at the anterior end of the longitudinal ridge on the pygidial axis are not known in the Diplagnostinae or Oidalagnostinae, although *Tomagnostus fissus* (Westergård 1946, pl. 7, fig. 29) has a pair of knobs in a comparable position but not on a ridge; and the median pygidial spine springs from a pit in the margin, somewhat as in *Aspidagnostus rugosus* Palmer (1962, pl. 1, fig. 25).

Cristagnostus papilio sp. nov.

Plate 25, figs. 5–13

1962 *Oidalagnostus* cf. *O. trispiniger* [*sic*] Westergard; Hutchinson, p. 80 [*pars*], pl. 7, fig. 20 only.
1972 *Oidalagnostus* sp. nov.; Taylor and Rushton, p. 18, pl. 4 [distribution].

Name. Papilio, Latin, butterfly, fancied resemblance to pygidial axis.

Holotype. BDA 1320–1321 (Pl. 25, fig. 5), an incomplete external mould and counterpart.

Paratypes. A poorly preserved dorsal shield (BDA 1502–1503), a small scattered exuvia (BDA 1587–1588), three cephala (BDA 1311, 1318–1319, 1349), and five pygidia (BDA 1312, 1322, 1579–1580, 1650–1651, Birmingham University BU 529).

Description. Cephalon semi-elliptical, length nine-tenths of width. Glabella three-quarters of cephalic length (slightly less in smaller specimens), about one-third of cephalic width just anterior to basal lobes. Anterior glabellar lobe a little more than one-quarter of glabellar length, indented anteriorly and weakly divided longitudinally in smaller specimens, but rounded in front and with barely a trace of a median depression in full-grown specimens; delimited behind by a weak furrow directed inwards and very slightly backwards. Posterior glabellar lobe parallel-sided with an elongate median ridge on its anterior half. A weak pair of lateral furrows at about one-third from the front of this lobe. The outline of the glabella is 'stepped' to accommodate the basal lobes and is rounded posteriorly. Basal lobes large, triangular, nearly continuous anteriorly with the main glabellar lobe but separated by only a very weak furrow (as in several diplagnostid cephala and also *Peronopsis scaphoa* Öpik, 1961). Acrolobes slightly constricted. Cheeks separated anteriorly by longitudinal preglabellar furrow, with weak scrobiculae. Border furrow broad, border narrow.

Pygidial length, excluding the articulating half-ring, about three-quarters of the width. Articulating furrow of diplagnostid type. Anterior part of axis nearly half of pygidial length, subtrapezoidal, length four-fifths of the width; it narrows slightly posteriorly, is indented medially in front and behind, and is divided into three lobes on either side of the median keel; anterior pair of lobes widen abaxially, second pair longer and roughly square, third pair small, semi-oval, widening abaxially. Median keel has two small knobs, side by side, at anterior end, rises towards the posterior end which is sharply rounded and drops steeply behind. Furrow behind the keel deep and wide. From the posterolateral end of the posterior pair of axial lobes weak furrows extend inwards and slightly backwards to delimit an indistinct transverse lenticular area of weak convexity. On the holotype, but no other specimen, a pair of faint furrows is seen behind this area, close to and parallel with the sagittal line; they may represent the intranotular axis. Behind the anterior part of the axis the axial region is swollen. A sinuous crest (pygidial collar) extends subparallel to, and lies about one-fifth of the pygidial length within, the posterior margin between the marginal spines. Acrolobes constricted. Flanks not scrobiculate. Border furrow wide, border narrow with a pair of posterolateral marginal spines and a median notch from which a tiny spine is directed backwards and downwards (Pl. 25, fig. 6).

Dimensions. The holotype has a cephalon 4·25 mm long and pygidium 3·8 mm long. The largest pygidium is 4·6 mm long.

Remarks. The cephalon of *C. papilio* is very like that of *Diplagnostus planicauda* (Angelin) (Westergård 1946, pl. 8, figs. 22, 24) and, apart from the strong preglabellar median furrow, also like *Oidalagnostus personatus* Öpik (1967, p. 136). It is more rounded in front than *Linguagnostus kjerulfi* and *O. trispinifer*.

The cephalon differs from that of *C. reconditus* (Poletaeva and Romanenko 1970, p. 75, pl. 10, figs. 10–12) from the early Upper Cambrian of the Altay Mountains, Siberia, because the anterior glabellar lobe is longer and shows a tendency to longitudinal division (in smaller specimens). The lateral furrows on the posterior glabellar lobe lie further back in *C. papilio* and the preglabellar median furrow is stronger. The basal lobes of *C. reconditus* are triangular and their anterior ends seem not to be confluent with the glabella.

The pygidium of *C. reconditus* differs from that of *C. papilio* in lacking the weak inwardly and slightly backwardly directed furrows behind the anterior part of the axis. Poletaeva and Romanenko's reconstruction (1970, text-fig. 4) suggests that the pygidial crest bends back to the posterolateral marginal spines and that the median spine is much stouter. Their plate 10, figs. 11 and 12, show that the anterior part of the pygidial axis has three pairs of lobes, the posterior pair with rounded posterolateral corners, and that there are paired tubercles at the anterior end of the axial keel; these are not in their reconstruction.

The pygidium figured by Hutchinson (1962, pl. 7, fig. 20) and referred to *L.? reconditus* by Poletaeva and Romanenko has faint furrows extending inwards and backwards behind the axis and a pygidial crest which does not reach the posterolateral spines; by these features it differs from *C. reconditus* and is referable to *C. papilio*.

Occurrence. Outwoods Formation in Merevale No. 3 Borehole, *C. papilio* occurs between 405 ft 8 in. (123·65 m) and 260 ft 0 in. (79·25 m), zone of *Agnostus pisiformis*. One pygidium was collected by Dr. I. Strachan from dumped shales 200 m north of the Royal Oak, Hartshill, by the south-west side of the cemetery (Birmingham University Collection No. BU 529). Newfoundland: above the base of the Elliott Cove Formation, where it is associated with *A. pisiformis* above beds referred to the *laevigata* Zone, as discussed under 'Correlation'.

Family CLAVAGNOSTIDAE Howell, 1937

Aspidagnostus Whitehouse, 1936

Öpik discussed and illustrated *Aspidagnostus* fully (1967, p. 115).

Aspidagnostus rugosus Palmer, 1962

Plate 25, fig. 14

1962 *Aspidagnostus rugosus* n. sp.; Palmer, p. 15, pl. 1, figs. 24–30.

1972 *Aspidagnostus* sp.; Taylor and Rushton, p. 19, pl. 4 [borehole record].

Material. One fragmentary cephalon 2·4 mm long, BDA 1720–1721 (counterparts).

Description. Main part of glabella kite-shaped, contracted behind to nearly half its greatest width which is at the anterior third. Anterior part depressed, pointed in front. Median keel crushed. Basal lobes project laterally at posterior margin. The glabella appears to widen backwards between its narrowest part and the basal lobes, as seen also in one of Palmer's figures (1962, pl. 1, fig. 26); it is possible that this widening represents the anterior part of the composite basal lobe, as in *A. inquilinus* Öpik (1967, pl. 56, figs. 1, 2). Cheeks show longitudinal median furrow and radiating pits and furrows (scrobiculae) nearly symmetrically disposed and very similar in distribution to those of *A. rugosus* (Palmer 1962, pl. 1, fig. 30). Margin not preserved (note that the narrow rim behind the glabella in Pl. 25, fig. 14 is the border of a juvenile *Agnostus pisiformis* underneath the *Aspidagnostus* cephalon).

Remarks. The radiating scrobiculae distinguish this cephalon from those of *A. laevis* Palmer, 1962, *A. lunulatus* (Kryskov, 1963), *A. stictus* Öpik, 1967, and *A. inquilinus* Öpik, 1967. Furthermore, the glabella contracts more strongly posteriorly (in the part between the anterior one-third and two-thirds of its length) than in those species and also *A. parmatus* Whitehouse. However, so far as it is preserved, the present specimen agrees with *A. rugosus*.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depth 435 ft 2 in. (132·64 m). Conasauga Formation, Alabama, and base of Dunderberg Formation, Nevada, U.S.A., in equivalents of the *pisiformis* Zone and basal *Olenus* Zone (Palmer 1962). Siberia, *A. pisiformis–Homagnostus fecundus* Zone and *Glyptagnostus reticulatus* Zone (Datsenko *et al.* 1968; Ivshin and Pokrovskaya 1968, p. 99; Poletaeva and Romanenko 1970, p. 72).

POLYMERID TRILOBITES

Family MARJUMIIDAE Kobayashi, 1935

Modocia Walcott, 1924*a*

Robison (1964, p. 550) and Rasetti (1965, p. 106) discussed the synonymy of *Modocia* and several other genera, including *Armonia* Walcott and *Perioura* Resser.

Modocia anglica sp. nov.

Plate 26, fig. 20

1972 trilobite n. gen.; Taylor and Rushton, p. 19 [recorded].

Holotype. One specimen in counterpart, RU 2210, well preserved but slightly flattened and crushed. It was prepared so as to show the right fixed cheek and the left free cheek.

Diagnosis. A species of *Modocia* with a smooth exoskeleton, a truncate glabella (not well rounded in front), an occipital tubercle, a backward bend in the anterior border furrow, genal spines in continuity with the margin of the free cheek, a median spine on the axis of the ninth thoracic segment, and a small pygidium with only one distinct pair of furrows.

Description. Cephalic axis three-quarters of cranidial length, sides straight and converging forwards, front not evenly rounded but slightly truncate. Glabella without furrows, width at occipital furrow nine-tenths of length (excluding occipital ring) and one and a half times width between proximal ends of eye-ridges. Occipital ring slightly wider than base of glabella, about one-fifth of glabellar length, simple, with small median tubercle. Frontal area one-quarter of cranidial length, preglabellar field three-quarters as long as anterior border at mid-line. Anterior border furrow makes slight backward bend medially. Width across preocular cheeks about equal to cranidial length. Interocular cheeks (axial furrow to palpebral furrow) about half as wide as glabella at eye-line, but width from axial furrow to ocular margin is two-thirds of glabellar width at eye-line. Palpebral lobe about one-third of length of cephalic axis, placed near mid-length of cranidium. Eye-ridges weak, oblique outwards and backwards, slightly curved. Preocular facial sutures diverge forwards from the eyes at about 30° to sagittal line, and curve sharply inwards at anterior border furrow to cross the anterior border obliquely. Postocular sutures curve out and back from eye to pleuroccipital furrow whence they curve inwards, so that they converge backwards across the posterior border. Postocular cheeks nearly as wide as occipital ring.

Free cheek with stout straight spine nearly as long as remainder of cheek. No genal caeca are visible but a principal genal vein (Öpik 1967, p. 172) extends back from the middle of the eye towards the genal angle. Lateral border slightly narrower than anterior border, striated parallel to margin; anteriorly doublure appears to extend towards mid-line such that rostrum was probably small (tr). Hypostoma unknown.

Thorax of thirteen segments with short pleural spines directed backwards. Anterior axial ring twice as wide as posterior ring. Ninth ring bears a backwardly pointing median spine of unknown length; the other rings lack median tubercles.

Pygidium twice as wide as long. Axis nearly two-fifths of total width, composed of two distinct rings, a faint third ring, and a terminal piece which is rounded behind. Pleural regions with distinct anterior pair of pleural grooves and an indistinct trace of a second pair. Posterior margin rounded, entire. There appears to be a posterior border but this may merely be caused by the edge of the doublure pressed through from below. Doublure sub-parallel to margin, narrows slightly behind axis, striated parallel to margin.

Internal and external surfaces of dorsal exoskeleton smooth. To judge from the convexity shown by the specimen the exoskeleton was thicker and stronger than that of *Olenus* which occurs in the overlying strata (Taylor and Rushton 1972, p. 15, text-fig. 4).

Dimensions. Length of cranidium 6·8 mm; length of cephalic axis 5·1 mm; width of cranidium across eyes 6·9 mm; width of occipital ring 4·0 mm; length of thorax 10·6 mm; length of pygidium 2·2 mm, width 4·4 mm; width of pygidial axis 1·6 mm.

Remarks. This specimen agrees with the description of the genus *Modocia* given by Robison (1964, p. 550) but differs because of the convergence of the posterior ends of the facial suture and the small size of the pygidium; the importance of the former difference is unknown but some other species of *Modocia* (Robison 1964, pl. 87, figs. 19–21) have pygidia relatively as small as that of the present specimen, which is accordingly referred to that genus. It may be distinguished from the type and many other species of *Modocia* (Lochman and Duncan 1944, pl. 11, figs. 35–43; Palmer 1954, pl. 87, figs. 3, 4, 6, 8; Robison 1964, pl. 87, figs. 5–19 and pl. 88, figs. 1–6; Rasetti 1963, pl. 70, figs. 20–25; Rasetti 1965, pl. 1, figs. 13–26 and pl. 2, figs. 1–9) because the glabella is slightly truncate anteriorly, the anterior border has a median backward bend, and the pygidium has only one distinct pair of pleural grooves. Furthermore, apart from *M. yellowstonensis* Duncan, *M.? spinosa* Rasetti, and *M. nuchaspina* Robison, none shows an occipital tubercle or spine; and, apart from *M. bidentata* Rasetti and *M. crassimarginata* Rasetti, none of those species has a smooth exoskeleton. *M.? agatho* (Walcott) (Rasetti 1965, pl. 1, figs. 27–30) has a more truncate glabella and a suggestion of a median backward bend in the anterior border furrow, which, however, is indistinct; it differs from the English form also because the interocular cheeks are narrower, less than one-third of the glabellar width. The cranidium of *M. elongata* (Walcott) [= *Armonia pelops* Walcott 1924*a*, *b*] is similar to the present specimen but the free cheeks have no spine, the thorax has fourteen segments, and the pygidium has several pairs of pleural grooves. *M. lata* (Howell and Duncan) generally has narrower interocular cheeks and the free cheek has a slender spine which makes an angle with the lateral margin of the cheek (Lochman and Duncan 1944, pl. 15, figs. 29–37). *M.* [*Perioura*] *typicalis* (Resser 1938, pl. 8, figs. 41–43) has fourteen thoracic segments of which the eleventh has long pleural spines, and several pairs of pygidial pleural furrows. The cranidium of *M. masoni* (Resser 1938, pl. 9, figs. 37, 38) is very similar to the English species but the anterior border furrow does not make a conspicuous backward median bend and the figure (Resser's fig. 37) suggests that the surface is granulose. The pygidium (fig. 38, presumably natural size) is 8 mm long yet shows only the anterior pleural and interpleural furrows and is at most weakly furrowed behind; it thus somewhat resembles the English specimen. *M. arctica* Walcott and Resser has a similar pygidium (Lazarenko and Nikiforov 1968, pl. 4, figs. 4–6) but the cranidium has a granulose surface.

Occurrence. Outwoods Formation, top of *pisiformis* Zone, about 15 m below the *Olenus* Zone, Purley Quarry (section No. 5 of Taylor and Rushton 1972, text-figs. 3, 4), about 25 m below the sill. In the U.S.A. *Modocia* species occur in the *Bolaspidella* Zone and *Cedaria* Zone (top Middle Cambrian to base of Upper Cambrian).

Family AGRAULIDAE Raymond, 1913
Cyclolorenzella Kobayashi, 1960

Remarks. According to Kobayashi's diagnosis (1960, p. 389) *Cyclolorenzella* has no glabellar furrows but some species he assigned to the genus show short furrows indenting the sides of the glabella, for example, *C. armata* (Walcott 1913, pl. 14, fig. 17*a*), *C. convexa* (Resser and Endo 1937, pl. 65, fig. 26), and *C. parabola* (Lu) (Chu 1959, pl. 2, fig. 1). The form described below has similar glabellar furrows.

Cyclolorenzella sp.

Plate 26, figs. 1–3

1972 Genus and species undet.; Taylor and Rushton, p. 19, pl. 4 [borehole record].

Material. A cephalon, a cranidium, a juvenile exoskeleton, and a very small pygidium with some thoracic segments (BDA 1565–1566, 1569–1572, 1574–1575); all are incomplete and all show signs of dorso-ventral compression during compaction of the sediment, the smaller specimens being least affected.

Description (based on BDA 1572, the largest specimen). Cephalic axis (excluding occipital spine) two-thirds of cephalic length. Glabella tapered forwards, truncate anteriorly, slightly longer than wide, most elevated at posterior quarter, declining forwards. Posterior glabellar furrows (S1) indent the sides of the glabella at posterior quarter, short; S2 indent sides of glabella near mid-length; creases extending inwards and forwards from S2 appear to be due to compression. S3 not seen. Occipital furrow widest medially, though this may be emphasized by compression. The occipital ring has a peculiar spine: the median part of the occipital ring is raised to form a thin transverse backwardly leaning ridge, which is interpreted as the base of a broad, flattened, occipital spine extending back over the simple posterior edge of the occipital ring, as partly seen in the smallest cephalon (Pl. 26, fig. 3). The spine resembles that of *Toxotis pusilla* Wallerius (Westergård 1948, pl. 3, figs. 17–21). Axial furrow deep. The semicircular depression of the cheeks around the front of the glabella may be partly due to compression. Frontal area is crushed down and slightly crumpled, and is now flat, but seems originally to have been swollen. Ocular ridges transverse, obsolescent laterally, palpebral lobes very indistinct, about one-fifth the length of cephalon. Pleuroccipital furrow wide and deep, shallowing laterally. Postocular cheeks about as wide as occipital ring, with fulcrum at posterior margin about two-thirds the distance from axial furrow to facial suture. Facial suture has a generally backward and outward course but makes an inward bend opposite the eye at two-fifths of the cranidial length from the front; the posterior ends of the facial suture turn inwards across the posterior margin.

The free cheek is narrow, shows no border furrow, but has a short spine continuous with the lateral margin.

The external mould shows that the surface was finely granulose.

The smallest cephalon (Pl. 26, fig. 3) differs from the largest (figs. 1, 2) because its glabella is relatively longer, less tapered, and is rounded anteriorly; the eye-ridges are barely perceptible. The specimen intermediate in size is intermediate in glabellar shape and the strength of the eye-ridges.

EXPLANATION OF PLATE 26

Figs. 1–3. *Cyclolorenzella* sp. 1, 2, crushed cranidium with left free cheek, dorsal and oblique side views. BDA 1572 latex, × 12, 387 ft 0 in. (117·96 m). 3, small exuvia, BDA 1566 latex, × 12, 386 ft 10 in. (117·91 m). M3.

Fig. 4. *Proceratopyge nathorsti* Westergård. Part of cranidium and thorax, RU 132, × 4. Section 5 of Taylor and Rushton (1972, figs. 3, 4), Purley Quarry, north-west of Nuneaton (SP 3060 9608).

Fig. 5. *Aedotes*? sp. Fragmentary cranidium, BDA 1889A, × 25. M3, 485 ft 0 in. (147·83 m).

Figs. 6, 7. *Walcottella* sp. Left valve, BDA 1788, 448 ft 10 in. (136·80 m); right valve, BDA 1825 latex, 466 ft 2 in. (142·09 m). Both × 15. M3.

Fig. 8. *Svealuta primordialis* (Linnarsson). Right valve, BDA 2313, × 4. M3, 639 ft 2 in. (194·82 m).

Figs. 9, 10. *Falites*? *minimus* (Kummarow). Left valves, BDA 1167, 208 ft. 7 in. (63·58 m); and BDA 1452, 275 ft 8 in. (84·02 m). Both × 20. M3.

Fig. 11. *Hesslandona trituberculata* (Lochman and Hu). Right valve, BDA 1817, × 25. M3, 464 ft 6 in. (141·58 m).

Fig. 12. *Falites fala* Müller. Left valve, BDA 1820, × 15. M3, 464 ft 6 in. (141·58 m).

Figs. 13, 14. *Bradoria* sp. Right valve, BDA 1192 latex, 221 ft 2 in. (67·41 m); and left valve, BDA 1826, 466 ft 8 in. (142·24 m). Both × 15. M3.

Fig. 15. *Cyclotron* sp. Left valve, BDA 1409, × 4. M3, 270 ft 6 in. (82·45 m).

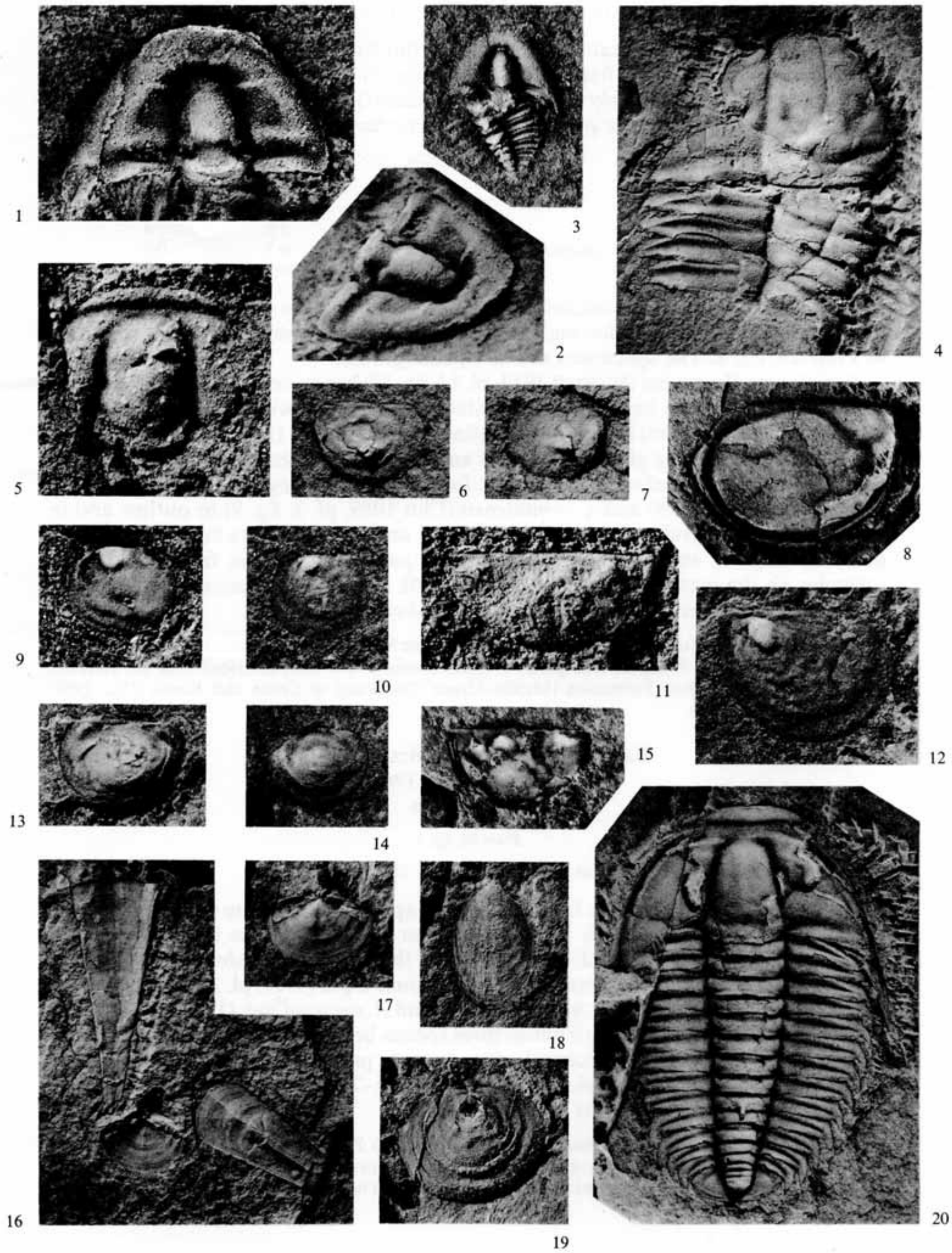
Figs. 16, 17. Hyolithid gen. and sp. undetermined. 16, dorsal and ventral views of conchs, RU 2216, × 3. 17, operculum, counterpart of 16, RU 2215, × 4. Locality as for 4.

Fig. 18. *Lingulella* sp. Pedicle valve, BDA 2162, × 8. M3, *laevigata* Zone, 575 ft 0 in. (175·26 m).

Fig. 19. *Acrothele* sp. Pedicle valve, BDA 2156, × 8. M3, *laevigata* Zone, 574 ft 6 in. (175·12 m).

Fig. 20. *Modocia anglica* sp. nov. Holotype, RU 2210 latex, × 3·3. Locality as for 4.

PLATE 26



RUSHTON, Cambrian shelly faunas

The number of thoracic segments is uncertain but BDA 1566, which is immature and may be incomplete, shows five segments of which the first three at least have axial spines. The pygidium (possibly a transitory pygidium) is poorly preserved but has three axial rings and two or three pairs of pleural grooves.

	BDA 1572 (mm)	BDA 1569 (mm)	BDA 1566 (mm)
Length of cranidium	2·2	—	0·95
Width of cranidium	3·2	1·9	1·4
Length of glabella (without occipital ring)	1·1	0·7	0·6
Width of glabella	1·0	0·5	0·4

Remarks. In recording the occurrence of this form (Taylor and Rushton 1972), I mentioned a fixigenal spine, having overlooked the facial suture shown by the specimen in Plate 26, fig. 3. The specimens are all opisthoparian.

Cyclolorenzella armata (Walcott 1913, pl. 14, fig. 17) has an occipital spine but differs from the present form because the occipital furrow is very weak, the frontal area is longer, and the palpebral lobe is more distinct. *C. tonkinensis* (Mansuy 1915, pl. 2, fig. 13*a–c*) differs in lacking glabellar furrows and the surface is finely and densely pitted. Apart from the occipital spine the present form resembles *C. ogurai* (Resser and Endo 1937, pl. 51, figs. 17–19) and *C. yentaiensis* (Chu 1959, pl. 2, fig. 9) in outline and in having a comparatively weakly inflated frontal area, but it differs in having distinct glabellar furrows and stronger eye-ridges. *C. parabola* (Lu) has free cheeks with tubercles on the margin (Chu 1959, pl. 1, fig. 35). Most other species have narrower postocular cheeks or a strongly granulose exoskeleton.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depths 387 ft 0 in. and 386 ft 10 in. (117·96 m and 117·91 m). Several species of *Cyclolorenzella* have been described from the Taitzuan and especially the Kushan Formation (Middle–Upper Cambrian) of China and Korea (Chu 1959; Kobayashi 1960, p. 389).

Family LEIOSTEGIIDAE Bradley, 1925
Aedotes Öpik, 1967
Aedotes? sp.

Plate 26, fig. 5

Material. One fragmentary cranidium 1·3 mm long, BDA 1889A.

Remarks. The palpebral lobe is fragmentary but appears to lie at the mid-length of the glabella. The interocular cheek is half as wide as the glabella. The long glabella, the unridged anterior border, and the position of the eye recall *Aedotes*. The glabella reaches nearly to the anterior border, as in *A. instans* Öpik (1967, pl. 21, fig. 3), and has distinct glabellar furrows as in *A. declivis* Öpik and *A. mutans* Öpik (1967, pl. 21, figs. 1, 6). The present specimen differs from all three species because the surface is sparsely but distinctly granulose. The occipital ring is not preserved, so distinction from *Prochuangia mansuyi* Kobayashi (1935, pl. 10, figs. 1–7) depends only on the stronger glabellar furrows shown by the present specimen.

Occurrence. Outwoods Formation, basal layer of the *pisiformis* Zone, at depth 485 ft 0 in. (147·83 m), Merevale No. 3 Borehole. Öpik recorded *Aedotes* from the lower part of the Mindyallan Stage in Queensland; Daily and Jago suggested that this horizon lies just below the base of the Upper Cambrian.

Family BURLINGIIDAE Walcott, 1908
Schmalenseeia Moberg, 1903

Jago (1972) has reviewed the species of *Schmalenseeia*.

Schmalenseeia amphionura Moberg, 1903

Plate 25, figs. 15, 17, 18

1903 *Schmalenseeia amphionura* n.g. et n. sp.; Moberg, p. 96, pl. 4, figs. 1, 2, 3?, 4, 7–10, *non* 5, 6?
1922 *Schmalenseeia amphionura* Moberg; Westergård, p. 119, pl. 1, fig. 19.
1972 *Schmalenseeia* cf. *amphionura* Moberg; Taylor and Rushton, pl. 4 [*pars*], *non* p. 18 [borehole record].

Lectotype. Selected here; Lund University LO 1660T, external mould of a cranidium, figured by Moberg 1903, plate 4, fig. 1; a cast is figured here, Plate 25, fig. 17.

New material. Four fragments showing the cephalic axis and parts of the frontal area; two fragmentary pygidia, one with two thoracic segments. BDA 1463, 1463A, 1464, 1532–1533.

Remarks. The syntypes of *S. amphionura* are preserved in limestone and are distinctly convex, the cranidia being about one-quarter as high as long and the greater part of the convexity being due to the down-sloping cheeks; but the exoskeleton is very thin and it is to be expected that if specimens become flattened the postocular cheeks, whose posterior margins are straight and nearly transverse when preserved in limestone (Pl. 25, fig. 17), might then be bent forwards from the base, their weakest part (cf. Pl. 25, fig. 16). Therefore the forward curvature of the posterior cranidial margin is not a reliable criterion for specific distinction unless reference is made to the state of preservation of the specimens.

Four cranidia from Moberg's material show that in some specimens the glabella tapers forwards more than in Westergård's figure. The longitudinal preglabellar ridge varies in strength but does not extend back on to the frontal glabellar lobe. All the specimens have an occipital tubercle though it is very weak in the smallest specimen (1·25 mm long), and all have a weak pleuroccipital furrow which fades out laterally (Moberg 1903, pl. 4, figs. 1, 2) or extends to the genal angle. The palpebral lobes are raised and the edge of the cranidium is turned up along the preocular and postocular sutures (Pl. 25, fig. 17) so that the free cheek may have been raised above the level of the fixed cheek. These upturned edges make the course of the sutures especially clear, even in shale-preserved specimens.

The cephalic fragments from Merevale No. 3 Borehole have a tapering glabella (1·0 to 1·4 mm long), and an occipital tubercle, but differ from *S. spinulosa* Lazarenko in having no other glabellar tubercles. The anterior glabellar lobe lacks the median ridge shown by *S. gostinensis* Jago. The pleural tips on the figured pygidial fragment seem slightly more pointed than in Westergård's figured specimen, an external mould of a small individual.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, the cephalic fragments at a depth of 277 ft 0 in. (84·43 m) and the figured pygidium at 374 ft 6 in. (114·15 m); lamprophyre sills are intruded between these two horizons and their corrected stratigraphical separation is estimated to be about 10 m. In Sweden *S. amphionura* occurs at the base of the *pisiformis* Zone (Westergård 1948, p. 3).

Schmalenseeia cf. *spinulosa* Lazarenko, 1960

Plate 25, fig. 16

cf. 1960 *Schmalenseeia spinulosa* sp. nov.; Lazarenko, p. 253, pl. 53, fig. 18.
1972 *Schmalenseeia* cf. *amphionura* Moberg; Taylor and Rushton, p. 18, pl. 4 [*pars*] [borehole record].

Material. A flattened cranidium 1·7 mm long (BDA 1890–1891) and several fragments, chiefly thoracic segments (BDA 1886A, 1887A–D, 1888–1889).

Remarks. *S. spinulosa* is distinguished especially by the median tubercles or spines on the glabella; Dr. J. B. Jago kindly lent me an enlarged photograph of the holotype of *S. spinulosa* which shows a tubercle and a trace of a longitudinal median ridge on the anterior glabellar lobe (L4). Each of L3, L2, and L1 are drawn up to form tubercles, and are also drawn backwards, so that in the case of L1 the tubercle lies opposite the occipital furrow. The cranidium figured here has tubercles opposite the occipital furrow, at the posterior edge of L2, and possibly a small one on L3 but one cannot be sure because the exoskeleton is crumpled there. The figured cranidium shows a thin longitudinal ridge on L4 continuous with the preglabellar ridge; this is probably an original feature but it is slightly irregular and it appears to have been accentuated by crumpling. No median node can be distinguished on L4 on this specimen but a fragmentary glabella on the same slab has a weak median node on L4 and shows the preglabellar ridge extending back on to L4 and quickly dying out without reaching the node. Apart from possible differences in the development of the glabellar tubercles the present form differs slightly from *S. spinulosa* because the preglabellar field is a little shorter (0·30 of the cranidial length compared with nearly 0·35 in *S. spinulosa*) and the anterior glabellar lobe is a little larger; but as the holotype of *S. spinulosa* is a larger specimen (cranidium 2·7 mm long) the importance of these differences is uncertain.

The proportions of the present cranidium agree closely with those of *S. amphionura* but the latter species has no glabellar spines (other than an occipital spine).

The clearest distinction of *S. gostinensis* Jago (1972) from the form figured here is the absence of a spine or tubercle on L2, but the sigmoidal curvature of the pleuroccipital furrow and the strong longitudinal ridge on L4 (Jago 1972, pl. 44, figs. 19–21) may also represent original differences. Judging from Jago's figures the cephalic axis is less than one-fifth of the cranidial width (not one-third as given by Jago on p. 234), narrower than that of *S. spinulosa* which is about one-quarter of the cranidial width. The glabella of *S. gostinensis* appears also to taper less strongly forwards but this may be because the specimens are comparatively small (the glabella of *S. amphionura* tends to taper less strongly in smaller specimens).

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, at depth 485 ft 0 in. (147·83 m). *S. spinulosa* was described from the *pisiformis* Zone of the middle reaches of the River Olenek, on the North Siberian Platform.

Family CERATOPYGIDAE Linnarsson, 1869
Proceratopyge Wallerius, 1895
Proceratopyge nathorsti Westergård, 1922

Plate 26, fig. 4; text-fig. 3*b*

1922 *Proceratopyge nathorsti* n. sp.; Westergård, p. 120, pl. 2, figs. 3–5.
1947 *Proceratopyge nathorsti* Westergård; Westergård, p. 10, pl. 2, figs. 2–7.
1958 *Proceratopyge nathorsti* Westergård 1922; Henningsmoen, p. 186, pl. 7, figs. 2, 3 [further synonymy].
1972 *Proceratopyge nathorsti* Westergård; Taylor and Rushton, p. 15, text-fig. 4 [recorded].

Material. A fragmentary cranidium with a tapered glabella and with some thoracic segments, RU 132; a small fragmentary pygidium, RU 122.

Remarks. The fragments illustrated here are distinguished from *P. conifrons* Wallerius (Westergård 1947, pl. 1, figs. 7–16) because the glabellar furrows are weaker and the pygidium is less transverse. *P. similis* Westergård (1947, pl. 2, fig. 1) has more nearly triangular postocular cheeks whereas those of *P. tullbergi* Westergård (1947, pl. 2, fig. 8) are more transverse ('strap-like'). *P. liaotungensis* Kobayashi and Ichikawa (1955) has no glabellar node and the occipital ring is thickened medially. *P. nectans* Whitehouse 1939 (see Henderson 1976) appears to have weaker glabellar furrows. No comparison is made with the many species of *Proceratopyge* which have a long pygidium or a parallel-sided glabella.

Occurrence. Outwoods Formation, *pisiformis* Zone, and possibly basal *Olenus* Zone, just below the lowest *Olenus* at Purley Quarry (Taylor and Rushton 1972, text-fig. 4, p. 15). *A. pisiformis* Zone and possibly base of *Olenus* Zone in Sweden. *A. pisiformis* Zone in Oslo district, Norway. *A. pisiformis–Homagnostus fecundus* Zone, River Lena, Siberia (Ivshin and Pokrovskaya 1968, p. 98).

CRUSTACEA
Order BRADORIIDA Raymond, 1935

This group of ostracod-like crustaceans has been studied recently by Fleming (1973) and Kozur (1974) who cite earlier work on the group. Kozur regarded the Bradoriida as forerunners of the Ostracoda, and stated that most of the Phosphatocopina of Müller (1964) cannot be distinguished from the Bradoriida; however, the genus *Hesslandona* Müller, 1964, which has a median dorsal plate (somewhat like the phyllocarid *Rhinocaris*), was excluded from the Ostracoda. Müller (1975, p. 178) has contested the basis of Kozur's conclusions. The shale-preserved material from the Nuneaton district yields no evidence contributory to this debate, but Kozur's classification is followed here for the present.

Superfamily BRADORIACEA Matthew, 1902
Family BRADORIIDAE Matthew, 1902
Bradoria Matthew, 1899
Bradoria sp.

Plate 26, figs. 13, 14

Material. Two figured valves, BDA 1192 and 1826, are assigned to *Bradoria* but some juvenile specimens may also belong here.

Description. Valves convex, without definitely distinguishable nodes. Dorsal margin straight, four-fifths of greatest length of valve. Cardinal angles obtuse. Anterior, ventral, and posterior margins form an unbroken curve, curvature strongest just below anterodorsal angle. Greatest height is three-quarters of the length and is placed at or just behind the mid-length. No marginal rim. Surface smooth.

Remarks. This form of *Bradoria* has a nearly symmetrical outline and the ocular node is absent or inconspicuous; it thus differs from most species but may be compared with *B. cambrica* (Matthew) (Ulrich and Bassler 1931, pl. 3, fig. 15) which is a little higher and has a punctate surface. *B. hicksii* (Jones) is a little longer and has more rounded cardinal angles. Andres (1969, p. 175) figured a similar but less symmetrical *Bradoria* sp. from the middle Middle Cambrian of Sweden.

Occurrence. Outwoods Formation, near the base and top of the *pisiformis* Zone, Merevale No. 3 Borehole, depths 466 ft 8 in. (142·24 m) and 221 ft 2 in. (67·41 m).

Walcottella Ulrich and Bassler, 1931
Walcottella sp.

Plate 26, figs. 6, 7

Material. Two specimens, BDA 1788 and 1825, are assigned to *Walcottella* but some juvenile and poorly preserved specimens may also belong here.

Description. Dorsal edge straight, four-fifths of greatest length of valve. Cardinal angles obtuse. Anterior, ventral, and posterior margins form a smooth curve. Greatest height nearly three-quarters of greatest length and placed just behind the mid-length. A strong tubercle is placed at the mid-length but well below the mid-height. Surface smooth.

Remarks. Of the thirteen species of *Walcottella* described by Ulrich and Bassler (1931) the present specimens most resemble *W. concentrica* which is a short species with the median tubercle subcentrally placed. It differs from this and all the other species because the surface is not punctate or reticulate (despite the preservation in shale, such detail should be visible if it was present originally).

Occurrence. Rare in the Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depths 466 ft 2 in. (142·09 m) and 448 ft 10 in. (136·80 m). All Ulrich and Bassler's species are from the Bright Angel Shale (Middle Cambrian) of Bass Canyon, Arizona, U.S.A.

Genus FALITES Müller, 1964
Falites fala Müller, 1964

Plate 26, fig. 12

1964 *Falites fala* n. sp.; Müller, p. 25, pl. 3, figs. 3–10; pl. 5, fig. 6.
1972 *Falites* sp.; Taylor and Rushton, p. 13.

Material. The description is based on a flattened left valve 1·85 mm long, BDA 1820. A few isolated valves are referred to this species (BDA 1824, 1844, 1855, 1863) but numerous imperfect valves may represent this or another species.

Description. Outline more than a semicircle. Dorsal edge straight, about five-sixths of maximum length. Anterodorsal angle a little more than 90°; posterodorsal angle very obtuse. Anterior, ventral, and posterior margins form a smooth curve. Greatest height at the mid-length, about three-quarters of the maximum length; the height is slightly less than the length of the hinge and lies at about its posterior one-third. Weakly marked border, narrow anteriorly, widening to nearly one-fifth of the total height ventrally and narrowing slightly posteriorly. One distinct node, just below hinge, at one-quarter of the length from the anterior end. No other nodes visible.

Remarks. This specimen agrees with Müller's description and figures (especially his pl. 3, fig. 6) but the anterior node seems to lie a little higher and further back. There is no trace of the two fainter nodes seen below the middle and posterior of the dorsal margin in some specimens (Müller 1964, pl. 5, fig. 6). The marginal rim on the present material is accentuated, probably because it reflects the edge of the duplicature.

Compared with *F. fala*, *F. angustiduplicatus* Müller has a narrower duplicature (narrower than one-tenth of the maximum height) and the posterodorsal angle is hardly more obtuse than the anterodorsal angle. *F. cycloides* Müller is slightly shorter, the height being four-fifths of the length, and the dorsal margin is about equal to the height. *F.*? *minimus* is discussed below.

Occurrence. In the Nuneaton district *F. fala* is rare in the Outwoods Formation, *pisiformis* Zone (481 ft 6 in. (146·76 m) to 464 ft 6 in. (141·58 m) in Merevale No. 3 Borehole) and occurs also rarely in the Monks Park Formation, between the *Leptoplastus angustatus* Subzone and *Ctenopyge postcurrens* Subzone (Taylor and Rushton 1972, pp. 25, 29, 30). Müller (1964, p. 37) recorded *F. fala* from the *pisiformis* Zone and the *Peltura* zones in Sweden.

Falites? *minimus* (Kummerow, 1931)

Plate 26, figs. 9, 10

1928 *Aristozoe*? cf. *primordialis* Linnss sp.; Kummerow, p. 42, pl. 2, fig. 19.
1931 *Aristozoe*? *minima* n. sp.; Kummerow, p. 255, fig. 18.
1964 *Falites*(?) *minima* (Kummerow, 1931); Müller, p. 29, pl. 4, figs. 8–12, 16.
1972 *Falites*? *minimus* (Kummerow); Taylor and Rushton, p. 13, pl. 4 [borehole record].

Material. Of four flattened valves, BDA 1167–1168, 1276–1277, 1452–1453, 1771, and 1774 (counterparts), two left valves are figured.

Description. Outline horseshoe shaped, nearly symmetrical about a dorsal to ventral line, height about seven-eighths of length; dorsal edge three-quarters of total length, and six-sevenths of the height. Anterior, ventral, and posterior margins make an even curve, slightly trapezoidal in aspect. Antero- and posterodorsal angles nearly equal, both a little over 90°. Node below dorsal margin, just forward of the mid-length. Flattened marginal zone indistinct, but suggestive of a duplicature of width about one-fifth of the total height. BDA 1452 is 0·78 mm long and 0·71 mm high; BDA 1167 is 0·82 mm long and 0·68 mm high.

Remarks. This form is distinguished from *F. fala* and *F. angustiduplicatus* by the relatively high valves. *F. cycloides* has high valves but the shape is generally less symmetrical and the anterior node is further forward.

Occurrence. In the Nuneaton district confined to the *pisiformis* Zone, in the Outwoods Formation, Merevale No. 3 Borehole, depths 446 ft 0 in. (135·94 m) to 208 ft 7 in. (63·58 m). Müller recorded this species from the *pisiformis*, *Olenus*, and *Peltura minor* zones in Sweden.

Superfamily HIPPONICHARIONACEA Sylvester-Bradley, 1961
Family HIPPONICHARIONIDAE Sylvester-Bradley, 1961
Cyclotron Rushton, 1969
Cyclotron sp.

Plate 26, fig. 15

1972 *Cyclotron* aff. *angelini* (Barrande); Taylor and Rushton, p. 18, pl. 4 [distribution].

Material. A large but slightly crumpled left valve, 6·3 mm long and 3·4 mm high (BDA 1408–1409); also a right valve and a fragmentary specimen (BDA 1254, 1261).

Remarks. The large undivided swelling low in the middle of the valve distinguishes the present form from *C. lapworthi* (Groom, 1902, p. 84, pl. 3) and *C. marginatum* (Ulrich and Bassler, 1931, pl. 8, figs. 28, 29). *C. angelini* (Barrande) has sharper cardinal angles and the node at the posterodorsal corner is weaker (Westergård 1947, pl. 1, fig. 15); the node low down in front is rounded in *C. angelini*, not elongated towards the anterodorsal corner as in the present form. *C. nodomarginatum* Schrank (1973, pl. 3, fig. 2) differs in having large posteroventral nodes projecting beyond the free margin: although the figured specimen is not well preserved in this region it seems improbable that it had such nodes originally.

Occurrence. Rare in the Outwoods Formation, upper part of the *pisiformis* Zone, Merevale No. 3 Borehole, depths 270 ft 6 in. (82·45 m), 252 ft 6 in. (76·96 m), and 252 ft 4 in. (76·91 m).

Family BEYRICHONIDAE Ulrich and Bassler, 1931
Svealuta Öpik, 1961
Svealuta primordialis (Linnarsson, 1869)

Plate 26, fig. 8

1869 *Leperditia primordialis* n. sp.; Linnarsson, p. 84, pl. 2, figs. 65, 66.
1931 *Aluta primordialis* (Linnarsson); Ulrich and Bassler, p. 59, pl. 8, figs. 11, 12 [synonymy].
1944 *Aluta primordialis* (Linnarsson); Westergård, p. 33 [distribution in Scanian borings].
1961 *Svealuta primordialis* (Linnarsson); Öpik, p. 174, text-fig. 58.
1972 *Svealuta primordialis* (Linnarsson); Taylor and Rushton, p. 8, pl. 4 [borehole record].

Material. The internal mould of a crushed right valve with scraps of the exoskeleton remaining (BDA 2313) is figured. Two further fragmentary left valves (BDA 2394, 2395).

Description (after Linnarsson). Equivalved, strongly convex, oblong, very broad in the middle; border depressed, obsolescent anterodorsally. Dorsal margin straight, occupying three-quarters of the length, making an angle with the posterior margin; evenly curved ventrally, confluent without angulation anteriorly. Each valve divided by indistinct grooves into three swollen parts, the posterior one large and ovate, the anterior ones small, the upper one subtriangular, the lower one globose, inflated, projecting beyond the margin. Ocular tubercle undifferentiated. Exterior of valve may either be smooth or finely granulated. Length 8 mm, height 5 mm.

Remarks. The specimen figured here is 8·2 mm long and 6·2 mm high; this is proportionally higher than Linnarsson's figured specimen, partly because it is 'spread' by crushing and partly because the anteriorly projecting node is broken off, reducing the length. The upper of the anterior nodes is one-third of the length and one-third of the height of the valve. The groove marking it off passes into the dorsal border furrow. The dorsal margin is three times as long as the short posterodorsal margin. Ventrally the width of the border is less than one-tenth of the height of the valve. The main body is rounded posteriorly as in Linnarsson's figure, not angulate as in Öpik's reconstruction (1961) and also the elongated valve of *S.* cf. *primordialis* (Öpik 1967, pl. 2, fig. 2).

Occurrence. In Britain, known only from the lower part of the Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole, 700 ft 0 in. (213·36 m) and 639 ft 2 in. (194·82 m). In Sweden *S. primordialis* is recorded from the *laevigata* Zone in Scania (Westergård 1944, p. 33; 1946, p. 11) and Västergötland (Wallerius 1930, p. 50). Öpik (1961, p. 175) stated that it also occurs abundantly in the *Solenopleura brachymetopa* Zone, but gave no bibliographic reference to such a record.

CRUSTACEA INCERTAE SEDIS

Hesslandona Müller, 1964

Remarks. Hesslandona is characterized by a dorsal median plate with a hinge along both its edges—a structure distinct from all ostracods but comparable with the ephippia of Cladocera (Adamczak 1965). *Hesslandona* was excluded from the Bradoriida by Kozur (1974).

Hesslandona trituberculata (Lochman and Hu, 1960)

Plate 26, fig. 11

1960 *Dielymella? trituberculata*, n. sp.; Lochman and Hu, p. 826, pl. 98, fig. 56.
1972 *Vestrogothia* sp.; Taylor and Rushton, p. 18 [*pars*].

Material. Four right valves and one left valve (BDA 1476, 1479, 1782, 1785, 1817). Several poorly preserved and juvenile valves may also be referable to this species.

Description. Height about half the length, greatest height just anterior to the mid-length. Dorsal edge straight. Anterior cardinal angle about 80°. Anterior and ventral margins evenly curved, lowest point of venter may be more sharply curved. Posteroventral margin nearly straight, posterior truncated obliquely downwards and forwards. Middle of valve slightly swollen, posterior end nearly flat. There are three low knobs at about one-fifth of the total height below the hinge-line, at one-fifth, two-fifths, and four-fifths of the total length from the front. Surface smooth. The smallest specimen (1·43 mm long) is proportionally slightly less high. One specimen (BDA 1814) and a few of the immature specimens show the median plate but do not show spines coming off this plate.

Remarks. In the present specimens the three knobs lie on a straight line as in *H. trituberculata* but not as in *H. necopina* (Müller 1964, pl. 1, fig. 2). The outline is more elongated than in *H. kinnekullensis* Müller.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depths 464 ft 6 in. (141·58 m) to 281 ft 10 in. (85·90 m). The holotype is from the Du Noir Limestone (early Upper Cambrian, *Cedaria* Zone) of the Sheep Mountain Section, Wyoming (Lochman and Hu 1960).

MOLLUSCA

Class HYOLITHA Marek, 1963

Order HYOLITHIDA Matthew, 1899

Hyolithid gen. et sp. undetermined

Plate 26, figs. 16, 17

Remarks. Of the hyolithids present those from the top of the *pisiformis* Zone at Purley Quarry (Nos. RU 2212–2216, 2218–2240) are best preserved. The conchs are flattened, so the cross-section and details of the lateral edges are unknown. The apical angle (as preserved) is 20° and the surface is marked only by growth lines which show a rounded ventral edge and transverse dorsal edge (Pl. 26, fig. 16). The opercula show a conical shield (Marek 1963, text-figs. 1, 2) with one pair of clavicles, but the cardinal shield is too poorly preserved for details other than a trace of the paired cardinal processes to be made out. Long curved appendages ('helens', Runnegar *et al.* 1975) are associated but show little detail apart from faint longitudinal (but not transverse) striae. The preservation is insufficient for the species or genus to be determined but the form appears to be related to the family Hyolithidae.

Acknowledgements. I thank Mr. K. Taylor for his care and assiduity in examining the cores and collecting fossils. I also thank Dr. D. Bruton, Messrs. F. J. Collier and J. Miller, Mr. L. Liljedahl, Mr. S. F. Morris, Drs. V. Jaanusson, L. Karis, R. B. Rickards, and I. Strachan for loaning specimens in their care, and Drs. B. Daily, R. A. Fortey, J. Jago, L. Karis, Professor A. R. Palmer, Professor R. A. Robison, Sir James Stubblefield, and Dr. J. T. Temple, whose help and suggestions have been of great value. This paper is published by permission of the Director, Institute of Geological Sciences.

REFERENCES

ADAMCZACK, F. 1965. On some Cambrian bivalved Crustacea and egg cases of the Cladocera. *Acta Univ. Stockh., Stockh. Contrib. Geol.* **13** (3), 27–34, 2 pls.

ANDRES, D. 1969. Ostracoden aus dem mittleren Kambrium von Öland. *Lethaia,* **2,** 165–180.

BOROVIKOV, L. T. and KRYSKOV, L. N. 1963. Cambrian deposits in the Kendyctas Mountains (south Kazakhstan). *Trudȳ vses nauchno-issled geol. Inst.* (*VSEGEI*) N.S. **94,** 266–280, pl. 1. Leningrad. [In Russian.]

BRADLEY, J. H. 1925. Trilobites of the Beekmantown in the Philipsburg region of Quebec. *Can. Fld Nat.* **39,** 5–9, fig.

BRÖGGER, W. C. 1878. Om Paradoxidesskifrene ved Krekling. *Nyt Mag. Naturvid.* **24,** 18–88, pls. 1–6.

BRONGNIART, A. 1822. Les Trilobites, pp. 1–65, pls. 1–4. *In* BRONGNIART, A. and DESMAREST, A.-G. *Histoire Naturelle des Crustacés Fossiles.* 154 pp., 11 pls. Paris.

BUTTS, C. 1926. *In* ADAMS, G. I. *et al.* Geology of Alabama. *Geol. Surv. Alabama,* Spec. Rep. No. 14, 312 pp. Univ. Alabama.

CHU, CHAO-LING. 1959. Trilobites from the Kushan Formation of North and Northeastern China. *Mem. Inst. Palaeont. Acad. Sinica,* **2,** 81–128, pls. 1–7.

COOK, H. E. and TAYLOR, M. E. 1975. Early Paleozoic continental margin sedimentation, trilobite biofacies, and the thermocline, western United States. *Geology,* **3,** 559–562.

DAILY, B. and JAGO, J. B. 1975. The trilobite *Lejopyge* Hawle and Corda and the Middle–Upper Cambrian boundary. *Palaeontology,* **18,** 527–550, pls. 62–63.

DALMAN, J. W. 1828. Om Palaeaderna, eller de så kallade Trilobiterna. *K. svenska Vetensk-Akad. Handl.* [for 1826], 113–152, 226–294, pls. 1–6.

DATSENKO, V. A. *et al.* 1968. Biostratigraphy and faunas of the Cambrian deposits of the north west part of the Siberian Platform, *Trudy nauchno-issled. Inst. Geol. Arkt.* (*NIIGA*), **155,** 213 pp., 23 pls. (text), 44 pp. (atlas). [In Russian.]

FLEMING, P. J. G. 1973. Bradoriids from the *Xystridura* Zone of the Georgina Basin, Queensland. *Publ. Queensl. Dep. Mines*, No. 356, *Palaeont. Pap.* No. 31, 9 pp., 4 pls.

FORTEY, R. A. 1975. Early Ordovician trilobite communities. *Fossils Strata*, **4**, 339–352.

—— and RUSHTON, A. W. A. 1976. Chelidonocephalus trilobite fauna from the Cambrian of Iran. *Bull. Br. Mus. nat. Hist.* (Geol.), **27**, 321–340, pls. 8–12.

GROOM, T. T. 1902. On *Polyphyma*, a new genus belonging to the Leperditiadae from the Cambrian shales of Malvern. *Quart. Jl geol. Soc. Lond.* **58**, 83–88, pl. 3.

HAWLE, I. and CORDA, A. J. C. 1847. *Prodrom einer Monographie der böhmischen Trilobiten.* 176 pp., 7 pls. Prague.

HENDERSON, R. A. 1976. Upper Cambrian (Idamean) trilobites from western Queensland, Australia. *Palaeontology*, **19**, 325–364, pls. 47–51.

HENNINGSMOEN, G. 1957. The trilobite family Olenidae. *Skr. Norske Vidensk.-Akad., Mat.-naturv. Kl.* **1**, 303 pp., 31 pls.

—— 1958. The Upper Cambrian faunas of Norway with descriptions of non-Olenid invertebrate fossils. *Norsk geol. Tidsskr.* **38**, 179–196, pls. 1–7.

—— 1975. Moulting in trilobites. *Fossils and Strata*, **4**, 179–200.

HOLM, G. and WESTERGÅRD, A. H. 1930. A Middle Cambrian fauna from Bennett Island. *Zap. Akad. Nauk S.S.S.R.* (8), **21**, (8), 25 pp., 4 pls.

HOWELL, B. F. 1935*a*. New Middle Cambrian agnostian trilobites from Vermont. *J. Paleont.* **9**, 218–221, pl. 22.

—— 1935*b*. Cambrian and Ordovician trilobites from Hérault, southern France. Ibid. 222–238, pls. 22, 23.

—— 1935*c*. Some New Brunswick Cambrian Agnostians. *Bull. Wagner Free Inst. Sci.* **10**, 13–15, 1 pl.

—— 1937. Cambrian *Centropleura vermontensis* fauna of northwestern Vermont. *Bull. geol. Soc. Am.* **48**, 1147–1210, 6 pls.

—— 1955. *Phalagnostus*, new genus for trilobite *Battus nudus* Beyrich. *J. Paleont.* **29**, 925–926.

HUTCHINSON, R. D. 1962. Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. *Bull. geol. Surv. Can.* **88**, 156 pp., 25 pls.

IVSHIN, N. K. and POKROVSKAYA, N. V. 1968. Stage and Zonal subdivision of the Upper Cambrian. *23rd Int. geol. Congr., Proc.* sec. 9, 97–108.

JAEKEL, O. 1909. Uber die Agnostiden. *Z. dt. geol. Gesell.* **61**, 380–401.

JAGO, J. B. 1972. Two new Cambrian trilobites from Tasmania. *Palaeontology*, **15**, 226–237, pl. 44.

—— 1976. Late Middle Cambrian agnostid trilobites from north-western Tasmania. Ibid. **19**, 133–172, pls. 21–26.

KOBAYASHI, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology. Part III. The Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. *J. Fac. Sci. Univ. Tokyo*, sec. II, **4**, 49–344, 24 pls.

—— 1937. The Cambro-Ordovician shelly faunas of South America. Ibid. **4**, 369–522, pls. 1–8.

—— 1939. On the Agnostids (Part 1). Ibid. **5**, 69–198, table.

—— 1960. The Cambro-Ordovician formation and faunas of South Korea, part VII, Palaeontology VI. Ibid. **12**, 329–420, pls. 19–21.

—— 1962. Idem, part VIII, Palaeontology VII. Ibid. **14**, 1–152, pls. 1–12.

—— and ICHIKAWA, T. 1955. Discovery of *Proceratopyge* in the *Chuangia* Zone in Manchuria, with a note on the Ceratopygidae. *Trans. Proc. Palaeont. Soc. Japan*, N.S. (19), 65–72, pl. 11.

KOZUR, H. 1974. Die Bedeutung der Bradoriida als Vorläufer der post-Kambrischen Ostracoden. *Z. geol. Wiss.* **2**, 823–830.

KUMMEROW, E. 1928. Beiträge zur Kenntnis der Fauna und der Herkunft der Diluvialgeschiebe. *Jb. Preuss. geol. Landesanst.* **48**, 1–59, pls. 1, 2.

—— 1931. Über die Unterschiede zwichen Phyllocariden und Ostracoden. *Cbl. Miner. Geol. Paläont.* 1931, Abt. B, 242–257.

LAZARENKO, N. P. 1960. *In* KRYSKOV, L. N. *et al.*, pp. 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.]

—— and NIKIFOROV, N. I. 1968. Assemblages of trilobites from Upper Cambrian strata on the River Kulyumbe (north-western Siberian Platform). *Uch. Zap. nauchno-issled. Inst. Geol. Arkt., Paleont. Biostrat.* **23**, 20–80, pls. 1–15. [In Russian.]

LERMONTOVA, E. V. 1951. *Upper Cambrian trilobites and brachiopods from Boshche-Kulya (North-east Kazakhstan)*. Moscow. [In Russian.]

LINNAEUS, C. 1757. *Skanska resa* [= *Iter. scan.*]. Stockholm. [Not seen.]

—— 1758. *Systema naturae*, 10th edition, vol. 1, 823 pp. Holmiae.

—— 1759. Petrificatet Entomolithus paradoxus. *K. Svenska Vidensk.-Akad. Handl.* for 1759, 19–24, pl. 1.

—— 1768. *Systema naturae*, 12th edition, vol. 3, 236 pp. Holmiae.

LINNARSSON, J. G. O. 1869. Om Vestergötlands Cambriska och Siluriska aflagringar. *K. svenska Vetensk-Akad. Handl.* **8** (2), 1–89, pls. 1, 2.

LOCHMAN, C. and DUNCAN, D. 1944. Early Upper Cambrian faunas of Central Montana. *Spec. Pap. Geol. Soc. Amer.* **54,** 181 pp., 19 pls.

—— and HU, C.-H. 1960. Upper Cambrian faunas from the north-west Wind River Mountains, Wyoming. Part 1. *J. Palaeont.* **34,** 793–834, pls. 95–100.

LU, YEN-HAO. 1974. Bioenvironmental Control Hypothesis and its application to the Cambrian biostratigraphy and palaeozoogeography. *Mem. Nanking Inst. Geol. Palaeont.* **5,** 27–116, 4 pls. [In Chinese.]

MANSUY, H. 1915. Faunas cambriennes du Haut-Tonkin. *Mém. Serv. géol. Indochine*, **4** (2), 35 pp., 3 pls.

MAREK, L. 1963. New knowledge on the morphology of Hyolithes. *Sb. geol. Ved, Paleont.* **1,** 53–72, pls. 1–4.

MARTINSSON, A. 1974. *The Cambrian of Norden*, pp. 185–283. *In* C. H. HOLLAND (ed.). *Cambrian of the British Isles, Norden, and Spitsbergen.* J. Wiley: London, New York, Sidney, Toronto.

MATTHEW, G. F. 1899. Preliminary notice of the Etcheminian fauna of Cape Breton. *Bull. nat. Hist. Soc. New Brunswick*, **4,** 198–208, 4 pls.

—— 1902. Ostracoda of the basal Cambrian rocks in Cape Breton. *Can. Rec. Sci.* **8,** 437–470, 2 pls.

McCOY, F. 1849. On the classification of some British fossil Crustacea, with notices of new forms in the University collection at Cambridge. *Ann. Mag. nat. Hist.* (2), **4,** 161–179, 330–335, 392–414. [Trilobites discussed in the last section.]

MOBERG, J. C. 1903. Schmalenseeia amphionura, en ny trilobit-typ. *Geol. Fören. Stockh. Förh*, **25,** 93–102, pl. 4.

MOORE, R. C. (ed.). 1959. *Treatise on invertebrate paleontology. Part O, Arthropoda* 1. xix + 560 pp. Geol. Soc. Amer. and Univ. Kansas Press.

MÜLLER, K. J. 1964. Ostracoda (Bradorina) mit phosphatischen Gehäusen aus dem Oberkambrium von Schweden. *Neues. Jb. Geol. Paläont. Abh.* **121,** 1–46, pls. 1–5.

—— 1975. '*Heraultia*' *varensalensis* Cobbold (Crustacea) aus dem Unteren Kambrium, der ältest Fall von Geschlechtsdimorphismus. *Paläont. Z.* **49,** 168–180, pl. 19.

ÖPIK, A. A. 1961. The geology and palaeontology of the headwaters of the Burke River, Queensland. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **53,** 249 pp., 24 pls.

—— 1963. Early Upper Cambrian fossils from Queensland. Ibid. **64,** 133 pp., 9 pls.

—— 1967. The Mindyallan fauna of northwestern Queensland. Ibid. **74,** vol. 1, 404 pp., vol. 2, 167 pp., 67 pls.

PALMER, A. R. 1954. The faunas of the Riley Formation in central Texas. *J. Paleont.* **28,** 709–786, pls. 76–92.

—— 1960. Trilobites of the Upper Cambrian Dunderberg Shale, Eureka District, Nevada. *Prof. Pap. U.S. geol. Surv.* **334-C,** 53–109, pls. 4–11.

—— 1962. *Glyptagnostus* and associated trilobites in the United States. Ibid. **374-F,** 49 pp., 6 pls.

—— 1968. Cambrian trilobites of east-central Alaska. Ibid. **559-B,** 115 pp., 15 pls.

—— 1972. Problems of Cambrian biogeography. *24th Int. geol. Congr., Proc.* sec. 7, 310–315.

POKROVSKAYA, N. V. 1958. Agnostidae from the Middle Cambrian of Yakutia: Part 1. *Trudy geol. Inst.* **16,** 96 pp., 5 pls. [In Russian.]

POLETAEVA, O. K. and ROMANENKO, YE. V. 1970. Middle and Late Cambrian trilobites of the Altay. *Paleont. Zh.* for 1970, (2), 72–83, pls. 10, 11. [Translation in *Paleont. J.* **4** (2), 216–228, pls. 10, 11.]

POULSEN, C. 1960. Fossils from the late Middle Cambrian Bolaspidella Zone of Mendoza, Argentina. *Mat. fys. Medd. Dan. Vid. Selsk.* **32** (11), 42 pp., 3 pls.

POULSEN, V. and ANDERSON, M. M. 1975. The Middle–Upper Cambrian transition in southeastern Newfoundland, Canada. *Can. J. Earth Sci.* **12,** 2065–2079, pls. 1, 2.

RASETTI, F. 1963. Middle Cambrian ptychoparioid trilobites from the conglomerates of Quebec. *J. Paleont.* **37,** 575–594, pls. 66–70.

—— 1965. Upper Cambrian trilobite faunas of northeastern Tennessee. *Smithson. misc. Collns*, **148** (3), 127 pp., 21 pls.

—— 1967. Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. Ibid. **152** (4), 111 pp., 14 pls.

RAYMOND, P. E. 1913. A revision of the species which have been referred to the genus Bathyurus. *Bull. Victoria Mem. Mus., geol. Surv. Can.* **1**, 51–79, pls. 3–7.

—— 1935. Leanchoilia and other Mid-Cambrian Arthropoda. *Bull. Mus. comp. Zool. Harvard*, **76** (6), 203–230.

RESSER, C. E. 1938. Cambrian System (restricted) of the Southern Appalachians. *Spec. Pap. Geol. Soc. Amer.* **15**, 140 pp., 15 pls.

—— and ENDO, R. 1937. *In* ENDO, R. and RESSER, C. E. The Sinian and Cambrian formations and fossils of Southern Manchoukuo. *Bull. Manchurian Sci. Mus.* **1**, 474 pp., 73 pls.

ROBISON, R. A. 1964. Late Middle Cambrian faunas from Western Utah. *J. Paleont.* **38**, 510–566, pls. 79–92.

—— 1972. Mode of life of Agnostid trilobites. *24th Int. geol. Congr., Proc.* sec. 7, 33–40.

RUNNEGAR, B., *et al.* 1975. Biology of the Hyolitha. *Lethaia*, **8**, 181–192.

RUSHTON, A. W. A. 1969. *Cyclotron*, a new name for *Polyphyma* Groom. *Geol. Mag.* **106**, 216–217.

—— 1976. In *Ann. Rep. Inst. geol. Sci.* for 1975, p. 115.

SCHRANK, E. 1973. Fauna und Kontakt Mittelkambrium/Oberkambrium in einem Geschiebe. *Z. geol. Wiss.* **1**, 85–99, pls. 1–3.

SDZUY, K. 1967. Trilobites del Cambrico medio de Asturias. *Trabajos Geol., Fac. Cienc., Univ. Oviedo*, **1**, 77–133, 10 pls.

ŠNAJDR, M. 1958. Trilobiti českého středniho kambria. *Rozpr ústred. Úst. geol.* **24**, 280 pp., 46 pls. [In Czech. English summary, pp. 237–280.]

SYLVESTER-BRADLEY, P. C. 1961. Archaeocopida, pp. 100–103. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part Q, Arthropoda 3.* xxiii + 442 pp. Geol. Soc. Amer. and Univ. Kansas Press.

TAYLOR, K. and RUSHTON, A. W. A. 1972 [dated 1971]. The pre-Westphalian geology of the Warwickshire Coalfield, with an account of three boreholes in the Merevale area. *Bull. geol. Surv. Gt Br.* **35**, 152 pp., 12 pls.

TJERNVIK, T. E. 1956. On the early Ordovician of Sweden. Stratigraphy and Fauna. *Bull. geol. Instn Upsala*, **36**, 107–284, pls. 1–11.

ULRICH, E. O. and BASSLER, R. S. 1931. Cambrian bivalved Crustacea of the order Conchostraca. *Proc. U.S. Natn. Mus.* **78**, Art. 4, 130 pp., 10 pls.

WAHLENBERG, G. 1818. Petrificata Telluris Svecanae. *Nova Acta R. Soc. Sci. Upsala.* **8**, 1–116, pls. 1–4.

WALCOTT, C. D. 1908. Cambrian geology and paleontology, No. 2, Cambrian trilobites. *Smithson. misc. Collns*, **53**, 13–52, pls. 1–6.

—— 1913. *The Cambrian faunas of China*, pp. 1–276, pls. 1–24. *In* WILLIS, B. *et al. Research in China*, vol. 3, Carnegie Inst., Washington, publ. 54.

—— 1924*a*. Cambrian geology and palaeontology, V, No. 2, Cambrian and Lower Ozarkian trilobites. *Smithson. misc. Collns*, **75**, 53–60, pls. 9–14.

—— 1924*b*. Idem, No. 3, Cambrian and Ozarkian trilobites. Ibid. 61–146, pls. 15–24.

WALLERIUS, I. D. 1895. *Undersökningar öfver zonen med* Agnostus laevigatus *i Vestergötland*. Lund. [Not seen.]

—— 1930. Fran Västergötlands mallankambrium. *Geol. Fören. Stockh. Förhandl.* **52**, 47–62.

WESTERGÅRD, A. H. 1922. Sveriges Olenidskiffer. *Sver. geol. Unders. Avh.* Ser Ca, **18**, 205 pp., 16 pls.

—— 1944. Borrnigar genom Skånes alunskiffer. Ibid. Ser. C, **459**, 45 pp., 6 pls.

—— 1946. Agnostidea of the Middle Cambrian of Sweden. Ibid. **477**, 140 pp., 16 pls.

—— 1947. Supplementary notes on the Upper Cambrian trilobites of Sweden. Ibid. **489**, 34 pp., 3 pls.

—— 1948. Non-Agnostidean trilobites of the Middle Cambrian of Sweden. I. Ibid. **498**, 32 pp., 4 pls.

—— 1953. Idem III. Ibid. **526**, 58 pp., 8 pls.

WHITEHOUSE, F. W. 1936. The Cambrian faunas of north-eastern Australia. Parts 1 and 2. *Mem. Queensland Mus.* **11**, 59–112, pls. 8–10.

—— 1939. Idem, part 3; the polymerid trilobites. Ibid. **11**, 179–282, pls. 19–25.

WHITTINGTON, H. B. 1965. Trilobites of the Ordovician Table Head Formation, western Newfoundland. *Bull. Mus. comp. Zool. Harv.* **132**, 275–442, pls. 1–68.

A. W. A. RUSHTON
Institute of Geological Sciences
Exhibition Road
London, SW7 2DE

Typescript received 19 January 1977
Revised typescript received 29 April 1977