The only known cyclopygid–'atheloptic' trilobite fauna from North America: the upper Ordovician fauna of the Pyle Mountain Argillite and its palaeoenvironmental significance

ALAN W. OWEN*† & DAVID L. BRUTON§

*School of Geographical and Earth Sciences, University of Glasgow, Gregory Building,
Lilybank Gardens, Glasgow G12 8QQ, Scotland, UK
§The Natural History Museum (Geology), University of Oslo, Postboks 1172 Blindern, N-0318, Oslo, Norway

Abstract – The trilobite fauna of the upper Ordovician (middle Katian) Pyle Mountain Argillite comprises a mixture of abundant mesopelagic cyclopygids and other pelagic taxa and a benthic fauna dominated by trilobites lacking eyes. Such faunas were widespread in deep water environments around Gondwana and terranes derived from that continent throughout Ordovician time but this is the only known record of such a fauna from North America and thus from Laurentia. It probably reflects a major sea level rise (the 'Linearis drowning events') as does the development of coeval cyclopygid-dominated deep water trilobite faunas in terranes that were marginal to Laurentia and are now preserved in Ireland and Scotland. The Pyle Mountain Argillite trilobite fauna occurs with a deep water *Foliomena* brachiopod fauna and comprises 22 species. Pelagic trilobites (mostly cyclopygids) constitute 36 % of the preserved sclerites, and 45 % of the fauna is the remains of trilobites lacking eyes, including one new species, *Dindymene whittingtoni* sp. nov. Three species of cyclopygid are present, belonging in *Cyclopyge*, *Symphysops* and *Microparia* (*Heterocyclopyge*). Cyclopygids are widely thought to have been stratified in the water column in life and thus their taxonomic diversity reflects the relative depths of the sea-beds on which their remains accumulated. A tabulation of middle and upper Katian cyclopygid-bearing faunas from several palaeoplates and terranes arranged on the basis of increasing numbers of cyclopygid genera allows an assessment of the relative depth ranges of the associated benthic taxa. The Pyle Mountain Argillite fauna lies towards the deeper end of this depth spectrum.

Keywords: Katian, water depth, Laurentia, Gondwana, Baltica, Avalonia.

1. Ordovician deep water trilobite faunas

Many Ordovician deep water trilobite faunas have two major components: an abundance of taxa that lived within the water column and species that were members of the underlying benthos. The former largely belong to the Cyclopygidae and have characteristically large eyes. Cyclopygids had wide palaeogeographical distributions but their remains are almost invariably restricted to deep water deposits from ocean-facing settings (Cocks & Fortey, 1990). They are therefore interpreted as having been mesopelagic (Fortey, 1985; Fortey & Owens, 1987; McCormick & Fortey, 1998), typically occupying levels in the water column at depths estimated to be between about 200 m and 700 m (Fortey, 1985; Fortey & Owens, 1987) or possibly a little shallower (e.g. McCormick & Fortey, 1998; Zhou, Zhou & Yuan, 2001; Zhou *et al*. 2003, 2011; Owens, 2002). Throughout the Ordovician period they lived above the outer shelves and upper continental slopes of the margins of Gondwana and continents and terranes derived from there (Fortey & Cocks, 2003). Occasionally, at times of high sea level

during early and middle Ordovician times, cyclopygids extended their range onto the margin of Baltica (e.g. Nielsen, 1995; Hoel, 1999) and terranes outboard of Laurentia (Williams *et al*. 1992; Fortey & Cocks, 2003). During late Ordovician time, however, they became increasingly frequent visitors to the Iapetus margin of Laurentia (e.g. Bartholomew & Tillman, 1977; Lespérance *et al*. 1987; Fortey & Owens, 1987, p. 107) and its outboard terranes now preserved in Scotland and Ireland (Owen & Romano, 2011).

Cyclopygid faunas are commonly associated with benthic species that lacked eyes or had smaller eyes than their shallow water relatives ('atheloptic' faunas of Fortey & Owens, 1987; see also Zhou *et al*. 2003; Fortey *in* Adrain *et al*. 2004). Although cyclopygids are abundant in some faunas from the upper Ordovician of the Laurentian margin, the only known occurrence in North America of a cyclopygid fauna with an associated benthic trilobite fauna dominated by species lacking eyes is that from the Pyle Mountain Argillite in Maine (Owen & Bruton, 2008). This fauna is described herein and assessed in terms of its likely relative bathymetric position compared to other upper Ordovician deep water trilobite faunas from a range of palaeogeographical settings.

† Author for correspondence: Alan.Owen@glasgow.ac.uk

Figure 1. (Colour online) The type locality of the Pyle Mountain Argillite, a roadside ditch and culvert from which fossil collections were made by H. B. Whittington with D. A. Whittington in 1961 and D. L. Bruton with R. B. Neuman in 1998. The gravel road above the culvert leads to what was once the site of Pyle School. Photo courtesy of W. H. Forbes, 2008.

2. Upper Ordovician cyclopygids in Laurentia

As is noted above, cyclopygids occur only rarely in upper Ordovician faunas from Laurentia and its marginal terranes within the Iapetus Ocean prior to middle Katian time (approximately latest Caradoc and earliest Ashgill in terms of Anglo-Welsh chronostratigraphy). Such recorded occurrences are from deep water deposits of Sandbian age and comprise a probable species of *Degamella* noted by Fortey & Owens (1987, p. 107) from the Normanskill Shale of New York State (= *Niobe*? *huberi* Roy, 1929); a specimen of *Microparia* from the Craigmalloch Formation (Albany Group) in the Girvan district of Scotland (Rushton, Tunnicliff & Tripp, 1996); a specimen of *Microparia* from the Laggan Member of the Balclatchie Formation at Girvan (Stewart & Owen, 2008) and six specimens, three complete, compared to *Microparia* (*M.*) *brachycephala* (Klouček) by Bartholomew & Tillman (1977) from the Liberty Hall Formation at Lusters Gate, Virginia.

However, at around the Caradoc–Ashgill boundary (middle Katian, see Bergström *et al*. 2009, fig. 1), abundant and diverse cyclopygid faunas appeared both on the Laurentian margin – as evinced by the Pyle Mountain Argillite fauna documented herein – and in the outboard terranes represented in the Whitehouse Subgroup at Girvan, Scotland (Ingham *in* Thomas, Owens & Rushton, 1984) and the Ballyvorgal Group and Oriel Brook Formation in Ireland (Weir, 1959; Owen & Romano, 2011). The benthic trilobite faunas associated with the last of these is most similar to the deep shelf *Phillipsinella parabola–Staurocephalus clavifrons* fauna seen in the upper Katian of Avalonia and Baltica, whereas the Whitehouse and Ballyvorgal Group faunas include a much more substantial component of trilobites lacking eyes.

Cyclopygids are also known from the subsequent part of the Katian of Laurentia. Species of *Cyclopyge*, *Heterocyclopyge* (now considered a subgenus of

Microparia) and *Symphysops* occur in, and locally dominate, the '*Stenopareia* Community' of Lespérance *et al*. (1987) in the Ashgill of the Percé region of Quebec but in association with 'normal-eyed' benthic taxa. A single cyclopygid specimen was ascribed to *Heterocyclopyge* by Sheehan & Lespérance (1978) amongst the 205 trilobite sclerites associated with a *Foliomena* brachiopod fauna that probably represents one of the shallower water developments of that fauna (Harper *in* Owen & Bruton, 2008). The low diversity trilobite fauna is composed almost entirely (84 %) of specimens of *Tretaspis* and, to a lesser extent, *Lonchodomas* (11 %). Both of these taxa lack eyes and, as noted by Owen & Bruton (2008), constitute a development of the trinucleid–raphiophorid association known through most of the Ordovician of Avalonia, Baltica and South China (see Owen & Parkes, 2000, p. 227).

3. The Pyle Mountain Argillite and its fauna

3.a. The Pyle Mountain Argillite

The geological setting of the Pyle Mountain Argillite in Castle Hill Township, Aroostook County, northeastern Maine was summarized by Neuman (1994), who provided a geological map showing the distribution of the formation (1994, fig. 2). The formation was originally named by Boucot *et al*. (1964) and although Roy (1987) recommended in an Open-File Report of the Maine Geological Survey that the name be amended to Pyle Mountain Formation, this has not been adopted by subsequent workers. The unit comprises fine-grained, olive-coloured mudstone, which, where calcareous, weathers to a brown 'gingerbread' rock that is commonly richly fossiliferous with abundant moulds of ostracods and agnostoid trilobites. Graptolites of the *Climacograptus spiniferus* Biozone occur in black shales near the top of the underlying Winterville Formation (Neuman, 1994, fig. 2) and indicate that the Pyle Mountain Argillite is probably equivalent to a level in or close to the lower part of the *Pleurograptus linearis* Biozone and thus approximately uppermost Caradoc in terms of the Anglo-Welsh chronostratigraphy. Pollock, Harper & Rhor (1994) discussed and provided a correlation of upper Ordovician successions in northern Maine and adjacent Canada and considered (1994, p. 930) that the Pyle Mountain Argillite was deposited in a 'deep, cold water basin on the outboard margin of Laurentia'.

Shelly fossils were first recorded from the Pyle Mountain Argillite by Boucot *et al*. (1964). The original plan for the present study was for a joint publication whereby, following joint collecting at the Pyle School locality in 1989, Robert B. Neuman (formerly of the US Geological Survey) was to describe the brachiopods and one of us (DLB), the trilobites. Regrettably this did not materialize and Neuman (1994) published the brachiopods separately but included a provisional list of the trilobites identified by Bruton (Neuman, 1994, p. 1221). This list was based on the 1989 collections,

Table 1. Composition of the trilobite fauna from the Pyle Mountain Argillite

Taxa in rank order of abundance	No of specimens	%	Ceph. & cran.	Fr. cheeks	Hyp.	Pyg.	Frags	Min. no of animals
Cyclopyge aff. *marginata* Hawle & Corda	37	19	4	6		27		27
Dindymene whittingtoni sp. nov.	26	13.5	19			5		19
Panderia megalophthalma Linnarsson	22	11	12			10		12
Dionide sp.	20	10	10			10		10
Trinodus cf. *tardus* (Barrande)	16	8	7			9		9
Amphitryon radians (Barrande)	11	5.5	9	1		1		9
Nankinolithus granulatus (Wahlenberg)	11	5.5	9	2				9
cyclopygids indet.	9	4.5		7		2		4
Symphysops sp.	9	4.5	5	2		2		5
Lonchodomas sp.	6	3	3			3		3
Dicranopeltis sp.	5	2.5				2	3	2
Telephina cf. *fracta* (Barrande)	4	2	2	2				2
harpetid indet.	4	2	4					2
Pseudosphaerexochus sp.	3	1.5	1			2		2
Raymondella? sp.	3	1.5	2			1		2
Novaspis cf. *albida* (Reed)	2	1	2					2
Nileus? sp.	2	1			1		1	1
proetid indet.	1	0.5		1				1
asaphid? indet.	1	0.5					1	1
Corrugatagnostus sp.	1	0.5	1					1
Staurocephalus cf. *clavifrons* Angelin	1	0.5	1					1
Microparia (Heterocyclopyge) sp.	1	0.5				1		1
Raphiophorus sp.	1	0.5	1					1
Total	196	99						126
Total cyclopygids	56	28.5						36
Total pelagic trilobites (excluding agnostoids)	71	36						60
Total eyeless trilobites	90	45.5						48
Total eyeless trilobites (excluding agnostoids)	73	37						38
Total benthic trilobites with eyes	35	17.5						20

Taxa are arranged in rank order of abundance based on both numerical abundance of specimens and the minimum number of animals indicated by the numbers of the different sclerites (cephala & cranidia, free cheeks, hypostomes, pygidia and indeterminate fragments) of each species. Cyclopygids comprise species of *Cyclopyge*, *Symphysops* and *Microparia* (*Heterocyclopyge*). *Amphitryon* and *Telephina* were also pelagic. See text for discussion of the benthic taxa.

supplemented by specimens collected on numerous occasions by Neuman with W. H. Forbes and others and those collected by Harry and Dorothy Whittington in 1961, which formed the basis for Whittington's report and faunal list published in Boucot *et al*. (1964, p. 21). Whittington recognized that the Pyle Mountain Argillite fauna was unlike those known from elsewhere in North America and had strong affinities with the Ashgill rocks of Europe, in particular Bohemia and Poland. We provided a preliminary assessment of the trilobite fauna (Owen & Bruton, 2008) prior to its detailed systematic treatment and analysis.

The type locality of the Pyle Mountain Argillite is a roadside ditch, now overgrown (Fig. 1), extending west across the north slope of Pyle Mountain at the intersection of the Turner Road and Dudley Road (Neuman, 1994, p. 1220, fig. 2) and at the site of the former Pyle School, now since gone. Collections from 1989 and later come from the spot marked PM on the map published by Neuman (1994, fig. 2), which corresponds to locality D-4 of the Presque Isle Quadrangle map (Boucot *et al*. 1964, pl. 1), whilst the 1961 collections contain additional specimens from locality E-3. In the field, the mudstone seems to lack bedding and the fossils appear widely scattered without any apparent orientation. Collections made by the Whittingtons and by Bruton have been prepared with the aid of a vibro-tool or fine needles, while those received from Neuman were those identified in rock samples that had already been treated in dilute hydrochloric acid to dissolve any remaining carbonate from the studied brachiopod shells. The majority of specimens are therefore internal moulds, or latex casts from external moulds that were first blackened with 'Opaque' and then whitened with ammonium chloride before photographing using Leitz Aristophot equipment with a film camera attachment. The developed films were later scanned and plates made using Adobe Photoshop™. A few specimens were photographed directly as digital images.

3.b. Trilobite fauna

The trilobite fauna of the Pyle Mountain Argillite comprises some 22 species. All of the specimens are isolated sclerites and thus the fauna reflects a degree of post-mortem transport. They range in size from a few millimetres in the case of some pygidia of *Cyclopyge* to a hypostome of *Nileus?* 23 mm wide. This is in marked contrast to the brachiopods, which are all small (even compared to related species elsewhere; most specimens being between 2 and 4 mm, none greater than 9 mm) (Neuman, 1994). The number of component sclerites of each trilobite species is listed in Table 1, with the taxa shown in rank order of abundance. The same order is obtained irrespective of whether the total number of sclerites of each taxon is counted or the minimum number of individual animals these might represent is

estimated. The latter is based on the maximum number of sclerites representing a single part in the exoskeleton (cranidium, pygidium or hypostome) or, if it is greater, half the number of paired sclerites (free cheeks). We recognize that this does not account for differences in the number of moult stages between species and hence the number of exuviae a single animal may leave during its life.

The fauna comprises a significant proportion of trilobites, largely cyclopygids, which lived in the water column, and a benthic fauna dominated by representatives of taxa lacking eyes. None of the benthic taxa that lack eyes have normal-eyed relatives, and whereas the original use of the term 'atheloptic association' was for faunas that included such secondarily blind or 'shrunken-eyed' taxa (Fortey & Owens, 1987, p. 106), the Pyle Mountain Argillite fauna conforms to the slightly broader sense in which the term 'atheloptic' has become used (e.g. Waisfeld *et al.* 2001).

Cyclopygids constitute 28.5 % of both the total number of identifiable sclerites and of the minimum number of individual trilobite animals. *Cyclopyge* is the most abundant but species of *Symphysops* and *Microparia* (*Heterocyclopyge*) are also present. The epipelagic *Telephina* is a rare component of the fauna and the remopleuridid *Amphitryon* was probably also a swimmer, and hence pelagic trilobites together constitute 36 % of the sclerites (37 % of the minimum number of individual animals). The agnostoids *Trinodus* and *Corrugatagnostus* constitute a further 8.5 % of the sclerites in the fauna (8 % of animals) and may also have had a pelagic mode of life, although this is a matter of some debate (e.g. see Fortey & Owens, 1999). Undoubted benthic trilobites lacking eyes (species of *Dindymene*, *Dionide*, *Nankinolithus*, *Lonchodomas*, harpetids, *Raymondella*?, *Novaspis* and *Raphiophorus*) constitute 37 % of the sclerites (30 % of the minimum number of individual animals). Including the agnostoids increased the figures for trilobites lacking eyes to 45.5 % and 48 %, respectively. Apart from *Panderia*, no benthic trilobite species with eyes represents more than 2.5 % of the fauna and such trilobites together comprise only 17.5 % of the sclerites and 16 % of the minimum number of individual animals represented by those isolated exoskeletal parts. The presence of benthic trilobites with normal eyes suggests some light penetration to the sea bed. It is possible that at least some of these trilobites could have been transported from shallower, more illuminated, waters. However, as is noted in Section 4.b, there seems to be some systematic arrangement of benthic taxa, including ones with normal eyes, down the palaeoslope below the waters inhabited by cyclopygids, suggesting that at least some were components of the deep water benthos.

3.c. Brachiopod fauna

The Pyle Mountain Argillite contains the only known *Foliomena* brachiopod fauna from North America (Neuman, 1994; Owen & Bruton, 2008), although such faunas are known from terranes in Ireland and Scotland that lay outboard of Laurentia during Ordovician time (Parkes & Harper, 1996; Harper & Stewart, 2008). Upper Ordovician cyclopygid faunas are commonly associated with such assemblages of typically small, thin-shelled brachiopods. Since its first description from Sweden (Sheehan, 1973), the *Foliomena* fauna has been documented from most palaeocontinents and has been the subject of several reviews (e.g. Cocks & Rong, 1988; Rong, Zhan & Harper, 1999; Zhan & Jin, 2005). It has become clear that the fauna occupied deep water (distal shelf) environments (Benthic Assemblage (BA) Zones 5–6) during Sandbian and early Katian times (Caradoc in terms of Anglo-Welsh chronostratigraphy) and extended its range into mid-shelf settings (BA 3–4) during late Katian time (Ashgill) (Villas, Hammann & Harper, 2002; Zhan & Jin, 2005) when it also reached its widest palaeogeographical extent. Cluster and Principal Component Analysis of 29 *Foliomena* faunas from nine Ordovician plates or microplates by Zhan & Jin (2005) placed the Pyle Mountain Argillite fauna in a group of younger faunas, which they interpreted as having occupied sites in the deeper water part of the environmental spectrum inhabited by the brachiopod fauna. Within that group the Pyle Mountain Argillite fauna occupied the deepest parts of the spectrum along with those of the Tangtou Formation in Nanjing, South China, the Jerrestad Mudstone of Sweden (Baltica) and the Domusnovas Formation of Sardinia. Other Ashgill faunas from what were interpreted as shallower (but none the less still deep) water settings within the same group include those of the Holy Cross Mountains in Poland (Baltica), the Crugan Mudstones of the Llŷn Peninsula of North Wales, the Tangtou Formation in Ningguo, South China, the Králův Dvůr Formation in Bohemia and the Jonstorp Formation of Västergötland, Sweden.

4. Environmental setting of the trilobite fauna

4.a. Deep water trilobite faunas

Analyses of cyclopygid trilobite faunas along depth gradients inferred from regional palaeogeographical and other criteria show an increasing abundance and diversity with increasing water depth and this is inferred to indicate depth stratification of taxa within the water column (e.g. Price & Magor, 1984; Zhou *et al.* 1994, 2003, 2011; Zhou, Zhou & Yuan, 2001, 2007). In simple terms, those cyclopygid taxa living at higher levels in the water column extended further shoreward above the outer shelf and are more likely to occur in otherwise shallower shelf successions at times of marine transgression. They may occur in low diversity cyclopygid-bearing assemblages in relatively shallow settings but increasingly higher diversity, higher abundance, cyclopygid faunas in deeper water environments. There are three cyclopygid genera, *Cyclopyge*, *Symphysops* and *Microparia*, in the Pyle

Mountain Argillite fauna. The question then arises as to what this might indicate in terms of the recorded spectrum of late Ordovician outer shelf to upper slope environments and whether that bathymetric 'signal' is also reflected in the associated benthic trilobite fauna.

4.b. Comparison of the Pyle Mountain Argillite faunas with other deep water faunas

Table 2 is a compilation of the occurrences of trilobite genera in the best-documented cyclopygid-bearing faunas in the middle and upper Katian of the Iapetus region (Avalonia, Baltica, Laurentia (including the Pyle Mountain Argillite fauna) and peri-Laurentian terranes in Scotland and Ireland), the high latitude margin of Gondwana (including Perunica) and South China. *Foliomena* brachiopod faunas have been documented from virtually all of the units yielding the trilobites. The trilobite faunas in Table 2 are arranged from left to right in terms of the increasing number of cyclopygid genera; this also reflects basinward transects determined using regional geological criteria for the Avalonian and Chinese faunas. The relative positions of faunas reflects a general deepening from left to right in the table and the Pyle Mountain Argillite fauna clearly plots towards the deeper water end of the spectrum, which accords with the interpretation of the brachiopod fauna (Zhan & Jin, 2005; see Section 3.b). The co-occurrence of the cyclopygids *Cyclopyge, Symphysops* and *Microparia* is a palaeogeographically widespread phenomenon (Table 2) and has a longer history on the Gondwanan margin such as in the Sandbian trilobite fauna recently documented from the Tarbagati Range in Kazakhstan by Ghobadi Pour *et al*. (2011).

The benthic trilobites in the Pyle Mountain Argillite fauna include some of the most ubiquitous genera across the analysed spectrum of deep water faunas shown in Table 2. The occurrence of the trinucleid *Novaspis* confirms a position for the fauna in the deeper part of the spectrum within what Price & Magor (1984) termed the '*Novaspis*-cyclopygid Association'. There are some interesting absences from the fauna, notably *Opsimasaphus/Birmanites* (the taxonomy of these genera requires clarification) and *Phillipsinella*, which are otherwise very widely distributed. Both have 'normal' eyes and occur in faunas in other peri-Iapetus settings including the occurrence of *Phillipsinella* in broadly coeval cyclopygid faunas in the Grangegeeth (Oriel Brook Fm) and Midland Valley (Upper Whitehouse Subgroup) terranes that lay on the margins of Laurentia. Their absence presumably reflects either very low abundance or some subtlety of the environment in Maine.

In terms of the peri-Iapetus faunas (Baltica, Avalonia and Laurentia and its marginal terranes), only 4 of the 34 genera in Table 2 (*Phillipsinella, Shumardia, Sphaeragnostus* and *Gravicalymene*) have ranges that unequivocally bracket the position of the Pyle Mountain Argillite but are not recorded from that formation. This lends support to the relative bathymetric position

of the Maine fauna established on the basis of the cyclopygids being also reflected in the benthos. *Shumardia* and *Sphaeragnostus* occur at Girvan, in what is interpreted as the deepest of the trilobite faunas, and *Gravicalymene* is known from more 'normal' shelf faunas on Laurentia (e.g. Ross, 1967; Lespérance & Weissenberger, 1998) so again, a local environmental rather than a wider biogeographical explanation for their absence must be sought.

5. Palaeobiogeographical interpretation

The increasing frequency of the appearances of cyclopygids on the Iapetus margin of Laurentia and its outboard terranes from the beginning of the late Ordovician period may reflect a long-term shift to higher global sea levels (Fortey, 1984). This began during the preceding Darriwilian age and persisted until well into Katian time (Haq & Schutter, 2008, fig. 1). On a shorter timescale, the development of diverse cyclopygid faunas on and close to the Iapetus margin of Laurentia, including ones associated with atheloptic benthic faunas such as in the Pyle Mountain Argillite, in middle Katian time may have been promoted by a major sea level rise, the 'Linearis drowning events' of Nielsen (2004), that led to the maximum extent of drowning of the Laurentian platform (Zhang, 2011). Although not fully established in the deep waters off Laurentia until late Ordovician time, it is somewhat ironic that the youngest record of a cyclopygid is from there and not from Gondwana or crustal blocks derived from it such as South China or Avalonia. Thus a species of *Cyclopyge* is known from the Hirnantian Tirnaskea Formation of Pomeroy, Co. Tyrone, northern Ireland (Thomas, Owens & Rushton, 1984; Owen, 1986), part of the marginal Laurentian Midland Valley terrane that includes Girvan (Woodcock *in* Fortey *et al*. 2000 and reference therein). Unlike most Hirnantian units, the Tirnaskea Formation also contains deep water brachiopod associations indicative of BA 5–6 (Candela, 2006).

6. Systematic palaeontology

The terminology and order of description of taxa follows that advocated in the *Treatise on Invertebrate Paleontology Part O* (Kaesler, 1997). All figured and listed material is housed in the type collections of the Geological Museum, University of Oslo (hereafter abbreviated PMO); the remaining material is in the US National Museum of Natural History, Washington, DC. With the exception of the new species of *Dindymene*, the records of the Pyle Mountain Argillite Formation taxa in the faunal lists of Whittington (*in* Boucot *et al*. 1964, p. 21), Bruton (*in* Neuman, 1994, p. 1221) and Owen & Bruton (2008, table 1) have not been compiled in synonymy lists. In most instances the generic affinity and even species comparison was the same as in the present paper. A note is made in the relevant discussion of those cases where the earlier generic determination differs from that used here.

A free cheek (Fig. 2o) of a proetid (?*Ogmocnemis* of Bruton *in* Neuman, 1994, p. 1221), three incomplete harpetid genal prolongations (Fig. 5s) and a fragment of harpetid brim

Table 2. Comparison of the trilobite fauna of the Pyle Mountain Argillite with that of other cyclopygid-bearing faunas from the middle and upper Katian (upper Caradoc to middle Ashgill) of Baltica (B), Avalonia (A), China (C), Gondwana (G), Perunica (P) and Laurentia and its marginal terranes (L)

Fauna	UM	JFD	RL	JFS	UT	CM	OB	Dom1	Por2b	BG	BC2	BC5	DM	SZ	PMA	UP1	UP2	UP3	UP4	KD	BC9	WS
Plate/terrane	B	B	A	B	C	A	L	G	G	L	A	A	A	B	**L**	C	C	C	C	P	A	L
CYCLOPYGID GENERA																						
Cyclopyge	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**x**		x	x	x	x	x	x
Microparia				x	x	?						?	x	x	**x**	x	x	x	x	x	?	x
Symphysops							x	x	x	x	x	x	x	x	**x**					x	x	x
Sagavia																x	x	x	x			x
Degamella																				x	?	x
Psilacella																					x	x
Novakella																						x
Ellipsotaphrus																						x
Girvanopyge																						x
gen nov 1																						x
gen nov 2																						x
NON-CYCLOPYGID GENERA IN PYLE MOUNTAIN ARGILLITE																						
Panderia	x	x		x			x				x	x		x	**x**	x	x	x	x			
Trinodus	x	x	x	x	x	x	x	x	x		x	x	x	x	**x**	x	x	x	x	x		
Pseudosphaerexochus	x	x	x	x	x	x		x		x	x	x	x	x	**x**	x		x		x		
Dionide	x	x	x	x	x	x	x			x	x	x	x	x	**x**			x		x	x	
Nankinolithus	x	x	x	x	x	x	x	x	x		x	x	x	x	**x**					x	x	x
Lonchodomas	x	x	x	x	x	x	x				x	x	x	x	**x**	x	x	x	x	x	x	x
Dindymene		x	x	x			x		x			x	x	x	**x**					x	x	x
Raphiophorus		x	x	x			x					x	x	x	**x**					x	x	x
Staurocephalus		x	x	x			x	x	x	x	x	x		x	**x**							
Amphitryon		x	x	x	x	x		?	?	x				x	**x**		x	x	x	x		
Nileus				x				?							**?**	x	x	x				?
Telephina				x				x		x					**x**	x	x	x		x		x
Corrugatagnostus				x				x		x				x	**x**	x	x	x				x
Hibbertia							?	x	x					x	**?**							
Novaspis												x		x	**x**						x	x
Dicranopeltis									x						**x**							
Raymondella							?								**?**							
OTHER NON-CYCLOPYGID GENERA																						
Tretaspis	x		x	x	x									x						x		
Diacanthaspis	x	x	x	x	x			x	x					x		x						x
Ectillaenus	x										?	x		x								?
Allolichas	x		x		x						x	x		x								
Cybeloides	x		x		x						x	x		x								
Sphaerocoryphe	x		x								x	x										
Rempleurides	x		x											x						x		
Brongniartella	x																			x		
Decoroproetus	x		x	?	x			?						x						x		
Stygina		x	x											x								
Ceraurinella		x	x	x	x						x	x		x								
Liocnemis		x	x	x							x	x	x	x								
Oedicybele		x	x	x								x		x				x				
Alceste		x		x	x									x			x	x	x			

Table 2. Continued

Fauna	UM	JFD	RL	JFS	UT	CM	OB	Dom1	Por2b	BG	BC2	BC5	DM	SZ	**PMA**	UP1	UP2	UP3	UP4	KD	BC9	WS
Zdicella		x												x						x		
Opsimasaphus/Birmanites		x	x	x	x	x		x			x	x	x	x		x		x	x		?	
Phillipsinella		x	x	x	x	x	x				x	x	x	x		x	x	x	x	x		x
Calyptaulax			x	x																		
Harpidella			x											x								
Prionocheilus			x						x													
Whittingtonia			x				?					x		x								
Encrinuroides			x			x					x	x										
Duftonia			x			x						x	x							x		
Illaenus [inc. *Parillaenus*]			x	x				?	?		x		x	x		x			x	x		x
Areia				x				x												x		
Flexicalymene				x																x		
Octillaenus				x									x							x		
Madygenia					x				x													
Paraphillipsinella					x			x								x	x	x				
Taklamakania					x			x	x													
Shumardia					x			x	x	x				x								x
Ovalocephalus					x			x						x		x	x	x	x			
Sphaeragnostus					x	x		x		x		x	x	x					x			x
Gravicalyene						x						x	x							x	x	
Actinopeltis								x	x					x						x		
Carmon														x						x		
Sphaerexochus							?									x				x		

The presence of a genus in a sample is marked by a cross. Cyclopygids are abundant in those faunas where more than one genus of that group is present, although quantitative data are not available in many instances. The faunas are arranged in terms of increasing water depth from left to right based on increasing cyclopygid diversity and, in the case of those from Avalonia and China, other regional geological evidence of bathymetry. The non-cyclopygid genera present in the Pyle Mountain Argillite (PMA) are arranged in stepwise order of occurrence from shallow to deep followed by a similar ordering of taxa that occur in more than one palaeogeographical region but not in the Pyle Mountain Argillite. Non-cyclopygid genera recorded from faunas restricted to a single palaeogeographical region have been excluded from this compilation. A limited amount of reassessment of taxonomic reassignment has been undertaken, but the main sources of data are: UM – Ulunda Mudstone, Västergötland, Sweden: Bergström (1973 with emendations by Owen, Harper & Rong, 1991); JFD – Jerrestad Fm, Bornholm, Denmark: Kielan (1960); RL – Rhiwlas Limestone, Wales: Whittington (1968 with emendations by Owen, Harper & Rong, 1991); JFS – Jerrestad Fm, Skåne, Sweden: Kielan (1960); UT – Upper Tangtou Fm, Jiangsu Province, China: Tripp, Zhou & Pan (1989); CM – Crugan Mudstone, North Wales: Price (1981); OB – Oriel Brook Fm, Ireland: Owen & Romano (2011); Dom1 and Por2b – Punta S'Argiola Member of the Domusnovas Fm, Sardinia: Hammann & Leone (2007); BG – Ballyvorgal Group, Ireland: Weir (1959 see also Whittington, 1968; Owen & Romano, 2011); BC 2, 5, 9 – upper Katian (Rawtheyan) between Bala and Corris, N Wales: Price & Magor (1984); DM – Dwyfor Mudstone, N Wales: Price (1981); SZ – *Staurocephalus clavifrons* Zone, Poland: Kielan (1960); UP1–4 – Upper Pagoda Limestone, northern Sichuan and southern Shaanxi provinces, China: Zhou, Zhou & Yuan (2007); KD – Králův Dvůr Formation, Czech Republic: faunas from localities yielding cyclopygids listed by Shaw (2000); WS – Upper Whitehouse Subgroup, Girvan, Scotland: Ingham *in* Thomas, Owens & Rushton (1984) and Ingham (in press).

(=*Hibbertia* sp. of Bruton *in* Neuman, 1994, p. 1221), and a possible asaphid fragment (Fig. 3j) do not warrant further description or discussion.

Family METAGNOSTIDAE Jaekel, 1909
Genus *Corrugatagnostus* Kobayashi, 1939

Type species. Agnostus morea Salter, 1864, from the Hope Shales (Llanvirn; Darriwilian), Shropshire, England (senior subjective synonym of *Agnostus perrugatus* Barrande, 1872). Holotype (by monotypy) cephalon refigured by Shergold & Laurie (1997, p. 375, fig. 236:5b).

Corrugatagnostus sp.
Figure 2a

Material. One cephalon.

Discussion. Nielsen (1997) provided an excellent survey of *Corrugatagnostus* and its distribution and noted that it contains both non-scrobiculate and scrobiculate forms (see also Shergold, Laurie & Sun, 1990; Shergold & Laurie, 1997). The Maine cephalon is of the latter type as are those of the type species and related species from Bohemia figured by Pek (1977, pls 5–7; Pek & Prokop, 1984, pl. 1, figs 1, 2). These species are older than the present specimen, which has a more pronounced and irregular pattern of small scrobicules arranged en échelon lateral to the glabella and divergent to chaotic in front. Owen & Ingham (1996, pp. 139–40, pl. 25, figs 1, 2) considered *C. sol* Whittard, 1955 from the Whitehouse Subgroup (uppermost Caradoc–lowest Ashgill) at Girvan, SW Scotland to be the most scrobiculate species of *Corrugatagnostus*. They considered that *C. convergens* Weir, 1959 from a broadly equivalent horizon in Ireland may prove synonymous with *C. sol*. Although probably laterally stretched, the present cephalon shows a comparable scrobiculation anteriorly and anterolaterally to that of *C. sol* figured by Owen & Ingham, but this becomes less pronounced posteriorly. The scrobiculation of the present specimen is like that of the much distorted cephalon from the upper Katian of Poland figured as *Geragnostus* sp. by Kielan (1960, pl.1, fig. 4) but the furrowing of the glabella is much more pronounced.

Genus *Trinodus* M'Coy, 1846

Type species. Trinodus agnostiformis M'Coy, 1846 from the Campanile Formation (Sandbian), Greenville, Enniscorthy, Co. Wexford, Ireland.

Discussion. Owen & Parkes (2000, pp. 229–32) discussed the complex nomenclatorial problems affecting *Trinodus* M'Coy, 1846 and *Arthrorhachis* Hawle & Corda, 1847 (type species *Battus tardus* Barrande, 1846 from the Králův Dvůr Formation in Bohemia). Fortey (1980, pp. 26–7) recommended that, in the absence of other material from its type locality, the name *Trinodus* should be restricted to the poorly preserved type cranidium of *T. agnostiformis*. This was widely followed and, although not without taxonomic problems of its own (see also Hammann & Leone 1997), *Arthrorhachis* became extensively used to accommodate material that had previously been assigned to *Trinodus*. In documenting topotype specimens, including pygidia, of *Trinodus agnostiformis*, Owen & Parkes (2000) reluctantly re-established *Trinodus* as a senior subjective synonym of *Arthrorhachis*. They noted that there may be a case for retaining *Arthrorhachis* as a subgenus of *Trinodus* for the *A. tarda* species group of Nielsen (1997). A detailed phylogenetic analysis would be necessary to establish this. Budil *et al.* (2011) have recently argued that there may be a case for promoting the use of *Arthrorhachis* and again

restricting the name *Trinodus* to material from the type locality. Pending the resolution of these issues we follow Owen & Parkes (2000) in using *Trinodus*.

Trinodus cf. *tardus* (Barrande, 1846)
Figure 2b–f

Material. Seven cranidia and nine pygidia.

Discussion. Hammann & Leone (1997) discussed the widely distributed, highly variable, upper Katian *Arthrorhachis* [= *Trinodus*] *tarda* in great detail. Suffice it to note here that previous authors have remarked on considerable variability of the species in the relative lengths of the glabella and pygidial axis (e.g. see Zhou & Dean 1986, p. 747) with two end morphotypes being recognized. This is certainly the case with the cephala figured here where the 'short' specimen (Fig. 2b) resembles closely that of *A.* aff. *tarda* of Tripp, Zhou & Pan (1989, fig. 3d, f) from the Ashgill Tangtou Fm, Jiangsu Province, China, and the 'long' specimen (Fig. 2c) is like that of *Trinodus* aff. *tardus* of Owen & Bruton (1980, pl. 1, fig. 4) from the upper Caradoc of Hadeland, Norway. The 'long' morphs have a glabella that is laterally constricted along its length; this is especially pronounced in the figured specimen (Fig. 2c). This feature is obvious on the lectotype of *A. tarda* selected by Pek (1977, pl. 8, fig. 2; but not figs 3, 4) but it is not obvious on other Bohemian material figured by Whittington (1950, pl. 68, fig. 6) and Fortey (1997, pl. 1, fig. 2) and is weak even on the internal moulds of material figured by Hammann & Leone (1997, pl. 2) from Sardinia. It is, however, present, albeit weak, on the articulated specimens figured by Kielan (1960, pl. 1, figs 9, 11) from Poland. The present specimens, like those from Poland, have deep marginal border furrows on both the cephalon and the pygidium. The latter is characterized by having a short axis outlined by deep furrows and three axial rings; the posterior ring furrow is complete and the first two are interrupted by a raised narrow strip terminating with an axial node. The short posterolateral spine is directed outwards rather than rearwards. In larger specimens (Fig. 2d, f), the convex pleural area narrows slightly towards the anterior and becomes steeper as in the Bohemian material figured by Whittington (1950, pl. 68, figs 4, 6), but on the smaller pygidium (Fig. 2e) the area behind the axis is longer (sag.) and less convex anteriorly, much the same as in the specimen figured by Kielan (1960, pl. 1, fig. 13) and the small pygidium figured by Tripp, Zhou & Pan (1989, fig. 3c). The present pygidia are very similar to those from the upper Caradoc of the Oslo-Asker area (Owen & Bruton, 1980, pl. 1, figs 1–3).

Family PANDERIIDAE Bruton, 1968
Genus *Panderia* Volborth, 1863

Type species. Panderia triquetra Volborth, 1863 from the middle Ordovician (probably Kunda Stage BIII; Darriwilian), Pavlovsk, St Petersburg District, Russia

Panderia megalophthalma Linnarsson, 1869
Figure 2g–l

1869 *Panderia megalophthalma* Linnarsson, p. 78, pl. 2, fig. 45.
1968 *Panderia megalophthalma* Linnarsson; Bruton, p. 26, pl. 10, figs 5, 6, 9; pl. 11, figs 1, 5–10.

For full synonymy see Bruton (1968, p. 26).
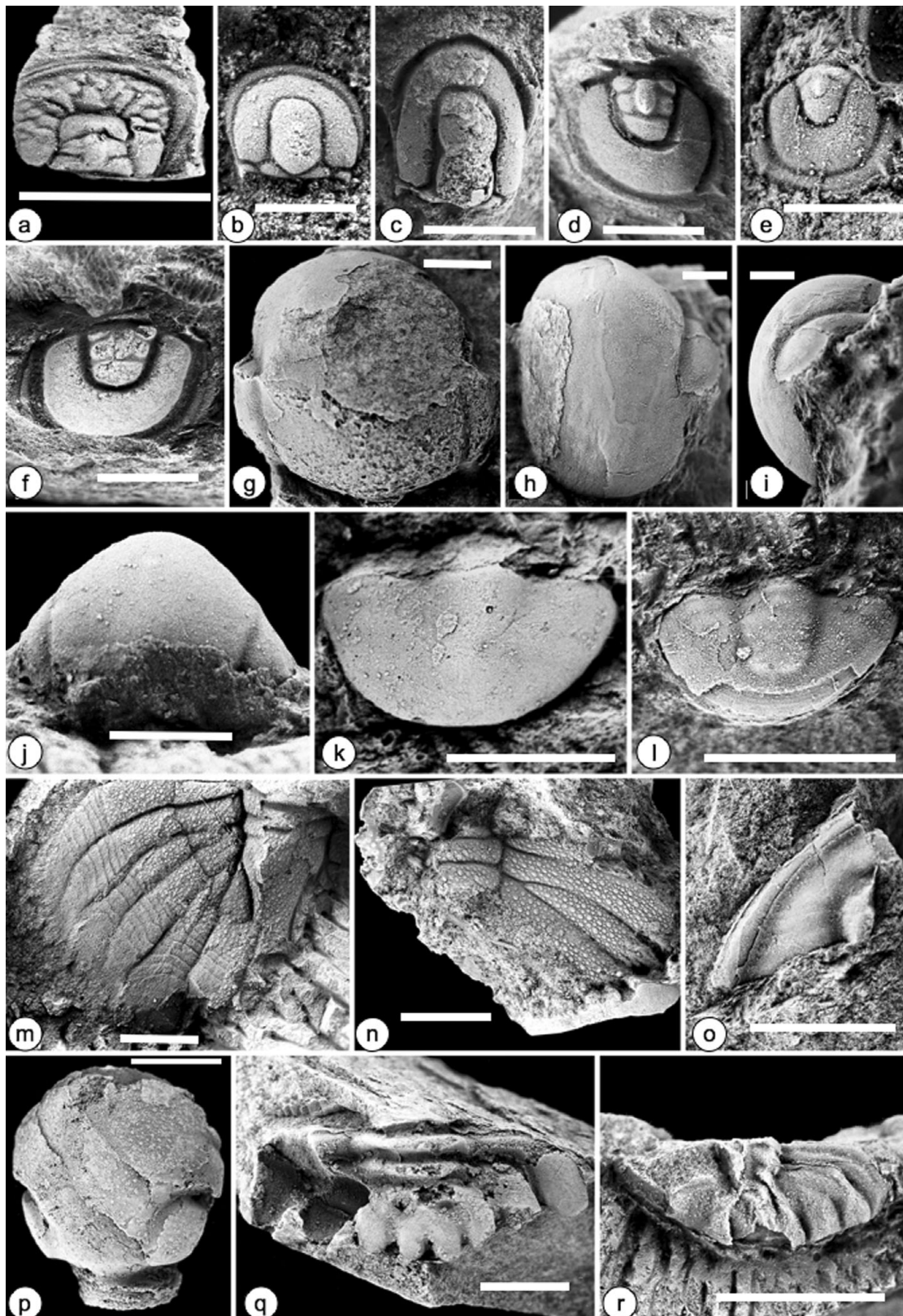
Material. Twelve cranidia and ten pygidia.

Figure 2. (a) *Corrugatagnostus* sp. incomplete cephalon, dorsal view, PMO 142.181, scale bar 2 mm. (b–f) *Trinodus* cf. *tardus* (Barrande, 1846) (b) cephalon, dorsal view, PMO 141.984, scale bar 1 mm; (c) elongated cephalon, dorsal view, PMO 141.986, scale bar 2 mm; (d) pygidium, dorsal view, PMO 141.985, scale bar 2 mm; (e) pygidium, dorsal view, PMO 141.982, scale bar 2 mm; (f) pygidium, dorsal view, PMO 141.986, scale bar 2 mm. (g–l) *Panderia megalophthalma* Linnarsson, 1869 (g) cranidium, palpebral view, PMO 142.018, scale bar 2 mm; (h, i) cranidium, anterior and left lateral views, PMO 142.176, scale bar 2 mm; (j) cranidium, dorsal view, PMO 208.308, scale bar 2 mm; (k) pygidium, dorsal view, latex cast, PMO 142.024, scale bar 4 mm; (l) pygidium, dorsal view, PMO 142.023, scale bar 4 mm. (m, n) *Dicranopeltis* sp. (m) pygidium, dorsal view, PMO 141.981, scale bar 4 mm; (n) pygidium, dorsal view, latex cast, PMO 141.962, scale bar 4 mm. (o) Proetid indet. free cheek, PMO 208.310, scale bar 4 mm. (p–r) *Pseudosphaerexochus* sp. (p) cranidium, dorsal view, PMO 142.150, scale bar 4 mm; (q) pygidium, dorsal view, PMO 142.176/1, scale bar 4 mm; (r) laterally distorted pygidium, dorsal view, PMO 142.148, scale bar 4 mm (n.b. grooves behind the pygidium are preparation marks).

Discussion. Although widely distributed throughout the Ordovician period in Baltoscandia where 12 species were described in detail by Bruton (1968), the genus has also been found in Poland (Kielan, 1960), the Anglo-Welsh area and southern Ireland (Morris, 1988 and references therein), Kazakhstan (Apollonov, 1974), southern Thailand (Fortey, 1997), the Turkistan-Altai region (Petrunina *in* Repina *et al*. 1975), Iran (Karim, 2009) and Guizhou Province, China (Yin *et al*. 2000). It may also occur in Iberia. Important criteria in discriminating species are the shape of the glabella in palpebral and dorsal views (Fig. 2g, j) and convexity in frontal and lateral view (Fig. 2h, i), while for the pygidium, the overall shape and width of the axis is important. Using these features, the present material is closest to the wide-ranging middle and upper Katian (upper Caradoc–Ashgill) species *P. megalophthalma* Linnarsson (see Bruton, 1968), although in frontal and lateral view the extended glabella forward of the front edge of the palpebral lobes resembles that of the youngest known species *P. edita* (see Bruton, 1968, pl. 9, figs 5, 7; pl. 10, figs 2, 8) from the upper Katian (middle Ashgill) Boda Limestone of Sweden. Ingham (1970, p. 26) assigned Ashgill material from northern England to *P. hadelandica* Bruton, but noted that the pygidium (Ingham, 1970, pl. 4, fig. 10) was rather like that of *P. megalophthalma*; both certainly have the axis segmented on the external surface (Ingham, 1970, pl. 4, fig. 10) as is also the case on the internal mould of the small pygidium figured here (Fig. 2l). The latter also shows a narrow, convex doublure with a terrace line pattern similar to that of the pygidium assigned to *P. megalophthalma* from the Ashgill of Sweden (Bruton, 1968, pl. 11, fig. 7). Fortey (1997, p. 7, figs 1–6) and Yin *et al*. (2000) described *P. orbiculata* Ji from the upper Caradoc of Thailand and South China, respectively. We agree with Yin *et al*. (2000), that in palpebral view *P. orbiculata* resembles *P. megalophthalma*, but in lateral view it differs in having a shorter glabella in front of the palpebral lobes. To judge from the figures of Fortey (1997, pl. 7, figs 1–3) the glabella of *P. orbiculata* is longer (sag.) in dorsal view than it is in *P. magalophthala* and the lateral profile shows a more convex glabella. The pygidium of *P. orbiculata* is semicircular in outline with a long axis defined by deep dorsal furrows anteriorly. The pygidial axis is well defined on the small specimen from Maine (Fig. 2l) but weakly defined on larger specimens (Fig. 2k) (cf. Bruton, 1968, pl. 11, figs 8, 10).

Family LICHIDAE Hawle & Corda, 1847
Subfamily LICHINAE Hawle & Corda, 1847
Genus *Dicranopeltis* Hawle & Corda, 1847

Type species. Lichas scabra Beyrich, 1845 from the Litĕn Formation (Wenlock) of Bohemia, Czech Republic.

Dicranopeltis sp.
Figure 2m, n

Material. Two pygidia and three fragments with typical lichid sculpture but of unknown provenance on the exoskeleton.

Discussion. Whittington (*in* Boucot *et al*. 1964) and Bruton (*in* Neuman, 1994) suggested that this material may belong in *Platylichas* but Owen & Bruton (2008) took a more cautious approach and simply ascribed it to the Lichidae. Even in the more complete of the two pygidia (Fig. 2m) the outermost parts of the pleurae are not preserved but there is enough to suggest an approximately semicircular pygidial outline. This together with the short axis with two rings, the short terminal piece in front of a long post-axial band and the presence of three pleural ribs strongly indicates that this material belongs in *Dicranopeltis*. The anterior band of the second segment on

the incomplete right anterolateral pygidium shown in Fig. 2n does not reach the axial furrow but this may be a teratological or injury repair feature. Such disruptions of the furrows or ribs on the pleural parts of pygidia are amongst the most common trilobite abnormalities (Owen, 1985). Apart from the area behind the tip of the axis possibly being a little narrower, the specimens could easily be accommodated in *D. polytoma* (Angelin, 1854), a widespread Ashgill species known from pure limestone units in Sweden (Warburg, 1939; Suzuki, Shiino & Bergström, 2009), the British Isles (Dean, 1974) and Spain (Hammann, 1992). Two cranidia, one from a cyclopygid-bearing fauna, were compared to Angelin's species by Hammann & Leone (2007) from the upper Katian of Sardinia and material considered to at least have affinity to *D. polytoma* has been described from the Hirnantian of Norway (Owen, 1981) and Rawtheyan of Inner Mongolia (Zhou & Zhou, 1982). *D. ubaldoi* Hammann & Leone, 2007 from the Ashgill of Sardinia (but not from any of the cyclopygid-bearing faunas) is characterized by weakly impressed pleural and interpleural furrows and thus differs from the present material.

Family CHEIRURIDAE Hawle & Corda, 1847
Subfamily ECCOPTOCHILINAE Lane, 1971
Genus *Pseudosphaerexochus* Schmidt, 1881

Type species. Sphaerexochus hemicranium Kutorga, 1854 from the Aseri Stage (Darriwilian), Estonia.

Pseudosphaerexochus sp.
Figure 2p–r

Material. A glabella and two incomplete pygidia.

Discussion. This material was assigned to *Actinopeltis* and *Liocnemis* by Bruton (*in* Neuman, 1994) but to *Pseudosphaerexochus* by Whittington (*in* Boucot *et al*. 1964) and Owen & Bruton (2008). Although incomplete, the pygidia have four pairs of posteriorly directed pleural spines, the posterior two of which at least are short and blunt. Such pygidia are typical of the group of species centred on *P. octolobatus* (M'Coy). M'Coy's species was based on material from the upper Katian (middle Ashgill–Rawtheyan Stage) Rhiwlas Limestone of North Wales and was redescribed by Lane (1971, p. 48, pl. 8, figs 1–8) from there and from the broadly equivalent Lady Burn Starfish Beds in the upper Drummuck Subgroup at Girvan, SW Scotland. Ingham (1974, p. 70, pl. 14, figs 1–5) tentatively ascribed material to M'Coy's species from Rawtheyan strata in northern England from where he also described a new, closely allied species, *P. tectus* from the underlying Cautleyan Stage (Ingham, 1974, pp. 68–70, pl. 13, figs 8–14). *P. laticeps* (Linnarsson) from the middle Ashgill of Västergötland and Scania in Sweden also has a broadly similar pygidium to that of *P. octolobatus* (see Kielan-Jaworowska, Bergström & Ahlberg, 1991; Pålsson, 1996). In marked contrast, *P. conformis* (Angelin, 1854) from the Ashgill Boda Limestone of Dalarne, Sweden has long, gently curved, more strongly radiating spines (see also Dean, 1971 and Owen, 1981, p. 45). The same applies to the broadly coeval *P. juvenis* (Salter) from Wales and northern England (see Price, 1980, pp. 858–9 and references therein) and *P. wolkae* Kielan, 1960 from the Ashgill *Staurocephalus clavifrons* Zone in Poland. *P. seabornei* Price, 1981 from the deep water Dwyfor Mudstone Formation of North Wales also has pointed pygidial spines but they are shorter and curve posteriorly to become sub-parallel.

Family ENCRINURIDAE Angelin, 1854
Subfamily DINDYMENINAE Přibyl, 1953
Genus *Dindymene* Hawle & Corda, 1847

Type species. Dindymene fridericiaugusti Hawle & Corda, 1847 from the Králův Dvůr Formation (middle Ashgill; upper Katian) of Bohemia, Czech Republic.

Dindymene whittingtoni sp. nov.
Figures 3a–b, 5h, k, o, p

1994 *Eodindymene* sp.; Bruton *in* Neuman, p. 1221.
1994 *Dindymene ornata* Linnarsson; Bruton *in* Neuman, p. 1221.
2008 *Dindymene* sp.; Owen & Bruton, table 1.

Holotype. External mould of a pygidium, PMO 141.947 (Fig. 3b).

Paratypes. External mould of cranidium, PMO 141.948 (Fig. 5h); internal mould of cranidium, PMO 141.954 (Fig. 5o, p); internal mould of pygidium, PMO 141.952 (Fig. 3a).

Other material. Eighteen cranidia and four pygidia.

Derivation of name. For Harry Whittington who first identified and interpreted the Pyle Mountain Argillite trilobites.

Diagnosis. Glabella narrow, especially posteriorly, bearing a median spine at about mid-glabellar length. Genal spine posterolaterally directed. Pygidium broad with 9–10 axial rings and three pairs of broad pygidial ribs that taper strongly distally.

Description. Semicircular cranidium strongly convex (tr., sag.). Glabella narrow, especially posteriorly where the ridge-like occipital ring occupies about 15 % of the posterior cephalic width, narrowing slightly in front of the occipital furrow but almost doubling in width anteriorly. Thorn-like median spine developed about half way along the glabella. Axial furrows deep, curved concave outwards although this may be exaggerated by post-mortem distortion. Triangular genal lobes convex. Posterior border transversely directed, narrow but broadening a little towards the genal angle where it is confluent with the lateral border. Genal spine very short, directed slightly rearwards. Posterior border furrow broad and shallow, arched very slightly forwards. Lateral border narrows considerably in front of the genal angle and becomes ridge-like and confluent with a narrow anterior border (Fig. 5k, p). Facial suture in front of the glabella delimits the outer edge of the cranidial border. External surface of glabella and genal lobes (excluding borders and border furrows) finely pitted and bearing irregularly distributed large granules that are more pronounced on the otherwise smooth internal moulds.

Free cheek, hypostome and thorax not known. Pygidium gently convex (tr.), broad; sagittal length (excluding spines) about three quarters of maximum width. Axis tapers evenly rearwards except over the posterior 15 % of its length where it tapers more strongly to a point a short distance from the posterior edge of the pygidium. Axis bears an anterior articulating half-ring, 9–10 (n = 4) rings and a short triangular terminal piece. Rings essentially transversely directed except for the posterior three or four, which are arched forward increasingly strongly. Ring furrows are very shallow mesially, deepening markedly abaxially into slot-like apodemal pits. This is especially the case on the external surface, and both here and on internal moulds, the mesial depth is greatest on the first two furrows. Axial furrow only impressed against the first two axial rings and the posterior-most part of the axis. Over the remainder, there is simply a slight break in slope between the axis and the inner pleural rib. Three pairs of ribs present, the first two originating opposite

the first two axial rings; the third extending alongside the axis and weakly differentiated from it except posteriorly. First two ribs divided into a larger strongly swollen inner band and a narrower, much more subdued outer one. Anterior rib curving strongly abaxially rearwards to become parallel to the other two ribs; all three taper very markedly distally. External surface and internal mould of pygidium bear scattered small granules.

Discussion. The presence of three rather than two ribs on the pygidium allies *Dindymene whittingtoni* sp. nov. to *D. longicaudata* Kielan, 1960 and *D. brevicaudata* Kolobova, 1972 and distinguishes it from most named species of *Dindymeme* including several broadly coeval species. These include the type species *D. fridericiaugusti* Hawle & Corda from Bohemia (= *D. speciosa* Hawle & Corda and *D. haidingeri* Barrande (see Shaw, 2000, p. 386; but see also Kozák & Vaněk, 1997) and possibly *D. cordai* Nicholson & Etheridge from the Rawtheyan of Girvan (see Ingham, 1974, p. 85)), *D. ornata* Linnarsson from Sweden, Poland and Wales (see Kielan, 1960; Whittington, 1968; Price & Magor, 1984), *D. hughesiae* Reynolds (see Ingham, 1974) from the North of England and *D. ovalis* Weir from Ireland. Owen & Ingham (1996, p. 159) suggested that the last of these may prove to be a junior synonym of *D. ornata*.

D. longicaudata was described originally from the *Staurocephalus clavifrons* Zone of the Holy Cross Mountains in Poland and equivalent horizons in Sweden (Kielan, 1960, pp. 153–6, pl. 26, fig. 5; pl. 28, fig. 5; pl. 29, fig. 4; pl. 30, figs 1–3; text-fig. 43; see also Kielan-Jaworowska, Bergström & Ahlberg, 1991, p. 240). Price (1980) subsequently described the species from the Ashgill of Wales. The present material differs from *D. longicaudata* in having a more slender glabella (occipital ring occupying about 15 % cf. about 25 % of the posterior cephalic width), a more forwardly placed median glabella spine, cephalic axial furrows curving outwards slightly rather than simply divergent forwards, shorter genal spines directed posterolaterally rather than anterolaterally, a proportionally broader pygidium, fewer pygidial axial rings (9–10 cf. 11–12) and pygidial pleural ribs that are proportionally broader over most of their length but taper more strongly distally.

D. brevicaudata from the Sandbian Karagach Formation of the Tarbagatai Range in Kazakhstan was redescribed by Ghobadi Pour *et al.* (2011, pp. 181–2, figs 5d, 12a–d, f–g). *D. whittingtoni* can be distinguished from it by the stronger anterior expansion of the glabella, the presence of genal spines, the pygidium having more axial rings (9–10 cf. 6–7) and the third pygidial rib being much less well differentiated from the axis. Ghobadi Pour *et al.* (2011, p. 184, fig. 13a–h) described as *D.* aff. *longicaudata* Kielan specimens co-occurring with, and having a similar cephalic morphology to, *D. brevicaudata* but with a pygidial axis comprising 9–12 rings. The third pygidial rib in these specimens is very short and thus unlike those of Kielan's species or *D. whittingtoni*.

Ingham (1974, p. 85) noted the presence of an undescribed species of *Dindymene* with three pygidial pleural ribs in the uppermost Caradoc–lower Ashgill Upper Whitehouse Subgroup at Girvan, SW Scotland. He noted the narrow posterior part of the glabella in this material; this also suggests some similarity to the present new species.

Three pygidial pleural ribs are also known in *Dindymene pulchra* Olin from the lower Ashgill of Sweden and Poland, which was redescribed by Kielan (1960, pp. 144–6, pl. 27, figs 1–2; pl. 28, figs 3–4; pl. 29, fig. 6; text-figs 9a, 40) who based her monotypic genus *Eodindymene* on it. *Eodindymene* was separated from *Dindymene* on the basis of the facial suture cutting across the anterior part of the glabella and the outer parts of the genal lobes rather than being located in front
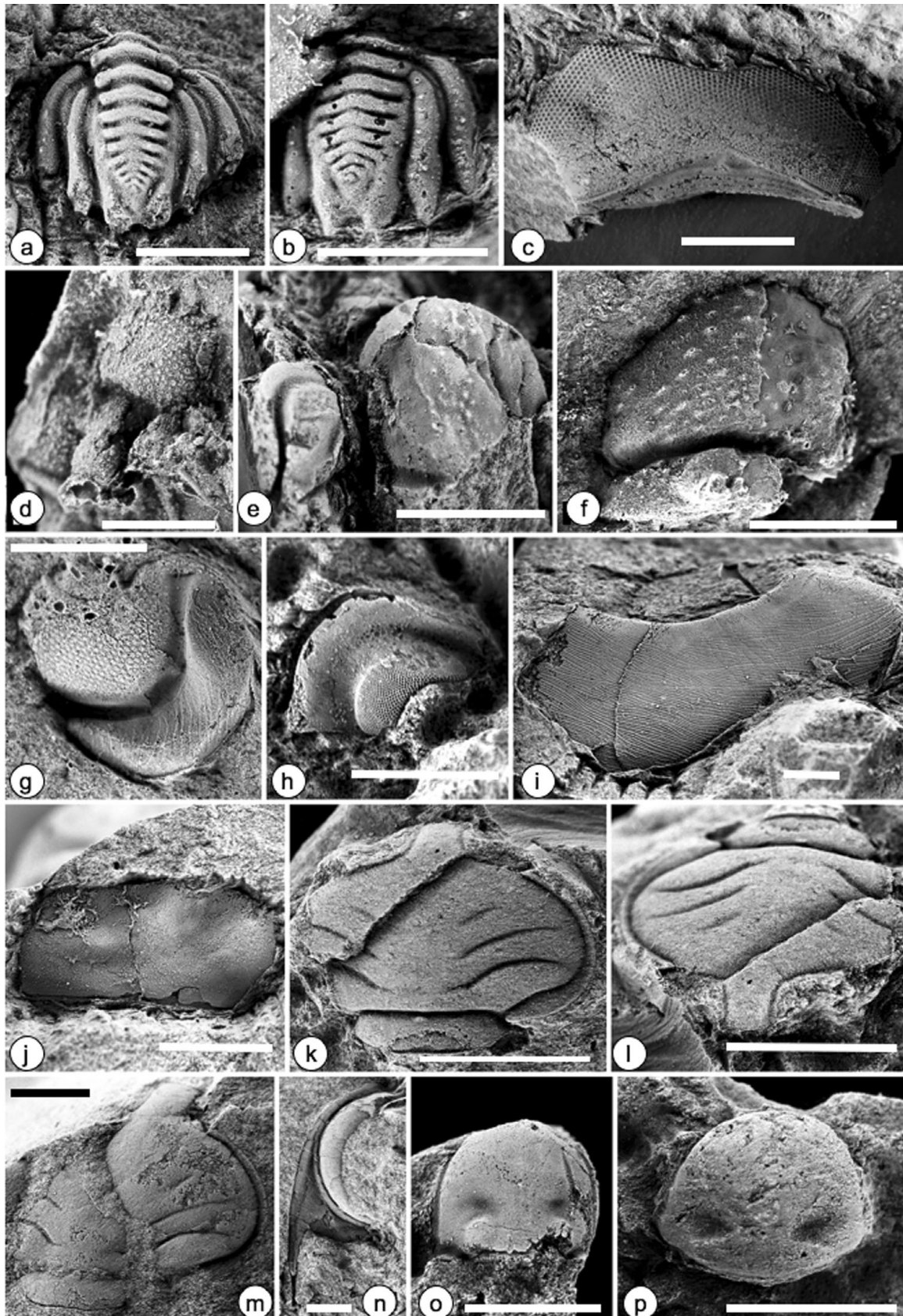
Figure 3. Scale bars are 4 mm unless otherwise stated. (a, b) *Dindymene whittingtoni* sp. nov. (a) pygidium, dorsal view, PMO 141.952, scale bar 2 mm; (b) pygidium, dorsal view, latex cast, PMO 141.947. (c) *Symphysops* sp. conjoined eyes with doublure below, anterior view, PMO 142,165. (d) *Staurocephalus* cf. *clavifrons* Angelin, 1854, cranidium, oblique lateral view, latex cast, PMO 208.309. (e–h) *Telephina* cf. *fracta* (Barrande, 1852) (e) incomplete cranidium, dorsal view, PMO 142.014; (f), glabella and occipital ring, dorsal view, latex cast, PMO 208.306; (g) latex cast of free cheek, PMO 142.143; (h) free cheek, PMO 142.142. (i) *Nileus*? sp.? ventral view of doublure, PMO 142.146. (j) Asaphid? indet. axial ring?, PMO 142.145. (k–n) *Amphitryon radians* (Barrande, 1846) (k, l) cranidium, dorsal and frontal views, PMO 142.008; (m) two cranidia, dorsal view, PMO 142.012; (n) free cheek, PMO 142.006. (o, p) *Cyclopyge* aff. *marginata* Hawle & Corda, 1847 (o) cranidium, dorsal view, PMO 142.156; (p) cranidium, dorsal view, PMO 142.160.

of the glabella and delimiting the outer edge of the cranidial border (see Kielan, 1960, text-fig 9). Fortey & Owens (1987, p. 235) doubted whether this character was sufficient to warrant generic separation of *Eodindymene* and suggested that Kielan's taxon should be relegated to subgeneric status. Dr Simon Peers (unpub. Ph.D. thesis, Univ. Glasgow, 1997) argued that *Eodindymene* should simply be synonymized within *Dindymene*. In addition to the course of the facial suture, *D. whittingtoni* differs from '*E*'. *pulchra* in its shorter, posterolaterally directed genal spines, narrower posterior part of the glabella, curved rather than simply divergent axial furrows and in its greater number of rings on the pygidial axis of some specimens (range of 9–10 cf. 8–9 rings).

Family STAUROCEPHALIDAE Prantl & Přibyl, 1947
Genus *Staurocephalus* Barrande, 1846

Type species. Staurocephalus murchisoni Barrande, 1846 from the Liteň Formation (Wenlock), Bohemia, Czech Republic.

Staurocephalus cf. *clavifrons* Angelin, 1854
Figure 3d

Material. An incomplete external mould of a cranidium.

Discussion. Although poorly preserved, this cranidium closely matches the redescription of *S. clavifrons* by Kielan (1957, pp. 163–7, pl. 3, figs 2, 3; pl. 4, figs 1, 2; text-figs 2, 3) based on the type specimen from the Rawtheyan of Västergötland, Sweden, other material from Västergötland and Scania in Sweden and a large collection from the *Staurocephalus clavifrons* Zone in the Holy Cross Mountains in Poland. Kielan-Jaworowska, Bergström & Ahlberg (1991, p. 240) noted the presence of 19 topotype specimens of *S. clavifrons* in the collections of the Riksmuseum, Stockholm but noted that they add nothing to the description provided by Kielan (1957). Hammann & Leone (2007, pp. 73–4, 76–7, pl. 46, figs 11, 12) assigned material from the Ashgill of Sardinia to *S. clavifrons* and reviewed the upper Ordovician species of *Staurocephalus*. They considered that differences in the surface sculpture of specimens described by Ingham (1977) from the uppermost Rawtheyan of the Cautley district of northern England compared to Kielan's Polish material were not significant and hence they reassigned this and other Ashgill material from northern England, Wales and eastern Ireland to Angelin's species unequivocally (see also Whittington, 1965*a*; Dean, 1971; Price, 1980; Owen & Romano, 2011). In addition to the European occurrences of *S. clavifrons*, Hammann & Leone (2007) supported the assignment of material from the Rawtheyan of Inner Mongolia by Zhou & Zhou (1982) to Angelin's species.

The present cranidium differs from that of *S.* aff. *clavifrons* from the Rawtheyan of Cross Fell in northern England described by Ingham (1977, p. 89, pl. 19, figs 8, 9) in its much finer tuberculation. It also differs from that of *S. pilafrons* Owen & Bruton (1980, pp. 30–1, pl. 9, figs 1–7) from the uppermost Caradoc of the Oslo Region, Norway in having a proportionally narrower glabella behind the swollen frontal lobe.

Family TELEPHINIDAE Marek, 1952
Genus *Telephina* Marek, 1952

Type species. Telephus fractus Barrande, 1852 from the Králův Dvůr Formation (middle Ashgill; upper Katian), Bohemia, Czech Republic.

Telephina cf. *fracta* (Barrande, 1852)
Figure 3e–h

Material. An incomplete cranidium, an external mould of a glabella and two free cheeks.

Discussion. The material is not well preserved and Bruton (*in* Neuman, 1994) provisionally assigned the cranidium to *Glaphurus*. However, the arrangement of the tubercles and associated lirae on the glabella and the configuration of the fixed cheek of the cranidium indicate that it belongs in *Telephina*. The latex peel of the broader glabella (Fig. 3f) has evenly distributed tubercles with a fine granulated background and traces of lirae, but the glabella on the internal cranidial mould (Fig. 3e) has tubercles on the central part only. The incomplete occipital ring (Fig. 3f) has the broken base of a spine.

Members of the Telephinidae had a world-wide distribution during Ordovician time and are thought to have formed part of the epipelagic trilobite community (Fortey, 1985). Bruton & Høyberget (2006, p. 363) considered that the occipital spine in species of *Telephina* is one of the features indicating a pelagic adaptation while cranidia lacking this feature may be immature and adapted to a benthic period of life. Shaw (2000, p. 387, pl. 7, fig. 15) refigured the lectotype of the type species, *T. fracta*, from the upper part of the Králův Dvůr Formation. This is an internal mould of a cranidium and together with fragmentary material was considered to represent a poorly defined species. However, the present specimens share with it a broad glabella bearing faint tubercles, an occipital ring with spine and an arcuate facial suture. *T. angulata* (Yi) from the Shihtzupu Formation (Darriwilian) of SW China, has an angulate facial suture (Zhou, Yin & Tripp, 1984, p. 23, fig. 5j, k, m, n) as does the Caradoc species *T.* cf. *convexa* Yin *et al*. (2000, p. 209, fig. 4a–c) from the Pagoda Formation, Guizhou Province and the Ashgill species *T. jui* Xiang & Ji (1987, pl. 1, fig. 11) from the Linxiang Formation of South China, which also lacks an occipital spine. A seemingly widespread Caradoc–Ashgill species is *T. convexa* Lu (see Tripp, Zhou & Pan, 1989, p. 44, fig. 9o; Fortey, 1997, p. 425, pl. 5, figs 16–17), but this has a narrow occipital ring and the inner portion of the fixed cheek is slim and curved convex outwards.

Family REMOPLEURIDIDAE Hawle & Corda, 1847
Genus *Amphitryon* Hawle & Corda, 1847

Type species. Caphyra radians Barrande, 1846 from the Králův Dvůr Formation (middle Ashgill; upper Katian) of Bohemia, Czech Republic. (Senior subjective synonym of *Amphitryon murchisonii* Hawle & Corda, 1847 (see Marek *in* Horný & Bastl, 1970).)

Discussion. Zhou & Zhou (2007) have made a convincing case that *Remopleurella* Dean, 1963 (type species *Remopleurides burmeisteri* Bancroft, 1949) is a junior subjective synonym of *Amphitryon* and that the supposedly diagnostic difference in the width of the glabellar tongue is an extremely variable character that is insufficient to sustain any taxonomic separation between the two.

Amphitryon cf. *radians* (Barrande, 1846)
Figure 3k–n

Material. Nine cranidia, one free cheek and one fragmentary pygidium.

Discussion. Whittington (*in* Boucot *et al*. 1964) originally assigned these specimens to *Remopleurides* but they were listed as belonging in *Amphitryon radians* by Bruton (*in* Neuman, 1994) and Owen & Bruton (2008). Hammann & Leone (1997, pp. 56–8) provided an extensive discussion of material assigned to *Amphitryon* which need not be repeated here. The type species, *A. radians*, has been widely described (see Kielan, 1960, p. 65 and Ingham, 1970, p. 14 for synonymies). Whittington (1966, p. 72, text-fig. 4)

reviewed its history and figured Bohemian material including topotypes from the Králuv Dvůr Formation at Králuv Dvůr and material from Lejškov, a locality from which specimens show variation in the width of the glabellar tongue (compare Whittington, 1966, text-fig. 4b and Shaw, 2000, pl. 2, fig. 21). Kielan (1960, pp. 65–6) discussed the length of the glabellar tongue and provided measurements of various specimens including those from Lejškov in the collections of the former Palaeontological (= Geological) Museum (PMO), in Oslo. These specimens together with those figured by Whittington (1966) and Shaw (2000) have longer glabella tongues than those from the upper Katian of the Holy Cross Mountains (Kielan, 1960, pl. 2, figs 3, 7; pl. 3, fig. 12). The present specimens closely resemble the Polish material in this respect. The former are not compressed and thus the tongue curves abruptly downwards when the cranidium is viewed in true dorsal view; if compressed, a similar view shows a flatter and seemingly straighter and longer tongue (Whittington, 1966, fig. 4b; Kielan, 1960, pl. 3, fig. 12). The material from Maine together with that from Poland and northern England (Ingham 1970, pl.1, figs 27, 28) shows a wider glabella and occipital ring than does material from Bohemia but it is not easy to define significant differences between these and specimens from the Ashgill of Wales (Whittington, 1966, pl. 22, figs 8, 10, 11). The present cranidia have the small occipital node close to the occipital furrow noted on internal moulds of *A. radians* by Kielan (1960, p. 66; see also Whittington, 1966 and Ingham, 1970) but lack a Bertillon pattern on the glabella; a variable feature that seems very much dependent on the mode of preservation. Two juxtaposed incomplete cranidia figured here (Fig. 3m) may represent a stage in the process of moulting, but the absence of associated, articulated, exoskeletal parts indicates that this is unlikely.

A. insculptum Ji and *A. asiaticum* Chen from the upper part of the Pagoda Formation (upper Caradoc) of southwestern Shaanxi were redescribed and reassigned to *Amphitryon* from *Remopleurides*, respectively, by Zhou & Zhou (2007). Both species have broad glabellar tongues. Zhou & Zhou (2007, p. 175) also reassigned several earlier records of early Ashgill Chinese specimens with narrow glabellar tongues to *A. zhejiangensis* Ji, 1986, within which they included *A. cheni* Tripp, Zhou & Pan, 1989. They distinguished *A. zhejiangensis* from *A. radians* on the basis of its broader pygidium with a shorter post-axial field and less well incised interpleural furrows.

<div align="center">

Family CYCLOPYGIDAE Raymond, 1925
Subfamily CYCLOPYGINAE Raymond, 1925
Genus *Cyclopyge* Hawle & Corda, 1847

</div>

Type species. Egle rediviva Barrande, 1846 from the Vinice Formation (upper Caradoc; lower Katian) of the Czech Republic.

Discussion. The genus *Phylacops* Cooper & Kindle, 1936 was established for species close to *Cyclopyge* in which the eyes are confluent frontally. Marek (1961) considered this to be insufficient to warrant the recognition of a separate taxon; a view that has been followed by most subsequent workers. However, Hammann & Leone (1997, p. 71) resurrected *Phylacops* as a subgenus of *Cyclopyge* and Jell & Adrain (2003, p. 469) retained its generic status in their compilation of available trilobite genus names. Neither view has been widely accepted. Shaw (2000, p. 389) and Karim (2009, p. 118) noted that anteriorly fused eyes occur in several cyclopygid lineages (see also Fortey, 1985, pp. 223–4). Karim (2009) argued that a phylogenetic analysis might resolve the relationships between taxa with such eyes and did not adopt

the use of *Phylacops* pending such an analysis; an approach followed herein.

<div align="center">

Cyclopyge aff. *marginata* Hawle & Corda, 1847
Figures 3o, p, 4a–e

</div>

Material. One cephalon, three cranidia, six free cheeks and 27 pygidia. A further seven indeterminate cyclopygid free cheeks (largely incomplete eyes) and two pygidia (= cyclopygids indet. of Owen & Bruton, 2008, table 1) may wholly or partly belong in *Cyclopyge*.

Discussion. Despite being the most abundant element of the fauna, the thin exoskeleton of *Cyclopyge* means that it is very prone to deformation and so it is not possible to provide a detailed description. Such deformation also applies to the many named upper Ordovician species of *Cyclopyge* and it is now widely recognized that several such taxa will prove to be synonymous. Hammann & Leone (1997) and Zhou & Zhou (2009) have undertaken such rationalization in redescribing *C. marginata* Hawle & Corda, 1847 and *C. recurva* Lu, 1962, respectively.

The glabellar proportions of the present material are very variable, but the more elongate specimens (e.g. Fig. 4e) also bear longitudinal ridges indicating lateral compression and suggesting that the proportionally broader specimens (e.g. Fig. 3o, p) are probably closer to the original shape. The glabella is invariably evenly rounded frontally which, together with the likely overall glabellar proportions, suggests an affinity to material ascribed to *C. marginata* Hawle & Corda, 1847 by Hammann & Leone (1997, pp. 76–80, pl. 8, figs 1–9; pl. 9, figs 1–16; text-figs 18–20) from the Katian of Sardinia. The original material of *C. marginata* is from the upper Katian Kráłův Dvůr Formation in the Czech Republic (see Marek, 1961) but, as noted by Shaw (2000, p. 389), it is poorly known from there. Dr J. K. Ingham of Glasgow University has kindly shown us illustrations of topotype material of Hawle & Corda's species that he will use to clarify the understanding of the species as part of his revision of the Girvan cyclopygids. Owen & Romano (2011) have recently compared material from the upper Katian of the Grangegeeth terrane in eastern Ireland to *C. marginata*. Hammann & Leone (1997) included *Phylacops bituberculatus* Weir, 1959 from Ireland and *Cyclopyge quadrangularis* Kielan, 1960 from Poland within Hawle & Corda's species along with material from the Girvan district of Scotland ascribed to *C. rediviva* (Barrande) by Nicholson & Etheridge (1880) and Reed (1904) as well as specimens assigned to various taxa from Kazakhstan, Central Asia and Turkey, giving *C. marginata* an extremely wide distribution.

Only one specimen from the Pyle Mountain Argillite (PMO 142.167) preserved the medial part of the conjoined free cheeks, but unfortunately this part of the cephalon was damaged following photography in dorsal and lateral orientations (Fig. 4d, e). It showed the eyes to be confluent frontally with a narrow median groove between the two sets of lenses as in material of *C. marginata* described by Hammann & Leone (1997). These authors considered that *Phylacops vigilans* Cooper & Kindle, 1936 from the upper Katian Grande Coupe Beds of the Matapédia Group in the Percé area of Quebec (see Lespérance *et al*. 1987) could be distinguished from *C. marginata* in having the visual surface of the eyes more completely confluent frontally where they also narrow (sag.) much less strongly. This may to some extent reflect preservational differences but perhaps more significantly, rather than a median groove, there is simply a slightly wider gap than between the rest of the lens files. Whether this is sufficient for the recognition of a separate
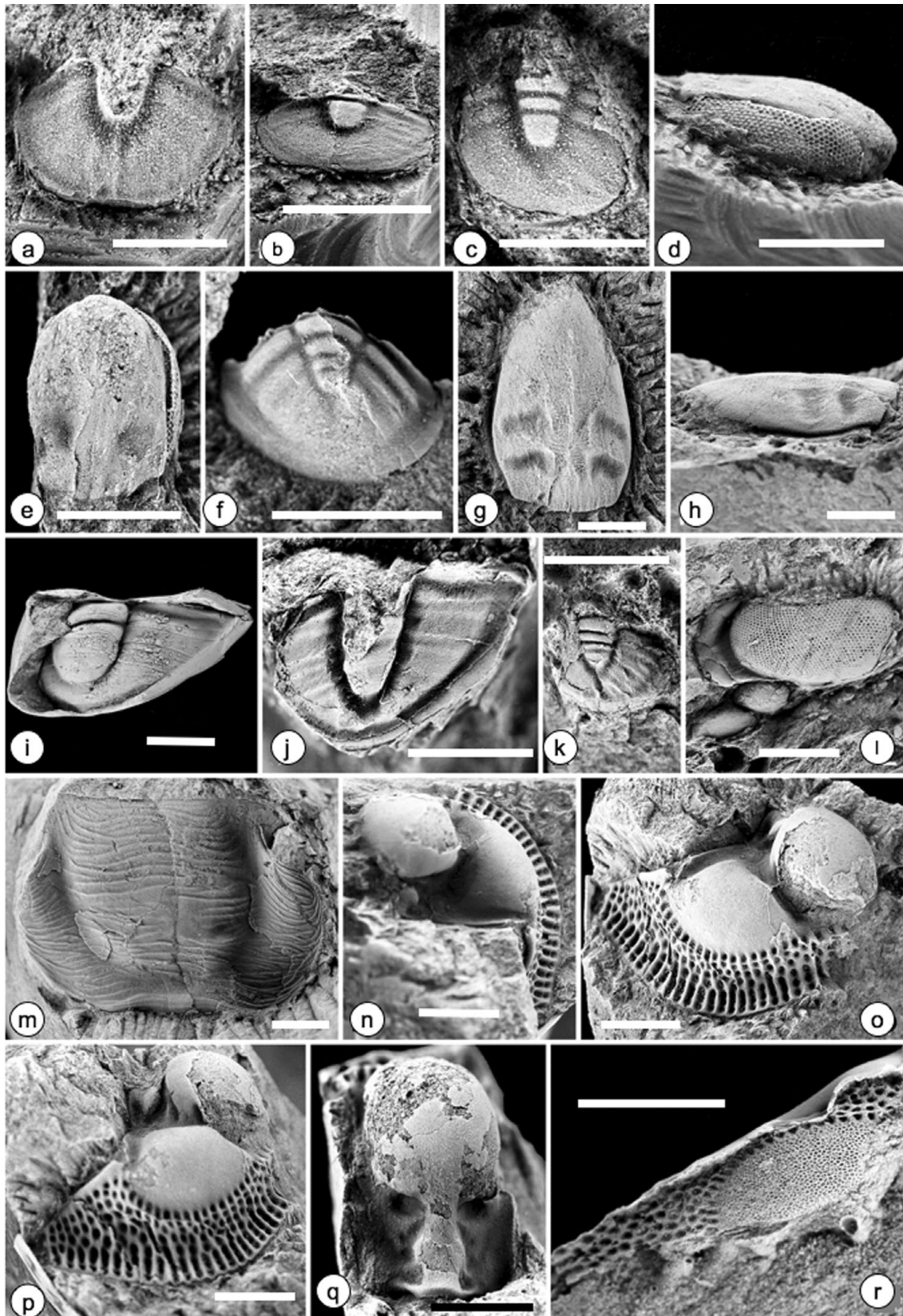
Figure 4. Scale bars are 4 mm unless otherwise stated. (a–e) *Cyclopyge* aff. *marginata* Hawle & Corda, 1847 (a) pygidium, dorsal view, PMO 142,168, scale bar 2 mm; (b) pygidium, dorsal view, PMO 142.16; (c) pygidium with two thoracic segments, dorsal view, PMO 142.155, scale bar 2 mm; (d, e) incomplete cephalon with right free cheek and eye, lateral and dorsal views, PMO 142.167. (f) *Microparia (Heterocyclopyge)* sp. pygidium, dorsal view, PMO 142.172. (g–l) *Symphysops* sp. (g–h) cranidium, dorsal and lateral views, PMO 142.151; (i) pygidium, dorsal view, latex cast, PMO 142.001; (j) pygidium, dorsal view, PMO 142,003; (k) pygidium, dorsal view, PMO 142.000; (l) cheek with eye, PMO 208.311. (m) *Nileus?* sp. hypostome, ventral view, PMO 141.978. (n–r) *Nankinolithus granulatus* (Wahlenberg, 1818) (n–p) incomplete cephalon, dorsal, oblique frontal and lateral views, PMO 141.971; (q) glabella, dorsal view, PMO 141.972; (r) detail of pitting on cheek inside brim, latex cast, PMO 208.307.

species is debatable. Hammann & Leone also suggested that the pygidium of the Canadian species differs from that of *C. marginata* in having a medial widening (sag., exsag.) of its border. This is not the case in most of the specimens illustrated by Cooper & Kindle but one (Cooper & Kindle, 1936, pl. 52, fig. 36) does have a very broad border posteriorly that tapers markedly laterally. This and the transversely rectangular outline of the pygidium distinguishes it from the other cyclopygids from the Matapédia Group. Hammann & Leone (1997, p. 75) considered *Cyclopyge angustata* Cooper & Kindle, 1936 from the same unit as *C. vigilans* to be similar to *C. marginata* but with the cranidium slightly more tapered forward. It was based on a single cranidium and detailed comparison must await further material.

Genus *Microparia* Hawle & Corda, 1847
Subgenus *Microparia* (*Heterocyclopyge*) Marek, 1961

Type species. Cyclopyge pachycephala Hawle & Corda, 1847, from the Vinice Formation (upper Caradoc; lower Katian) of the Czech Republic.

Microparia (*Heterocyclopyge*) sp.
Figure 4f

Material. One pygidium.

Discussion. The strongly ribbed axis and the presence of two distinct pleural ribs in this slightly deformed internal mould suggest an affinity to *Microparia* (*Heterocyclopyge*) *abunda* Zhou *et al*. 1994 from the Sandbian of Tarim. Although its axis is not as strongly tapered and the overall pygidial outline less transverse, the specimen is also reminiscent of the pygidium of *M.* (*H.*) *shelvensis* Whittard, 1961 from the lower Llanvirn (middle Darriwilian) of the Shelve district, Shropshire and the upper Llanvirn (upper Darriwilian) of Builth, central Wales (Owens, 2002). The overall outline is closer to that of *M.* (*H.*) *nigra* (Hörbinger & Vaněk, 1985) from the Dobrotivá Formation (uppermost Darriwilian–lower Sandbian) of Bohemia and also described by Owens (2002) from Builth. The axis is less tapered and the pygidial segmentation more strongly developed than in that species, however.

Cyclopyge kindlei Cooper *in* Schuchert & Cooper, 1930 and *C. insolens* Cooper *in* Schuchert & Cooper, 1930 from the upper Katian Grande Coupe Beds of the Matapédia Group in the Percé area of Quebec are in need of modern redescription but were reassigned to *Heterocyclopyge* by Lespérance (1968, pp. 813, 815). The pygidial axis of *M.* (*C.*) *kindlei* is short and shows subdued rings on the external surface; it is feasible that they may be more pronounced on internal moulds. The overall shape of the present pygidium is also comparable to that of Cooper's species but its preservation as an internal mound precludes detailed comparison with the named taxon.

Subfamily PRICYCLOPYGINAE Fortey & Owens, 1987
Genus *Symphysops* Raymond, 1925

Type species. Aeglina armata Barrande, 1872 from the Králův Dvůr Formation (middle Ashgill; upper Katian) of the Czech Republic.

Symphysops sp.
Figures 3c, 4g–l

Material. Five cranidia, two free cheeks and four pygidia.

Discussion. The present specimens are too poorly preserved to enable detailed comparison with the named upper Katian species of *Symphysops*. Moreover, as argued by several authors (e.g. Marek, 1961; Owen & Ingham, 1996; Hammann

& Leone, 1997; Shaw, 2000), the supposed differences between these upper Ordovician taxa are at best very limited and some or all may prove to be conspecific. As noted by Shaw (2000) the paucity of well-preserved specimens makes unequivocal comparisons impossible. The supposedly diagnostic characters are based on features that are highly susceptible to distortion and other preservational effects and there may also be substantial differences in material from the same locality between external surfaces and internal moulds (cf. Fig 4i, j herein) and between specimens of different size (cf. Fig 4j, k herein).

Shaw (2000, p. 390, pl. 8, figs 2–4) reillustrated the lectotype of the type species, *S. armata* (Barrande, 1872), selected by Marek (1961). He noted that no further specimens beyond those discussed by Marek had come to light. Hammann & Leone (1997) assigned material from the Katian of Sardinia to *S. armata* and provided an extensive comparison to all the other named upper Katian species and subspecies. They suggested that *S. spinifera* Cooper & Kindle, 1936 from the Matapédia Group in Quebec may be distinguishable from the type species in having the glabella less vaulted (tr.) and more elongate frontally and in having more pronounced terrace ridges on the glabella and posterior margin for the free cheeks. None of these distinctions seem to be sustainable. Owen & Ingham (1996, p. 146) included *S. spinifera* and *S. subarmata elongata* Kielan, 1960 from the upper Katian of Poland in the synonymy of *S. subarmata* (Reed, 1914) from the Whitehouse Subgroup (uppermost Caradoc–lowest Ashgill) at Girvan, SW Scotland. Whether or not *S. subarmata* can be distinguished from *S. armata* must await the redescription of the Girvan material.

Family NILEIDAE Angelin, 1854
Genus *Nileus* Dalman, 1827

Type species. Nileus armadillo, Dalman, 1827, from the uppermost Arenig–lower Llanvirn (Darriwilian) of Sweden (see Nielsen, 1995).

Nileus? sp.
Figures 4m, ?3i

Material. One hypostome and possibly a large fragment of doublure.

Description. The well-preserved hypostome was assigned to *Nileus* by Owen & Bruton (2008, table 1) and has a maximum width of 23 mm, the largest specimen in our collection. It is quadrate with a straight anterior margin and gently concave posterior margin upturned medially. The lateral margins are gently curved from behind the wing with rounded posterolateral corners. The anterior wings are not visible on the figured specimen but a fragment of the external mould of the broken left side does show a short wing. The gently convex median body tapers slightly rearwards and is rounded posteriorly inside the upturned margin. Weak maculae occur posteriorly and are most obvious where the area is not crossed by the well-defined terrace lines. These are transverse across the median body but curve strongly rearwards posterior to the wings and straighten and bifurcate on the lateral margins behind a line drawn transversely through the maculae.

Discussion. Nielsen's (1995) detailed study of early Ordovician nileids excluded consideration of the hypostome beyond brief reference to illustrations in the literature. Brøgger (1886, pl. 3, fig. 40) and Hansen (2009, pl. 17, fig. 6) have illustrated hypostomes of the type species showing a slight median projection on the posterior border. There is no projection in the present specimen and, where developed, this is a variable feature within *Nileus* (e.g. compare that of *N. affinis* Billings illustrated by Whittington, 1965*b*, pl. 31,

fig. 4 from Newfoundland with that of *N. porosus* Fortey, 1975, pl. 12, fig. 6 from Spitsbergen). Schrank (1972) illustrated hypostomes ascribed to *N. exarmatus* Tjernvik both with and without a median projection (1972, pl. 2, fig. 5 and pl. 2, fig. 9, respectively). The forward curvature of the posterior margin of the present specimen is less than that of the hypostome assigned to *Nileus transversus* Lu, 1957 by Tripp, Zhou & Pan (1989, p. 37, fig. 6a, b) from the middle Katian (upper Caradoc–lower Ashgill) of South China, which also lacks a median projection.

The Pyle Mountain Argillite specimen differs from the Scandinavian, Spitsbergen, Newfoundland and Chinese hypostomes assigned to *Nileus* in having less pronounced, more posteriorly placed maculae. It is identical to undescribed hypostomes in the Hunterian Museum, University of Glasgow, from the upper Myoch Fm and overlying Gray Member of the Mill Fm, Upper Whitehouse Subgroup at Girvan, SW Scotland. The Girvan material may be very slightly younger than the Maine fauna and includes other sclerites including free cheeks with typical *Nileus* eyes but bearing genal spines. Such spines are well developed in *Kodymaspis* Prantl & Přibyl (see Whittington, 2003, p. 638), *Peraspis* Whittington (but see Whittington, 2003, p. 642 concerning familial placement) and *Elongatanileus* Ji (see Fortey, 1997, p. 412). Genal spines are generally absent in *Nileus* but were reported in some specimens of *N. transversus* Lu by Tripp, Zhou & Pan (1989, p. 37) and a minute spine was illustrated in a small cephalon of *N. orbiculatoides svalbardensis* Fortey (Fortey, 1975, pl. 11, figs 1, 2). The poorly preserved hypostome of *Nileus? domusnovensis* Hammann & Leone (1997, p. 84, pl. 11, fig. 2; text-fig. 22) from the upper Katian of Sardinia has the maculae far back on the median body but the posterior margin has a median projection. Turvey (2007, p. 386) suggested that the Sardinian species may belong in *Elongatanileus*.

A large fragment of doublure (Fig. 3i) has a Bertillon pattern similar to that on the dorsal surface of the atheloptic nileid *Illaenopsis* Salter (see Fortey & Owens, 1987, pp. 197–8), the normal-eyed *Kodymaspis* Prantl & Přibyl (see Šnajdr, 1984, p. 147) and at least one species of *Nileus*, *N. implexus* Nielsen (1995, fig. 208B) from the lower Darriwilian of Sweden. The ventral cephalic doublure of the third of these has not been described but that of the other two bears 'normal' terrace ridges. The same applies to the Girvan nileid noted above, suggesting that if the Pyle Mountain Argillite hypostome is from the same species as that from Girvan, then the doublure fragment represents a different taxon.

Family TRINUCLEIDAE Hawle & Corda, 1847
Subfamily TRINUCLEINAE Hawle & Corda, 1847
Genus *Nankinolithus* Lu, 1957

Type species. *Nankinolithus nankinensis* Lu, 1957 from the Tangtou Formation (lower Ashgill; upper Katian), Tangtou, Tangshan, Jiangning County, Jiangsu, China. (See Zhou & Hughes, 1989, p. 68 for discussion of the date of the first formal description of the species and therefore the genus.)

Nankinolithus granulatus (Wahlenberg, 1818)
Figure 4n–r

1818 *Entomostracites granulatus* Wahlenberg, p. 15, pl. 2, fig. 4.
1996 *Nankinolithus granulatus* (Wahlenberg); Pålsson, p. 157, fig. 5H.
1997 *Nankinolithus granulatus* (Wahlenberg); Hammann & Leone, pp. 59–62, pl. 24, figs 1–12.
2011 *Nankinolithus granulatus* (Wahlenberg); Owen & Romano, p. 423, fig. 3F.

For full synonymy see Hammann & Leone (1997, p. 59).

Material. Two cephala, seven cranidia and two lower lamellae.

Discussion. The broad fringe with a large genal prolongation bears about 30 sulci (half-fringe) containing arcs I_1, E_{1-2}. There are up to four other I arcs (including I_n) on the anterolateral part of the fringe and an increasing amount of pit irregularity towards the posterior of the fringe. The material falls well within the range of variation of the widely distributed upper Katian (middle Ashgill) *Nankinolithus granulatus*. The history of the species and its junior synonyms was summarized by Hammann & Leone (1997) who included material within it from Sweden (including the type locality), Poland, Bohemia, Sardinia, Wales and the Girvan district of Scotland. They also included records of the species from the upper Katian of Quebec (e.g. Lespérance, 1968) but noted that these have yet to be supported by illustrations. Hammann & Leone described a wide range of variation in the extent of the E_2 arc (which is complete or nearly so in the present material) and in the depth of the radial sulci. They attributed the latter to preservational differences, but the extremely weak development of these depressions in some of the material described from South Wales by Price (1980, pl. 109, figs 3, 4, 10) indicates that there is at least a degree of original phenotypic variation in this feature.

In describing a large sample of topotype material of the type species of *Nankinolithus*, *N. nankinensis* Lu, Tripp, Zhou & Pan (1989, pp. 47–9, 51, figs 2M, 10b–f, j–m, 11A–J) noted that all the Chinese species are typified by the presence of a single E arc. *N. yanhaoi* Zhou & Hughes, 1989 is an exception in having E_2 pits present anteriorly and anterolaterally. *N. granulatus* differs from this species, however, in having a much broader fringe with more I arcs and a larger genal prolongation.

All of the Chinese species of *Nankinolithus* are early to middle Ashgill in age in terms of the Anglo-Welsh chronostratigraphy (see Zhou & Zhou, 2008, table 8.1) and the material from around the Iapetus and Rheic oceans ascribed to *N. granulatus* is of middle Ashgill age. However, the poorly known *N. portrainensis* (Reed, 1897) from the 'Trilobite Shales' within the upper Portrane Volcanic Formation in eastern Ireland is broadly constrained as late Caradoc–early Ashgill in age (Harper & Parkes *in* Fortey *et al.* 2000, p. 56) and material from the Myoch and Mill formations at Girvan, SW Scotland currently being described by Dr J. K. Ingham of Glasgow University spans that interval. Preliminary analysis of *N. portrainensis* by one of us (AWO) and of the Girvan material by Ms K. Keefe (unpub. M.Sc. thesis, Univ. Glasgow, 2004) suggests strong affinities to *N. granulatus*. Hughes, Ingham & Addison (1975, p. 559) placed *Bergamia praecedens* (Klouček) from the upper Dobrotivá Formation (approximately lowest Sandbian) in Bohemia in *Nankinolithus* but Zhou & Hughes (1989, pp. 67–8) and Shaw (1995, pp. 5–7) have since argued that Klouček's species should remain in *Bergamia*.

Genus *Novaspis* Whittington, 1941

Type species. *Tretaspis elevata* Cooper & Kindle, 1936 from the Ashgill (= upper Katian) of Quebec.

Discussion. The holotype specimen is from Cooper & Kindle's locality 1 at Priest's Road in what have became known as the Grande Coupe beds within the Matapédia Group (see Lespérance *et al.* 1987, p. 125). Whittington (1941, p. 40) also collected and described a specimen from here. Cooper & Kindle also recorded the species from their locality 13 in what is now termed the Pabos Formation near

Grande Rivière. Lespérance & Weissenberger (1998, p. 304) stated that this is the type locality and that the species does not occur outside that formation. No reasons were given for this contradiction of the earlier stated occurrences in the Grande Coupe beds at Priest's Road, nor was there any mention of *N. elevata* in that unit by Lespérance *et al.* (1987) or Lespérance (1968).

Novaspis cf. *albida* (Reed, 1914)
Figure 5a–d

Material. One almost complete cranidium and one postero-lateral part of a cephalon including genal spine.

Discussion. The specimens show the narrow cephalic fringe with two complete arcs (I_n and E_1) and a few pits in I_1 posterolaterally typical of the genus. The more complete of the specimens shows the almost spherical pseudofrontal lobe and swollen genal lobes seen in *Novaspis albida* (Reed). Reed's species from the Upper Whitehouse Subgroup at Girvan, SW Scotland is being revised by Dr J. K. Ingham of Glasgow University and specimens were illustrated by Hughes, Ingham & Addison (1975, pl. 4, figs 55–8). Kielan (1960, pp. 175–8, pl. 34, fig. 3; pl. 36, figs 1–5; text-fig. 50) ascribed specimens to *N. albida* from the upper Katian of the Holy Cross Mountains having also examined type and topotype material of Reed's species in the Natural History Museum, London. She considered similar ranges of apparent variation in the overall shape and inflation of the pseudofrontal lobe to be a result of post-mortem deformation in both the Girvan and the Polish samples. Kielan distinguished *N. albida* from the type species, *N. elevata* (Cooper & Kindle) on the basis of its less strongly inflated pseudofrontal lobe, more rounded cephalic outline and less elongated posterior parts of the fringe. In the holotype cranidium of *N. elevata* (Cooper & Kindle, 1936, pl. 52, figs 19, 25, 28) the glabella stands well above the very weakly convex genal lobes. This is difficult to reconcile with post-mortem deformation although the rather transverse cephalic outline and posterior fringe may well reflect such distortion. The cranidium figured by Whittington (1941, pl. 6, figs 7, 8) is less transverse and the glabella may not be as elevated as in the holotype, although Whittington did not illustrate his specimen in frontal view.

A single specimen from the *Staurocephalus clavifrons* Zone (upper Katian) in the Holy Cross Mountains was described as *N.* sp. by Kielan (1960, p. 178, pl. 35, fig. 3) on the basis of its unusually large pit count. In modern terminology, this is reflected in there being about 21 pits in E_1 between the axial furrow and posterior margin (cf. about 19 or fewer in the entire half-fringes of the illustrated material of *N. elevata* and *N. albida*). This may simply represent an extreme value in the natural range of variation in pit numbers.

Weir (1959, pp. 371–2) described material from the upper Katian (Ashgill) of County Clare, Ireland as *N.* aff *albida*, but as Hughes, Ingham & Addison noted (1975, p. 567), it is clear from the description and some of the illustrations that other trinucleines may be present in addition to *Novaspis*. The similarity of specimens from the Abercwmeiddaw Group in North Wales to *N. albida* suggested by Price & Magor (1984, fig. 4a, b) seems reasonable.

Novaspis abbatialis Lespérance *in* Lespérance & Sheehan, 1988 was based on a single, incomplete, distorted cranidium from the upper Katian of Belgium. Only a part of the fringe is preserved and shows a few anterolateral I_n pits, outside of which is a distinct list beyond which the fringe is deflected steeply downwards and bears an arc of pits in radial alignment with those of I_n. It is not clear whether this is the outermost arc or whether it is simply the inner part of a much broader

fringe extending down into the matrix. However, the genal lobe is strongly reticulate and bears a lateral eye tubercle: features unknown in *Novaspis* but also present in *Tretaspis*, which is also described from the same locality and seems the likely identification for this specimen.

Family DIONIDIDAE Gürich, 1907
Genus *Dionide* Barrande, 1847

Type species. *Dione formosa* Barrande, 1846 from the Zahořany Formation (upper Caradoc; lower Katian) of Bohemia, Czech Republic.

Dionide sp.
Figure 5e–g, i–j

Material. Ten cranidia and ten pygidia.

Discussion. The present specimens include pygidia previously assigned to *Dalmanitina* by Bruton (*in* Neuman 1994, p. 1221) and are similar in various combinations of characters to several middle and upper Katian (uppermost Caradoc and Ashgill) species of *Dionide*, some of which are in need of modern description and illustration. In addition, it is clear that some features such as the preservation of glabellar spines and details of genal caeca can be strongly influenced by preservation (Shaw, 2000, p. 390) or by ontogenetic development even within the holaspis stage (Ingham *in* Tripp, Zhou & Pan, 1989, pp. 51–2). Original cranidial proportions are difficult to determine with certainty because of the effects of post-mortem distortion but probably lie somewhere between a semicircular outline (as in Fig. 5f which has undergone some transverse shortening) and one in which the sagittal length is equivalent to about 40 % of the posterior width (as in Fig. 5e). The apparent absence of a median glabellar swelling or spines may be diagnostic but given the degree of crushing of the present specimens, the possibility of an originally weak, broad swelling cannot be excluded. Pending a more thorough investigation of the upper Ordovician species of *Dionide*, the present material is retained under open nomenclature but a fairly extensive review of its possible affinities is given.

In its glabellar features, the lack of differentiation of the genal lobe from the fringe and the medial extent of the fringe, the Maine specimens strongly resemble *D. magnifica* Owen & Bruton, 1980 from the uppermost Caradoc (middle Katian) of the Oslo Region and *D. jemtlandica* Månsson, 2000 from the upper Llanvirn to the middle Caradoc (approximately upper Darriwilian to lower Katian) of Jämtland, Sweden but the cranidium can be distinguished in the absence of a median glabellar swelling, the more subdued genal caeca and probably in having a less transverse outline. The pygidium of the Pyle Mountain Argillite taxon has fewer pleural ribs (12–14; n = 5) than those of *D. magnifica* (17–19) and *D. jemtlandica* (16) and, to some extent, axial rings (15–17; n = 3 cf. 17–19 and 16–18, respectively). The American material differs from another Baltic taxon, *D. euglypta* (Angelin) from the uppermost Katian Upper Jonstorp Formation in Västergötland Sweden (see Månsson, 2000, pp. 320–1, fig. 5), primarily in having the fringe extending in front of the glabella and in the essentially transverse posterior margin of the cranidium; that of *D. euglypta* curves strongly rearwards over its outer parts.

The present material also resembles *D. speciosa* (Hawle & Corda) from the Ashgill Králův Dvůr Formation in Bohemia illustrated by Shaw (2000, 390–1, pl. 8, figs 10–15), differing in the more distinct glabellar constriction, prominent longitudinal glabellar furrows and probably lower glabellar convexity. One of the specimens illustrated by Shaw (2000, pl. 8, fig. 15) shows a marked coarsening of the fringe
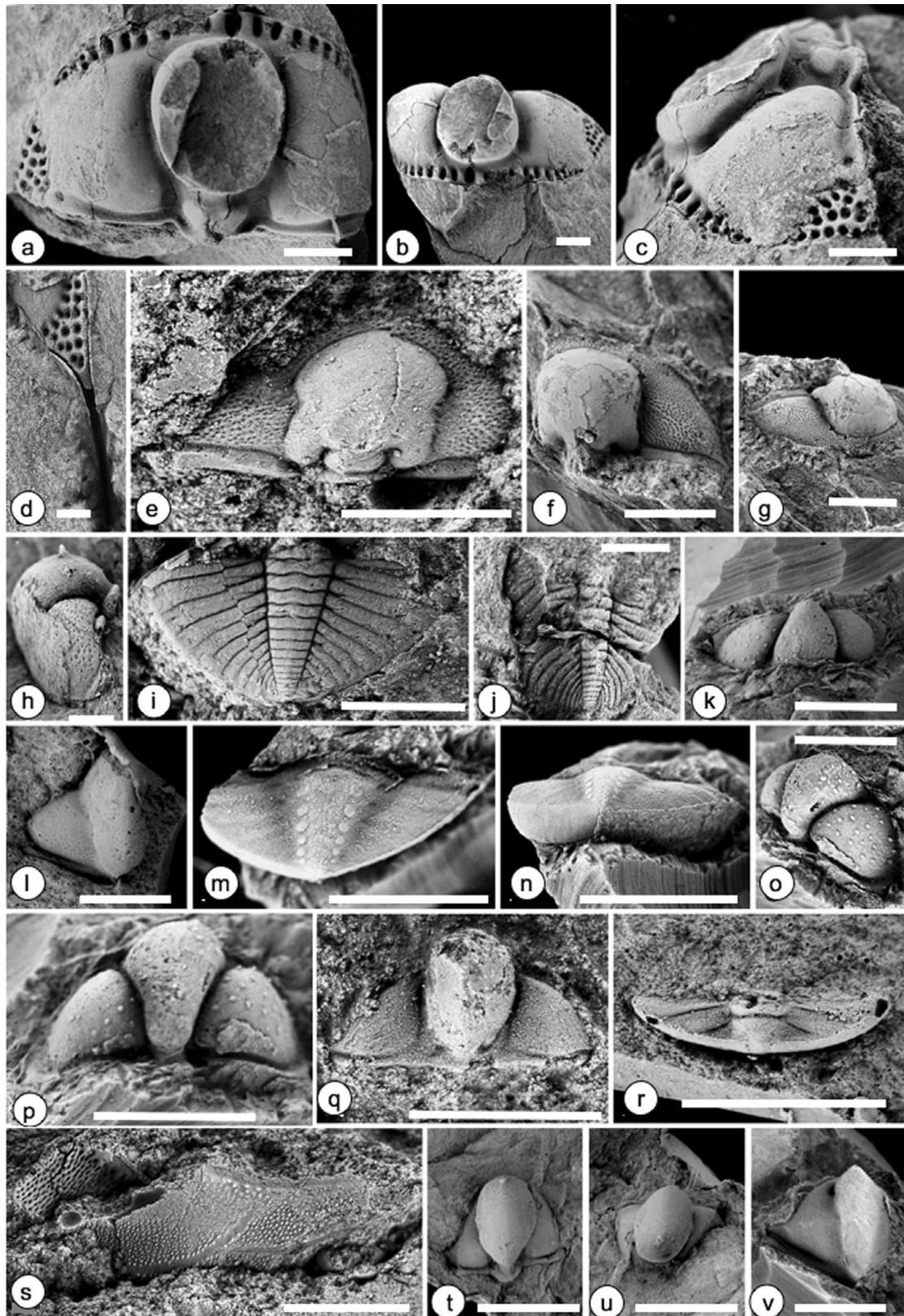
Figure 5. Scale bars are 4 mm unless otherwise stated. (a–d) *Novaspis* cf. *albida* (Reed, 1914) (a–c) cephalon, dorsal, frontal and lateral views, PMO 141.976; (d) cheek with long spine, PMO 141.974. (e–g, i–j) *Dionide* sp. (e) cranidium, dorsal view, latex cast, PMO 141.962/1, scale bar 2 mm; (f, g) cranidium, dorsal and anterior views, PMO 141.966; (i) pygidium, dorsal view, PMO 142.013; (j) pygidium with part thorax, PMO 142.016, scale bar 2 mm. (h, k, o, p) *Dindymene whittingtoni* sp. nov. (h) cephalon, lateral view showing glabellar spine, latex cast, PMO 141.948, scale bar 2 mm; (k, o, p) cephalon, anterior, oblique posterolateral and dorsal views, PMO 141.954. (l–n, v) *Lonchodomas* sp. (l) incomplete cranidium, latex cast from external mould showing pitted surface on fixed cheek, PMO 208.312; (m, n) pygidium, dorsal and posterior views, PMO 142.03; (v) incomplete cranidium showing glabellar muscle scars and anterior pit, PMO 142.036. (q, r) *Raymondella?* sp. (q) cranidium, dorsal view, PMO 142.035, scale bar 2 mm; (r) latex cast from external mould of pygidium, dorsal view, PMO 142.029. (s) Harpetid indet. PMO 142.035. (t, u) *Raphiophorus* sp. latex cast from external mould of cranidium dorsal and anterior views, PMO 142.040.

pitting towards the margin. Setting aside the small, complete holaspid specimen figured by Shaw (2000, pl. 8, fig. 11), the number of axial rings in the Maine pygidia fall in the middle of the range given by Shaw for *D. speciosa* (13–18), although judging from his illustrations, the Bohemian specimens may have slightly fewer ribs (10–13 cf. 12–14). The glabella of *D. speciosa* is very similar to that of *D. decorata* Kielan, 1960 from the Ashgill *Staurocephalus clavifrons* Zone in the Holy Cross Mountains, Poland, but that species differs from both *D. speciosa* and the Maine specimens in the pitting on the genal lobes being much coarser than on the fringe and in having more pygidial ribs (16). The glabella of *D. semicircula* Owen, 1981 from the Rawtheyan of the Oslo Region, Norway, is to some extent intermediate between those of the specimens from Maine and *D. speciosa* but the genal lobe of the Norwegian species has a convexity independent of the fringe and the pitting on both lobe and fringe is extremely subdued. The glabellar spines are also more forwardly placed than in the Bohemian species.

Family RAPHIOPHORIDAE Angelin, 1854
Genus *Raphiophorus* Angelin, 1854

Type species. Raphiophorus setirostris Angelin, 1854, from the Fjäcka Shale Formation (upper Katian, lower Ashgill) of the Siljan district, Sweden.

Raphiophorus sp.
Figure 5t–u

Material. The external mould of a cranidium.

Discussion. The glabella of this specimen does not extend very far in front of the fixed cheeks, a feature considered characteristic of *Raphiophorus gratus* (Barrande) by Shaw (2000, p. 391) from the upper Katian Králův Dvůr Formation in Bohemia. *R. gratus* was also described by Kielan (1960, pp. 166–7, pl. 32, fig 6; pl. 33, figs 4, 5; pl. 36, fig. 7; text-fig. 48) from the upper Katian of Poland and Sweden. The present specimen is distinguished from *R. gratus* by its more pear-shaped glabella and arched occipital ring, and in these respects it resembles *R. tenellus* (Barrande) from the upper Katian of Bohemia (Whittington, 1968; Shaw, 2000), Poland (Kielan, 1960), Sweden (Kielan, 1960; Pålsson, 1996) and possibly Wales (Price, 1980).

Genus *Lonchodomas* Angelin, 1854

Type species. Ampyx rostratus Sars, 1835 from the Vollen Formation (Sandbian) on Bygdøy, Oslo, Norway.

Lonchodomas sp.
Figure 5l–n, v

Material. Three cranidia and three pygidia.

Discussion. Owen (1981, pp. 39–40) pointed out the need for a thorough revision of the many Ashgill species assigned to *Lonchodomas*. The genus is long-ranging and only well-preserved material in which details of the frontal spine and hypostome together with surface sculpture are known, can be directly compared. An incomplete cranidium from Maine (Fig. 5l) shows finer pitting than is present on *L. portlocki* (Barrande, 1846) from the upper Katian of Bohemia and Poland (Kielan, 1960) although Shaw (2000, p. 392) noted that the Bohemian material is not well preserved and it is difficult to see features of the surface sculpture. This is well preserved on the cranidium of *L.* aff. *pennatus* La Touche figured by Owen & Bruton (1980, pl. 7, fig. 1) from the upper Caradoc of the Oslo Region, Norway, and on similar material assigned to *L.* aff. *depressus* (Angelin) from the succeeding Ashgill (Owen, 1981, pl. 9, fig. 4). The Maine pygidium (Fig.

5m, n) is very like that of *L.* sp. from the uppermost Katian of Norway figured by Owen (1981, pl. 9, fig. 10) in having an evenly rounded margin with rim and poorly defined axial rings and pleural furrows on the internal mould but with six well-defined axial muscle scars.

Genus *Raymondella* Reed, 1935

Type species. Ampyx? macconochiei Etheridge & Nicholson *in* Nicholson & Etheridge, 1879, from the Balclatchie Formation (upper Sandbian) of Girvan, SW Scotland.

Raymondella? sp.
Figure 5q, r

Material. Two cranidia and one pygidium.

Discussion. Whittington (1959, p. 487) and Owen & Bruton (1980, p. 25) discussed the differences between the cephala of *Raymondella* and *Ampyxina*, which are remarkably similar, but the pattern of lirae with minute tubercles on the fixed cheek distinguishes *Raymondella* from most species of *Ampyxina* (but see Owen & Parkes, 2000, p. 261 for exceptions). Fine lirae and minute tubercles are present in the Maine specimens, which seem to be closer to *R. elegans* (Cooper, 1953) from the Lower Edinburg Formation of Virginia, USA (see Whittington, 1959, pp. 487–91) and *R.* sp of Owen & Bruton (1980, p. 25, pl. 7, figs 19–21) from the upper Caradoc–lower Ashgill (middle–upper Katian) of the Oslo Region, Norway than to the type species, *R. macconochiei* described by Whittington (1950, p. 558, p. 74, fig. 10; pl. 75, figs 1, 2). The only other Ashgill species known to us is *R. erratica* Krueger (1972, pp. 856–8, figs 1–4) described from Baltic erratic blocks. The present cranidia differ in having a more elongate frontal glabellar lobe, a shorter (sag.) posterior part of the glabella and much less prominent bacculae. Apart from the presence of only one well-developed axial ring, the short pygidium from Maine bears some resemblance to that of *Raphiophorus*.

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Note added in proof

A case for promoting the use of the genus name *Arthrorhachis* and restricting the name *Trinodus* to its type and topotype material anticipated in the discussion of the latter genus herein has now been published (Budil *et al.* 2011).

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