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Description and ecology of a new Middle Ordovician (Llanvirn) odontopleurid trilobite from the Builth Inlier of Mid-Wales, with a review of the genus *Meadowtownella*

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Abstract – A new odontopleurid trilobite, *Meadowtownella serrata*, is described from a new Llanvirnian (Darriwilian; *Didymograptus murchisoni* Biozone) locality in the Builth Inlier, Mid-Wales. This unusually spinose species displays a remarkable array of pygidial spines and extends the stratigraphic range of the genus back into the Abereiddian. Benthic faunas are rare in the predominantly 'anoxic' *D. murchisoni* Biozone of the Welsh Basin, and these beds are an unusual habitat for odontopleurids. Environmental analyses (framboidal pyrite and associated total organic carbon) in this study, together with the distribution of benthic faunas (described and figured) in the section, indicate a likely oxic water column and episodically oxic bottom waters. A new diagnosis for *Meadowtownella* is presented with a review of the genus, as a clarification of previous work. The greater spinosity of earlier members of the lineage may reflect either changing environmental preferences, or the derivation of *Meadowtownella* from an original more spinose lineage.

Keywords: Odontopleuridae, Builth–Llandrindod Inlier, *Primaspis*, spinosity, *Meadowtownella*.

1. Introduction

Trilobites of the superfamily Odontopleuridae (order Lichida) are striking but generally rare members of Middle Ordovician trilobite assemblages. The family (stratigraphic range Early Ordovician–Late Devonian) is generally well documented, probably owing to their distinctive appearance, wide geographic distribution and relatively easy identification. Despite this, and although the trilobite faunas of the Builth Inlier have been extensively studied (Hughes, 1969, 1971, 1979), only two indeterminate odontopleurids have been reported (Hughes, 1979, pp. 171–72). This scarcity may be due largely to the general preference of odontopleurids for carbonate platform environments, which are entirely lacking in the Builth Inlier succession. However, some odontopleurids have been described from deep-shelf environments, such as the blind *Diacanthaspis trippi* (Harper & Owen, 1986) from Upper Ordovician (Sandbian) siltstones in the Girvan succession (Harper & Owen, 1986; Stewart & Owen, 2008). Odontopleurids are also described from shelf siliciclastic rocks of late Darriwilian (Llandeilan) age in the nearby Shelve Inlier (Whittard, 1961; MacGregor, 1963). Several species of *Meadowtownella* are described from Shelve, but most are restricted to a few specimens recovered from sandstones. Only two species, *M. simulatrix* and the rarer *M. rorringtonensis*, occur in units composed primarily of silt- and mudstones.

Abundant (several hundred) fragments of a new, unusually spinose (many small librigenal and pygidial border spines) odontopleurid have been collected from graptolitic mudstones at a previously undescribed locality in the *Didymograptus murchisoni* Biozone (Abereiddian) of the Builth Inlier. Samples are from within a stratigraphic sequence of offshore sediments usually lacking benthic faunas, and description of a new odontopleurid species from the area is therefore significant both for the general understanding of the group and in a local ecological context. An ecological analysis and a detailed examination of this atypical environment have been carried out to look at the implications for its mode of life. Odontopleurid fragments are present throughout the section, but are very abundant in certain horizons. They are distinctively tuberculate, and easily distinguishable from the other fauna. Despite this, no entirely or even nearly articulated specimens were recovered, and specimens were fragmented to a greater extent than would be expected simply from moulting. This may indicate either transported death assemblages or benthic colonization when conditions became suitably oxygenated, but after which remains were exposed on the sea floor for a considerable time before burial.

2. Geological setting and stratigraphy of the Builth Inlier

The Builth–Llandrindod Inlier (inset of Fig. 1) of Mid-Wales is an area of Middle–Upper Ordovician (lower Llanvirn–lower Caradoc; Darriwilian–Sandbian) rocks, encompassing the graptolite biozones *Didymograptus artus* to *Nemagraptus gracilis*. The basic stratigraphy of the area was established by Elles

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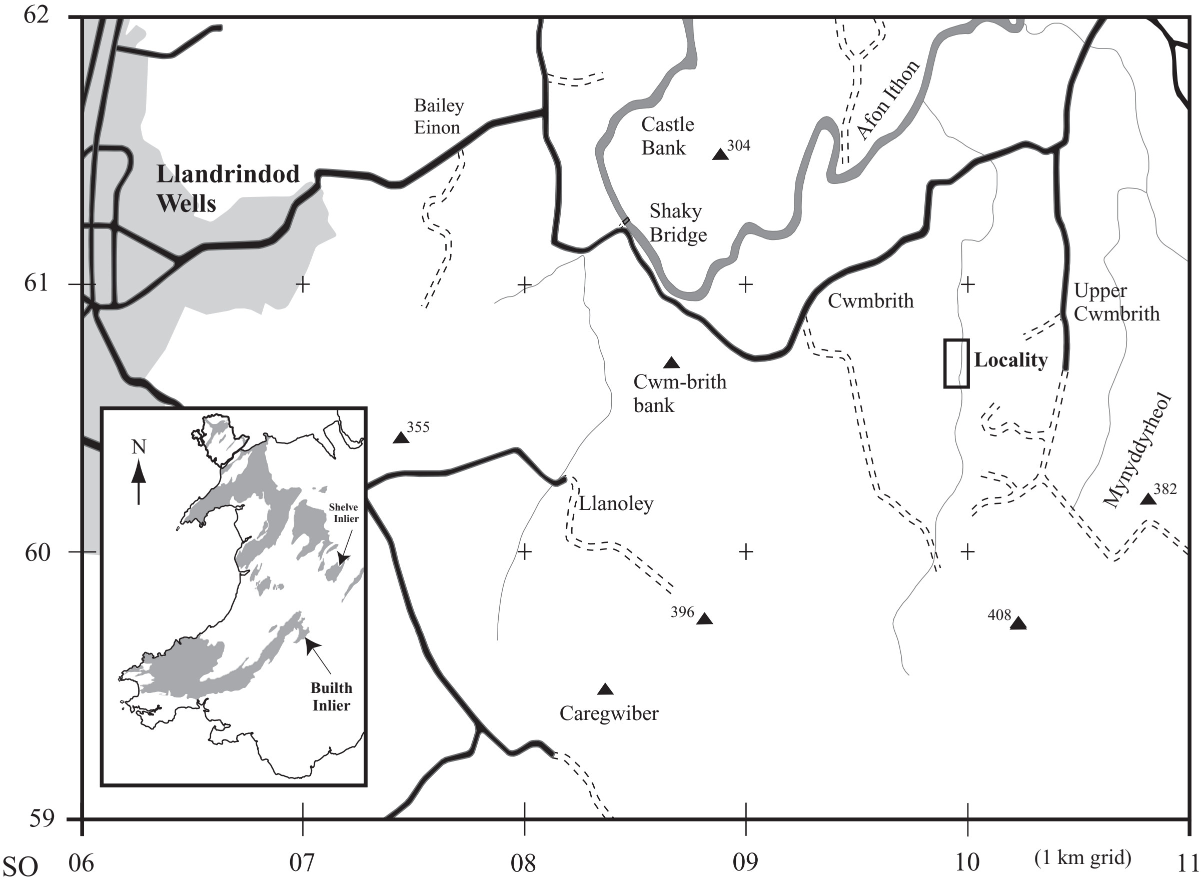

Figure 1. Location map, showing Llandrindod Wells and the Carreg-grog stream section. Map is based on the Ordnance Survey Landranger Map 147 (scale 1:50 000) and shows National Grid coordinates. Grey shading delimits the town of Llandrindod Wells. Inset shows outcrop of Ordovician rocks (shaded grey) in Wales, reproduced from Bettley, Fortey & Siveter (2001).

(1940) and Jones & Pugh (1941, 1949), with the latter describing the volcanic rocks and providing a reconstruction of the area as a volcanic island environment. Figure 2 shows a revised stratigraphy for the Inlier, based on more recent work by the British Geological Survey (BGS) (Davies *et al*. 1997; British Geological Survey, 2005), and correlated with the latest British (Fortey *et al*. 2000) and global (Finney, 2005; Bergström *et al*. 2006) chronostratigraphy.

Rocks of upper Llanvirn (Darriwilian) age in the Inlier are dominated by mudstones and siltstones, believed by some authors to have been deposited in a low-energy shelf environment (Davies *et al.* 1997), but with more complex interpretations also described (Botting & Muir, 2008). The lower part of the *murchisoni* Biozone mudstone sequence is referred to as the Gilwern Volcanic Formation of the Builth Volcanic Group, and interbedded within it are volcanogenic deposits (ash, tuff, reworked tuff, lava). This volcanic activity has been related to a volcanic island environment (Jones & Pugh, 1949), within the regional back-arc Welsh Basin (Dunkley, 1980), as part of the ongoing subduction of the Iapetus Ocean (Phillips, Stillman & Murphy, 1976) during Ordovician time. The bulk of the volcanic activity is slightly older, with the island development mainly restricted to the *Didymograptus murchisoni* Biozone (Bevins & Metcalfe, 1993), but discrete ash bands continue well into the *teretiusculus* Biozone, partly equivalent to the nearshore Newmead Sandstone Formation in the south of the area.

3. Location of sites

The material was all collected from a stream near Carreg-grog, east of Llandrindod Wells (Fig. 1). The section exposes mudstones of the Gilwern Volcanic Formation, between the major volcanic units of the Llandrindod and Cwm-amliw Tuff formations. An associated graptolite fauna confirms the biostratigraphy (Fig. 2), and provides a reasonably precise age for the fauna. Odontopleurid fragments were mainly collected from two horizons along the section, designated b and f on the detailed section log (Fig. 3), although additional remains were recovered from several other levels.

4. Palaeoenvironment reconstruction and analyses

4.a. Lithological description

The locality (Fig. 1) lies in the siliciclastic sequence of the Gilwern Volcanic Formation, faulted over the underlying reworked tuff and conformably overlain by the Cwm-Amliw Tuff Formation. The section

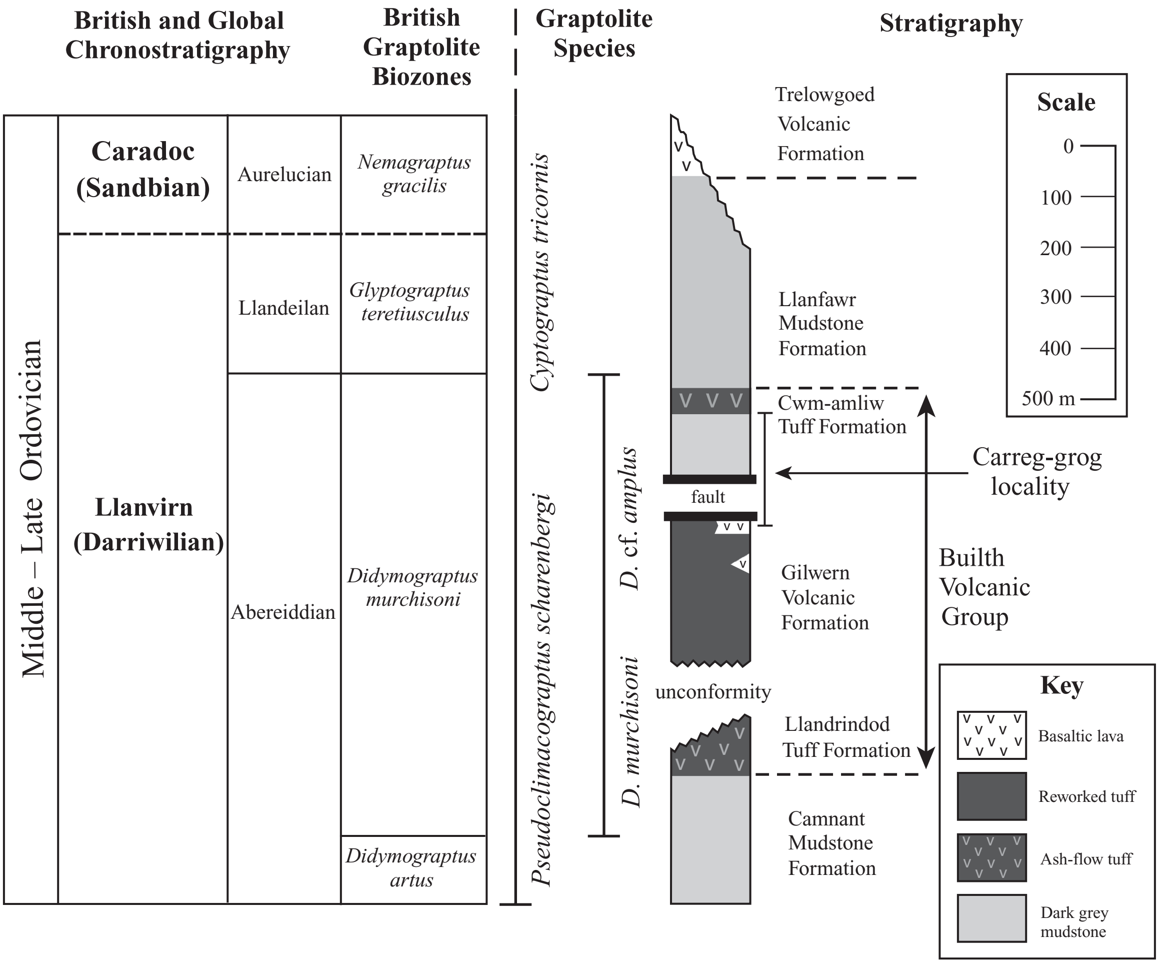

Figure 2. Stratigraphy of the area, adapted from Davies *et al.* (1997), updated in line with more recent work (Fortey *et al.* 2000; Finney, 2005; Bergström *et al.* 2006; British Geological Survey, 2005) and confirmed with graptolite species collected during this study.

comprises three main rock types, which have all been sectioned (CAMSM X.50154.49–58) and analysed.

The basal unit is a poorly-sorted, fine-grained, silty volcaniclastic sandstone with little evidence of sedimentary structures; euhedral plagioclase crystals and sand-sized fragments of volcanic tuff suggest a local volcanic source. This unit is likely to represent the more distal deposits resulting from high-energy reworking of a silica-rich volcanic unit (perhaps dominantly the eroded Llandrindod Tuff Formation; Davies *et al.* 1997). Above this, the lower mudstone unit is composed of clay aggregates, with abundant quartz and plagioclase (coarse silt to fine sand) grains. The unit probably represents a transitional period from the high-energy deposition of the underlying sandstones to the low-energy mudstones above. There is some slight deformation around large volcanic clasts, perhaps indicative of ash falls into soft, poorly consolidated sediments. Lamination is present but generally less well developed than in the overlying graptolitic mudstones.

The majority of the section comprises normally laminated, locally bioturbated grey mudstones, indicating a low-energy depositional environment. The absence of ripples or cross-bedding suggests a quiet basinal environment or shelf setting, below storm wave base. Local slumping and small-scale deformation may also indicate relatively steep local topography, although it is not clear at what stage this took place. Pyrite framboids and quartz and plagioclase (sub-angular silt) grains are abundant throughout. There are numerous discrete ash horizons, with volcanic clasts and poorly-sorted euhedral muscovite crystals, suggesting occasional ash falls into the basin from a local volcanic source.

4.b. Faunal assemblage

The section contains a fairly restricted fauna (Fig. 4), dominated by *Didymograptus* (*Didymograptus*) *murchisoni*, and the partly pseudoplanktonic (Botting & Thomas, 1999) phosphatic brachiopod *Apatobolus? micula*. Other graptolites distributed throughout the section include *Didymograptus* (*Didymograptellus*) cf. *amplus*, *Orthograptus* sp., *Diplograptus foliaceus*, *Pseudoclimacograptus scharenbergi*, *Cryptograptus tricornis* and the (possibly benthic) dendroid *Callograptus* sp.

In addition to the odontopleurids, at several other horizons along the section (Fig. 3, horizons a, b and f), there is good evidence of both nektonic

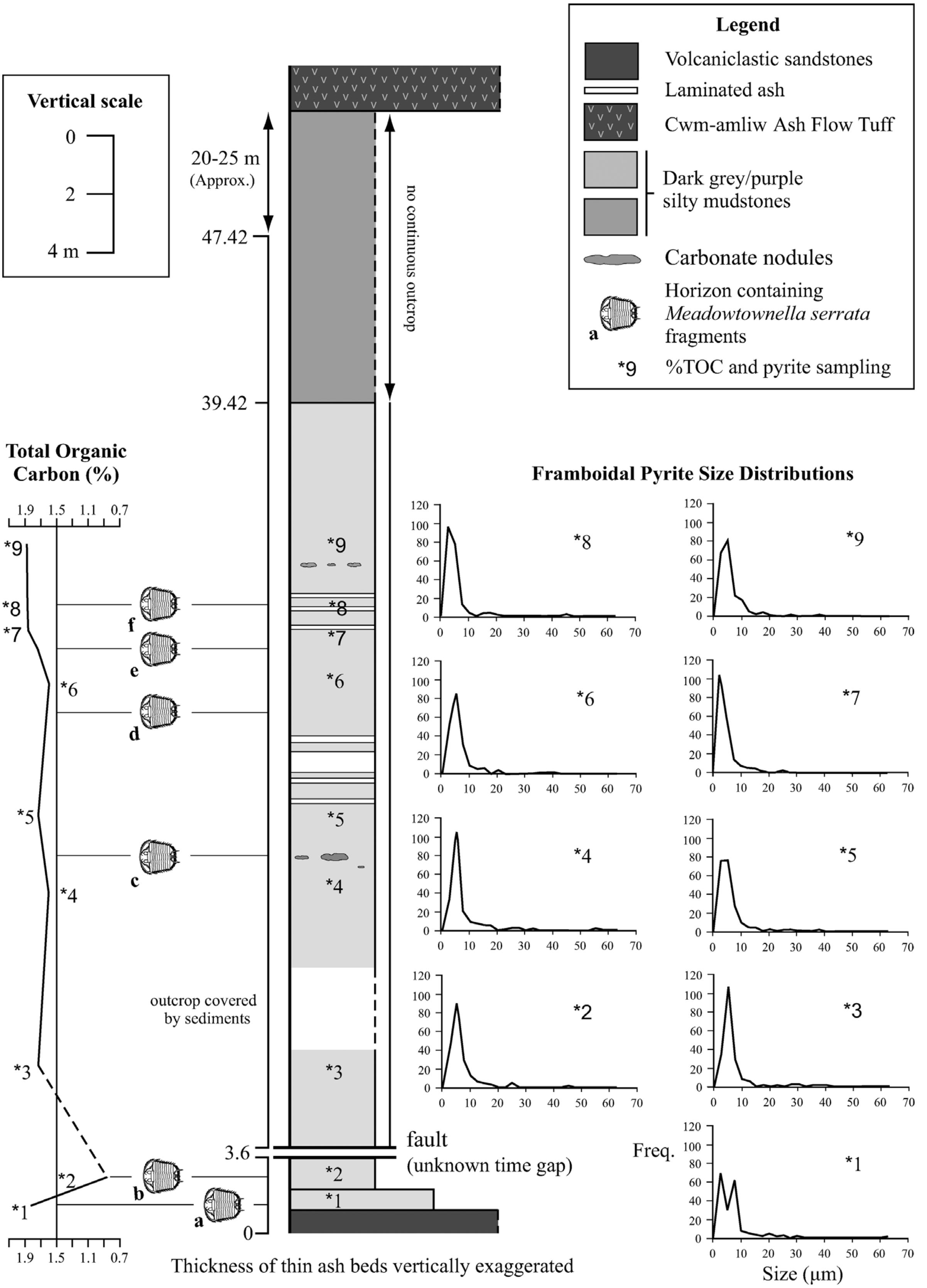

Figure 3. Stratigraphic log of Carreg-grog stream section, showing *Meadowtownella serrata* horizons and % TOC and framboidal pyrite size distributions at nine sampling points along the section.

and benthic activity. The nekton includes orthoconic nautiloids and arthropods (ceratiocarid carapaces and other unidentified non-mineralized remains), although none are abundant. The benthic fauna is more diverse, including trilobites (*Ogyginus corndensis*, *Ogygiocarella debuchii*, an undetermined calymenid,

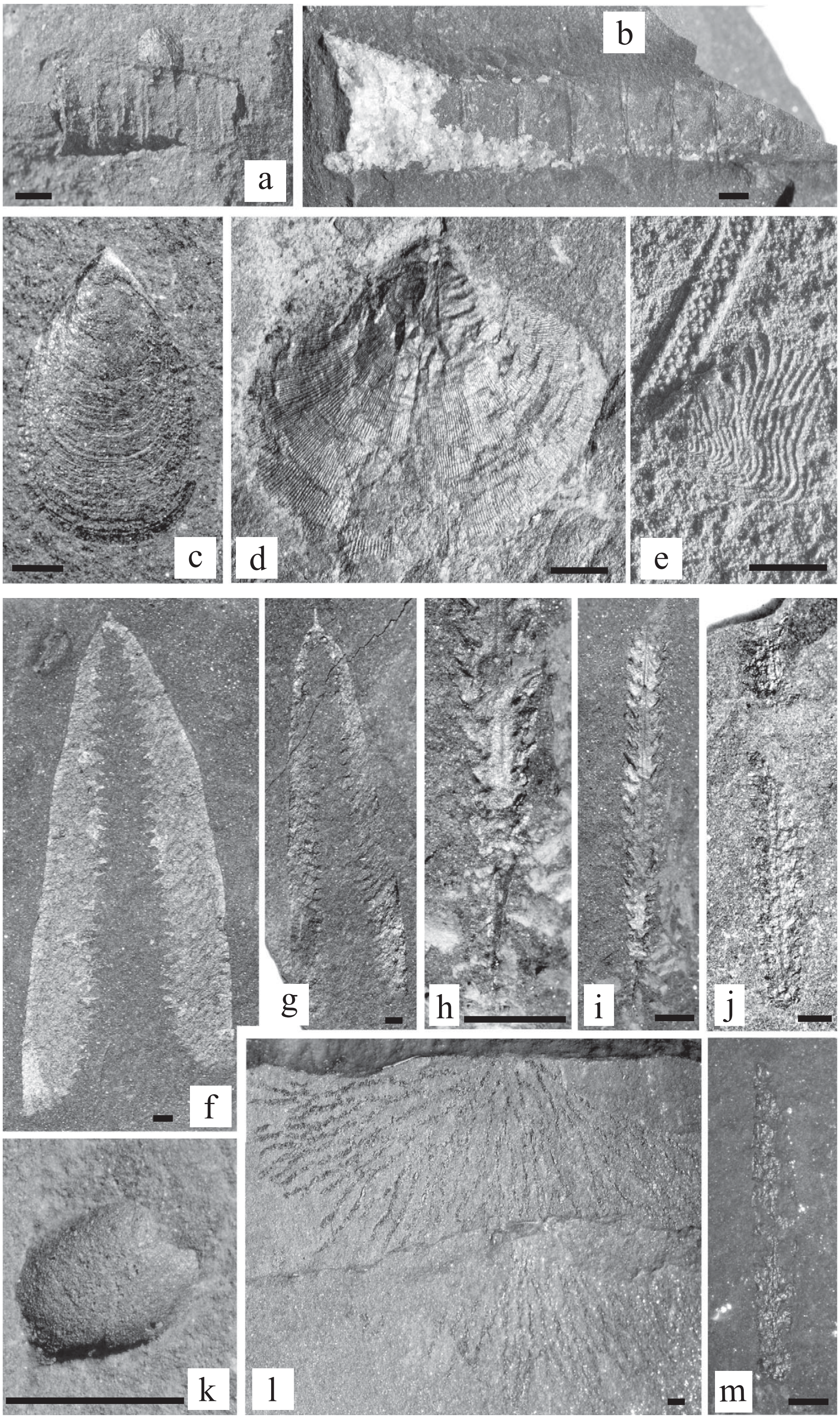

Figure 4. (a, b) Orthoconic nautiloids (CAMSM X.50154.40.a, CAMSM X.50154.41.a). (c) *Palaeoglossa attenuata* (Sowerby; CAMSM X.50154.37.a). (d) *Monobolina ramsayi* (Salter; CAMSM X.50154.38.a). (e) Machaeridian sclerite and partial *Meadowtownella serrata* sp. nov. thoracic segment (CAMSM X.50154.39.a). (f) *Didymograptus (Didymograptellus)* cf. *amplus* (Elles & Wood; CAMSM X.50154.47.a). (g) *Didymograptus (Didymograptus) murchisoni* (Beck, CAMSM X.50154.44.a). (h, i) *Orthograptus* sp. (CAMSM X.50154.48.a). (j) *Diplograptus foliaceus* (Murchison; CAMSM X.50154.43.1.a). (k) Smooth ostracode (CAMSM X.50154.35.a). (l) *Callograptus* sp. (CAMSM X. 50154.42.a). (m) *Pseudoclimacograptus scharenbergi* (Lapworth; CAMSM X.50154.46.a). Scale bars are 1 mm long.

Table 1. Per cent total organic carbon and framboidal size distribution results

	% Framboid size distributions						
Horizon	<7 μm	<25 μm	7–25 μm	Mean (μm)	Standard deviation	Number of framboids measured	Total organic carbon (%)
*1	86	99	13	6.70	6.33	200	1.80
*2	84.5	99.5	15	6.40	5.09	200	0.87
*3	83	98	15	7.05	6.83	200	1.60
*4	89	97	8	6.48	5.67	200	1.73
*5	90	99	9	5.44	4.28	200	1.73
*6	86	99	13	6.34	5.28	200	1.56
*7	90	100	10	4.69	3.54	200	1.74
*8	93	100	7	4.86	4.37	200	1.86
*9	85	100	15	5.75	4.35	200	1.89

Refer to Figure 3 for sampling horizon information.

Trinucleus abruptus and an undetermined trinucleid), sponge spicules, machaeridian sclerites, echinoderms (fragmentary mitrates and cornutes), brachiopods (*Monobolina ramsayi*, *Palaeoglossa attenuata*), ostracodes (smooth and rare ornamented but indeterminate forms), gastropods and encrusting bryozoans. At least at these horizons, the base of the water column was oxic, although there is little evidence of infaunal activity.

The absence of any certain infaunal benthos may be indicative of anoxic sediments. The small lingulid *Palaeoglossa* appears sometimes to have been burrowing, but the evidence so far is weak, and it may have been at least largely epibenthic or even pseudoplanktonic. Many of the rarer elements of the benthic fauna are of poorly understood groups, making their palaeoecological significance uncertain. Remains of carpoids are locally abundant in the Builth Inlier (under description by B. Lefebvre and J. P. Botting), but are otherwise very rare fossils. Equally important, machaeridian sclerites are now known to come from armoured worms (Vinther, Van Roy & Briggs, 2008), although their mode of life is unclear. Both are rare in rocks of this age in the Welsh Basin; two other sclerites are known from the Builth Inlier, both from one site in a similar facies.

4.c. Total organic carbon and framboidal pyrite

The rocks were sampled at nine places along the section for both framboidal pyrite and % total organic carbon (TOC). For TOC, the rock was powdered and reacted with potassium dichromate and sulphuric acid. The spectroscopic colour change of the solution is a quantitative indicator of organic carbon in the sample (Walkley & Black, 1934). TOC in a rock is mostly affected by organic matter preservation (controlled by sedimentation rate, organic matter influx and the presence of oxygenated bottom waters), and the relative presence of other components (Tyson, 2005). Because it is usually unclear which of these plays a major role in a preserved sediment, TOC percentages can only be of limited use, although low values (less than 1 %) may indicate oxygenated conditions, and higher values ($\geq$ 5–10 %) are indicative of anoxia. Values for TOC ($\sim$ 1.8 %) in this section (Table 1; Fig. 3) are suggestive of slightly oxic bottom conditions, especially at locality 2 ($\sim$ 0.8 %).

The mudstones contain abundant primary framboidal pyrite (densely packed spheroidal aggregates of sub-micron sized pyrite crystals) in addition to authigenic (later diagenetic) pyrite grains. Framboids form just below the redox interface (Muramoto *et al.* 1991; Kaplan, Emery & Rittenburg, 1963), and their mean size and variability are controlled by residence time near this boundary (Wilkin, Barnes & Brantley, 1996); framboids forming in an anoxic water column have shorter growth times than those forming in anoxic sediment pore waters (Randolf & Larson, 1988). Framboid size and size distribution therefore provides an indicator of the level of this anoxic/oxic boundary in the water column (Wilkin, Barnes & Brantley, 1996), with framboids formed in modern euxinic (anoxic water columns) basins (5 ± 1.7 μm) being smaller and less variable than those formed under an oxic/dysoxic water column (7.7 ± 4.1 μm) with the redox interface within the sediments (Wilkin, Barnes & Brantley, 1996). Framboid size distributions (based on a survey of 200) from this study (Fig. 3) have mean values (Table 1) that, together with the presence of large framboid clusters and TOC percentages, correlate with data for an oxic water column (Wilkin, Barnes & Brantley, 1996; Wilkin, Arthur & Dean, 1997; Wilkin & Barnes, 1997), and so it seems likely that the water column was oxygenated, with a redox interface at or close to the sediment–water interface. The restriction of benthos to distinct horizons suggests the possibility of episodically anoxic bottom waters and permanently anoxic sediments, although there is little variation of framboidal size distribution or TOC along the section to support the identification of specific euxinic intervals.

4.d. Palaeoenvironmental interpretation

The section is composed of well-laminated silty mudstones, with little evidence of bioturbation, suggesting a quiet low-energy environment, with a low sedimentation rate (low siliciclastic input). TOC and framboidal pyrite data indicate anoxic sediments with an oxic water column; it is likely that the redox interface was close to the sediment–water interface. At various points, the sediment–water interface also appears to have become anoxic, indicating some fluctuations in local oxygenation; this correlates with the restriction of the fauna to graptolites and *A.*? *micula* at certain levels. The absence of definite infaunal benthos and bioturbation, and epifaunal benthos being limited to certain horizons (when bottom waters may be sufficiently oxic) is also indicative of low oxygen availability. Persistent benthic anoxia is typical of much of the *D. murchisoni* Biozone, both within the Builth Inlier (Botting, 2002; Botting & Muir, 2008) and more widely across at least the Welsh Basin, and this environment is therefore unusual in showing some benthic activity.

The reason for this section showing benthic colonization, when equivalent strata in the Inlier do not, is not clear. Local topography at this time would have been complicated by the presence of at least one volcanic island (Botting & Muir, 2008). The location of this section falls close to the channel between the main Builth volcanic cone and the remainder of the cone for the Llandegley Tuffs volcano (Botting & Muir, 2008), and it may be that there was enhanced circulation of bottom water during the deposition of this section. The fauna is not indicative of shallow conditions, but the asaphids and odontopleurids have eyes, which suggest habitation within the photic zone or slightly below. The presence of blind trinucleids is not diagnostic as their sensory system also functioned in light-rich environments; they occur in many different facies in the area and elsewhere. The section represents a period of limited volcanic activity, but with numerous influxes of ash into the basin, which may have had a significant negative effect on benthos, perhaps promoting periodic eliminations and recolonizations (Botting, 2002).

There are transported beds of sandstone at the base of the section, but these stop abruptly to leave relatively homogeneous silty mudstones. Volcanically induced changes in the local topography could account for such a change in sediment input without needing rapid changes in local sea level. One possible interpretation is that the formation of a dividing ridge abruptly cut off the coarse sediment supply and created a relatively isolated basinal area. It may be that benthic colonization occurred following sediment slumps into this region, but that sedimentation between these events was slow; following the return of euxinic conditions and death of the community, the skeletons would have been exposed for significant lengths of time on the sea floor, leading to the complete disarticulation and fragmentation (above that expected from moulting) observed in the odontopleurid fossils. The limited opportunity for benthic colonization may explain the presence of so few trilobite species, and just one odontopleurid. A similar occurrence is described by Thomas (1981), who reported over 1800 disarticulated exoskeletal parts of *Odontopleura ovata* in Late Llandovery Shales from the Builth succession. It is possible that some odontopleurids were environmental opportunists, with either a long-lived larval stage or a greater adult dispersal potential than most trilobites.

5. Systematic palaeontology

Terminology follows Whittington & Kelly (*in* Kaesler, 1997). Lateral glabellar lobes are designated L1, L2, L3, etc., with corresponding lateral furrows S1, S2, S3.

Order LICHIDA
Superfamily ODONTOPLEUROIDEA
Family ODONTOPLEURIDAE Burmeister, 1843
Subfamily ACIDASPIDINAE Salter, 1864
Genus *Meadowtownella* Přibyl & Vaňek, 1965

Type species. *Primaspis whitei* Whittard, 1961 from the Shelve Inlier, Shropshire.

Diagnosis. Glabella with three lateral lobes (L2 much smaller than L1), widest across L1 and occipital ring, lateral lobes narrow anteriorly; narrow glabellar frontal lobe well developed. Convex occipital ring bears occipital lobe with median tubercle and well-defined lateral occipital lobes. Wide librigenae; short posterior genal spine, with small border spines. Palpebral lobe approximately two thirds down (sag.) cephalon, opposite mid-L1. Two major pygidial border spines linked to axis by major ridge, and 6 to 19 pairs of posterior border spines.

Discussion. *Primaspis* was established (Richter & Richter, 1917) as *Acidaspis* (*Primaspis*), one of nine subgenera of *Acidaspis*, with *Odontopleura primordialis* (Barrande, 1852) designated as type species. Warburg (1933) raised *Primaspis* to generic rank, but the first detailed examination of the genus (Prantl & Přibyl, 1949) focused on Bohemian material, together with a review of previous work. Although this provided the first diagnosis, the group was still regarded as a subgenus of *Acidaspis*. Whittington (1956) rediagnosed *Primaspis* (raised to generic rank) and commented on the genus as being well represented in Bohemia (late Llandeilan–Ashgill), with several North American examples possessing median tubercules, but not occipital spines (a feature of the type species).

Přibyl & Vaňek (1965) noted the differences between some members of the genus and the type species and re-assigned all the Anglo-Scandinavian and North American species to a new subgenus, *Primaspis* (*Meadowtownella*), on the basis of significant differences from *Primaspis primordialis* (lack of occipital spines, presence of smooth occipital ring and median tubercule). However, Bruton (1967) later deemed *P.* (*Meadowtownella*) to be a junior subjective synonym of *Primaspis*. He suggested that too much importance was given to trivial differences, whilst noting that some have a minor pygidial border spine fused

Table 2. Details of all species within the genus *Meadowtownella*, shown with British and Global Series Ages

Species	Described	Geographic occurrence	Age	Minor pygidial spines
M. ascitus	Whittington (1956)	United States	Caradoc (Sandbian)	10
M. bestorpensis	Bruton (1966)	Sweden	Caradoc—Ashgill (Katian)	14
M. bucculenta	McNamara (1979)	England, Norway	Ashgill (Katian)	8
M. caractaci	Salter (1853), Dean (1963)	England	Late Caradoc (Katian)	10
M. aff. *caractaci*	Tripp & Morris (1986)	Ireland	Late Caradoc (Katian)	12
M. crosotus	Locke (1843)	United States	Late Caradoc (Katian)	–
M. evoluta	Törnquist (1884), Bruton (1966)	Sweden, Wales, England, Norway	Ashgill (Katian)	10
M. cf. *evoluta*	Törnquist (1884), Bruton (1968)	Latvia	Ashgill (Katian)	12
M. evoluta canadia	Bolton (1972)	Canada	Ashgill (Katian)	–
M. evoluta evoluta	Törnquist (1884)	–	Ashgill (Katian)	–
M. girvanesis	Reed (1914)	Scotland	Ashgill (Katian–Hirnatian)	10
M. harnagensis	Bancroft (1949), Dean (1963)	England	Early Caradoc (Sandbian)	12
M. horani	Billings (1863)	–	Early Caradoc (Sandbian)	14
M. llandowrensis	Price (1980)	S. Wales	Ashgill (Katian)	6
M. mendica	Siveter (1989)	Ireland	Silturian (Wenlock)	8
M. multispinosa	Bruton (1965), Hansen (2009)	Norway	Late Llanvirn (Darriwilian)	17
M. rorringtonensis	Whittard (1961)	Shelve Inlier, Wales	Caradoc (Katian)	–
M. sacerdos	Lespérance (1998)	Quebec	Late Ashgill (Katian–Hirnantian)	8
M. semievoluta	Reed (1910), Dean (1962)	England	Caradoc (Sandbian)	–
M. cf. *semievoluta*	Reed (1910), Whittington (1962, 1968)	Wales	Caradoc (Sandbian)	10
M. serrata sp. nov.	(This study)	Builth Inlier, Wales	Early Llanvirn (Darriwilian)	34–37
M. simulatrix	Whittard (1961)	Shelve Inlier, Wales	Late Llanvirn (Darriwilian)	14
M. trentonensis	Hall (1847), Brett *et al.* (1999)	United States	Late Caradoc (Katian)	8
M. whitei	Whittard (1961)	Shelve Inlier, Wales	Late Llanvirn (Darriwilian)	12
M. sp. (a)	Lespérance (1968)	Canada	Caradoc– Ashgill (Katian)	–
M. sp. (b)	(x) Ross (1979)	United States	Late Caradoc (Katian)	8
M. sp. (c)	(y) Ross (1979)	United States	Late Caradoc (Katian)	10
M. sp. (d)	Lespérance (1998)	Quebec	Late Ashgill (Hirnantian)	–
M. sp. (e)	MacGregor (1963)	Shelve Inlier, Wales	Late Llanvirn (Darriwilian)	14
M. sp. (f)	Bruton (1965)	Norway	Caradoc (Katian)	12
M. sp. (g)	Bolton (1972, 1981)	Canada	Ashgill (Katian)	–
M. sp. (h)	Price (1980)	S. Wales	Ashgill (Katian)	–
M. sp. (i)	Delgado (1908), Romano (1982)	Portugal	Caradoc (Sandbian–Katian)	–

All species are of Ordovician age except *M. mendica*

to the major spine, but again concluded that this was not significant enough to subdivide the group. Šnajdr (1984) redescribed the Bohemian members of *Primaspis* in a stratigraphic sequence from Llandeilan to Ashgill (Darriwilian to Hirnantian) and proposed that they evolved to adapt to lithofacies changes (as with *Chlustinia* and *Selenopeltis*), on the basis that odontopleurids were intimately connected with their lithofacies because of their benthic mode of life.

Ramsköld & Chatterton (1991) agreed with Přibyl & Vaňek (1965) and assigned all the non-Bohemian members of *Primaspis* to *Meadowtownella* (raised to generic rank) and restricted *Primaspis* to those species previously assigned by Šnajdr (1984) to *Primaspis* (*Primaspis*). Ramsköld also re-evaluated the subgenera proposed by various authors, regarding *Anacaenaspis*, *Chlustinia*, *Primaspis* and *Meadowtownella* as separate genera (within the subfamily Acidaspidinae). Siveter (1989) regarded the differences as not significant enough to divide the genus, but since 1990, *Meadowtownella* has been regarded as a separate genus, although not formally diagnosed. Ramsköld & Chatterton (1991), Lespérance (1998), Brett *et al.* (1999) and others have used the designation. This paper includes the first formal definition of the genus. The corresponding diagnosis for *Primaspis* should differ only by the presence of two paired occipital and minor border spines on the occipital ring. Hansen (2009) rediagnosed *Primaspis* to include both species with and without the occipital spines, but we believe the separation based on these is appropriate and should be used.

Other species. See Table 2.

Meadowtownella serrata sp. nov.
Figures 5, 6, 7

Derivation of name. From Latin *serratus* (serrated), referring to the numerous small pygidial and librigenal spines, which generate a serrated appearance to the

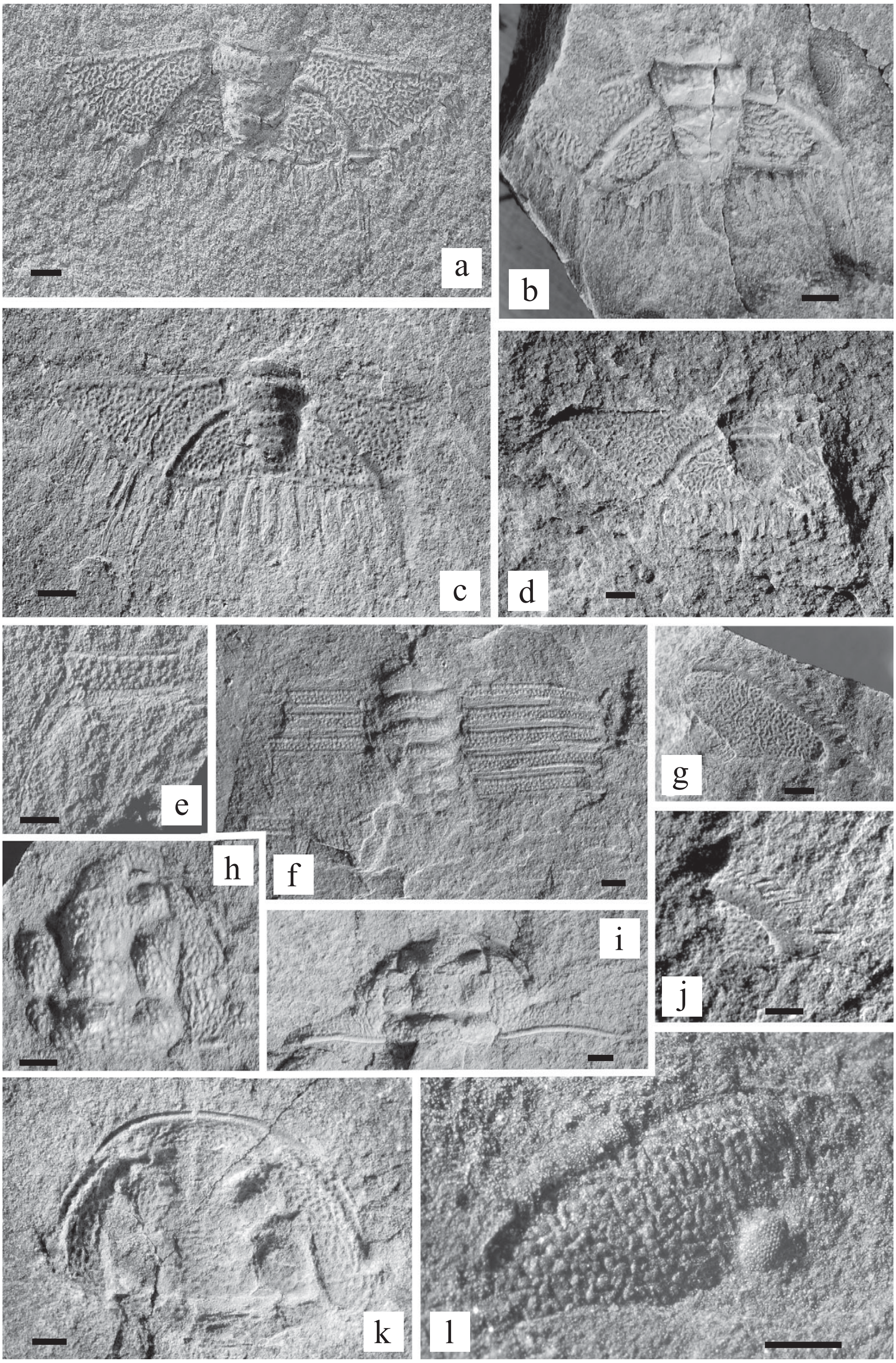

Figure 5. (a–d) *Meadowtownella serrata* sp. nov. pygidia (CAMSM X.50154.23.1.a (holotype), CAMSM X.50154.25.1.a, CAMSM X.50154.27.2.a, CAMSM X.50154.22.1.a); (e) *M. serrata* sp. nov. partial thoracic segment displaying anterior and posterior spines and structure (CAMSM X.50154.20.a); (f) *M. serrata* sp. nov. partial thorax displaying thoracic structure and ornamentation (CAMSM X.50154.17.a); (g) *M. serrata* sp. nov. librigena displaying border and spines (CAMSM X.50154.31.a); (h, i) *M. serrata* sp. nov. cranidia (CAMSM X.50154.5.2.a, CAMSM X.50154.3.1.a); (j) *M. serrata* librigena sp. nov. displaying border and genal spine (CAMSM, X.50154.29.1.a); (k) *M. serrata* cranidium sp. nov. displaying occipital and L1–3 lobes (CAMSM X.50154.8.1.a); (l) *M. serrata* sp. nov. librigena displaying eye and genal surface (CAMSM X.50154.33.1.a). Scale bars are 1 mm long.

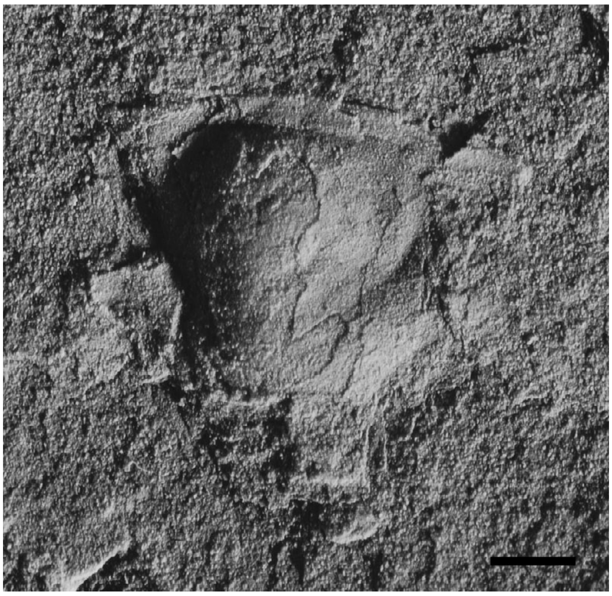

Figure 6. *Meadowtownella serrata* sp. nov. hypostome (CAMSM X.50154.16.a). Scale bar is 1 mm long.

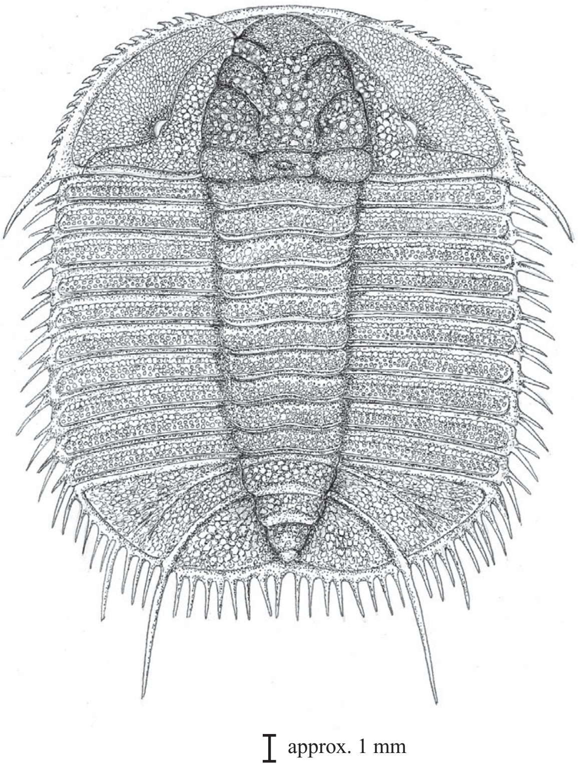

Figure 7. Reconstruction of *Meadowtownella serrata*, showing complete dorsal carapace (reconstructed from fragments).

carapace in comparison with other members of the genus.

Holotype. CAMSM X.50154.23.1 pygidium.

Paratypes. CAMSM X.50154.3 partial cephalon with complete fixigenae; CAMSM X.50154.1, CAMSM X.50154.2, CAMSM X.50154.4.a, CAMSM X.50154.5, CAMSM X.50154.6.a, CAMSM X.50154.7, CAMSM X.50154.8, CAMSM X.50154.9.a, CAMSM X.50154.10, CAMSM X.50154.11.a, CAMSM X.50154.12.a, CAMSM X.50154.13, CAMSM X.50154.14.a partial cephala; CAMSM X.50154.29, CAMSM X.50154.30, CAMSM X.50154.31.a, CAMSM X.50154.32 partial librigena; CAMSM X.50154.33 partial librigena with eye; CAMSM X.50154.17.a, CAMSM X.50154.18, CAMSM X.50154.19.a articulated thoracic segments; CAMSM X.50154.20.a thoracic pleural spines; CAMSM X.50154.21, CAMSM X.50154.22, CAMSM X.50154.24, CAMSM X.50154.25, CAMSM X.50154.26.a, CAMSM X.50154.27, CAMSM X.50154.28 partial and complete pygidia; CAMSM X.50154.15.a, CAMSM X.50154.16.a hypostomes.

Other material. A large number of odontopleurid specimens were collected from the stream section. Preservation is mouldic or with apparent replacement of the original carapace by clay minerals or by silica or pyrite in some specimens. Material is mostly undeformed, but fragments with greater relief (mostly glabellae) are often slightly deformed. Material from horizon f show more deformation than the others, whereas pygidia from horizon b are usually flattened rather than deformed.

Diagnosis. *Meadowtownella* with strongly convex occipital ring and librigenae bearing more than 20 short robust anterior border spines. Thorax with broad strongly convex posterior principal pleural ridges, separated from lower anterior ridges (fused row of granules) by depressed central pleural band (ornamented with two lateral rows of granules). Pygidium with 32–37 minor border spines; outer spines not fused with the major spine base. Pleural area ornamented with a dense granulation.

Description. Cephalon convex, approximately three times as wide (tr.) as long (sag.), semi-elliptical in outline, grading into short, posterolateral genal spines. Glabella slightly wider than long, occupying the centre third (tr.) of cephalon. Glabella widest (tr.) opposite mid-L1, narrows slightly along L2 and then narrows rapidly along L3 and the frontal lobe. Glabella divided from smooth anterior border by narrow furrow. Anterior cephalic border merges laterally with anterior librigenal border. Three pairs of inflated lateral glabellar lobes; L1 is largest, sub-oval, strongly convex and elliptical (elongated tr.) and divided from median glabellar lobe by deep S1; L1 occupies approximately 30 % of glabellar (tr.) width and just under half of glabella (sag.) length. L2 is smaller, and expands laterally, fused to median glabellar lobe. L3 is as small elongated convex swelling extending laterally (45° to sag.), with weakly defined S3. S1 and S2 well defined, S3 weakly defined. S2 (inclined at 45° from sag. line) and S3 (inclined at approximately 60° from sag. line) only partially separate L2 and L3. Median glabellar lobe sub-rectangular, widest across base of L1, narrowest at mid-length of L2; widens into anterior frontal lobe. Shallow, narrow axial furrows. Glabellar and occipital surfaces covered in large granules (0.2–0.3 mm), irregularly arranged. Occipital ring strongly convex (tr.), with a centrally positioned medial granule, well-defined deep occipital furrow (S0). Two well-defined sub-oval lateral occipital lobes.

Wide fixigenae, widest (as wide as L1) across palpebral lobes, narrowing anteriorly. Slightly convex posterior border (with flattened posterior flange), which grades into posterolateral librigenal border. No posterior border spines or granulation. Fixigenal surface coarsely granulated (0.1–0.2 mm), with smooth borders and eye ridge. Palpebral lobe opposite mid-L1, two thirds of the way from the anterior to posterior border, narrowing anteriorly and grading into narrow eye ridge which curves inwards and forwards to merge with anterior cephalic border. Anterior branch of the facial suture runs parallel, before diverging to cut anterior margin perpendicularly, creating sub-triangular elongation of the fixed cheek. Posterior branch of facial suture longer than anterior, directed outwards from eye lobe, curves outwards and backwards to cut posterior border inside genal spine. Wide anterior border (curving and tapering into the genal spine) bearing more than 20 short, robust spines (increasing in length posteriorly). Genal spine is approximately one third the length of anterior border and curves backwards from an enlarged base with a small subgenal notch. Border and spines are smooth, with cheek surface covered by a dense granulation (granules 0.1–0.2 mm), showing some orientation close to eye. Genal surface becomes more convex towards the inner posterior corner that bears the eye. Eye sub-spherical and composed of 10–15 rows of lenses.

Hypostome slightly wider than long, subquadrate with relatively straight anterior margin. Smooth anterior border, grades laterally into small triangular anterior wings and divided from median body by a shallow furrow. Material poorly preserved but median body shows slight anterior and posterior lobes; divided by a shallow furrow. Lobes are slightly convex, both slope down to the margin. Broad posteriolateral border, grading anteriorly into the shoulder.

Thorax with at least eight segments (ten is presumed, as with all Acidaspidinae). Thoracic pleurae have low, horizontal, smooth anterior and posterior flanges, which overlap with adjacent pleurae. Inner pleural regions horizontal, with lateral fulcral regions deflected posteriorly. Posterior ridges widen to form pronounced fulcral region, and major pleural spine. Anterior bands grade into smooth anterior spine. Wide axial region granulated, showing continuation of main pleural ridge. Little apparent segmental length differentiation; main pleural spines become elongated and more backwards directed posteriorly.

Pygidium approximately 3.5–4.5 times as wide (tr.) as long (sag.). Axis occupies approximately 20 % of total width, narrowing anteriorly and divided into three granulated rings, separated by smooth areas. Anterior ring convex, with rings narrowing posteriorly; the posterior triangular portion of axis is contiguous with posterior border. Anterior flattened flange and a granulated anterior border ridge. Raised pygidial ridge curves backwards and outwards from first ring to join major border spines at approximately ¼–⅓ width (tr.). Major border spines long, curving slightly inwards. Smooth posterolateral border with 32–37 minor spines; 12–15 posterior secondary spines (outer spines not fused with the major spine base), 20–22 anterior secondary spines. Pleural area with a dense granulation (0.1–0.2 mm), axial rings show irregularly arranged granules and borders and spines are smooth. Granules orientated to form a partial secondary major ridge, parallel to main ridge.

Discussion. Figure 7 shows a reconstruction of *M. serrata*. Ten thoracic segments were assumed, and pleural spine variation was interpolated from isolated segments (the relative proportions of thoracic and pygidial transverse widths are based on cephala, pygidia and several complete thoracic segments). The hypostomes (see Fig. 6) identified as odontopleurid show marked similarity to previously described species (Whittington, 1956; Bruton, 1965).

The glabellae of *M. serrata* show marked similarity to those of other species of Llanvin (Darriwilian) age: *M. whitei* (Whittard, 1961) and *M. simulatrix* (Whittard, 1961) from the Llandeilan of the Welsh basin, and *M. multispinosa* (Bruton, 1965) from the Llandeilan of Norway. The new species differs from other members of the genus principally by the large number of small pygidial lateral border spines, and to some extent the thoracic pleural sculpture (although this is not described for several other species). *M. serrata* pygidia are most similar to those of *M. multispinosa* in terms of spine number, and to those members of the genus that do not have the secondary posterior minor spine fused with the major spine base; several species of *Meadowtownella* show this. The pleural structures show marked similarity to *M. bestorpensis* (Bruton, 1966).

Remarks on morphometric analyses and functional morphology. Detailed morphometric data were plotted, with the majority of the parameters displaying varying degrees of allometry. However, the number of anterior pygidial border spines varies isometrically, proportionately with pygidial width (Fig. 8), whilst the posterior spine number changes negligibly. This change in spine number with size raises questions about the classification of *Meadowtownella*, as defining species on spine number may result in the separation of members of the same species. This may be important for species with few spines, but *M. serrata* and *M. multispinosa* can easily be distinguished by their large number of border spines; it is clear that even small *M. serrata* pygidia have many more minor spines than any of the others.

Palaeogeographic distribution and spinosity. *Primaspis* was restricted entirely to Bohemia, but

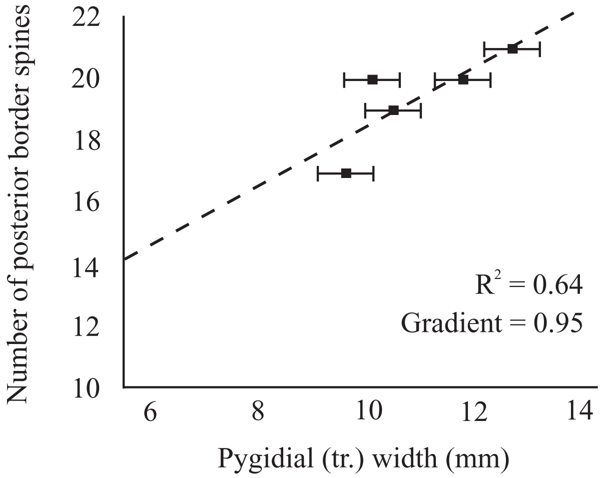

Figure 8. *Meadowtownella serrata* morphometric data showing isometric increase of pygidial posterior border spines with growth (width ± 0.5 mm).

Meadowtownella had a wider geographic range, spanning the Baltic (Norway, Sweden, Latvia and Estonia), the British Isles (Wales, Shropshire, Ireland and Scotland) and North America (USA and Canada). Species were present initially in Avalonia during the Llanvirn (Darriwilian; Abereiddian) and Baltica (Darriwilian; Llandeilan) and then also Laurentia by the Caradoc and Ashgill (Sandbian–Katian). Figure 9 shows the changing distribution of *Meadowtownella* and *Primaspis* overlaid on reconstructions of continental configuration (Llanvirn and Caradoc based on Toghill, 2004; Ashgill adapted from Trench *et al.* 1991) during the Ordovician. This shift is most likely related to the gradual closing of the Iapetus Ocean during Late Ordovician time, with the consequent narrowing of basins allowing migrations across the previously impassable Iapetus Ocean. *Meadowtownella serrata* appears to be the only species to inhabit an offshore environment, with the majority of the others found in limestone and sandstone facies. It is unclear from the current record whether the genus originated in deeper or shallower settings, and *M. serrata* may represent an early adaptation to offshore conditions that was not repeated subsequently. Even here, though, it is not a true deep-water inhabitant, and cross-oceanic dispersal was not possible.

This new species is the oldest known occurrence of the genus, and also possesses the most spines. There is a general trend of spine reduction over time, albeit with some variability and exceptions; there is a gradual average shift from 32–37 in the Abereiddian (early Llanvirn; Darriwilian), 12–17 during the Llandeilan (late Llanvirn; Darriwilian), 10–12 dominating the Caradoc (Sandbian–Katian) and 8–10 during the Ashgill (Katian). The most common form is 10–12, with the genus being best represented in the late Caradoc–Ashgill (Katian–Hirnantian). The youngest member of the genus in the Silurian (*M. mendica*; Siveter, 1989) shows only eight minor spines. The apparent rapid loss of spines between *M. serrata* and *M. multispinosa* (Bruton, 1965), in contrast to the later

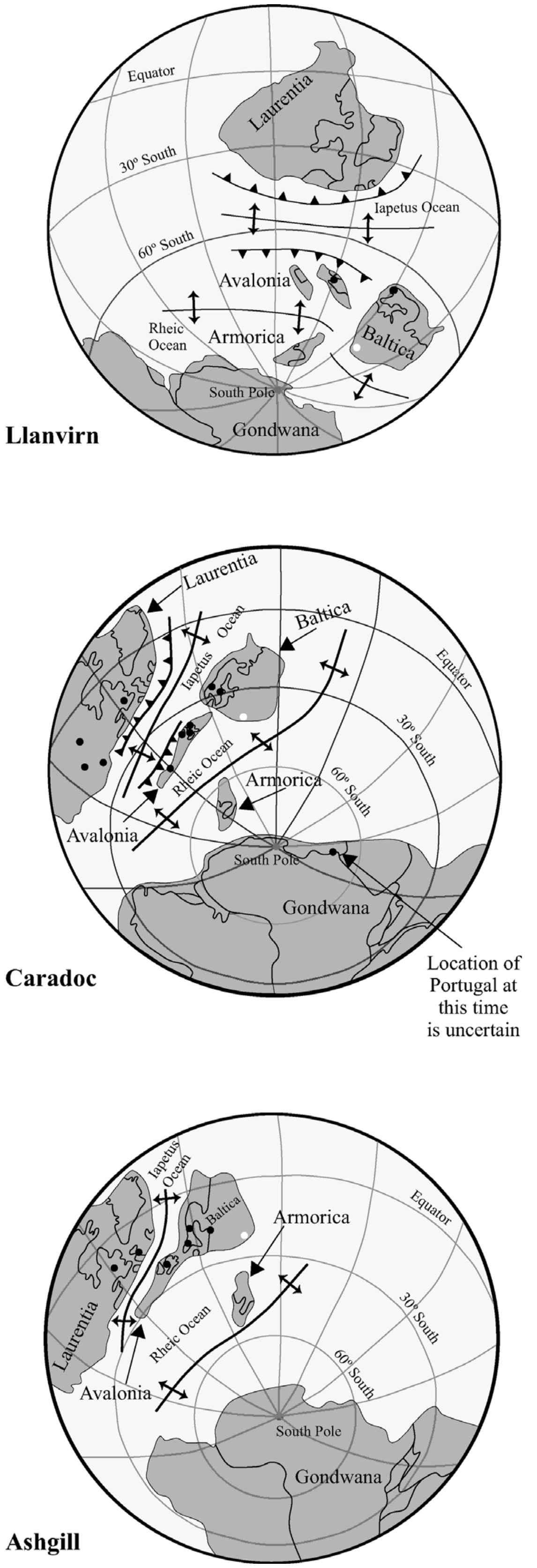

Figure 9. Palaeogeographical distributions of *Meadowtownella* (black dots) and *Primaspis* (white dots). Species are plotted on reconstructions of Ordovician continental configurations; Llanvirn (late Darriwilian) and Caradoc (Sandbian–Katian) are based on Toghill (2004) and Ashgill (Katian–Hirnantian) is adapted from Trench *et al.* (1991).

gradual changes, may suggest an origin for the genus from an even spinier odontopleurid lineage, although it is difficult to establish any definite relationships. The recent discovery of a less spiny member of the genus (unpub.; in private collection of P. Lawrence) from a nearby, slightly older, Builth Inlier locality, illustrates that more information is potentially available with further collecting.

The gradual shift in spine number may be a result of selection by a number of evolutionary pressures; one option is changing lithofacies, as having fewer but more robust spines may be beneficial in higher-energy clastic environments. This new species inhabited an unusually deep environment in contrast to most of the others, and so the colonization of new habitats could be linked to a change in spine number. It is notable that the blind deep-water odontopleurid *Diacanthaspis trippi* (Harper & Owen, 1986), which displays two long pygidial anterior border spines not present in other members of *Diacanthaspis*, is also thought to have inhabited a deeper-water environment than other members of the genus (Harper & Owen, 1986; Stewart & Owen, 2008). The presence of fused spines in some members of *Meadowtownella* may suggest that fusing spines together was genetically easy, providing a possible mechanism for spine reduction.

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References

BANCROFT, B. B. 1949. Upper Ordovician trilobites of zonal value in south-east Shropshire. *Proceedings of the Royal Society Series B, Biological Sciences* **136**, 291–315.

BARRANDE, J. 1852. *Systême Silurien du centre de la Bohême. 1ère partie: Recherches Paléontologiques. Vol. I. Trilobites*. Praha & Paris, 935 pp.

BERGSTRÖM, S. M., FINNEY, S. C., XU, C., GOLDMAN, D. & LESLIE, S. A. 2006. Three new Ordovician global stage names. *Lethaia* **39**, 287–8.

BETTLEY, R. M., FORTEY, R. A. & SIVETER, D. J. 2001. High-resolution correlation of Anglo-Welsh Middle to Upper Ordovician sequences and its relevance to international chronostratigraphy. *Journal of the Geological Society* **158**, 937–62.

BEVINS, R. E. & METCALFE, R. 1993. Ordovician igneous rocks of the Builth Inlier. In *Geological Excursions in Powys, Central Wales* (eds N. H. Woodcock & M. G. Bassett), pp. 243–58. University of Wales Press/National Museum of Wales, Geological Series 14.

BILLINGS, E. 1863. On the parallelism of the Quebec group with the Llandeilo of England and Australia, and with the Chazy and Calciferous formations. *Canadian Naturalist* **8**, 19–35.

BOLTON, T. E. 1972. Geological map and notes on the Ordovician and Silurian litho- and biostratigraphy, Anticosti Island, Quebec. *Geological Survey of Canada Paper* **71**, 1–45.

BOLTON, T. E. 1981. Ordovician and Silurian biostratigraphy, Anticosti Island, Québec. In *IUGS Field Meeting, Anticosti-Gaspé, Québec, 1981. Volume 2, Stratigraphy and Paleontology*, pp. 41–59. Department de Geologie, Université De Montréal.

BOTTING, J. P. 2002. The role of pyroclastic volcanism in Ordovician diversification. In *Palaeobiogeography and Biodiversity Change: The Ordovician and Mesozoic-Cenozoic Radiations* (eds J. A. Crame & A. W. Owen), pp. 99–113. Geological Society of London, Special Publication no. 194.

BOTTING, J. P. & THOMAS, A. T. 1999. A pseudoplanktonic inarticulate brachiopod attached to graptolites and algae. *Acta Universitatis Carolinae Geologica* **43**, 333–5.

BOTTING, J. P & MUIR, L. A. 2008. Unravelling causal components of the Ordovician Radiation: the Builth Inlier (central Wales) as a case study. *Lethaia* **41**, 111–25.

BRETT, C. E., WHITELEY, T. E., ALLISON, P. A. & YOCHELSON, E. L. 1999. The Walcott-Rust Quarry: Middle Ordovician trilobite Konservat-Lagerstätten. *Journal of Paleontology* **73**, 288–305.

BRITISH GEOLOGICAL SURVEY. 2005. *Builth Wells, England and Wales Sheet 196. Solid Geology. 1:50 000.* Keyworth, Nottingham: British Geological Survey.

BRUTON, D. L. 1965. The Middle Ordovician of the Oslo Region, Norway: 19. The trilobite family Odontopleuridae. *Norsk Geologisk Tidsskrift* **45**, 339–56.

BRUTON, D. L. 1966. A review of the Swedish Ordovician Odontopleuridae (Trilobita). *Bulletin of the Geological Institutions of the University of Uppsala* **43**, 1–44.

BRUTON, D. L. 1967. Silurian odontopleurids from Sweden, Estonia and Latvia. *Palaeontology* **10**, 214–44.

BRUTON, D. L. 1968. Ordovician odontopleurid trilobites from Estonia and Latvia. *Lethaia* **1**, 288–302.

BURMEISTER, H. 1843. *Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Übersicht aller zeither beschriebenen Arten*. Berlin: G. Reimer, 147 pp.

DAVIES, J. R., FLETCHER, C. J. N., WATERS, R. A., WILSON, D., WOODHALL, D. G. & ZALASIEWICZ, J. A. 1997. Geology of the country around Llanilar and Rhayader. *Memoir of the British Geological Survey, Sheets 178 and 179 (England and Wales)*, 267 pp.

DEAN, W. T. 1962. The Ordovician trilobite faunas of South Shropshire II. *Bulletin of the British Museum of Natural History: Geological Series* **5**, 311–58.

DEAN, W. T. 1963. The trilobites of the Caradoc Series in the Cross Fell inlier of Northern England. *Bulletin of the British Museum of Natural History: Geological Series* **7**, 65–134.

DELGADO, J. F. N. 1908. Système silurique du Portugal; étude de stratigraphie paléontologie. *Memoires de la Commission Géologique du Portugal, Lisbon*, 1–245.

DUNKLEY, P. N. 1980. Ordovician volcanicity of the SE Harlech Dome. In *The Caledonides of the British Isles; reviewed* (eds A. L. Harris, C. H. Holland & B. E. Leake), pp. 597–601. Geological Society of London, Special Publication no. 8.

Elles, G. L. 1940. The stratigraphy and faunal succession in the Ordovician rocks of the Builth-Llandrindod Inlier, Radnorshire. *Quarterly Journal of the Geological Society of London* **95**, 338–445.

Finney, S. 2005. Global Series and Stages for the Ordovician System: a progress report. *Geologica Acta* **3**, 309–16.

Fortey, R. A., Harper, D. A. T., Ingham, J. K., Owen, A. W., Parkes, M. A., Rushton, A. W. A. & Woodcock, N. H. 2000. *A Revised Correlation of Ordovician Rocks in the British Isles*. Geological Society Special Report no. 24. London: Geological Society of London, 83 pp.

Hall, P. 1847. Description of the organic remains of the lower division of the New York System. *Paleontology of New York* **1**, 1–338.

Hansen, T. 2009. Trilobites of the Middle Ordovician Elnes Formation of the Oslo region, Norway. *Fossils and Strata* **56**, 149, pl. 25.

Harper, D. A. T. & Owen, A. W. 1986. A shelly facies from graptolitic mudstones of the lower Balclatchie Group (Lower Caradoc) near Laggan, Girvan district. *Scottish Journal of Geology* **22**, 271–83.

Hughes, C. P. 1969. The Ordovician trilobite faunas of the Builth-Llandrindod Inlier, central Wales. Part I. *Bulletin of the British Museum of Natural History: Geological Series* **18**, 39–103.

Hughes, C. P. 1971. The Ordovician trilobite faunas of the Builth-Llandrindod Inlier, central Wales. Part II. *Bulletin of the British Museum of Natural History: Geological Series* **20**, 115–82.

Hughes, C. P. 1979. The Ordovician trilobite faunas of the Builth-Llandrindod Inlier, central Wales. Part III. *Bulletin of the British Museum of Natural History: Geological Series* **32**, 109–81.

Jones, O. T. & Pugh, W. J. 1941. The Ordovician rocks of the Builth district – a preliminary account. *Geological Magazine* **78**, 185–91.

Jones, O. T. & Pugh, W. J. 1949. An Early Ordovician shoreline in Radnorshire, near Builth Wells. *Quarterly Journal of the Geological Society* **105**, 65–99.

Kaplan, I. R., Emery, K. O. & Rittenburg, S. C. 1963. The distribution of and isotopic abundance of sulphur in recent marine sediments off southern California. *Geochemica et Cosmochima Acta* **27**, 297–331.

Lespérance, P. J. 1968. Ordovician and Silurian trilobite faunas of the White Head Formation, Perce region, Quebec. *Journal of Paleontology* **42**, 811–26.

Lespérance, P. J. 1998. Trilobites of the Pabos Formation (Ashgillian, Upper Ordovician), Percé area, Quebec. *Journal of Paleontology* **72**, 303–16.

Locke, J. 1843. Notice of a new trilobite, *Ceraurus crosotus*. *American Journal of Science* **44**, 346.

Macgregor, A. R. 1963. Upper Llandeilo Trilobites from the Berwyn Hills, North Wales. *Palaeontology* **5**, 790–816.

Mcnamara, K. J. 1979. Trilobites from the Coniston Limestone Group (Ashgill Series) of the Lake District, England. *Palaeontology* **22**, 53–92.

Kaesler, R. L. (ed.) 1997. *Treatise on Invertebrate Paleontology. Part O. Arthopoda (Revised), Volume 1*. Lawrence: Geological Society of America and University of Kansas Press, 530 pp.

Muramoto, J. A., Honjo, S., Fry, B., Hay, B. J., Howarth, R. W. & Cisne, J. L. 1991. Sulfur, iron and organic carbon fluxes in the Black Sea: sulfur isotropic evidence for origin of sulfur fluxes. *Deep-Sea Research* **38**, S1151–87.

Phillips, W. E. A., Stillman, C. J. & Murphy, T. 1976. A Caledonian plate tectonics model. *Journal of the Geological Society, London* **132**, 579–609.

Prantl, F. & Přibyl, A. 1949. A study of the superfamily Odontopleuracea nov. superfam. (trilobites). *Rozpravy Státniho Geologického ústavu ČSR* **12**, 1–221.

Přibyl, A. & Vaňek, J. 1965. Neue Trilobiten des Bohmischen Ordoviziums. *Vestnik Ustredniho Ustav Geologicky* **40**, 277–82.

Price, D. 1980. The Ordovician trilobite fauna of the Sholeshook Limestone Formation of South Wales. *Palaeontology* **23**, 839–87.

Ramsköld, L. & Chatterton, B. D. E. 1991. Revision and subdivision of the polyphyletic "*Leonaspis*". *Transactions of the Royal Society of Edinburgh: Earth Sciences* **82**, 333–71.

Randolf, A. D. & Larson, M. A. 1988. *Theory of Particulate Processes*, 2nd ed. San Diego: Academic Press Inc, 369 pp.

Richter, R. & Richter, E. 1917. Über die Einteilung der Familie Acidaspidinae und über einige ihrer devonischen Vertreter. *Zentralblatt für Mineralogie, Geologie und Paläontologie, for 1917*, 462–72.

Reed, F. R. 1910. New fossils from the Dufton Shales. *Geological Magazine* **7**, 211–20.

Reed, F. R. 1914. Supplement to the lower Palaeozoic trilobites of the Girvan district, Ayshire. *Palaeontographical Society Monograph* **329**, 1–56.

Romano, M. 1982. A revision of the Portuguese Ordovician Odontopleuridae (Trilobita): *Selnopeltis* and *Primaspis*. *Communiacacoes dos Servicos Geologicos de Portugal* **68**, 213–23.

Ross, R. J. 1979. Additional trilobites from the Ordovician of Kentucky. *United States Geological Survey Professional Paper* **1066**-D, 1–13.

Salter, J. W. 1853. Figures and descriptions illustrative of British organic remains. Decade 7. *Memoir of the Geological Survey of the United Kingdom*, 1–78.

Salter, J. W. 1864. A monograph of the British Trilobites from Cambrian, Silurian and Devonian Formations. *Palaeontographical Society Monograph* **1**, 1–80.

Siveter, D. 1989. Silurian trilobites from the Annascaul Inlier, Dingle Peninsula, Ireland. *Palaeontology* **32**, 109–61.

Šnajdr, M. 1984. O českých trilobitech z rodu *Orphanaspis*, *Selnopleltoides* a *Taemaspis* (Odontopleuridae). *Ústřední Ústav Geologický, Praha, Czechslovakia* **153**, 212–16.

Stewart, S. E. & Owen, A. W. 2008. Probing the deep shelf: a Lagerstätte from the Upper Ordovician of Girvan, southwestern Scotland. *Lethaia* **41**, 139–46.

Thomas, A. T. 1981. British Wenlock trilobites. Part 2. *Palaeontographical Society Monograph* **134**, 57–99.

Toghill, P. 2004. *The Geology of Britain; An Introduction*. Marlborough: Airlife Publishing, 244 pp.

Törnquist, S. L. 1884. Undersökningar öfver Siljansomrĺdets trilobitfauna. *Sveriges Geologiska Undersökning Series C* **66**, 1–101.

Tripp, R. P. & Morris, S. F. 1986. The trilobite fauna of the Raheen Formation (Upper Caradoc), Co. Waterford, Ireland. *Bulletin of the British Museum of Natural History Geological Series* **40**, 91–122.

Trench, A., Torsvik, T. H., Smethurst, M. A., Woodcock, N. H. & Metcalfe, R. 1991. A palaeomagnetic study of the Builth Wells-Llandrindod Wells Ordovician inlier, Wales; palaeogeographic and structural implications. *Geophysical Journal International* **105**, 477–89.

TYSON, R. V. 2005. The "productivity versus preservation" controversy; cause, flaws, and resolution. *SEPM Special Publication* **82**, 17–33.

VINTHER, J., VAN ROY, P. & BRIGGS, D. E. G. 2008. Machaeridians are Palaeozoic armoured annelids. *Nature* **451**, 185–8.

WALKLEY, A. & BLACK, I. A. 1934. Method for determining soil organic matter. *Soil Science* **37**, 29–38.

WARBURG, E. 1933. On the structure of the occipital ring of the Odontopleuridae. *Arkiv för Zoologi* **25A**, 1–19.

WHITTARD, W. F. 1961. The Ordovician trilobites of the Shelve Inlier, west Shropshire pt. 5. *Palaeontographical Society Monograph* **491**, 163–96.

WHITTINGTON, H. B. 1956. Silicified Middle Ordovician trilobites; the Odontopleuridae. *Bulletin of the Museum of Comparative Zoology. Harvard University* **114**, 153–288.

WHITTINGTON, H. B. 1962. The Ordovician trilobites of the Bala area, Merioneth. Part I. *Palaeontographical Society Monograph* **116**, 1–32, pls 1–8.

WHITTINGTON, H. B. 1968. The Ordovician trilobites of the Bala area. Merioneth. Part IV. *Palaeontographical Society Monograph* **120**, 93–138, pls 29–32.

WILKIN, R. T., ARTHUR, M. A. & DEAN, W. E. 1997. History of water-column anoxia in the Black Sea indicated by pyrite framboid size distributions. *Earth and Planetary Science Letters* **148**, 517–25.

WILKIN, R. T. & BARNES, H. L. 1997. Pyrite formation in an anoxic estuarine basin. *American Journal of Science* **297**, 620–50.

WILKIN, R. T., BARNES, H. L. & BRANTLEY, S. L. 1996. The size distribution of framboidal pyrite in modern sediments; an indicator of redox conditions. *Geochemica et Cosmochima Acta* **60**, 3897–912.