LATE SILURIAN TRILOBITE PALAEOBIOLOGY AND BIODIVERSITY

by

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ABSTRACT

Trilobites from the Ludlow and Přídolí of England and Wales are described. A total of 15 families; 36 genera and 53 species are documented herein, including a new genus and seventeen new species; fourteen of which remain under open nomenclature. Most of the trilobites in the British late Silurian are restricted to the shelf, and predominantly occur in the Elton, Bringewood, Leintwardine, and Whitcliffe groups of Wales and the Welsh Borderland. The Elton to Whitcliffe groups represent a shallowing upwards sequence overall; each is characterised by a distinct lithofacies and fauna. The trilobites and brachiopods of the Coldwell Formation of the Lake District Basin are documented, and are comparable with faunas in the Swedish Colonus Shale and the Mottled Mudstones of North Wales. Ludlow trilobite associations, containing commonly co-occurring trilobite taxa, are defined for each palaeoenvironment. Trilobites in the British Přídolí are too rare and sporadic to systematize them into distinct associations. A preliminary study on the global diversity of Silurian trilobites is presented also. A total of six trilobite bioevents are recognised for the Silurian occurring in the argenteus-leptotheca, sedgwickii, centrifugus-murchisoni, nilssoni, formosus, and bouceki-transgrediens graptolite biozones, characterised by elevated extinction rates.

For my late grandmothers, Olive Storey and Irene Robins

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‘I have nothing to offer but blood, toil, tears, and sweat. We have before us an ordeal of the most grievous kind. We have before us many, many long months of struggle and of suffering. You ask, what is our aim? I can answer in one word: Victory. Victory at all costs – Victory in spite of all terror – Victory, however long and hard the road may be.’

Winston Churchill, 13 May 1940.

TABLE OF CONTENTS

LIST OF TEXT-FIGURES

LIST OF PLATES

LIST OF TABLES

CHAPTER ONE

INTRODUCTION

1.1 BACKGROUND: THE BRITISH SILURIAN AND TRILOBITE SYSTEMATICS

THE geology of Great Britain is characterized by a diverse succession of rocks representing all geological systems, from the Precambrian through the Phanerozoic. The British rock record is one of the best samples of Earth's history and it has thus received a great deal of international attention over the last 200 years. The Silurian System (443-416 Ma, Ogg *et al.* 2008) is well represented by sedimentary rocks exposed in numerous outcrops throughout Britain, from the Mendips (Somerset) in the south, westwards to Pembrokeshire, and northwards to the Midland Valley of Scotland. *The Silurian System* of Murchison (1839) comprised the first detailed description of Silurian strata and the British towns of Llandovery, Much Wenlock, and Ludlow now define the type localities for the Silurian international series of the same names (Holland 1980, 1982, 1985; Bassett 1985). British rocks of Silurian age and their faunas rapidly gained international importance which the Ludlow Research Group continues to develop (see Rosenbaum 2008).

Murchison (1839) not only highlighted the importance of the Silurian geology of Britain but its palaeontology too, as fossils were utilised in mapping and identifying strata (see Murchison 1839, p. 579). Numerous fossil groups were described and illustrated by Murchison (1839) and these rapidly became the focus of systematic study. Consequently extensive collecting led to the discovery of many fossil groups resulting in the publication of numerous monographs. Some of the most notable 19th century publications containing descriptions and illustrations of Britain Silurian trilobites include Murchison (1839), Phillips (1841), Fletcher (1850*a*, *b*), Sedgwick and M^{c}Coy (1851-1855), Salter (1849, 1853, 1864-1867, 1873, 1883), and La Touche (1884).

Silurian trilobites were globally distributed, commonly constituting a significant percentage of fossil assemblages, and displaying a substantial degree of variation in morphology and mode of life (Thomas and Lane 1984). Due to their hard exoskeleton and moulting trilobites have a high preservation potential, and this makes them a useful group when studying the evolution of marine ecosystems, phylogeny, palaeobiogeography, and biodiversity. Trilobites have been described from the various Silurian outcrops worldwide including Europe (Angelin 1854; Bruton 1967; Tomczykowa 1975, 1991; Šnajdr 1980; Chlupáč 1987; Lindström 1885, 1901; Hede 1915; Ramsköld 1983, 1984, 1985, 1986), North Greenland (see Lane 1972), North America (Campbell 1967; Holloway 1980, 1981), Canada (Ludvidsen and Tripp 1990, Adrain and Edgecombe 1997), Asia (Kobayashi 1988, Kobayashi and Sakagami 1989, Tianrui 2008, Ivanova *et al.* 2009), and Australia (Holloway 1994, Edgecombe and Sherwin 2001, Sandford 2000, Sandford and Holloway 2006).

In Britain, comprehensive studies have focussed on the trilobite faunas of the Llandovery (Temple 1970, 1975; Howells 1982; Curtis and Lane 1997-1998; Thomas and Lane 1999) and Wenlock (Thomas 1978, 1979, 1981; Thomas and Lane 1999). Many of the trilobite taxa previously described from the late Silurian of Britain were originally identified by Murchison (1839) and Salter (1864). Several of these species were revised by later authors; most notably the calymenids by Shirley (1936) and Siveter (1983), the cheirurids by Lane (1971), the proetids by Owens (1973), the phacopids by Shergold (1967, 1966), and the dalmanitids from the Lake District by Rickards (1965). In spite of this several trilobite species occurring in the late Silurian of Britain have not been revised in the last 150 years, and many remain unidentified or undescribed. In addition, several species previously thought to occur in the late Silurian of Britain are restricted to the Wenlock, and there are several species in Britain that are junior synonyms of species occurring abroad. This project will account for these and complete the systematics of the trilobites in the Ludlow and Přídolí series of Britain.

1.2 GEOLOGICAL AND PALAEOENVIRONMENTAL CONTEXT

The collision of Avalonia and Laurentia was significant in the development of the geology and geography of Britain during the Silurian. It allowed the development of the foreland basin setting of the Lake District Basin whereby subsidence was increased by flexure of the Avalonian lithosphere, as the microcontinent of Eastern Avalonia was loaded by Laurentia (King 1994). In the late Silurian Avalonia and Laurentia were driven more tightly together (Aldridge *et al.* 2000) resulting in the closure of the Iapetus Ocean and the joining of Wales and England (Avalonian Plate) with Scotland (Laurentian Plate). Consequently new uplands were created which resulted in increased amounts of sediment infilling the basins. Due to the increase in sedimentation and the general shallowing of late Silurian seas, the Lake District and Welsh basins were above sea level by the end of the Silurian (Aldridge *et al.* 2000). The Ludlow platform facies of England and Wales also exhibit a shallowing upwards sequence (Watkins 1979, Mikulic and Watkins 1981). The various palaeoenvironments represented are characterised by distinctive faunas (e.g. Watkins 1979, Mikulic and Watkins 1981, Cherns 1988, Lawson 1999*a*, *b*), and this provides an opportunity to study their depth relationships. Herein, the trilobite faunas occurring in the Elton to Whitcliffe groups of England and Wales and those occurring in the Coldwell Formation of the Lake District Basin are documented.

A total of nine events, which Jeppsson (1990) related to ocean-atmosphere changes, are documented for graptolites and conodonts during the Silurian. Extinctions in graptolites and conodonts often occur during glacial episodes and carbon/oxygen isotope excursions. The Sandvika (late Aeronian), Ireviken (late Telychian to early Sheinwoodian), and Mulde (early Homerian) events affect trilobites locally (Chatterton *et al.* 1990, Calner 2008) and are associated with elevated extinctions. As part of this project a high resolution trilobite global diversity curve is constructed from the Hirnantian through the Silurian, for the first time. The purpose of such a study is to determine how widespread the Silurian events are and their effects on trilobite global diversity and taxonomic rates.

1.3 PROJECT AIMS

Substantial collections from the Coldwell Formation of the English Lake District and the various Ludlow outcrops of the Welsh Borderlands and Wales have been amassed by supervisors A. T. Thomas and P. D. Lane over the last 40 years, and this forms the bulk of material for this project. Late Silurian trilobite collections stored in the British Geological Survey (Keyworth), the Lapworth Museum of Geology (University of Birmingham), the Ludlow Museum (Shropshire), the National Museum of Wales (Cardiff), the Natural History Museum (London), the Naturhistoriska riksmuseet (Stockholm), Oxford University Museum, and the Sedgwick Museum (Cambridge) were also surveyed. In addition, field work to the Howgill Fells, Lake District in 2009 and 2010 have supplemented existing collections.

The material available for this project is mostly represented by internal moulds. External moulds do occur, however, and latex casts are made from the well preserved specimens. Features such as furrows, eye lenses, and tubercles are generally sharper and better defined on external moulds and they are preferentially used together with well preserved internal moulds when describing and comparing species. For several of the trilobites material is restricted to compressed or distorted specimens and descriptions/comparisons for those species remains incomplete.

The wealth of material available to this project is significantly larger than that of previous studies and has permitted the extension of previous work, by researching the systematics, palaeoenvironmental relationships and distribution of the trilobites from the British Ludlow and Přídolí series.

A summary of the project aims are as follows:

- To document formally and describe the deep-water trilobite fauna from the Coldwell Formation of the Lake District Basin.
- To document formally and describe the trilobites occurring in the platform facies of England and Wales.
- To describe the various trilobite associations that occur in the British late Silurian with regards to their palaeoenvironment.
- To construct a global diversity curve of trilobite species from the Hirnantian through Silurian (at graptolite biozone level), and to compare this to the several extinction events known to affect graptolites and conodonts.

This study represents the first comprehensive account of the trilobites that occur in the British late Silurian and completes the documentation of the British Silurian trilobite fauna. An extensive systematic revision of the trilobites and their stratigraphic and environmental distribution is presented in Chapters Two and Three. Chapter Four comprises an in-depth literature survey of trilobite occurrence data resulting in a global diversity curve for the Hirnantian and Silurian. It is anticipated that this project will refine understanding on the temporal and environmental controls on trilobite distribution and provide a basis for wider studies on trilobite palaeobiogeography.

CHAPTER TWO

A DEEP-WATER TRILOBITE ASSOCIATION FROM THE LATE WENLOCK/EARLY LUDLOW OF THE ENGLISH LAKE DISTRICT

2.1 INTRODUCTION

THE most abundant and diverse Silurian trilobite faunas occur in shelf facies commonly associated with benthic assemblages (BA) 1-4, with more basinal settings characterised by graptolite and cephalopod bearing mudstones. The Tranearth Group, of the English Lake District, which stratigraphically covers the base of the Wenlock to the early Ludlow, is mostly laminated hemipelagic mudstones. Fossils occur rarely and are mostly restricted to nekton. The Coldwell Formation, however, is characterised by two calcareous members yielding a rich benthic fauna and it is thought to represent intervals of oxygenated bottom waters. The late Wenlock Randy Pike Member occurred during a phase of widespread deposition of fossiliferous calcareous mudstones (Warren 1971), associated with a eustatic fall in sea level (Johnson 2006). A widespread transgression at the start of the Ludlow resulted in graptolitic mudstones predominantly returning to the basins. In the early Ludlow of the Lake District Basin deposition of the calcareous High Cross Member of the Coldwell Formation is associated with continuing shallowing, presumably due to local tectonic effects.

The Homerian (late Wenlock) to Gorstian (early Ludlow) Coldwell Formation of the English Lake District contains a BA5 assemblage which is dominated by trilobites.

Other examples of Silurian deep-water faunas (*c.* BA5) include the Mottled Mudstones of the Welsh Basin (Warren *et al.* 1984), the Bylands Siltstone of Australia (Sandford and Holloway 2006), and the Swedish Colonus Shale (Hede 1915) . The prevalence of graptolitic mudstones in the basins highlights the importance of horizons like the Coldwell Formation, as they offer a rare glimpse into Silurian benthonic life in a basinal setting.

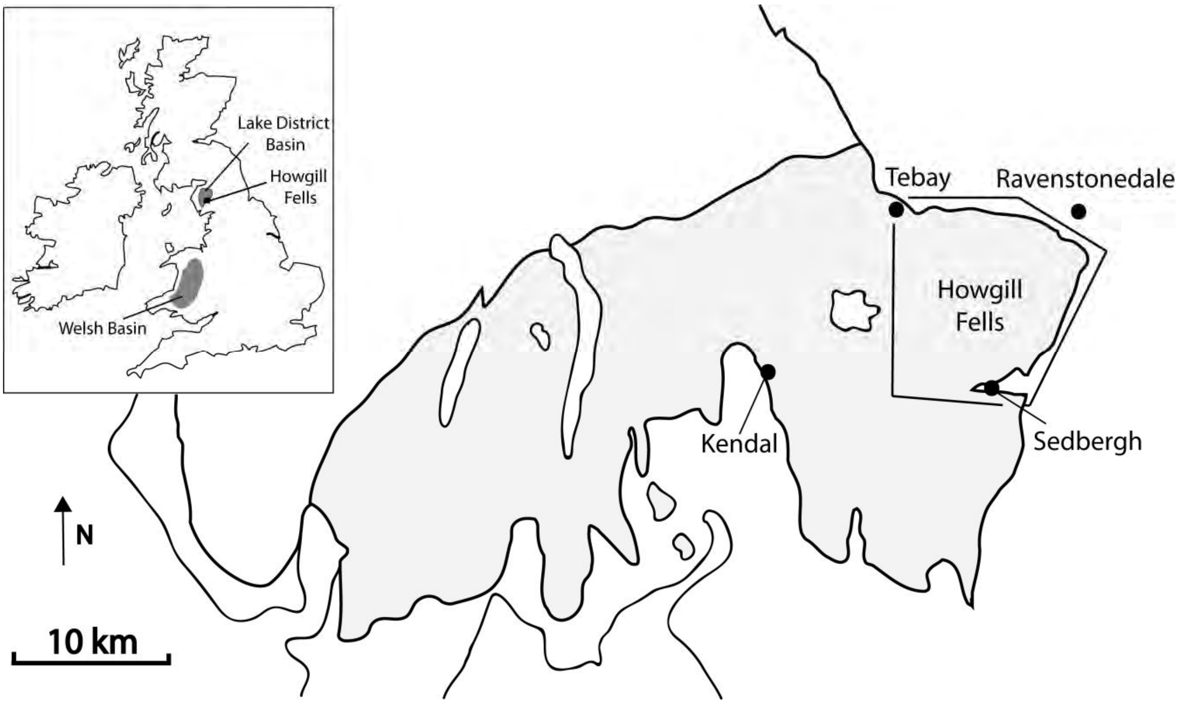
Although systematic descriptions have been published for some of the Coldwell Formation taxa (Rickards 1965, Owens 1973, Thomas 1978, 1981) there are only two brief accounts of the assemblage (Thomas and Lane 1999, Storey and Thomas 2008). Substantial collections made over the last 40 years significantly increased the amount of material from the Coldwell Formation (Randy Pike Member), together with older museum collections, and these provide a basis for the systematic revision of the trilobite taxa. *Sphaerocoryphe* occurs here, the first appearance in the record since the late Llandovery. The types of '*Dalmanites mobergi*' Hede, 1915 (=*Barriepiscator mobergi* gen. nov.) and '*Dalmanites simrica*' Hede, 1915 (=*Struveria simrica*) are figured photographically here for the first time.

The trilobite assemblage from the Coldwell Formation demonstrates strong similarities with those from the Swedish Colonus Shale (Homerian), the Mottled Mudstones of North Wales (Homerian), the Builth Mudstones Formation of mid-Wales (Homerian), and the uppermost Motol Formation (Homerian) to the lowermost Kopanina Formation (Gorstian) of Bohemia.

Affinities of the dalmanitids from the Coldwell Formation have been outlined by previous authors but no formal cladistic analysis has been undertaken. As part of this work such an analysis is included to assess the relationships between *Barriepiscator mobergi*, *Delops obtusicaudatus*, and *Struveria simrica* and other Silurian dalmanitids. This provides a better understanding of the early evolutionary history and divergence of the Dalmanitinae and Synphoriinae.

2.2 GEOLOGICAL AND STRATIGRAPHICAL SETTING

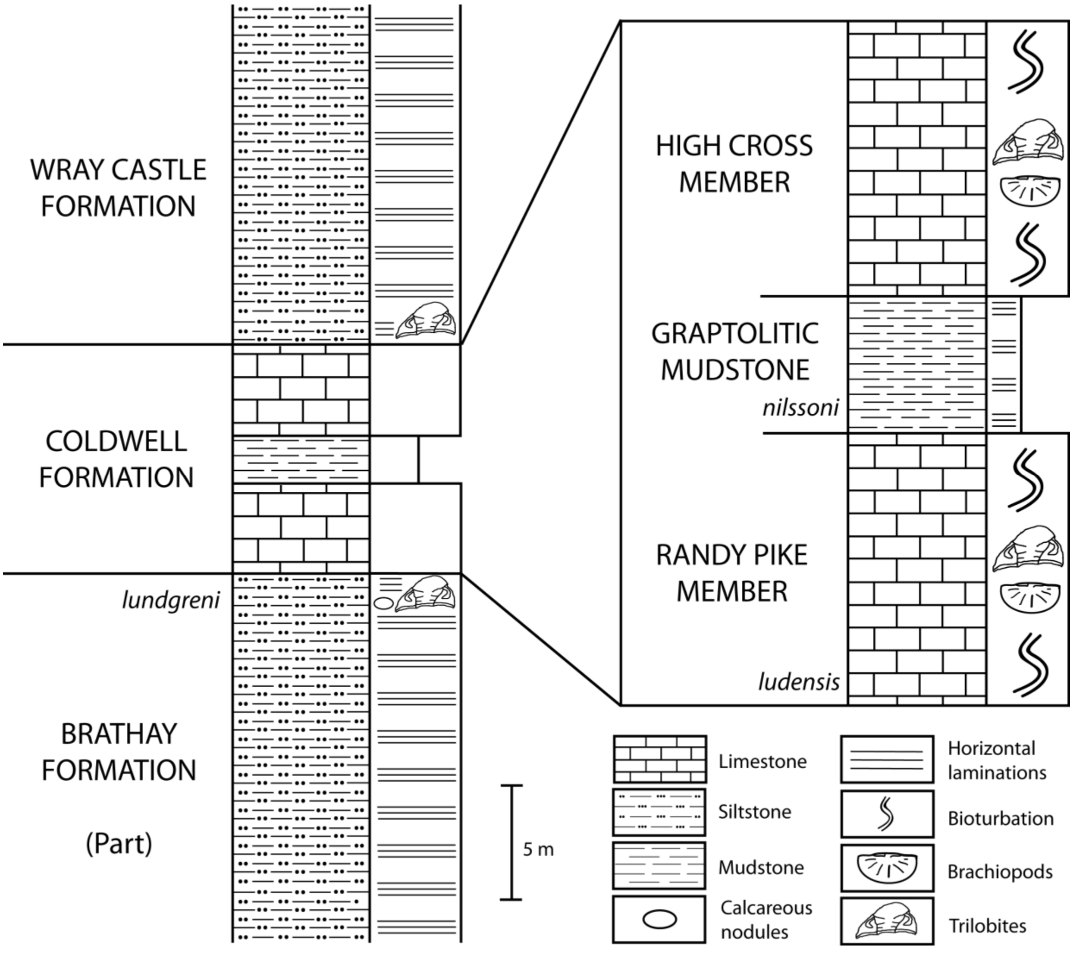
The Howgill Fells, Cumbria, north-west England, are located north of the town of Sedbergh and south of Ravenstonedale (Text-Figure 2.1), and are bordered to the west by the River Lune and to the east by the Dent Fault. Exposures encompass the Windermere Supergroup which consists of five groups and nine formations ranging from late Caradoc (mid Katian) to Přídolí in age.



Text-Figure 2.1. Map showing location of the Howgill Fells area. Silurian rock is shaded light grey (adapted and redrawn, with permission, from Storey and Thomas 2008, fig. 1).

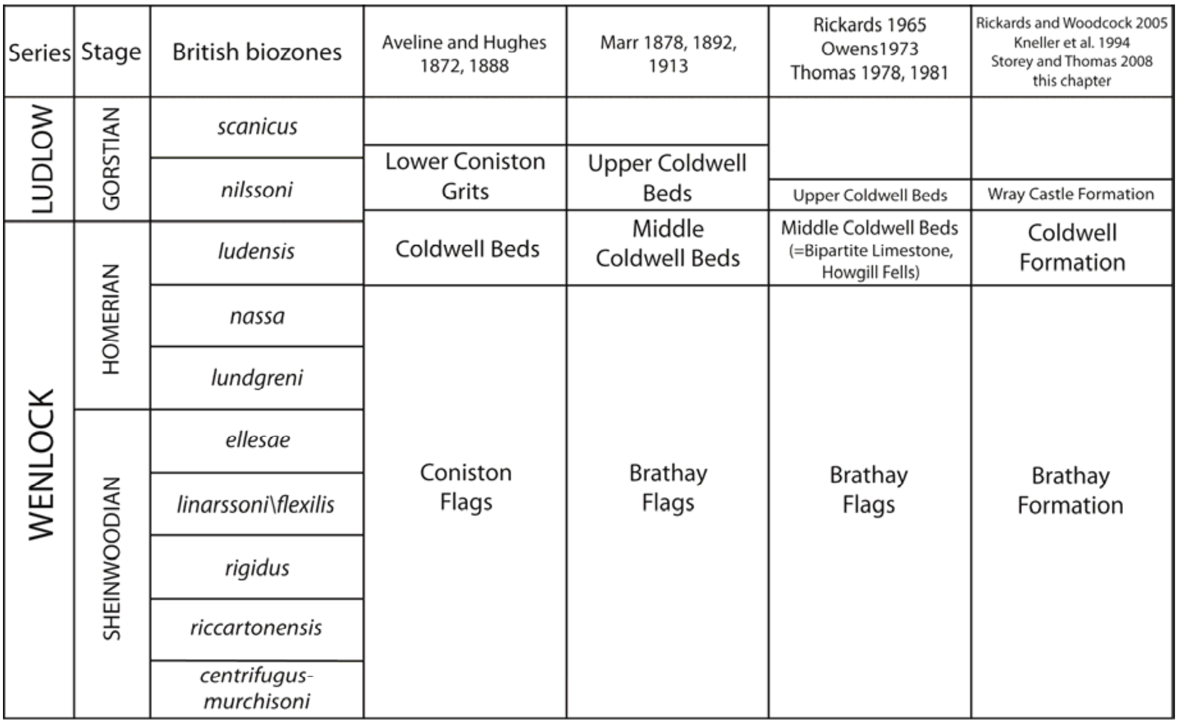
The Windermere Supergroup represents a foreland basin succession (King 1994) which developed as the microcontinent of Eastern Avalonia was loaded by Laurentia. The sedimentology and stratigraphy of the Windermere Supergroup were outlined in full by Kneller *et al.* (1994) and Rickards and Woodcock (2005).

Located towards the top of the Windermere Supergroup, the Tranearth Group has a maximum thickness of 260 m, and it is predominately composed of laminated hemipelagic silty mudstones. The Brathay and Wray Castle formations are composed almost entirely of the latter, and are separated by a thin calcareous interval, the Coldwell Formation (Text-Figure 2.2).



Text-Figure 2.2. Summary stratigraphical log of part of the Tranearth Group, Howgill Fells, showing the position of the Coldwell Formation (modified and updated, with permission, from Storey and Thomas 2008, fig. 2).

The Coldwell Formation (Coldwell Beds) was first described by Aveline and Hughes (1872) from Coldwell Quarry, Coldwell, Westmoreland. Later Marr (1878, 1892, 1913) extended the term to include the top of the Coniston Flags, Coldwell Beds and Lower Coniston Grits of Aveline and Hughes (1872), and respectively named them the Lower, Middle, and Upper Coldwell beds (Text-Figure 2.3).



Series	Stage	British biozones	Aveline and Hughes 1872, 1888	Marr 1878, 1892, 1913	Rickards 1965 Owens1973 Thomas 1978, 1981	Rickards and Woodcock 2005 Kneller et al. 1994 Storey and Thomas 2008 this chapter
LUDLOW	GORSTIAN	*scanicus*				
		nilssoni	Lower Coniston Grits	Upper Coldwell Beds	Upper Coldwell Beds	Wray Castle Formation
WENLOCK	HOMERIAN	*ludensis*	Coldwell Beds	Middle Coldwell Beds	Middle Coldwell Beds (=Bipartite Limestone, Howgill Fells)	Coldwell Formation
		nassa	Coniston Flags	Brathay Flags	Brathay Flags	Brathay Formation
		lundgreni				
	SHEINWOODIAN	*ellesae*				
		linarssoni\flexilis				
		rigidus				
		riccartonensis				
		centrifugus-murchisoni				

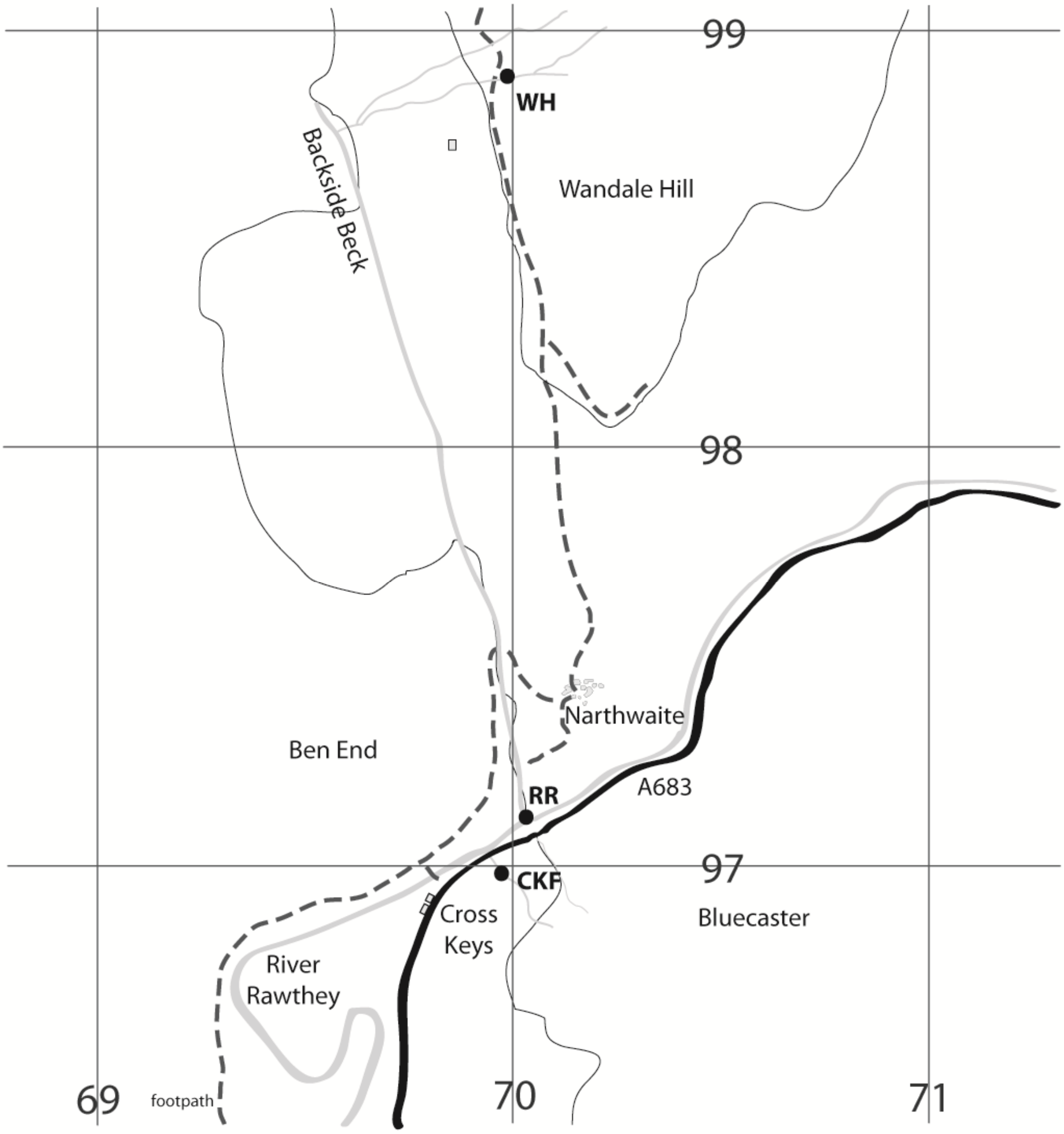
Text-Figure 2.3. Correlation of the Tranearth Group reported in key publications since 1872. Adapted from Rickards and Woodcock (2005, p. 266). In Sedgwick (1845, 1846) the Brathay, Coldwell, and Wray Castle formations were contained within the Coniston Flags, which then also contained the Llandovery Stockdale Group and the Ludlow Coniston Group (lower part).

Kneller *et al.* (1994) saw no sedimentological basis for the use of Lower, Middle, and Upper Coldwell beds, and instead adopted the original usage of the term Coldwell Beds. The Wray Castle Formation of Kneller *et al.* (1992) is the equivalent of the Upper

Coldwell Beds. The Lower Coldwell Beds, equivalent to the Birk Riggs Formation of Kneller *et al.* (1994), do not outcrop in the Howgill Fells area. The Coldwell Formation is exposed at various localities in the Lake District and reaches a maximum thickness of 80 m. In the Howgill Fells, the Formation is typically 10 m thick, and is characterised by calcareous mudstones and sporadic fossiliferous silty limestones. The Coldwell Formation is divided into two calcareous members separated by a graptolitic mudstone, leading to the use of the term 'Bipartite Limestone' in the literature.

The lower Randy Pike Member contains graptolites of the late Wenlock *Colonograptus ludensis* Biozone and the overlying mudstone interval yields graptolites indicative of the *Neodiversograptus nilssoni* Biozone (Rickards 1967). No graptolites are known from the High Cross Member, the upper division of the Coldwell Formation. The overlying Wray Castle Formation contains graptolites of the *nilssoni* Biozone constraining the High Cross Member to the base of the Ludlow. The laminated mudstone and siltstones of the Tranearth Group, with their lack of bioturbation and benthic fossils, have been interpreted as reflecting deposition under anaerobic bottom waters (Rickards 1967). In comparison to the Brathay and Wray Castle formations, the lower and upper bioturbated members of the Coldwell Formation yield a rich shelly fauna dominated by disarticulated trilobites and including subsidiary brachiopods.

There are two main fossiliferous localities for the Coldwell Formation in the Howgill Fells, the River Rawthey (Locality RR, SD 68899 96978-70070 97251) between the mouth of Backside Beck and the Cross Keys, and in a field along strike from the River Rawthey (Cross Keys Field Locality = CKF, SD 69976 96980, Plate 1, figures 1-2). Both localities are situated close to the Cross Keys Inn, south of Narthwaite (Text-Figure 2.4).



Text-Figure 2.4. Simplified map showing the three fossiliferous localities of the Coldwell Formation in the Howgill Fells. Modified from digimaps sd69 and sd79. © Crown Copyright 2010; an EDINA supplied service. Locality RR represents water-washed sections of the River Rawthey, the full extent of which is SD 68899 96978-70070 97251.

Fossils can be found also in a stream section on the west side of Wandale Hill (Locality WH, SD 69920 98924), although there they are less common. Localities RR and CKF have yielded the most extensive fossil finds, and includes material collected by Rickards (1965, RR), and Owens (1973, CKF). There are also several specimens from the Coldwell Formation collected by Marr from an unspecified locality 'North-north-west of Narthwaite' (see Marr 1913, p. 12).

As part of the present study outcrops at the mouth of Ecker Secker Beck (SD 69148 95405), Gais Gill (NY 7184 0117), Screes Gill (SD 6886 9743), and Crosshaw Beck (SD 6867 9382) were also surveyed but no fossils were found.

Material described includes collections made over the last 40 years by A.T. Thomas, P.D. Lane, and their students from RR and CKF, supplemented by recent field collections by Storey from CKF and WH. At localities RR, CKF, and WH the Coldwell Formation is represented by the Randy Pike Member. Graptolites of the *ludensis* Biozone have been found in the Coldwell Formation at localities RR and WH, but not at CKF. The contact between the Coldwell Formation and underlying Brathay Formation can be found in a dried up stream only 40 m SSE from where fossils were collected at CKF.

Many of the taxa known from the Coldwell Formation were originally described by Hede (1915) from calcareous mudstones at Smedstorp, Sweden. This sequence was originally described by Holst (1892) as the Colonus Shale but was later referred to as the Cyrtograptus Shale by Hede (1915) and Regnéll and Hede (1960). Later a comparison of the lithology, shelly fauna, and chitinozoans from the Colonus Shale at Östra Odarslöv with that of Smedstorp (Laufeld *et al.* 1975, p. 215) showed that both belong to the base of the Colonus Shale (*ludensis* Biozone); The reference by Laufeld *et al.* (1975, p. 218) to Hede's (1915) fauna being from the Cyrtograptus Shale is in error (J. Bergström, personal communication 2011).

2.3 THE COLDWELL FORMATION: TRILOBITE FAUNA

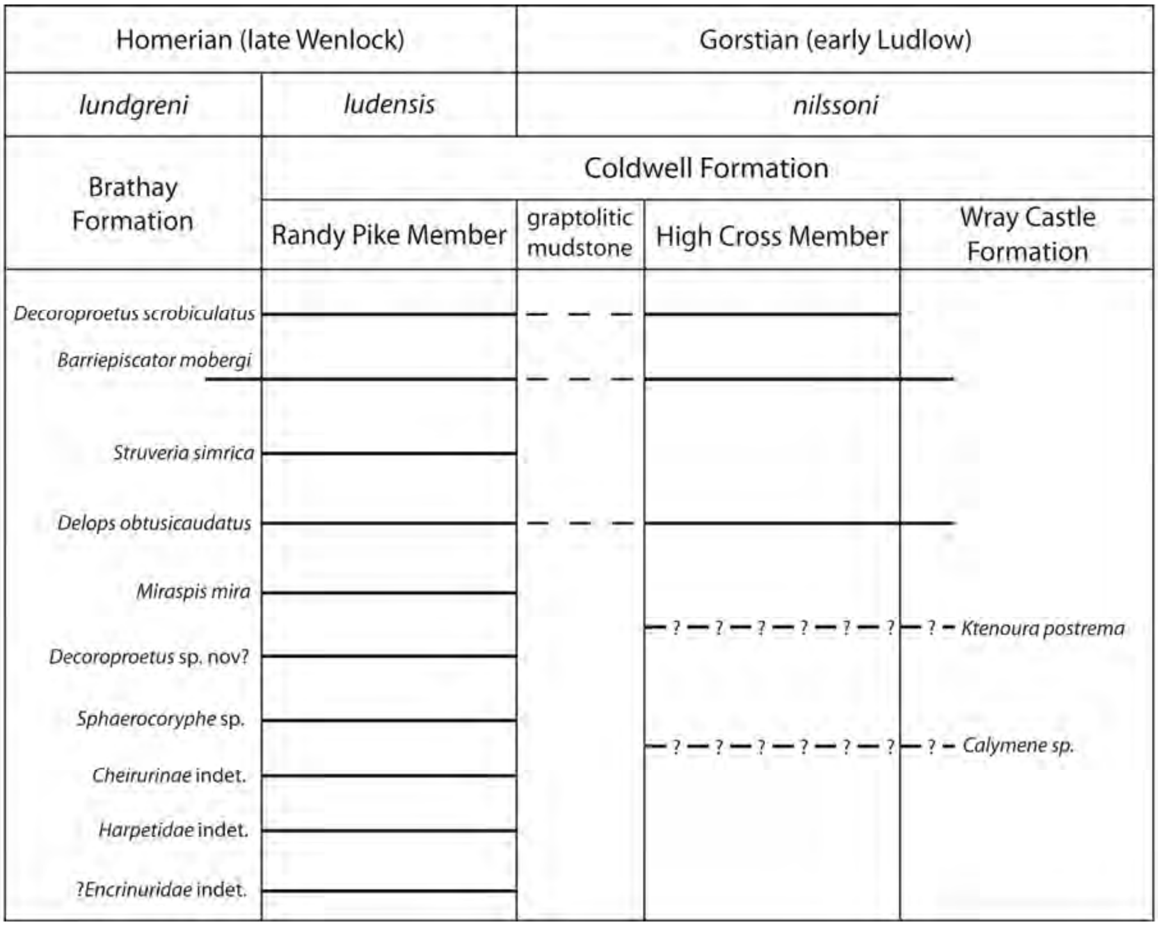
Fossils in the Coldwell Formation occur in calcareous mudstones and scattered lenses of silty limestone. The fauna listed here is based on collections, amassed as part of the present study, from the Randy Pike Member. Based on specimen counts trilobites (minimum 247 individuals) represent around 90 per cent of the fauna, with brachiopods (minimum 27 individuals) constituting most of the remainder. Bryozoans, crinoid ossicles and a solitary rugose coral occur also, but are rare. Relative abundances of trilobites were determined by counting librigena (left and right), cephala, and pygidia (Table 2.1). The highest number of any of these elements indicates the minimum number of individuals per species represented.

Taxon	Cranidia	Pygidia	Librigenae (L+R)	Hypostomes	Thoracic segments
Decoroproetus scrobiculatus	49	124	46L, 55R	-	-
Barriepiscator mobergi	63	58	11L, 14R	6	60
Struveria simrica	31	50	5L, 6R	1	23
Miraspis sp.	4	-	-	-	-
Decoroproetus sp. nov?	1	2	1R		
Cheiruridae indet.	1	1	-	1	-
Delops obtusicaudatus	1	-	-	-	-
Sphaerocoryphe sp.	-	1	-	-	-
Harpetidae indet.	1	-	-	-	-

Table 2.1. Specimen details for the taxa collected from the Coldwell Formation (Randy Pike Member). There are some specimens that could belong to either *Barriepiscator mobergi* or *Struveria simrica* (mostly partial thoracic segments) and these are assigned equally to each, for the purpose of estimating abundance.

Based on 616 trilobite specimens representing a minimum of 247 individuals, *Decoroproetus scrobiculatus* (Owen, 1973) makes up 50 per cent of the fauna with *Barriepiscator mobergi* (Hede, 1915) 25.5 per cent, *Struveria simrica* (Hede, 1915) 20 per cent, *Miraspis* sp. 1.6 per cent, and *Decoroproetus* sp. nov? around 1 percent. *Sphaerocoryphe* sp., *Delops obtusicaudatus* (Salter, 1865), a cheirurid, and a harpetid are rare and collectively they represent 1.5 per cent of the trilobite fauna. Thomas (1981) figured *Miraspis mira* (Barrande, 1846) from the Randy Pike Member, and *Miraspis* sp. most likely belongs to that species.

Based on a survey of museum collections from the High Cross Member (BGS, NHM, SM) the trilobites *Decoroproetus scrobiculatus*, *Barriepiscator mobergi*, and *Delops obtusicaudatus* occur but *Struveria simrica* and rare taxa such as *Miraspis* are absent. Collections from the Randy Pike Member are much larger than that of the High Cross Member and the faunal differences between the two is most likely a result of sampling. *Barriepiscator mobergi* is known rarely from the underlying Brathay Formation, and occurs rarely with *Delops obtusicaudatus* in the Wray Castle Formation. *Ktenoura postrema* (Lane, 1971) and *Calymene* sp. are known from the Tranearth Group too, and were either collected from the High Cross Member of the Coldwell Formation or the Wray Castle Formation. The distribution of trilobite taxa in the Tranearth Group is summarized in Text-Figure 2.5.



Text-Figure 2.5. Chart summarising the distribution of trilobite taxa in the Tranearth Group.

2.4 SYSTEMATIC PALAEONTOLOGY

2.4.1 *Material and Methods*

In total the collection comprises over 600 specimens and this represents the largest from the Coldwell Formation to date. The systematic work in this chapter is largely based on this material and is deposited in the Lapworth Museum of Geology, University of Birmingham.

Rock samples were broken using a hammer and anvil. Where possible blocks were broken down to 1 mm size pieces to ensure small specimens were not missed. Specimens were prepared using a pneumatic air brush. Many of the specimens from the Coldwell Formation exist as internal moulds, although some external moulds do occur. For photography, casts of external moulds were made using latex. In order to better illustrate features and achieve the best contrast all specimens were whitened with ammonium chloride sublimate, and those collected by the authors were stained with Indian ink beforehand. Most of the photographs were taken with a Sony a300 and Sony DT 30mm F2.8 prime macro lens (SAL30M28). A Canon EOS 40D body, attached to a Carl Zeiss Tessovar, was used for specimens too small to photograph with a conventional macro lens.

In addition to material stored in the Lapworth Museum existing museum collections were also surveyed. Specimens from the University of Birmingham (Lapworth Museum of Geology) are registered with the prefix BU, British Geological Survey BGS, Lund University LO, Natural History Museum NHM, National Museum of Wales NMW, Oxford University Museum OUM, and Sedgwick Museum (Cambridge) SM.

The morphological terms used in this chapter follow that of Whittington *et al.* (1997), and additionally Owens (1973) for the proetids. In the descriptions here (and Chapter Three), unless otherwise indicated, 'long', 'length', 'short' etc. normally refer to sagittal (sag.) and exsagittal (exsag.) dimensions, and 'wide', 'narrow' etc. to transverse (tr.) ones. However, in structures such as cephalic anterior and posterior borders and border furrows and pygidial inter-rib furrows, bands and ridges, the conventional use of 'narrow' refers to the direction orthogonal to the length of the structure, whatever the orientation, when this is obvious from the context. Thus the terms transverse ('tr.'), sagittal ('sag.'), and exsagittal ('exsag.') are only indicated when the sense is ambiguous. In Whittington *et al.* (1997) the glabella includes the occipital ring in all trilobites (except agnostoids). The term 'preoccipital area of the glabella' is used herein when referring to the glabella excluding the occipital ring.

2.4.2 *Trilobite classification: genera/subgenera and species/subspecies*

Features used to classify trilobite genera and species vary between trilobite families. The shape of the anterior border, condition of the eye solce, and the profile of the pygidial axis can be used to distinguish proetid genera (Šnajdr 1980) but these features would be of no use when differentiating between dalmanitids, for example. However, there are several features that are commonly used in different trilobite families when differentiating between genera and these include the convexity of the glabella, the size of the genal spines (if present), the nature of the glabella furrows, the size and shape of the glabella lobes, the number of thoracic segments, convexity of the pygidium, the length of the pygidial axis, and sculpture.

The use of the term ‘subgenus’ is widely used in trilobite systematics, and examples include Schrank (1972), Owens (1973), Thomas and Owens (1978), Šnajdr (1980), Thomas and Holloway (1988), Palmer and Repina (1993), and Sandford (2005). Subgenera unite groups of closely related species based on shared characters that are often easily recognised within a genus but are too subtle or few in number to define a new genus, and may include characters which occur in other genera and subgenera (Thomas and Owens 1978). In the dalmanitids, for example, the size and shape of the frontal lobe, orientation of S2, the degree of expansion at L3, the number of thoracic segments, the length of the axis, the nature of the pygidial border (present, absent, weak), the length of pleural furrows, and the sculpture of the cephalon and pygidium (smooth, tubercles, granules) are important features when differentiating between different genera. Features such as the short anterior process and distinct lateral nodes on thoracic axial rings seen in species close to

Dalmanites caudatus (Brünnich, 1781) are of subgeneric importance (Ramsköld 1985).

In older publications there was a tendency for genera to contain a large number of species (Murchison 1839, Salter 1864-1867), displaying wide ranging morphologies that were later defined at the subgeneric level, most notably in the proetids (Owens 1973, Šnajdr 1980) and encrinurids (Schrank 1972, Ramsköld 1986). Advances in taxonomic practice and the use of cladistics increased the number of trilobite genera (Edgecombe and Chatterton 1990, Ramsköld and Chatterton 1991, Ramsköld and Werdelin 1991, Lieberman 1994), which doubled between 1983 and 2002 (Jell and Adrain 2002), by dividing genera into smaller taxonomic groups. Subsequently many previously recognised subgenera are now regarded as distinct genera (for example Lütke 1990, Edgecombe 1994, Lieberman 1994, Lieberman and Kloc 1997).

The tendency for a trilobite subgenus to be weak [such as *Harpidella* (*Rhinotarion*) Whittington and Campbell, 1967] or as in many cases later be proved to represent a distinct genus (for example *Tetinia* Chlupáč, 1971), questions the value of such a taxonomic grouping. In circumstances where subgenera are used to define groups of species with very strong cranidial differences, but where there is a great deal of variation in pygidial morphology (see Thomas and Holloway 1988), seems a reasonable approach and that is adopted here.

Species are based on minor morphological differences that are fewer in number in comparison to genera. In dalmanitids the length of the eye, the shape and extent of the anterior process and posterior pygidial spine (if present), the number of pygidial pleural ribs, the width of the pygidial axis, and the number of incomplete axial rings, the presence/absence or size (sag., tr.) of the post-axial ridge, and subtle differences in sculpture are useful when differentiating species. Additionally subtle variations in the diagnostic features of a genus can also define its species. In *Barriepiscator* gen. nov., for example, the frontal lobe is swollen so that it transgresses the anterior border, but in *B. nobilis* (Thomas, 1900) this is more pronounced than in *B. mobergi* (Hede, 1915).

The concept of a subspecies and its use in palaeontology was discussed by Sylvester-Bradley (1951). Subspecies are common in trilobite systematics, examples can be found in Bruton (1968), Owens (1973), Burton and Eldredge (1974), Šnajdr (1980), and Feist (2002), and are based on subtle differences between groups of specimens that are geographically separate. *Decoroproetus scrobiculatus* Owen, 1973 (England, Wales, and southern Sweden) and *Decoroproetus yassensis* Sun, 1989 (Yass Basin, New South Wales), for example, are regarded here as belonging to the same species. *D. yassensis* differs from *D. scrobiculatus* only in possessing continuous striations in the lateral parts of the preglabellar field and a slightly wider librigena. Both *D. scrobiculatus* and *D. yassensis* contain tropidial ridges on the preglabellar field, a diagnostic feature of the former (Owens 1973), and their pygidia are indistinguishable. *Decoroproetus* species are mainly separated on the degree to which the glabella narrows forwards, the nature of the eye solce, presence or absence of granules, the profile of the preglabella field, the number of pygidial axial rings and pleural ribs (see Owens 1973). The differences between *D. scrobiculatus* and *D. yassensis* are too small to separate them at the specific level and for this reason, along with their geographic separation, they are regarded as separate subspecies (*D. scrobiculatus scrobiculatus* and *D. scrobiculatus yassensis*). Only one other subspecies is used herein, where *Balizoma rosensteinae* (Tripp *et. al.*, 1977*b*) and *B. obtusus* (Angelin, 1851) are regarded as separate subspecies (see Chapter Three).

Order PHACOPIDA Salter, 1864

Suborder PHACOPINA Struve *in* Harrington *et al.*, 1959

Superfamily DALMANITOIDEA Vogdes, 1890

Family DALMANITIDAE Vogdes, 1890

Subfamily SYNPHORIINAE Delo, 1935

2.4.3 Genus BARRIEPISCATOR gen. nov.

Derivation of name. After the late Barrie Rickards and the Latin *piscator* (fisherman); Professor Barrie Rickards was a celebrated angler.

Type species. Dalmanites mobergi Hede, 1915, from the Colonus Shale (Homerian; *ludensis* Biozone), Smedstorp, south Sweden.

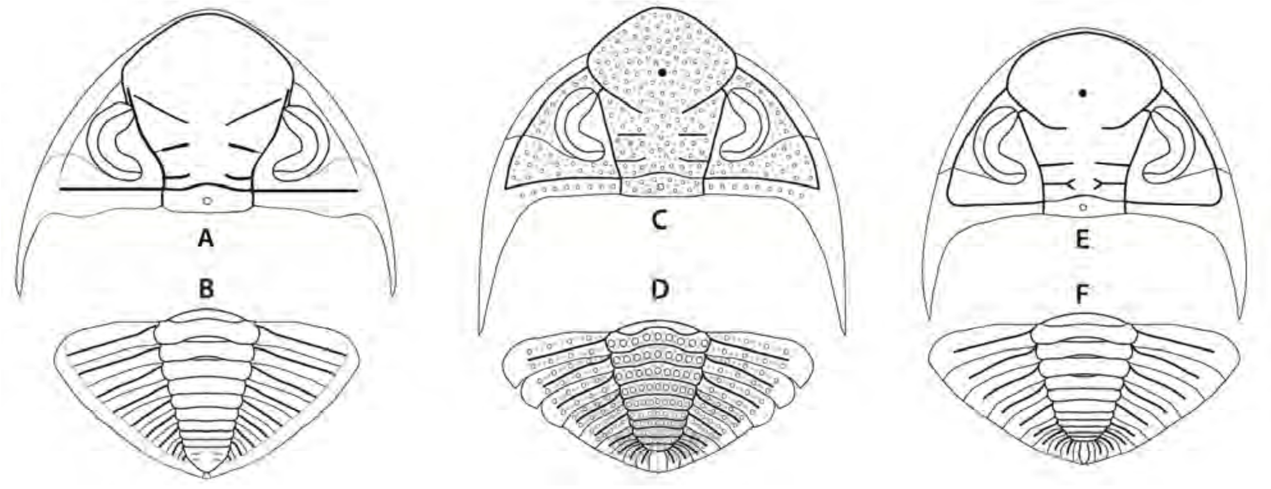
Diagnosis. Eye large, at a maximum extending from half-way between occipital ring and S1 to most anterior end of L3; axial furrows gently diverging anteriorly; S1 gently curving adaxially; S2 transverse, not reaching axial furrow; L2 *c.* 1.4-1.6 times longer than L1; L3 *c.* 1.8-2.5 times longer than L1; frontal lobe subtriangular, transgressing anterior border. Pygidial axial rings strongly arched anteriorly with deep and long furrows; pygidial axial rings flatten posteriorly becoming less distinct; nine to thirteen axial rings, six to nine pygidial pleural ribs; pygidial margin denticulate.

Other species. B. dermaloc (Šnajdr, 1981), *B. nobilis* (Thomas, 1900).

Remarks. Based on its type species *D. obtusicaudatus* (Salter, 1865), *Delops* is regarded as a synonym of *Lygdozoon* Holloway, 1981 (see remarks under *Delops* below).

Barriepiscator gen. nov. is erected herein for three taxa formerly assigned to *Delops*: *D. nobilis marri* (=*B. mobergi*), *D. nobilis nobilis* (=*B. nobilis),* and *D. dermaloc.*

Barriepiscator differs from both *Delops* and the closely related *Struveria*, in several respects including large genal spines, axial furrows diverging gently from occipital ring, S2 transverse, shorter L3, frontal lobe transgressing the anterior border, a denticulate pygidial margin, pygidial axial rings strongly arched anteriorly with deep and long furrows, and the presence of tubercles on the cephalon and pygidium (Text-Figure 2.6).



Text-Figure 2.6. Line drawings highlighting key cephalic and pygidial differences between *Delops* (A and B), *Barriepiscator* gen. nov. (C and D), and *Struveria* (E and F). Genera shown are based on *D. collatus* (Holloway 1981), *B. mobergi* (Hede 1915), and *S. simrica* (Hede 1915). Grey shading indicates faint features. Cephala modified, with permission, from Holloway (1981, text-fig. 2a and 2f) and Rickards (1965 text-fig. 1).

Additional differences between *Barriepsicator* and *Delops* include the former possessing a central pit in the frontal lobe, distinct epiborder furrows, lateral and posterior border furrows equal in depth, a shorter pygidial axis, and inter pleural furrows consistent in depth towards pygidial margin. Additional differences between *Barriepsicator* and *Struveria* include the absence of S1 adaxial bifurcation, inner ends of S3 oblique, frontal lobe swollen and pointing forwards, longer S2 in comparison to S1, the eye situated further from the antero-lateral border furrow, absence of a strong postaxial ridge.

Barriepiscator mobergi is the best known species of this genus and it is here selected as type species.

Barriepiscator mobergi (Hede, 1915)

Text-Figure 2.6.C-D; Plate 2, figures 1-18

1878 *Phacops obtusicaudatus*, Salt.; Marr, pp. 882, 883.

1878 *Phacops* (*Odontochile*) *obtusicaudatus*, Salter.; Marr, p. 885.

1864 *Phacops* (*Odontochile*) *obtusicaudatus* Salter; Salter (pars) pl. 1, fig. 42, *non* figs 43-45 [=*Delops obtusicaudatus*]. (Specimen untraced).

? *1911* *Phacops obtusicaudatus*; Watney and Welch, pp. 217, 223, 227-228, 234.

v. 1913 *Phacops (Dalmanites*?) sp. 1; Marr, p. 12, 17 [SM A38995].

v. 1913 *Phacops* (*Dalmanites*) sp. 2; Marr, p. 12, 17 [SM A38996].

*v** 1915 *Dalmanites Mobergi* n. sp., Hede, 1915, p. 40, pl. 4, figs 3-8; p. 50.

v. 1965 *Delops nobilis marri* subsp. nov., Rickards, p. 546, pl. 84, figs 3-7; pl. 85, figs 8-9; text-fig. 1a.

. 1975 *D. mobergi* (Hede); Laufeld *et al.*, pp. 217-219 [*D. mobergi* on p. 217 and 219, *Dalmanites mobergi* on p. 218].

. 1979 *Delops nobilis marri* Rickards; Thomas, p. 450, pl. 1, fig. 20.

. 1979 *Delops;* Thomas, p. 448 (*pars*) [of the Wenlock/Ludlow Bipartite Limestone].

. 1984 *Delops nobilis marri* Rickards; Thomas *et al.*, pp. 52, 56.

. 1988 *Delops nobilis marri* Rickards, 1965; Morris, p. 74.

v. 2008 *Delops*; Storey and Thomas, pp. 376-378.

Type material. The lectotype selected herein is a cephalon (LO 2824t), original of Hede (1915, pl. 4, fig. 3). The paralectotypes are a cephalon (LO 2825t), a thoracic segment (LO 2828t), pygidium (LO 2829t), an eye (LO 2826t), and hypostome (LO 2827t) from the base of the Colonus Shale (Homerian; *ludensis* Biozone), Smedstorp, locality a of Hede (1915), southern Sweden.

Other material. There are 59 cranidia, 45 pygidia, and 5 hypostomes from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), localities RR and CKF, stored at BU, and there are many specimens belonging to this species at SM, NHM, and BGS. There are also 2 cephala (BGS RX 1519-1520) from the Lower Mottled Mudstones Member (Homerian; *nassa* Biozone) of the Nantglyn Flags Formation, roadside, Garth Hwylbren, Llanrwst, housed at BGS. The holotype of *Delops nobilis marri* Rickards, 1965 is SM X.22199 (cephalon) from the Coldwell Formation, locality RR (Rickards 1965, pl. 84, fig. 3).

Diagnosis. Revised from Rickards (1965, pp. 546, 547). Genal spine long, 47-55 per cent of cephalic length (n=2); eye extends from opposite S1 to most anterior end of L3; frontal lobe swollen (sag.). Pygidial axis with 9-10 axial rings; pygidial margin with 2-4 prominent denticles, becoming less distinct posteriorly, doublure flattened.

Description. Only points additional to those documented by Hede (1915) and Rickards (1965) are included. Cephalon, excluding spines, semicircular, bearing coarse rounded tubercles with finer ones between. Coarser tubercles generally evenly spaced, extending from frontal lobe to lateral border. Anterior border has no coarse tubercles, but finer ones occur and extend onto genal spine. Eye 1.5-2 times as long as high. Glabellar lobes increase in length gradually anteriorly. Frontal lobe swollen, *c.* 57-60 per cent of glabellar length (excluding occipital ring). Pygidial axial rings gently arched anteriorly with deep furrows, posteriorly rings flatten and furrows become less distinct. 6-9 pygidial pleural ribs. Coarse tubercles on pygidium, arranged transversely, extending from centre of each axial ring onto pleura, running parallel to anterior edge of pygidial margin. Tubercles arranged in two rows on pleura, separated by pleural furrow. Finer tubercles occur between coarser ones; randomly distributed. Tubercles not reaching margin, concluding at distal end of pleural furrows. Thoracic segments tuberculate also, with tubercles on pleural fields oriented as pygidium. Coarse and fine tubercles on thoracic axis like pygidium but also covered with closely spaced granules. Weak postaxial ridge seen on one specimen (SM A38995a, b).

Remarks. '*Dalmanites mobergi*' Hede, 1915 and '*Delops nobilis marri*' Rickards, 1965 are here regarded as synonymous. The only notable difference between them is the presence of very fine tubercles on the anterior border and genal spines of '*D. mobergi*' which are absent from '*D. nobilis marri*'. These tubercles are not only very small but faint, and their absence from '*D. nobilis marri*' is likely to be due to preservation.

A single cephalon figured by Salter (1864, pl. 1, fig. 42) from the Coldwell Formation, assigned to '*P. obtusi-caudatus*', probably belongs to *Barriepiscator*. The cephalon differs from *B. mobergi* in several respects, including the absence of an epiborder furrow, short genal spines, and a less swollen frontal lobe (sag.). The specimen may represent an undescribed species, but unfortunately it has yet to be traced.

Stratigraphical range. Wenlock (Homerian; *lundgreni* Biozone) to Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. This taxon was originally described from the Swedish Colonus Shale (Homerian; *ludensis* Biozone) of Smedstorp (locality a of Hede, 1915). Rare in the upper few metres of the Brathay Formation (Homerian; *lundgreni* Biozone) but occurs commonly in the overlying Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), of the Howgill Fells area, localities RR and CKF. It occurs rarely in Coldwell Formation, High Cross Member, and the overlying Wray Castle Formation (Gorstian; *nilssoni* Biozone) of the Lake District. Several specimens from the Lower Mottled Mudstones (Homerian; *nassa* Biozone), Nantglyn Flags Formation are housed at the BGS (Keyworth).

Barriepiscator nobilis (Thomas, 1900)

Plate 2, figures 19-21

*v**1900 *Phacops (Dalmania) nobilis;* Thomas, p. 617, pl. 34, figs 1-3.

v. 1965 *Delops nobilis nobilis* (Thomas); Rickards, p. 545, pl. 85, figs 7, 10.

v. 1981 *Delops nobilis nobilis* (Thomas); Holloway, p. 714, pl. 100, figs 7, 10.

. 1984 *Delops nobilis nobilis* (Thomas); Thomas *et al.*, p. 53.

Type material. OUM C.24-25 is the original of Thomas (1900, pl. 34, figs 1, 2) from the Builth Mudstones Formation (Homerian; ?*lundgreni* Biozone), 140 m from the bank of the River Wye, 1.6 km east of Builth, Builth Wells, Powys, Wales, was selected by Rickards (1965, p. 545) as the 'holotype' and is selected here as the lectotype. Three partial cephala with partial thoraces (OUM C.30-C.32), and a partial thorax (OUM C.29) are designated here paralectotypes.

Other material. A single cranidium (OUM C.558), Builth Mudstones Formation (Homerian), 140 m from bank of the River Wye, 1.6 km east of Builth.

Diagnosis. Revised from Rickards (1965, p. 545). Cephalic axial furrows diverge gently to most anterior end of L3 then diverge strongly; eye extends from midway between occipital ring and S1 to most anterior L3; frontal lobe greatly swollen (sag.). Pygidial axis with 9-11 axial rings; most anterior pleural rib shows faint denticulation.

Description. In addition to features recorded by Thomas (1900) and Rickards (1965), frontal lobe 68 per cent (n=1) length of glabella (excluding occipital ring). Thorax with most anterior segments curving gently anteriorly at the pleural tips and posterior most segments gently curving posteriorly. Thoracic segments between these transverse.

Remarks. The thorax of *B. nobilis* is the only complete one known for this genus. The curvature of the anterior and posterior pleural trips is distinctive.

Stratigraphical range. Wenlock (Homerian; ?*lundgreni* Biozone).

Discussion. *B. nobilis* differs from *B. mobergi* in possessing a longer eye, the cephalic axial furrows widen more rapidly from the most anterior part of L3, the frontal lobe is more swollen and extends farther past the anterior border, only the most anterior pleural rib shows faint denticulation. Both *B. mobergi* and *B. nobilis* resemble *B. dermolac* (Šnajdr, 1981) from Bohemia. Differences include the condition of the pygidial margin, and S2 in *B. dermolac* does not extend as far abaxially as in *B. mobergi* and *B. nobilis*. In *B. dermolac* (Šnajdr 1981, tab II, fig. 2) there are signs of a slight denticulation of the anterior most pygidial pleural rib but this could be preservational; this feature is greatly exaggerated in Šnajdr’s pygidial reconstruction (Šnajdr 1981, p. 154). The eye in *B. dermolac* is similar in length to that of *B. mobergi*. The material available for *B. dermolac* from the top Liten Formation (Homerian; *ludensis* Biozone) and base of the Kopanina Formation (Gorstian; *nilssoni* Biozone) of Bohemia is poorly preserved and incomplete making it difficult to be sure that these differences are significant.

2.4.4 Genus DELOPS Rickards, 1965

[*Synonyms*: *Lygdozoon* Holloway, 1981].

Type species. By original designation; *Phacops obtusicaudatus* Salter, 1849, from the Coldwell Formation, High Cross Member (Gorstian; *nilssoni* Biozone), Coldwell, Westmoreland.

Diagnosis. This diagnosis is based on that for *Lygdozoon* by Holloway (1981, p. 717). Epiborder furrow faint; cephalic axial furrows exsaggital or slightly diverging from the posterior border to S1 then strongly diverging abaxially; L2 *c.* 1.8-2.4 times longer than L1; S2 generally oblique, not reaching or only weakly joining axial furrow; L3 *c.* 3.7-5 times longer than L1; cephalic doublure sometimes with faint vincular furrow laterally; anterior cephalic border short (sag.), lacking in front of frontal lobe. Pygidium with weak border and faint border furrow; pleural furrows reach border furrow while interpleural furrows extend faintly to margin; axial terminus poorly defined, well rounded; short postaxial ridge. Surface sculpture granular.

Other species. D. analops (Holloway, 1981), *D. arkansanus* (Van Ingen, 1901), *D. collatus* (Holloway, 1981), *D.* (s.l.) *weaveri* (Salter, 1849).

Remarks. Delops obtusicaudatus was designated as the type species of *Delops* by Rickards (1965) but the species was then known only from poorly preserved cephala and pygidia. Newly collected material displays features that are more consistent with *Lygdozoon* than other taxa assigned by Rickards (1965) to *Delops*. Features of *Lygdozoon* that are seen in *Delops obtusicaudatus* include small genal spines, oblique S2, posterior border deeper than lateral border, L2 significantly longer than L1 (*c.* 1.8-2.4 times), a long pygidial axis, interpleural furrows faintly extending to margin edge, and a weak pygidial border. *Delops* is therefore considered the senior synonym of *Lygdozoon* Holloway (1981). Taxa formerly assigned to *Delops* differ in characters such as the presence of a denticulate margin, and these are reassigned to *Barriepiscator* gen. nov. as noted above. The Llandovery species ‘*Phacops weaveri*’ Salter, 1849 was assigned to *Lygdozoon* by Curtis and Lane (1998). *Delops weaveri* (Salter, 1849) shows a number of symplesiomorphic features not seen in *Delops* species *sensu stricto*, which are a long L1, a less convex glabella, a medial pit on the frontal lobe, and the abaxial slope of pygidium is gentle (rather than steep). Nevertheless, *D. weaveri* is closer to *Delops* than to *Barriepiscator* with regards to cephalic sculpture (fine granules only), the cephalic axial furrows are divergent from S1, the occipital ring is a little wider than L1, the presence of a weak pygidial border, the long pygidial axis, and the pygidial margin is entire (rather than denticulate), hence the reassignment to *Delops sensu lato*.

Delops shows strong similarity to *Barriepiscator* gen. nov. (see remarks under *Barriepiscator*) and *Struveria* Rickards. *Delops* differs from *Struveria* mainly in possessing a longer occipital ring, a short L1 (rather than L1 and L2 roughly equal in length), no adaxial bifurcation of S1, the S2 does not reach axial furrows or only faintly reaches it, the posterior border is deeper and longer than the lateral border, the epiborder furrow is indistinct, the inner ends of S3 are oblique (rather than horizontal), the eye is situated farther from the antero-lateral border furrow, pygidial interpleural furrows become very faint abaxially, the pygidial axis is longer, and the postaxial ridge is indistinct (Text-Figure 2.6).

Delops obtusicaudatus (Salter, 1849)

Plate 3, figures 1-8, ?9, 10-13

1845 *Asaphus caudatus*; Sedgwick, p. 446.

* 1849 *Phacops obtusicaudatus* Salter, p. 7 of pl. 1.

v. 1851 *Phacops* (*Odontochile*) *obtusi-caudata* Salter; M^{c}Coy *in* Sedgwick and M^{c}Coy (1855), p. 161, pl. 1G, figs 15-16.

. 1852 *Phacops* (*Odontochile*) *obtusicaudatus* Salter; Salter *in* Sedgwick and M^{c}Coy (1855), appendix A, p. 2.

. 1864 *Phacops* (*Odontochile*) *obtusicaudatus* Salter; Salter (*pars*) p. 45, pl. 1, figs 43-45, *non* fig. 42 [=?*Barriepiscator* sp.].

v. 1865 *Calymene*? *Daviesii*, *n. sp.*; Salter p. 103, text-fig. 23.

non 1911 *Phacops obtusicaudatus*; Watney and Welch, pp. 217, 223, 227-228, 234 [=*Barriepiscator mobergi*].

non 1913 *Phacops* (*D*) *obtusicaudatus*; Marr, pp. 12, 17 [=*Barriepiscator mobergi*].

v. 1965 *Delops obtusicaudatus* (Salter); Rickards, pp. 543-545, pl. 84, figs 1-2.

1984 *Delops obtusicaudatus* (Salter); Thomas *et al.*, pp. 53, 56.

. 1988 *Delops obtusicaudatus* (Salter, 1849); Morris, p. 74

. 1988 *Struveria*? *daviesii* (Salter, 1865); Morris, p. 223.

Type material. Lectotype selected by Rickards (1965, p. 543, pl. 84; fig. 1); SM A38682, original of Salter 1851, pl. 1G, fig. 15, Coldwell Formation, High Cross Member

(Gorstian; *nilssoni* Biozone), Coldwell, Cumbria, England. Paralectotype figured McCoy (1851), pl. 1G, figs. 16 (specimen not traced).

Other material. There are many specimens belonging to this species housed at SM, OUM, NHM, BGS, and NMW. A single cephalon (BU 4741), Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), locality RR, Howgill Fells area, Bluecaster, is housed at BU. The holotype of '*Calymene*? *daviesii*' Salter, 1865 is pygidium NHM 59195 (pygidium), late Wenlock Series, ?Llangammarch Formation (Caer Beris Member) of Glan Wye (Gwy), 3.2 km NW of Builth Wells, Powys, Wales (Salter 1865, text-fig. 23).

Diagnosis. Genal spine short; eye extends from opposite S1 to most anterior end of L3; S2 oblique, becoming faint abaxially weakly reaching axial furrow; S3 reaches axial furrow. 11-13 pygidial axial rings and 9 pairs of pleural ribs; most posterior axial rings weak.

Description. Frontal lobe pointing forwards gently, 56-59 per cent sagittal glabellar length (excluding occipital ring). L2 short, L3 *c.* 1.8-2.4 and L3 *c.* 3.6-5 times longer than L1. S1 generally transverse but gently curves anteriorly adaxially. S2 oblique, oriented at *c.* 45 degrees abaxially. S3 oblique and deep reaching axial furrow, L3 strongly expanding abaxially. Posterior border deeper than lateral border. Thoracic segments not known. Pygidium 1.5 times wider than longer, pygidial width three times widest point of axis. Weak and narrow pygidial border, interpleural furrows extend faintly onto border and reach margin. Pygidial axial rings convex with deep furrows, most anterior axial rings gently arched anteriorly. Axial rings flatten and furrows become faint posteriorly so that most posterior axial rings are poorly defined. Pygidial axis almost touching border, faint postaxial ridge extending to margin.

Stratigraphical range. Wenlock (Homerian; *nassa* Biozone) to Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. Represented by a single specimen in the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), of the Howgill Fells. Common in the Coldwell (High Cross Member), and Wray Castle formations (Gorstian; *nilssoni* Biozone) of the Lake District, Cumbria. Also occurs in the Lower Mottled Mudstones (Homerian; *nassa-ludensis* biozones) of the Llanrwst District; the burrow mottled mudstones of the Builth Mudstones Formation (Homerian; *nassa* to *ludensis* biozones), Builth Wells, Powys; and the Llangammarch Formation, Caer Beris Member (Homerian), road cutting on the A483 just south of Howey.

Discussion. D. obtusicaudatus resembles *D. collatus* (Holloway, 1981) from the St Claire Limestone (Wenlock), Arkansas, USA. Similarities with *D. collatus* include S2 steeply slanted abaxially, S2 faintly reaching axial furrow, and presence of a short genal spine. In both *D. arkansanus* (Van Ingen, 1901) and *D. analops* S2 does not reach the axial furrow, *D. arkansanus* has longer genal spines, whereas in *D. analops* (Holloway, 1981) genal spines are absent. Differences between *Delops obtusicaudatus* and other *Delops* species include S3 reaching axial furrows, anterior portion of eye in line with anterior most end of L3 (rather than just below), and stronger pygidial border furrows.

In older publications, cephala bearing tubercles, and a frontal lobe transgressing the anterior border, have been assigned to *D. obtusicaudatus* in error and belong to

Barriepiscator mobergi. A single specimen figured by Salter (1865), and assigned to *Calymene*? *daviesii* is considered conspecific with *D. obtusicaudatus*. An almost complete specimen (NHM I 4233) most likely belongs to *D. obtusicaudatus* but it is not sufficiently preserved to be certain.

2.4.5 Genus STRUVERIA Rickards, 1965

Type species. Dalmanites simricus Hede, 1915 (=*S. howgillensis* Rickards, 1965), originally described from the Colonus Shale (Homerian; *ludensis* Biozone), Smedstorp, southern Sweden.

Diagnosis. Revised from Rickards (1965, p. 548). Cephalic axial furrows parallel or slightly diverging until S2 then strongly diverging abaxially; eye extends from opposite S1 to anterior end of L3, situated close to antero-lateral border furrow; L1 1-1.25 times longer than L1; S2 reaches axial furrows and slopes gently anteriorly adaxially; L3 *c.* 2.8-3.3 times longer than L1; frontal lobe transversely elliptical in outline, anterior cephalic border short (sag.), border furrow does not pass in front of frontal lobe. Pygidial margin entire; 9-11 axial rings, 7-9 pleural ribs, most anterior 2 or 3 pygidial axial rings gently arched anteriorly flattening posteriorly; pygidial axial ring furrows narrow, axial rings ill defined posteriorly.

Remarks. The cladistic analysis of this chapter indicates that *Struveria* is a basal member of the Synphoriinae. For a comparison between this genus with *Delops* and *Barriepsicator* gen. nov. see under the remarks for each, and Text-Figure 2.6.

Other species. S. orba (Šnajdr, 1981), *S*? *plinthourgos* Sandford and Holloway, 2006.

Struveria simrica (Hede, 1915)

Text-Figure 2.6.E-F; Plate 3, figures 14-21; Plate 4, figures 1-3

v* 1915 *Dalmanites simricus* n. sp., Hede, p. 42, pl. 4, figs 9-10; p. 50.

. 1965 *Struveria howgillensis* sp. nov., Rickards, p. 549, pl. 85, figs 1-6, text-fig. 1b.

. 1975 *Dalmanitina* (*Struveria*) *simrica* (Hede); Laufeld *et al.*, p. 218, figs 8 A-B, 9A; p. 217, fig. 7.

. 1979 *Struveria;* Thomas, p. 448 (*pars*) [of the Wenlock/Ludlow Bipartite Limestone and upper Wenlock beds in N Wales].

v. 1983 *Struveria simrica* (Hede); Tomczykowa, p. 52.

v. 1913 *Phacops* (*Dalmanites*) sp. 2; Marr, p. 12, 17 [SM A38996].

. 1984 *Struveria howgillensis* Rickards; Thomas *et al.*, pp. 53, 56.

. 1988 *Struveria howgillensis* Rickards 1965; Morris, p. 223.

v. 1991 *Struveria simrica* (Hede, 1915); Tomczykowa, p. 33, pl. 6, figs 8-12.

v. 2008 *Struveria*; Storey and Thomas, pp. 376-378.

Type material. From the syntypes of Hede (1915) the lectotype is selected herein as a pygidium (LO 2830t), original of Hede (1915, pl.4, fig. 9). The paralectotype is a pygidium (LO 2831t) from the base of the Colonus Shale (Homerian; *ludensis* Biozone), Smedstop, Scania, southern Sweden (original of Hede, 1915).

Other material. 23 cranidia and 33 pygidia, stored at BU, from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), localities RR and CKF, Howgill Fells area, Bluecaster, England, and are stored in BU. Other collections can be found in SM, BGS, and NMW. The holotype of *Struveria howgillensis* Rickards, 1965 is cephalon SM X.22194 (Rickards 1965, pl. 85, fig. 1) from the Coldwell Formation, locality RR.

Diagnosis. Revised from Rickards (1965) to take account of new material and the synonymy of *S. howgillensis* within *S. simrica*. Eye extends from opposite S1 to front of L3; S1 showing strong adaxial bifurcation; L1 and L2 of approximately equal length but L3 much larger. Pygidial axis with 9-11 well defined rings; 7-9 pygidial pleural ribs; distinct postaxial ridge extending to pygidial margin.

Description. In addition to features noted by Rickards (1965), L3 *c.* 1.8-3 times longer than L2. Eye large, *c.* 2.75-3.5 times as long as high (n=2). Pygidium *c.* 1.6-2 times as wide as long. Axis with 9-11 well defined axial rings. Some specimens may have 12 and possibly 13 axial rings, but these are ill defined posteriorly.

Remarks. Tomczykowa (1991) and Laufeld *et al.* (1975) suggested that *Struveria howgillensis* Rickards (1965) and *Struveria simrica* (Hede 1915) might be conspecific. The main differences between the two species given by Tomczykowa (1991) and Laufeld *et al.* (1975) were that *S. howgillensis* has 9-10 pygidial axial rings and 7-8 pygidial pleural ribs compared with 10-11 axial rings, 8-9 pygidial pleural ribs, and a postaxial ridge in *S. simrica*. Based on new material from the Coldwell Formation the range of variation in *S. howgillensis* overlaps with that seen in *S. simrica*. Many of the specimens from the

Coldwell Formation have a distinct postaxial ridge and its absence from others is likely to be a result of preservation. *S. howgillensis* is thus considered a junior subjective synonym of *S. simrica.*

The number of pygidial axial rings given in the diagnosis for *S. simrica* (=*S. howgillensis*) is restricted to well defined rings only (9-11). Additional pygidial axial rings are ill defined, even in well preserved specimens, and are not included in the diagnosis as they cannot be easily counted. From the present material available around 1-2 indistinct posterior most axial rings can be observed in better preserved specimens.

Stratigraphical range. Wenlock (Homerian; *nassa* Biozone) to ?Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. This species is known from the base of the Colonus Shale (Homerian; *ludensis* Biozone) at Smedstorp and Östra Odarslöv; the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), of the Howgill Fells area, Bluecaster, Cumbria; and from the Lower and Upper Mottled Mudstones (Homerian; *nassa* to *ludensis* biozones), Nantglyn Flags Formation, of North Wales.

Suborder CALYMENINA Swinnerton, 1915

Family CALYMENIDAE Burmeister, 1843

Subfamily CALYMENINAE Burmeister, 1843

2.4.6 Genus CALYMENE Brongniart, 1822

Type species. Calymena [*sic*] *Blumenbachii* [Brong. MS] Desmarest, 1817, p. 517 from the Much Wenlock Limestone Formation (Wenlock, Homerian), Dudley, West Midlands, England.

Calymene sp.

Plate 4, figure 4

Material. A single pygidium (SM A38676) from the Tranearth Group of Helms Knott, Howgill Fells, Cumbria.

Remarks. The collector of SM A38676 is unknown. Marr (1878, 1892) collected from the Tranearth Group of Helm's Knott but did not list any *Calymene* species.

It is not clear if this species was collected from the Coldwell Formation (High Cross Member) or Wray Castle Formation of Helms Knott. This species resembles *C. oliveae* sp. nov. (see Chapter Three) but differs in possessing a slightly wider pygidial axis and an extra pleural rib. The pygidial axis appears to taper backwards rather strongly as in *C. oliveae,* but the posterior end is missing, and it is unclear how close the axis extends to the pygidial margin.

Suborder CHEIRURINA Harrington and Leanza, 1957

Family CHEIRURIDAE Salter, 1864

2.4.7 Subfamily CHEIRURINAE Salter, 1864

Genus KTENOURA Lane, 1971

Type species. By original designation; *Ktenoura retrospinosa* Lane, 1971, p. 31 from the Much Wenlock Limestone Formation (Homerian) of Dudley, West Midlands, England.

Ktenoura postrema (Lane, 1971)

Plate 4, figure 10

*v** 1971 *Cheirurus postremus* Lane, p. 16, pl. 2, figs 2-3.
. 1984 *Cheirurus postremus* Lane; Thomas *et al.*, p. 56.
. 1985 *Ktenoura postrema* (Lane); Přibyl *et al.*, p. 146.
. 1988 *Ktenoura postrema* (Lane, 1971); Morris, p. 122.

Type material. Holotype by original designation is cephalon SM A38677, from the Tranearth Group (Gorstian; *nilssoni* Biozone) of the Howgill Fells, Helms Knott, near Dent, Cumbria, England.

Other material. A cranidium (NHM 42905) from the ?Kirkby Moor Formation

(Ludfordian; ?*bohemicus* Biozone) Benson Knott, Kendal, Westmoreland, Lake District.

Remarks. This species was described by Lane (1971) as occurring in the "Upper Coniston Flags" of Helms Knott and was assumed by Thomas *et al.* (1984, p. 56) to be of Ludfordian age. The Upper Coniston Flags comprise the upper part of the Tranearth Group and the Coniston Group (see Rickards and Woodcock 2005, p. 266). Based on the locality from which this species was collected, it is almost certainly from the Tranearth Group, and is therefore of an early Ludlow age.

The only other named *Ktenoura* species to occur in Britain is the type species, *Ktenoura retrospinosa* Lane, 1971 from the Wenlock Limestone Formation (Wenlock; Homerian) of Dudley and the Coalbrookdale Formation (Wenlock; Sheinwoodian and Homerian) of Dudley and Malvern. *K. postrema* is similar to *K. retrospinosa* but differs in possessing a distinct oblique ridge running from the eye anteriorly towards the axial furrows opposite S3, a more convex frontal lobe, and the eye is situated a litter farther from the antero-lateral border furrow.

Occurrence. This species is known from the Tranearth Group of Helms Knott, Howgill Fells and the ?Kirkby Moor Formation at Benson Knott, Kendal, Westmoreland.

Stratigraphic range. Ludlow (Gorstian; *nilssoni* Biozone to Ludfordian; ?*bohemicus* Biozone).

Cheirurinae indet.

Plate 4, figures 5-7

? *1892* *Cheirurus* sp.; Marr, p. 537.

Material. A poorly preserved cranidium BU 4753a, b from the Coldwell Formation, (locality WH), a hypostome BU 4776 and a pygidium BU 4754 (locality RR). Two partial pygidia (BGS LZ1549-50) from locality WH. All are from the Randy Pike Member (Homerian; *ludensis* Biozone).

Remarks. This material is represented in the Coldwell Formation by only a few poorly preserved specimens that cannot be identified below subfamily level. The only named cheirurid known from the Tranearth Group of the Howgill Fells is *Ktenoura postrema* (Lane, 1971) and these specimens could belong to that species.

Subfamily SPHAEREXOCHINAE Öpik, 1937

2.4.8 Genus SPHAEROCORYPHE Angelin, 1854

Type species. By subsequent designation of ICZN Opinion 614; *Sphaerocoryphe dentata* Angelin, 1854 from the Late Ordovician of Sweden.

Sphaerocoryphe sp.

Plate 4, figure 8

v. 1999 *Sphaerocoryphe*; Thomas and Lane, p. 454.

v. 2008 *Sphaerocoryphe*; Storey and Thomas, p. 377.

Material. One pygidium (BU 4757a+b) from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), locality CKF, Howgill Fells area, Bluecaster, England.

Remarks. This genus is common in the Ordovician, but is not known from outside of the Lake District in the late Silurian. The only other Silurian record of *Sphaerocoryphe* is a cranidium and pygidium from the Telychian of the Broken River Area, north Queensland, Australia (Holloway 1994).

2.4.9 Family ENCRINURIDAE Angelin, 1854

?Encrinuridae indet.

Plate 4, figure 9

1913 *Encrinurus variolaris* Brongn. var.? 2; Marr, p. 12.

Material. A single pygidium (SM A38992a-b) collected by Marr (1913) from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), locality RR, Howgill Fells area, Bluecaster, England, was originally identified as *Encrinurus*. The specimen resembles a laterally compressed *Decoroproetus* pygidium but the preservation is too poor to be certain.

Order PROETIDA Fortey and Owens, 1975

Family PROETIDAE Salter, 1864

2.4.10 Genus DECOROPROETUS Přibyl, 1946

[*Synonyms: Warburgaspis* Přibyl, 1946; *Proetidella* Bancroft, 1949; *Ogmocnemis* Kielan, 1960].

Type species. Proetus decorus Barrande, 1846 p. 64, from the Liteň Formation (Wenlock Series), Loděnice, near Prague, Czech Republic.

Diagnosis. See Owens (1973) and Šnajdr (1980).

Decoroproetus scrobiculatus scrobiculatus Owens, 1973

Plate 4, figures 11-18

v. 1913 *Proëtus*; Marr, p. 12.

v. 1846 *Proetus gracilis*; Barrande, p. 87.

. 1852 *Proetus gracilis*; Barrande, p. 449, pl. 15, fig. 47-49.

v. 1915 *Proetus gracilis* BARR.; Hede, p. 45, pl. 4, figs 22-24; p. 50 [table].

v. 1965 *Decoroproetus* sp.; Rickards, p. 548.

v. 1967 *Decoroproetus*; Rickards, p. 230.

*v** 1973 *Decoroproetus scrobiculatus* sp. nov., Owens, p. 52, pl. 9, figs 10-20; pl. 10, figs 1-8, text-fig. 7.

v. 1978 *Decoroproetus scrobiculatus* Owens; Thomas, p. 44, pl. 12, figs 1-4.

v. 1979 *Decoroproetus;* Thomas, p. 448 (*pars*) [of the Wenlock/Ludlow Bipartite Limestone only].

. 1984 *Decoroproetus scrobiculatus* Owens; Thomas *et al.*, pp. 53, 56.

. 1988 *Decoroproetus scrobiculatus* Owens, 1973; Morris, p. 72.

v. 2008 *Decoroproetus;* Storey and Thomas, p. 376.

v. 2008 *D. scrobiculatus;* Storey and Thomas, p. 377 (*pars*).

Type material. Holotype; by NMW 71.6G512a, from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), locality CKF.

Other material. Around 50 cranidia, 97 librigenae, and over 100 pygidia, stored at BU, from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), localities RR and CKF, Howgill Fells area, Bluecaster, England. 2 cranidia: LO 2843t (Hede 1915, pl. 4, fig. 22; Owens 1973, pl. 9, fig 17.), LO 2844t (Hede 1915, pl. 4, fig. 23; Owens 1973, pl. 9, fig 12.), and a pygidium LO 2845t (Hede, pl. 4, fig. 24; Owens 1973, pl. 9, fig. 19) from the base of the Colonus Shale (Homerian; *ludensis* Biozone), Smedstop, Scania, southern Sweden (originals of Hede 1915). Material belonging to this species can also be found in SM and NMW.

Diagnosis. The following diagnosis is based on that of Owens (1973, p. 52) but with minor modifications to take account of newly collected material. Glabella with 3 pairs of weakly impressed furrows; preglabellar field sigmoidal; anterior border broad, flattened, lateral border broadening markedly towards base of genal spine; short irregular tropidial ridges on lateral parts of preglabellar field and on anterior part of free cheek; pygidial axis with 7-9 ill-defined rings, pleural areas with 5-7 pairs of ribs; weak postaxial ridge. Sculpture of fine striations.

Description. In addition to the features noted by Owens (1973) *Decoroproetus scrobiculatus* has a pygidial length to width ratio of 0.5-0.7. In some specimens this ratio appears a little higher due to compression. Pleural ribs with deep furrows extending close to pygidial margin. Interpleural furrows poorly developed, only distinguishable on most anterior three pairs of pleural ribs, the latter commonly extremely faint or absent. Pygidial doublure with 6-9 prominent terrace ridges with faint secondary terrace ridges running parallel and between these. Spacing between prominent terrace ridges decreases anteriorly, due in part to doublure curvature. Better preserved specimens show a corresponding decrease in the number of secondary ridges from around eight posteriorly and six to four anteriorly. Weak postaxial ridge present but often indistinct or absent due to compression.

Remarks. D. scrobiculatus closely resembles *D. yassensis* Sun, 1989 from the Ludfordian of the Yass Basin, New South Wales. The only differences are less well impressed glabellar furrows, continuous striations in the lateral parts of the preglabellar field, and a broader librigena in *D. yassensis*. The first of these may be preservational as several of the *D. scrobiculatus* specimens in the Coldwell Formation show faint glabellar furrows. Cephalic differences between these two taxa are subtle, and given that their associated pygidia are indistinguishable they are herein regarded as separate subspecies.

Stratigraphical range. Wenlock (Homerian; *lundgreni* Biozone) to Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. This taxon is known from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), Howgill Fells area, Cumbria; the Coldwell Formation, High Cross Member (Gorstian; *nilssoni* Biozone) of Helms Knott, near Dent, Cumbria; Trewern Brook Formation (Homerian; *lundgreni* to *nassa* biozones) of the Long Mountain, Welsh Borderland; Builth Mudstones Formation (Homerian), Builth Wells; and the Swedish Colonus Shale (Homerian; *ludensis* Biozone), Smedstorp (locality a of Hede 1915), Scania, southern Sweden.

Decoroproetus sp. nov?

Plate 4, figures 19-23

v. 2008 *Decoroproetus;* Storey and Thomas, p. 377 (*pars*). [Referred to as specimens distinguished from *D. scrobiculatus* by a raised first pygidial axial ring with deep furrows].

Material. One cranidium (BU 4765), 2 pygidia (BU 4766-67), and a librigena (BU 4769) from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), locality RR, Howgill Fells area, Bluecaster, England.

Description. Cranidium with wide preglabellar field *c.* 1/3 the length of the cranidium bounded by a broad anterior border. Tropidial ridges absent from preglabellar field, but a series of continuous striations occur instead. In longitudinal section preglabellar field sigmoidal in profile. Glabella narrows slightly forwards, a little longer than wide. Librigena broad, with a length width ratio of 1.64 (n=1). Lateral border yields a high radius of curvature. Posterior border curving gently adaxially. Librigena doublure contains a series of distinct terrace ridges, the spacing between these narrow adaxially. Anterior most end of eye terminates far from lateral border. Eye socle absent. Pygidium around 1.6 times as wide as long, margin gently sloping posteriorly. Axis *c.* 1/5 pygidial width anteriorly, narrowing gently posteriorly. Axial furrows well pronounced, most anterior axial ring slightly raised with deep furrow. Six pleural ribs curving backwards, progressively steepening so that posterior most rib is exsagittal. Pleural furrows deep but are only prominent on the first 3 pleura and terminate around half way from the margin edge. Pygidial doublure contains 6 prominent terrace ridges, and in between these a series of faint secondary terrace ridges. A distinct postaxial ridge is present.

Remarks. The pygidium differs from *D. scrobiculatus* in possessing a narrower axis, a more gently sloping pygidial margin, more prominent furrows, a raised first axial ring, and a distinct postaxial ridge. Although bearing some similarities to *D. scrobiculatus* this appears to represent a distinct species and is unlike other *Decoroproetus* taxa described thus far from the Silurian. The cranidium and librigena are assigned to the same species on the basis of co-occurrence, and because these do not belong to *D. scrobiculatus.* The cranidium differs from *D. scrobiculatus* in possessing a wider preglabellar field without tropidal ridges, and a wide anterior border. The librigena differs from *D. scrobiculatus* in being wider, possessing a higher length width ratio, a higher radius of curvature of the lateral border, a more posteriorly positioned eye, and a lack of an eye socle. More material is necessary to evaluate its taxonomic status.

Order LICHIDA Harrington *et al.*,1959

Superfamily ODONTOPLEUROIDEA (Whittington *in* Harrington *et al.*, 1959)

Family ODONTOPLEURIDAE Burmeister, 1843

2.4.11 Genus MIRASPIS Richter and Richter, 1917

Type species. By original designation; *Odontopleura mira* Barrande, 1846, Liteň Formation (Wenlock Series), Czech Republic.

Miraspis sp.

Plate 4, figures 24-25

v. 1913 *Acidaspis*; Marr, p. 12.

v. 2008 *Miraspis*; Storey and Thomas, pp. 376-377.

Material. Four cranidia from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), localities RR, CKF, and WH, housed at BU; a cranidium (SM A38991)

Coldwell Formation (collected by Marr 1913), from an unspecified locality NNW of Narthwaite, Howgill Fells, Bluecaster, England.

Remarks. Only cranidia are available for this species. The material probably belongs to *M. mira* (Barrande, 1846) as described by Thomas (1981) from the Coldwell Formation. Cranidial differences between *M. mira* and other species of the same genus are the absence of a prominent median occipital spine, the L3 is reduced and indistinct being defined only by weak lateral furrows, and the presence of long occipital spines. The material is not of sufficient quality to distinguish these differences.

Order HARPETIDA Ebach & McNamara, 2002

2.4.12 Family HARPETIDAE Hawle and Corda, 1847

Harpetidae indet.

Plate 4, figure 28

v. 2008 *Scotoharpes*; Storey and Thomas, pp. 377-378.

Material. One specimen from the Coldwell Formation, Randy Pike Member (Homerian; *ludensis* Biozone), locality CKF, Howgill Fells area, Bluecaster, England.

Description. Cephalon poorly preserved and incomplete, with brim missing. Occipital ring convex, strongly arched anteriorly. Axial rings 0.25 times width of thorax, axial ring furrows faintly furrowed laterally, becoming stronger posteriorly. Thoracic segments generally transverse but at distal end curve gently abaxially. Thorax incomplete, but with at least 18 segments.

Remarks. The specimen described here is too incomplete to identify beyond the family level.

2.5 CLADISTIC ANALYSIS OF SILURIAN DALMANITIDS

Although the evolutionary relationships of Silurian dalmanitids have been discussed (Holloway 1981), no formal cladistic analysis has been undertaken. A cladistic analysis is presented to clarify the relationships between *Barriepiscator* and *Delops* (subfamily Synphoriinae), *Struveria,* and representatives of the subfamily Dalmanitinae (*Dalmanites, Ommokris,* and *Daytonia*). For this analysis 11 ingroup taxa were selected, with each genus being represented by its type species. In addition *Delops collatus, D. arkansanus, D. analops*, and *Delops* (s.l.) *weaveri* were included to analyse the relationships between them and *D. obtusicaudatus*. *Dalmanites* and *Ommokris* resemble each other closely, particularly in pygidial characters, and they were regarded as synonymous by Ramsköld (1985) and Jell and Adrain (2002). They are coded separately here pending a full revision of the taxa concerned.

The *Dalmanitina*-group (subfamily Zeliskellinae), genera close to *Dalmanitina, Chattiaspis*, and *Eudolatites*, is thought to be ancestral to members of the Dalmanitinae (Harrington *et al.* 1959) but many of the taxa concerned are represented only by poorly preserved material. Although *Zeliszkella* (Middle Ordovician) does not belong to the *Dalmanitina*-group, it is a member of the Zeliskellinae and its many primitive characters make it an appropriate outgroup. *Zeliszkella nenaudae* is represented by some well preserved and uncompressed material.

The taxa included in this analysis are listed here along with references to photographic illustrations: *Zeliszkella nenaudae* (Henry 1980, pl. 26, figs 1-2, pl. 27 figs 1-2), *Barriepiscator mobergi* (Plate 2, figures 1-18), *Barriepiscator nobilis* (Plate 2, figures 19-21), *Dalmanites myops* (Plate 12, figures 4-8; Ramsköld 1985, pl. 10, figs 1-8, 10-11 only), *Daytonia werthneri* (Holloway 1981, pl. 96, figs 1-9, 13, 14), *Delops* (s.l.) *weaveri* (Curtis and Lane 1998, pl. 10, figs 1, 10, 11, 12), *Delops analops* (Holloway 1981, pl. 102, figs 14-21), *Delops arkansanus* (Holloway 1981, pl. 98, fig. 14; pl. 103, figs 9, 12, 14-16, 18, 19), *Delops collatus* (Holloway 1981, pl. 101, figs. 1-17; pl. 102, figs 1-13), *Delops obtusicaudatus* (Plate 3, figures 1-8, ?9, 10-13), *Ommokris bassleri* (Holloway 1981, pl. 96, figs 10-12; pl. 97, figs 1-12); *Struveria simrica* (Plate 3, figures 14-21; Plate 4, figures 1-3); Wenlock. All of the species listed above are known only from the Wenlock with the exception of *Zeliszkella nenaudae* (Mid Ordovician), *Daytonia werthneri* (Llandovery), *D.* (s.l.) *weaveri* (Llandovery) and *B. mobergi* (Wenlock-Ludlow).

2.5.1 *Method*

40 characters (unordered) were coded for this analysis (Table 2.1) and the resulting data matrix (Table 2.2) was constructed using Nexus data editor (Page 2001). The cladistic analysis was performed using WINCLADA (Nixon 2002) and NONA 2.0 (Goloboff 1998). For the analysis the heuristic search algorithm was used with 10,000 maximum trees to keep (hold) and 1000 search repetitions. The ratchet algorithm was also used and produced the same result as the heuristic search. It was noted that the former search produced the final result using fewer characters than the latter. It is possible that the ratchet algorithm is better than the heuristic method in dealing with fewer characters and when there are

conflicts. A character map is also included with the analysis, and comprises unambiguous optimisations only. Ambiguities are omitted when the exact placement of a character on the tree is unknown. This is often the result of homoplasy. Bootstrap support, performed using WINCLADA, for each node was tested based on 10,000 replications and 1000 number of search repetitions.

Table 2.2 showing characters used in phylogenetic analysis. CI and RI values are listed for each character.

1. Exsagittal eye length
[0] from point opposite abaxial end of occipital ring to ½-¾ between abaxial ends of S2 and S3
[1] placed abaxial of a point opposite occipital ring or S1, to in contact with S3
[2] placed abaxial of a point opposite S1 or between S1 and occipital ring to almost in contact with S3
(CI 0.66, RI 0.80)

2. Position of eye relative to lateral border
[0] anterior end not positioned close to lateral border furrow
[1] anterior end positioned close to lateral border furrow
(CI 1.00, RI 1.00)

3. Posterior end of eye relative to the sagittal line
[0] not closely situated
[1] closely situated
(CI 1.00, RI 1.00)

4. Relative length of L1 and L2
[0] L2 1-1.3 times longer than L1
[1] L2 1.4-1.6 times longer than L1
[2] L2 1.75-2.33 times longer than L1
(CI 0.66, RI 0.80)

5. Relative length of L3 and L1
[0] length of L3 2.8 or more times that of L1
[1] L3 less than 2.6 times length of L1
(CI 0.33, RI 0.33)

6. Divergence of axial furrows
[0] divergent from base of L1
[1] divergent from S1
[2] divergent from S2
(CI 0.66, RI 0.75)

7. L3 anteriorly expanding abaxially
[0] absent
[1] weak
[2] strong
(CI 0.66, RI 0.75)

8. Shape of S1
[0] straight
[1] bowed anteriorly adaxially
[2] bifurcate adaxially
(CI 1.00, RI 1.00)
9. Abaxial nature of S1
[0] extends to axial furrow
[1] does not reach axial furrow
(CI 0.50, RI 0.50)

10. Abaxial nature of S2
[0] extends to axial furrow and is deep and distinct abaxially
[1] weakly extends to axial furrow- very narrow and faint abaxially
[2] does not reach axial furrow
(CI 0.50, RI 0.50)

11. Orientation of S2
[0] transverse to gently oblique abaxially
[1] strongly oblique abaxially
(CI 0.25, RI 0.25)

12. Abaxial nature of S3
[0] reaches axial furrow
[1] does not reach axial furrow
(CI 0.33, RI 0.60)
13. Inner section of S3
[0] transverse
[1] oblique
(CI 1.00, RI 1.00)

14. Width of occipital ring compared with L1
[0] equal width
[1] Occipital ring wider
(CI 0.50, RI 0.50)

15. Relationship between frontal lobe and anterior border
[0] frontal lobe does not extend more than half-way across anterior border
[1] frontal lobe almost reaches anterior margin
[2] frontal lobe transgresses anterior border
(CI 1.00, RI 1.00)

16. Length of frontal lobe as a percentage of pre-occipital glabellar length
[0] 60% or less
[1] 61% or more
(CI 0.25, RI 0)
17. Shape of frontal lobe
[0] transversely elliptical in outline
[1] pointing forwards sagittally (sub-triangular to sub-rhombic)
(CI 1.00, RI 1.00)

18. Epiborder furrow
[0] absent
[1] faint
[2] deep
(CI 0.66, RI 0.75)

19. Depth of posterior and lateral border furrows
[0] posterior and lateral border furrows equally deep
[1] posterior border furrow deeper than lateral
(CI 0.50, RI 0.66)

20. Maximum anterior extent of facial suture curving abaxially
[0] in line with S1
[1] half way between S1 and S2
[2] almost in line with S2
(CI 0.66, RI 0.80)

21. Convexity of glabella
[0] low or flat
[1] high
(CI 1.00, RI 1.00)

22. Length of genal spine as a percentage of total cephalic length
[0] spine absent
[1] <39%
[2] 40-49%
[3] >50%
(CI 0.50, RI 0)

23. Medial pit on frontal lobe
[0] absent
[1] present
(CI 1.00, RI 1.00)

24. Spines or crenulations on anterior border
[0] absent
[1] present
(CI 1.00, RI 1.00)

25. Cephalic sculpture
[0] smooth
[1] fine granules only
[2] coarse granules present
[3] coarse tubercles present
(CI 0.75, RI 0.75)

26. Shape of pleural tips of anterior thoracic segments
[0] pointed
[1] well rounded
(CI 1.00, RI 1.00)

27. Sub-rectangular embayment on first pygidial axial ring
[0] indistinct or absent
[1] distinct
(CI 0.50, RI 0.80)

28. Anterior arching of pygidial axial rings
[0] most anterior axial ring weakly arched or transverse
[1] most anterior axial ring strongly arched
(CI 0.50, RI 0.80)

29. Condition of the pygidial margin
[0] entire
[1] denticulate
(CI 1.00, RI 1.00)

30. Pygidial border
[0] absent
[1] weak
[2] distinct
(CI 1.00, RI 1.00)
31. Length of pygidial axis as a percentage of sagittal pygidial length, excluding caudal spine
[0] 86% or less
[1] >88%
(CI 0.50, RI 0.66)

32. Number of incomplete axial rings
[0] 0
[1] 1-2
[2] 3
(CI 0.66, RI 0.75)

33. Crecentic depressions on pleural furrows
[0] absent
[1] present
(CI 1.00, RI 1.00)

34. Relationship between interpleural furrows and pygidial margin
[0] interpleural furrows do not reach pygdial margin
[1] interpleural furrows reach pygidial margin but become faint before margin is reached
[2] interpleural furrows reach pygidial margin: consistent in depth abaxially
(CI 0.66, RI 0.80)

35. Nature of pleural furrows abaxially
[0] consistent in depth and length abaxially
[1] deepen and widen abaxially
(CI 1.00, RI 1.00)

36. Pleural furrows strongly curved abaxially towards distal tip of pleural rib
[0] absent
[1] present
(CI 1.00, RI 1.00)
37. Comparison of pleural and interpleural furrow termination
[0] interpleural furrows extend closer to margin
[1] both terminate at equal distance from margin
(CI 0.50, RI 0.50)

38. Abaxial slope of pygidium, as seen in lateral view
[0] gentle/flattened
[1] steep
(CI 1.00, RI 1.00)

39. Caudal spine
[0] absent
[1] present
(CI 1.00, RI 1.00)

40. Postaxial ridge
[0] absent
[1] short
[2] long
(CI 1.00, RI 1.00)

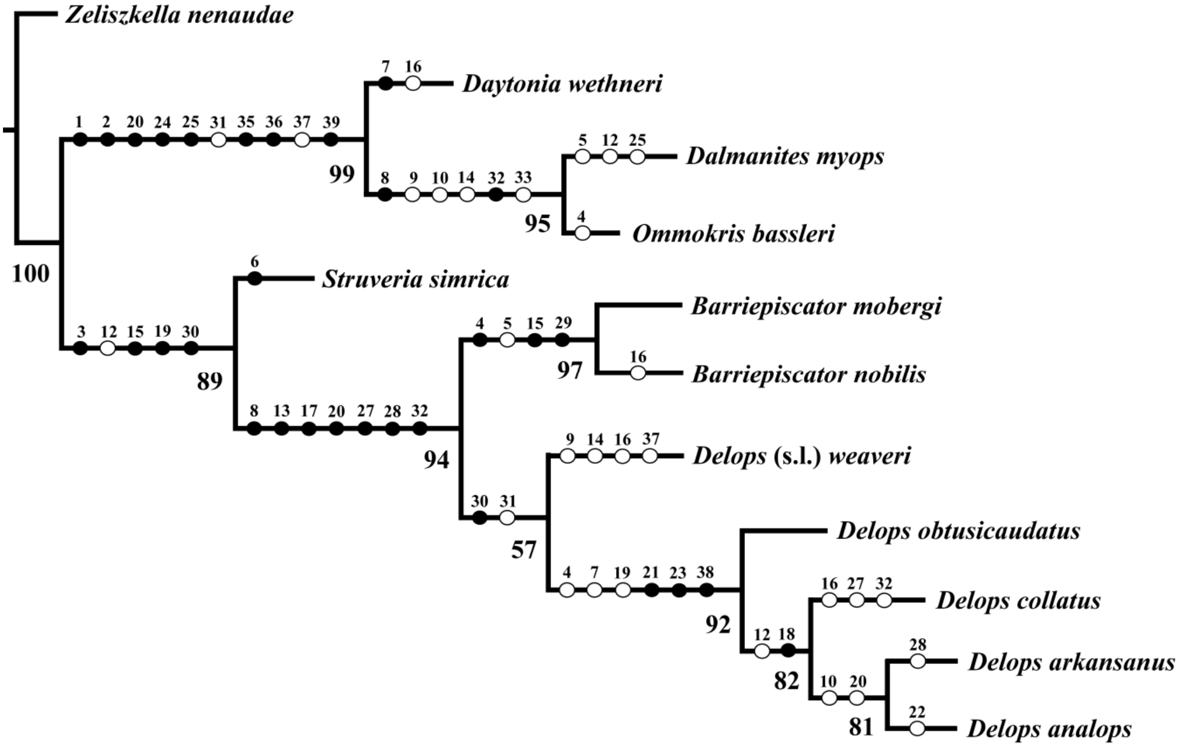
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Zeliszkella nenaudae	2	1	0	0	1	1	2	2	0	0	1	1	0	0	0	0	0	0	1	1
Barriepiscator mobergi	2	1	1	1	1	0	1	1	0	2	0	0	1	0	2	0	1	2	0	2
Barriepiscator nobilis	2	1	1	1	1	0	1	1	0	2	0	0	1	0	2	1	1	2	0	2
Dalmanites myops	0	0	0	0	1	0	1	0	1	2	0	0	0	1	0	0	0	0	1	0
Daytonia wethneri	0	0	0	0	0	1	0	2	0	0	0	1	0	0	0	1	0	2	1	0
Delops (s.l.) weaveri	1	1	1	0	0	1	1	1	1	1	0	0	1	1	1	1	1	2	0	2
Delops analops	1	1	1	2	0	1	2	1	0	2	1	1	1	0	1	0	1	1	1	1
Delops arkansanus	1	1	1	2	0	1	2	1	0	2	1	1	1	0	1	0	1	1	1	1
Delops collatus	1	1	1	2	0	1	2	1	0	1	1	1	1	0	1	1	1	1	1	2
Delops obtusicaudatus	2	1	1	2	0	1	2	1	0	1	1	0	1	0	1	0	1	2	1	2
Ommokris bassleri	0	0	0	2	0	0	1	0	1	2	1	1	0	1	0	0	0	0	1	0
Struveria simrica	2	1	1	0	0	2	1	2	0	0	1	0	0	0	1	0	0	2	0	1

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Zeliszkella nenaudae	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	0
Barriepiscator mobergi	0	3	1	0	3	0	0	1	1	0	0	0	0	2	0	0	0	0	0	1
Barriepiscator nobilis	0	?	1	0	3	0	0	1	1	0	0	0	0	2	0	0	0	0	0	?
Dalmanites myops	0	3	1	1	3	0	1	0	0	2	1	2	1	0	1	1	1	0	1	2
Daytonia wethneri	0	1	1	1	2	0	1	0	0	2	1	1	0	0	1	1	1	0	1	2
Delops (s.l.) weaveri	0	1	1	0	1	?	0	1	0	1	1	0	0	0	0	0	1	0	0	1
Delops analops	1	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	1	0	1
Delops arkansanus	1	1	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	1
Delops collatus	1	1	0	0	1	1	1	1	0	1	1	1	0	1	0	0	0	1	0	1
Delops obtusicaudatus	1	1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	1	0	1
Ommokris bassleri	0	2	1	1	2	0	1	0	0	2	1	2	1	0	1	1	1	0	1	2
Struveria simrica	0	2	1	0	0	0	1	0	0	0	0	1	0	2	0	0	0	0	0	1

Table 2.3: Characters and character states for each taxon used in the cladistic analysis.

2.5.2 *Results*

18 characters in the analysis scored a Retention Index (RI) and Consistency Index (CI) of 1.0 and are thought to be the most important. Those scoring an RI and CI of 1.0 are character numbers 2, 3, 8, 13, 15, 17, 21, 23, 24, 25, 26, 29, 30, 33, 35, 36, 38, 39, and 40. Of these characters, most relate to features of the glabella, frontal lobe and pleura. Less important characters (RI and CI of less than 0.5) are character numbers 5, 11, and 16. Characters such as the lateral orientation of S1, eye length, number of pygidial axial rings and pleural ribs are uninformative and are excluded.



Text-Figure 2.7: Cladogram resulting from the cladistic analysis. Black circles= non homoplasies, white circles= homoplasies. Character map shows unambiguous optimizations only. Bootstrap values are in bold and are listed at the base of each node.

From this cladistic analysis one most parsimonious tree was produced (Text-Figure 2.6) with a length of 88, a CI of 0.64, and an RI of 0.76. The resulting cladogram supports the synonymy of *Lygdozoon* with *Delops obtusicaudatus* by grouping this with species formally assigned to *Lygdozoon*. *D. obtusicaudatus* contains more symplesiomorphic features (see characters 12 and 18) than *D. collatus*, *D. arkansanus*, and *D. analops*, and forms the base of that clade. The exsagittal eye length of *D. obtusicaudatus* (character 1) also differs from other *Delops* species and *D.* (s.l.) *weaveri* states 1 and 2 respectively. *Struveria* and *Barriepiscator* also show character state 2 for character 1) and it is therefore unclear if this represents convergence between *D.* (s.l.) *weaveri* and the base of the *D. collatus* clade or reversal in *D. obtusicaudatus*. The designation of *sensu lato* to *D. weaveri* appears to be justified as the node containing this and other *Delops* species has low bootstrap support. This is due to several homoplasic characters shared with taxa in the Dalmanitinae and Synphoriinae. Although *Delops* (s.l.) *weaveri* groups with other *Delops* species its node is supported by a low bootstrap value due to the sharing of several characters with *Dalmanites*, *Ommokris* and *Daytonia* to the exclusion of other taxa in the Synphoriinae.

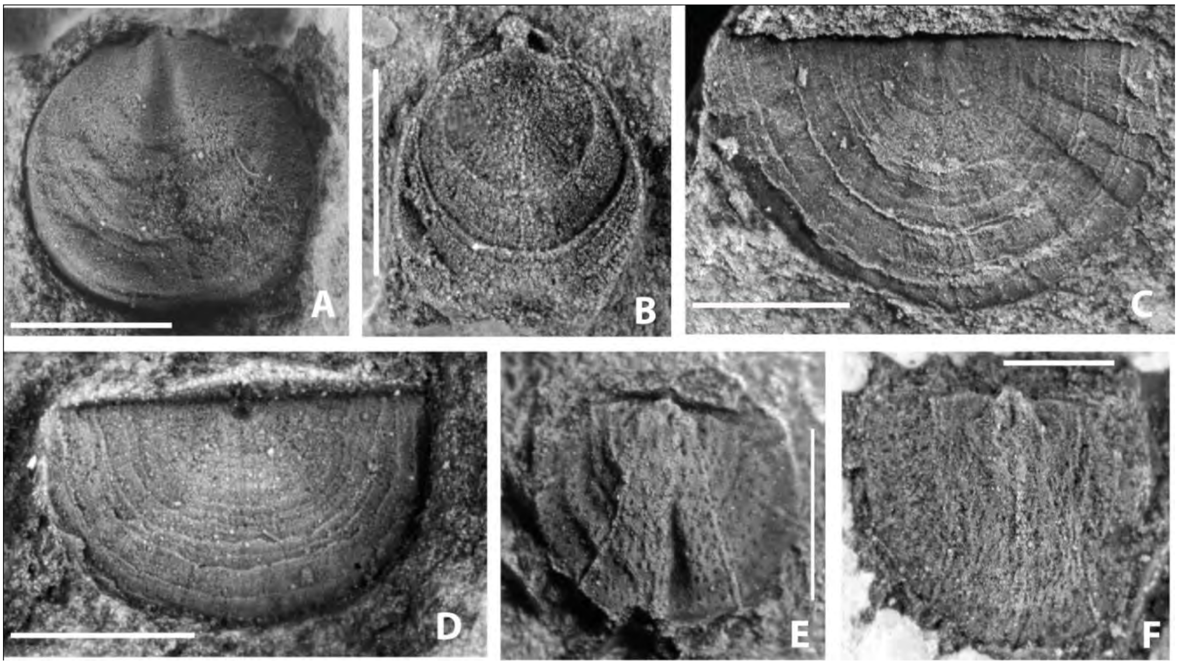
The analysis supports the interpretation of Holloway (1981) that *Delops* (=*Lygdozoon*) forms the sister group of specimens now assigned to *Barriepiscator*, and that *Daytonia* forms the base of a clade containing *Dalmanites* and *Ommokris*. These clades represent the subfamily Synphoriinae and Dalmanitinae respectively, and both are supported by strong bootstrap values. When *Struveria* was erected, Rickards (1965) placed the taxon in the *Dalmanitina*-group. In this analysis *Struveria* occupies an intermediate position between *Zeliszkella*, and the Dalmanitinae on the one hand, and the Synphoriinae on the other. It seems appropriate therefore, to include *Struveria* alongside *Barriepiscator* and *Delops* in the Synphoriinae.

Daytonia werthneri (Aeronian) and *Delops* (s.l.) *weaveri* (Telychian) represent the oldest known occurrences of the Dalmanitinae and Synphoriinae respectively, and this suggests the two subfamilies diverged around the mid to late Llandovery or earlier. Morphological developments in the Dalmanitinae included the eye moving posteriorly, a decrease in the maximum anterior extent of the facial suture, the development of spines and crenulations on the lateral border, and the deepening and lengthening of the pleural furrows abaxially. *Daytonia* which was probably related to the stock that gave rise to the more derived forms, such as *Dalmanites* and *Ommokris*, by modifications including the straightening of S1 and loss of adaxial bifurcation, an increase in the number of complete pygidial axial rings, S1 not reaching axial furrow, and an increase in the width of the occipital ring relative to L1. Early Synphoriinae, including *Struveria*, diverged from dalmaninitids by modifications including the reduction of the length of the anterior border, and steepening of the pygidial pleural ribs. More derived members of this clade showed a continuing reduction in the length of the anterior border, as in *Delops*, or the frontal lobe transgressing the anterior border altogether, as in *Barriepiscator.* Other modifications include the loss of S1 adaxial bifurcation, the frontal lobe pointing forwards strongly, an increase in the length of L2 relative to L2, and S2 not reaching axial furrows. In the case of *Delops*, the latter took place more gradually than *Barriepiscator*, with S2 joining the axial furrows weakly (as in *D. obtusicaudatus* and *D. collatus*) initially. *Delops* and *Barriepiscator* are the most derived forms of the Synphoriinae included in the analysis, and were most likely related to the stock that gave rise to most of the Devonian Synphoriinae genera. The cladogram shown here is congruent with the stratigraphic occurrences except in the case of *Delops* (s.l.) *weaveri* which occurs in older rock than *Struveria* and *Barriepiscator* suggesting that the latter two represent a late off-shot of the basal

Synphoriinae, or that they have a ghost range extending down at least to the Llandovery.

2.6 THE COLDWELL FORMATION: SHELLY FAUNA

Two brachiopods occur in the Coldwell Formation (Randy Pike Member), both recorded for the first time: *Leangella segmentum* (Lindström, 1861) and ?*Protozyga* sp. (Text-Figure 2.7).



Text-Figure 2.8. Photographic figures of brachiopods occurring in the Coldwell Formation.?*Protozyga* sp.: BU 4770 (A), ventral view; BU 4772 (B), dorsal view. *Leangella segmentum*: BU 4774a (C), dorsal view; BU 4771 (D), dorsal view; BU 4775 (E), ventral view; BU 4773 (F), ventral view. Scale bars=2mm.

Leangella is the most abundant brachiopod in the assemblage and is represented by 7 brachial valves and 24 pedicle valves. Only 3 brachial valves and 1 pedicle valve have been recognised for *?Protozyga*. All of the main constituents of the fauna in the Randy

Pike Member can be found at localities RR and CKF, but at locality WH only cheirurid indet., *Miraspis,* and *Leangella* occur. These differences probably reflect sampling from different horizons in the unit.

Other taxa previously recorded from the Coldwell Formation (Marr 1878, 1892) include orthoconic cephalopods, the bivalve *Cardiola*, and the brachiopod *Mezounia*. These taxa have not been found as part of the present study and are therefore considered to represent rare elements of the fauna. Burrows occur frequently thought the Coldwell Formation, the most frequent of which are *Zoophycos* and *Chondrites* (Salam and Kelling 1993).

2.7 THE COLDWELL FORMATION: PALAEOENVIRONMENT

The sediments above and below the Coldwell Formation are laminated graptolitic shales and turbidites. The laminations could have been formed from hemipelagic fallout or weak turbidity flows (Rickards and Woodcock 2005). A detailed study by Salam and Kelling (1993), however, concluded that the laminated mudstone formed from low density and low velocity gravity flows in a density stratified basin. By contrast, the calcareous upper and lower divisions of the Coldwell Formation represent slow and continuous sedimentation during times of oxygenated bottom water (Salam and Kelling 1993). These aerobic conditions represent periods of sea floor ventilation, possibly associated with temporary shallowing (Kneller *et al.* 1994). The Randy Pike Member (Homerian, *ludensis* Biozone) was deposited during a time of eustatic lowstand (Johnson 2006), but the High Cross Member (Gorstian, *nilssoni* Biozone) represents a localized shallowing event and reflects the tectonically active foreland basin setting of the Lake District Basin.

The fragmentary nature of the assemblage indicates transport. *Decoroproetus* shows the highest disparity of pygidia to cephala (ratio 2.3), in comparison to *Barriepiscator* (0.9) and *Struveria* (1.6), suggesting that the proetid may have undergone more transport and possibly occupied shallower depths. Transport was probably local as none of the trilobite species described are known from platform environments, however.

Fossil finds in the mudstone facies of the Tranearth Group are predominantly restricted to nekton. Some taxa characteristic of the Coldwell Formation, for example *Barriepiscator* and *Delops*, occur as rarities in the Brathay and Wray Castle formations. These occurrences could be due to transport into a deeper-water setting, or may reflect a capacity to survive in less well oxygenated conditions.

2.8 COMPARISON WITH OTHER TRILOBITE FAUNAS

The fauna of the Coldwell Formation was termed the *Delops*-*Miraspis* Assemblage by Thomas and Lane (1999) and represents a subgroup of the Odontopleuridae Community Group. Although this assemblage-type has to date only been applied to the fauna of the Coldwell Formation, similar faunas are known also from other basinal settings (Table 2.4).

Taxon	Coldwell Formation (Randy Pike Mbr)	Colonus Shale (Smedstorp)	Mottled Mudstones (Llanrwst District)	Builth Mudstones Formation (Builth Wells)
trilobites				
Acaste	-	-	*A*? sp.	-
Ananaspis	-	-	*A.* aff. *communis* *A.* cf. *stokesii*	-
Barriepiscator	*B. mobergi*	*B. mobergi*	*B. mobergi*	*B. nobilis*
Calymene	?	-	sp.	-
Cheiruridae	gen. et. sp. indet	-	-	-
Dalmanites	-	-	*D. myops* *D. caudatus*	-
Decoroproetus	*D. scrobiculatus* *D. sp. nov*?	*D. scrobiculatus*	-	*D. scrobiculatus*
Delops	*D. obtusicaudatus*	-	*D. obtusicaudatus*	*D. obtusicaudatus*
Exallaspis	-	-	*E.* cf. *coronata*	-
Harpetidae	gen. et. sp. indet	-	-	-
Odontopleura	-	-	sp.	-
Raphiophorus	-	*R. parvulus*	*R. parvulus*	-
Sphaerocoryphe	sp.	-	-	-
Struveria	*S. simrica*	*S. simrica*	*S. simrica*	*S. simrica*
Miraspis	*M. mira*	*M. cardiolarum*	*M. mira*	-
brachiopods				
Bracteoleptaena	-	*B. bracteola*	*B. bracteola*	-
Dualina	-	*D*? sp.	-	-
'Clorinda'	-	*'C' dormitzeri*	*'C' dormitzeri*	-
Glassia	-	-	sp.	-
Howellella	-	-	*H.* cf. *elegans*	
Leangella	*L. segmentum*	-	sp.	-
Mezounia	sp.	sp.	sp.	-
'Orthis'	-	*'O'. holsti*	-	-
Pholidops	-	*P. ellipitica*	-	-
Protathyris	-	-	sp.	-
Protozyga?	sp.	-	-	-
Strophochonetes	-	*S. cingulatus*	sp.	-
Visbyella	-	?	*V.* cf. *trewerna*	-
bivalves				
Cardiola	*C. interrupta*	*C. interrupta* *C. migrans*	*C. interrupta* *C. migrans*	-
Ambonychia	-	*A. antiquissima*	-	-
Antipleura	-	*A*? *cucullaeiformis*	-	-
Butovicella	-	*B. migrans*	-	-
Ctenodonta	-	*retusa*	sp.	-
Lunulicardium	-	*L. caudagalli*	-	-
Maminka	-	*M. suecica*	*M.* cf. *suecica*	-
Modiolopsis	-	*M. senilis*	-	-
Mytilus	-	*M. esuriens*	-	-
Nucula	-	spp.	-	-
Stolidotus	-	*S. siluricus*	*S. siluricus*	-

Taxon	Coldwell Formation (Randy Pike Mbr)	Colonus Shale (Smedstorp)	Mottled Mudstones (Llanrwst District)	Builth Mudstones Formation (Builth Wells)
cephalopods				
Kinoceras	-	-	*K*? sp.	-
Othoceras	*O.* ?*subannulare* *O. tennuistriatim*	*O. originale* sp.	*O.* cf. *dimidiatum* *O.* cf. *mocktreense* *O.* cf. *primaevum*	sp.
gastropods				
Archinacella	-	*A. dubiosa*	-	-
Bellerophon	-	*B. buccinatus*	*B.* cf. *buccinatus*	-
Hormotoma	-	-	*H*? sp.	-
Platyceras	-	-	*P*? sp.	-
hyolithids				indet.
Hyolithes	-	-	*H.* cf. *forbesii*	-
Hyolithus	-	*H. fabaceus*	-	-
ostracods				
Hemsiella	-	-	*H.* sp.	-
Sleia	-	-	*S.* cf. kochii	-
bryozoans				
indet.	gen et. sp. indet.	gen et. sp. indet.	gen et. sp. indet.	-

Table 2.4. Faunal lists of the Coldwell Formation (Randy Pike Member), Lake District, the Colonus Shale (Smedstorp, locality a of Hede 1915), south Sweden, the Mottled Mudstones (Nantglyn Flags Formation), Llanrwst District (Warren *et al.* 1984, BGS and NMW collections), and the Builth Mudstones Formation of Builth Wells (NMW collections).

The Mottled Mudstones (Homerian; *nassa* to *ludensis* biozones), Nantglyn Flags Formation of the Llanrwst District (North Wales) is one example, and yields a fauna dominated by trilobites and brachiopods. *Barriepiscator mobergi*, *Struveria simrica*, *Delops obtusicaudatus*, Miraspis *mira, Leangella*, and *Cardiola* occur, but differences include the presence of *Ananaspis, Dalmanites, Raphiophorus* (Warren *et al.* 1984), and a more diverse brachiopod and bivalve fauna.

The Colonus Shale of Sweden contains another example of a fauna like that of the Coldwell Formation. Of the five trilobite species described by Hede (1915) from Smedstorp, at least three are known to occur in the Coldwell Formation: *Barriepiscator* *mobergi*, *Struveria simrica*, and *Decoroproetus scrobiculatus scrobiculatus* (Owens 1973, pl. 9, figs 12, 17, 19). In addition *Miraspis* occurs in both the Colonus Shale and the Coldwell Formation, but in the former it is represented by *Miraspis cardiolarum* (Hede 1915). *Raphiophorus parvulus* (Forbes, 1848), *Ampyx roualti* in Hede (1915), and the bivalve *Cardiola* are also known from the Colonus Shale. The former is not included in the systematic section of this chapter but is figured photographically for the first time (Plate 4, figures 26-27).

A similar trilobite fauna occurs in burrow mottled mudstones (Homerian; *lundgreni* to *ludensis* biozones) of the Builth Mudstones Formation, Builth Wells, ('shales of Wenlock age' in Rickards 1965), where the trilobites *Decoroproetus scrobiculatus scrobiculatus*, *Delops obtusicaudatus,* and *Barriepiscator nobilis* are known. Despite the strong similarities with the trilobite fauna of the Coldwell Formation, the faunas of the Mottled Mudstones (Nantglyn Flags Formation) and Colonus Shale seem to be particularly close. The Mottled Mudstones (Nantglyn Flags Formation), and possibly the Colonus Shale, belong to the *Visbyella* Community of Calef and Hancock (1974). Due to the scarcity of brachiopods in the Coldwell Formation it is difficult to be certain about the benthic assemblage point. The presence of *Cardiola*, *Mezounia,* orthoconic cephalopods, and graptolites are consistent with the *Visbyella* Community too, but all are rare. Ostracods are a common element of the *Visbyella* Community but neither they nor the nominate brachiopod *Visbyella* cf. *trewerna* are known from the Coldwell Formation. The differences could reflect paleobiogeographical factors, but the presence of several taxa known from shallower-water settings makes it more likely that the Mottled Mudstones and Colonus Shale were deposited at somewhat shallower depths than the Coldwell Formation. The benthic community of the Coldwell Formation may either represent a deeper extension of the *Visbyella* Community (so that many of the taxa are rare and have not been found in the Coldwell Formation) or it may reflect a similar but subtly different shelly community.

The *Raphiophorus-Rabuloproetus* Assemblage (Chlupáč 1987), recorded from the upper Motol Formation (late Wenlock) to lower Kopanina Formation (early Ludlow) of Bohemia, bears some resemblance to the fauna of the Coldwell Formation and similarities include the presence of *Decoroproetus, Struveria, Barriepiscator*, and *Miraspis.* A significant difference, however, is the presence of trilobites either with reduced or absent eyes, including *Rabuloproetus*, *Borkopleura*, and *Raphiophorus*. In the Coldwell Formation, Harpetidae indet. is the only taxon with reduced eyes and this is only represented by one specimen. The reduced or absent eyes of most of the trilobites and the preservation of articulated exoskeletons, suggests that the *Raphiophorus-Rabuloproetus* Assemblage may have occupied greater depths than the fauna of the Coldwell Formation.

The absence of *Miraspis* from the Builth Formation may also reflect subtle palaeoenvironmental differences. *Miraspis,* however, is rare in the Coldwell Formation, and it is possible that its absence is due to sampling bias. Based on the discussion above it seems reasonable to include the fauna of the Mottled Mudstones, Colonus Shale, and possibly the Builth Formation under the same assemblage type as the Coldwell Formation. The *Delops-Miraspis* Assemblage is renamed as the *Barriepiscator-Miraspis* Association to account for the inclusion of *Delops nobilis marri* in the genus *Barriepiscator* and the absence of *Delops* from the Mottled Mudstones and Colonus Shale. The *Barriepiscator-Miraspis* Association is also redefined to take account of differences between this and the *Raphiophorus-Rabuloproetus* Assemblage of Chlupáč (1987) from Bohemia. The *Barriepiscator-Miraspis* Association is defined, herein, as containing *Barriepiscator*, *Miraspis*, *Struveria*, and *Mezounia*, with *Delops* and *Decoroproetus* only sometimes co-occurring with these.

The palaeogeographical setting and fauna of the Coldwell Formation suggests relatively deep-water. There are many descriptions of deep-water trilobite faunas from the Ordovician (Fortey 2006), Devonian, and Carboniferous (Owens and Tilsey 1995), including ‘atheloptic’ assemblages which are dominated by eyeless trilobites. Typical atheloptic assemblage-types occur at depths of at least 300 m (Owens and Tilsey 1995) and possibly much deeper. No such associations are known from the late Silurian, although one possible atheloptic assemblage has been described from the Wenlock Bylands Siltstone of Australia (Sandford and Holloway 2006). There are no blind trilobites in the Coldwell Formation and the lack of reduced eyes in the assemblage may suggest that the fauna of the represents shallower conditions than that of atheloptic assemblages.

The lack of sedimentary structures produced by storms for the entire interval of the Tranearth Group suggests a depth well below that of storm wave base for an extended period of time. The *Barriepiscator-Miraspis* association described herein occupied depths around BA5 and possibly much deeper. The presence of eyes suggests that the assemblage occurred within the photic zone (around 40-100 m). Whittington (1966) suggested a depth range of over 300 m for eyed trilobites, however, and the schizochoral eyes present in phacopids (such as *Barriepiscator*, *Struveria,* and *Delops*) may have been better suited for a range of light levels (Schoenemann 2007), including dim conditions. It is entirely possible that the fauna of the Coldwell Formation occupied depths beyond BA5, into BA6. In that case bioluminescence may have been the main source of light (Brett *et al.* 1993).

PLATES 1-4

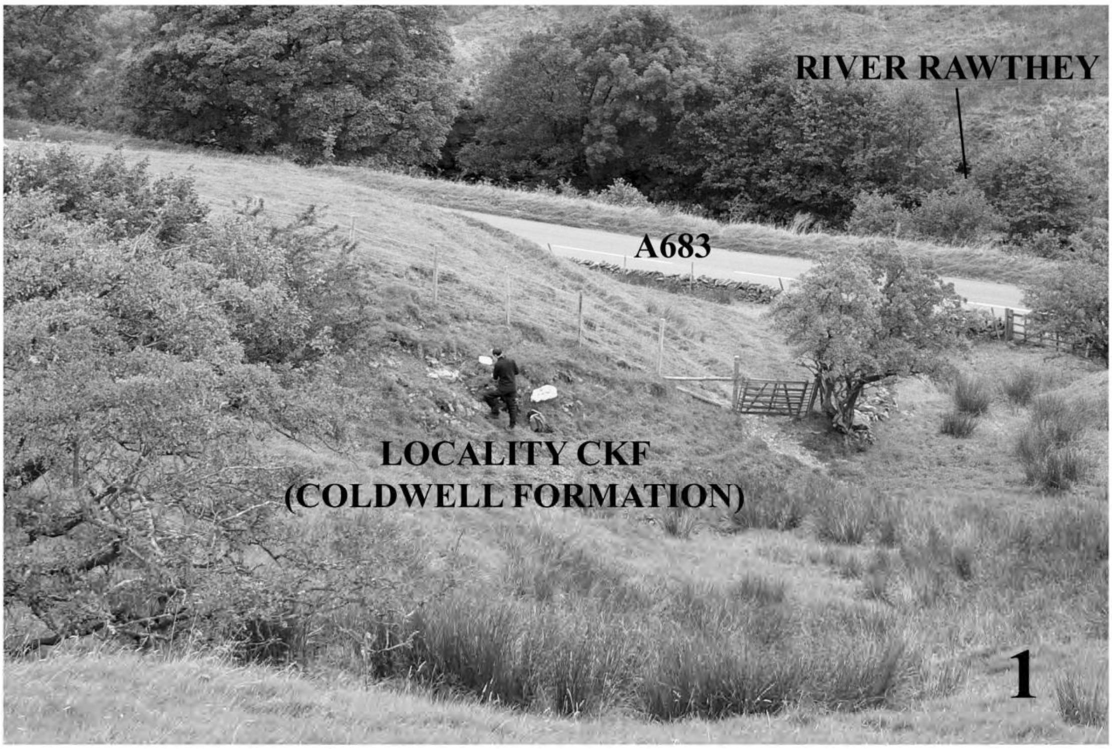
Plates 2-4 comprise figures of either internal moulds or latex casts of external moulds, most of which belong to the former. Photographs are of internal moulds except where stated otherwise.

EXPLANATION OF PLATE 1

Figure 1. Photograph of the Cross Keys Field locality (CKF), looking NW. The locality is just off the A683 north of Sedbergh, along strike from the River Rawthey, and is around 200 metres NE from the Cross Keys Inn. A small exposure of the Coldwell Formation (Randy Pike Member) can be seen where the author is standing. Photograph taken by Ray Storey, 2009.

Figure 2. Photograph of the Coldwell Formation at the Cross Keys Field locality (CKF), looking SW, where the Randy Pike Member is represented by a small exposure. Most of the fossils collected from CKF occurred in loose blocks and scree at the bottom of the photograph. The bag, located towards the bottom right of the picture, measures 0.5 m in length. Photograph taken by the author, 2009.

PLATE 1

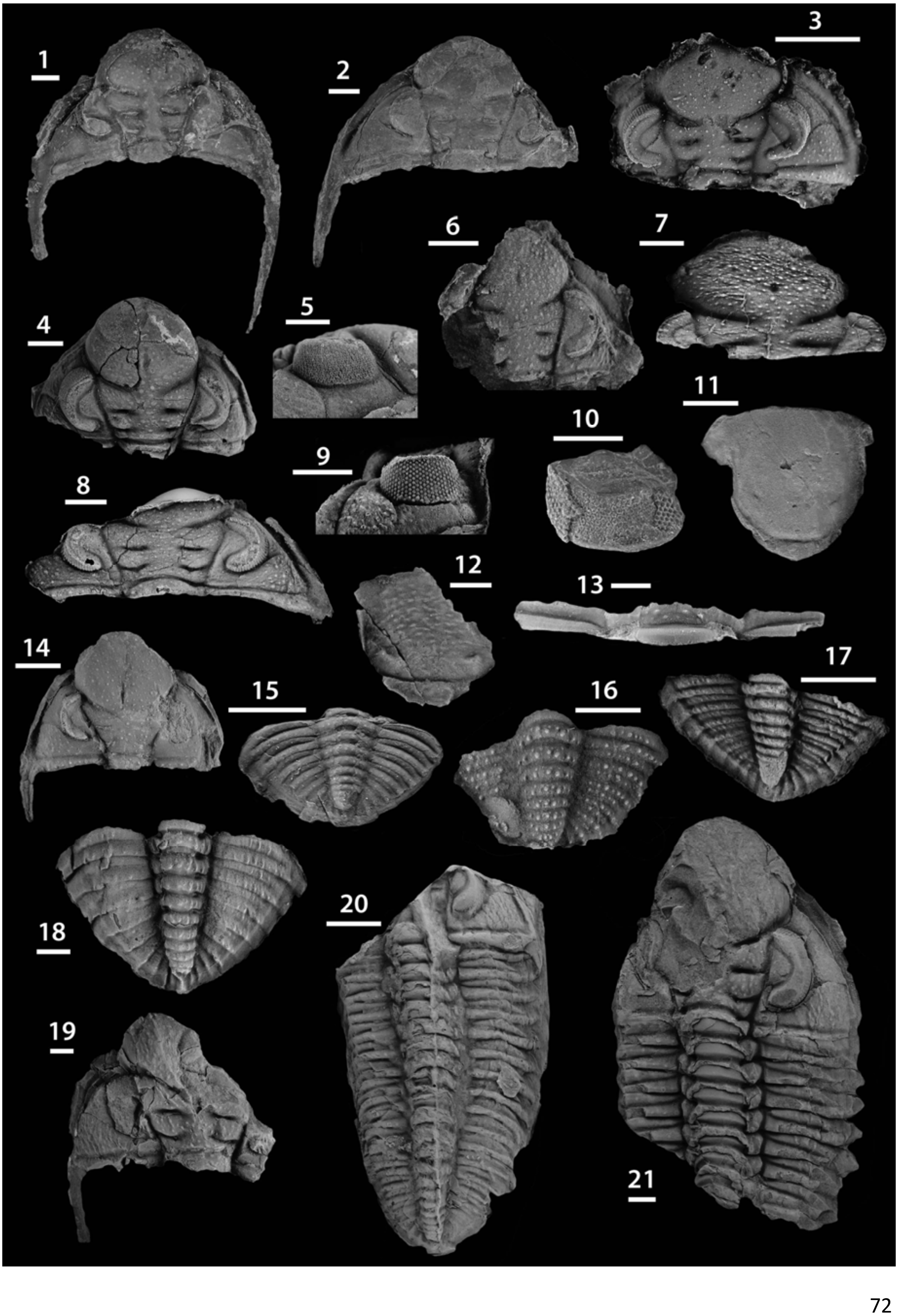


EXPLANATION OF PLATE 2

Figures 1-18. *Barriepiscator mobergi* (Hede, 1915). 1-2, 10-11, 13, 15 are from the Colonus Shale, Smedstorp. 3-9, 12, 16-18 are from the Coldwell Formation, Randy Pike Member, of the Howgill Fells. **1.** lectotype, cephalon LO 2824t, original of Hede (1915, pl. 4, fig. 3); dorsal view. **2.** paralectotype, cephalon LO 2825t, original of Hede (1915, pl. 4, fig. 4); dorsal view. **3.** Latex cast of external mould of cephalon BU 4738; dorsal view, locality CKF. **4-5.** cephalon SM X.22199, original of Rickards (1965, pl. 84, fig. 3); dorsal and lateral views, locality RR. **6.** latex cast of external mould of cephalon BU 4744, dorsal view, locality RR. **7.** cranidium BU 4743; dorsal view, locality RR. **8-9.** latex cast of external mould of cephalon BU 4742; dorsal and lateral view, locality RR. **10.** paralectotype, eye LO 2826t, original of Hede (1915, pl. 4, fig. 5); lateral view. **11.** paralectotype, hypostome LO 2827t, original of Hede, (1915, pl. 4, fig. 6); ventral view. **12.** partial hypostome BU 4745; ventral view, locality RR. 13. paralectotype thoracic, original of Hede (1915, pl. 4, fig. 7); ventral view. **14.** cephalon BGS RX 1519; dorsal view, Lower Mottled Mudstones (*nassa* Biozone), Nantglyn Flags Formation, roadside, Garth yr Hwylbren, Llanrwst. **15.** paralectotype, pygidium LO 2829t, original of Hede (1915, pl. 4, fig. 8); dorsal view. **16.** latex cast of external mould of pygidium BU 4746a; dorsal view, locality RR. **17.** pygidium; dorsal view, locality RR. **18.** pygidium SM A38945a; dorsal view, NNW of Narthwaite. Scale bars represent 5 mm.

Figures 19-21. *Barriepiscator nobilis* (Thomas, 1900), Builth Formation, 1.6 km E of Builth, Builth Wells, Powys. **19.** cephalon OUM C.558; dorsal view. **20.** lectotype, latex cast of external mould of almost complete specimen OUM C.25; dorsal view. **21.** lectotype, head and thorax OUM C.24; dorsal view. Scale bars represent 5 mm.

PLATE 2



EXPLANATION OF PLATE 3

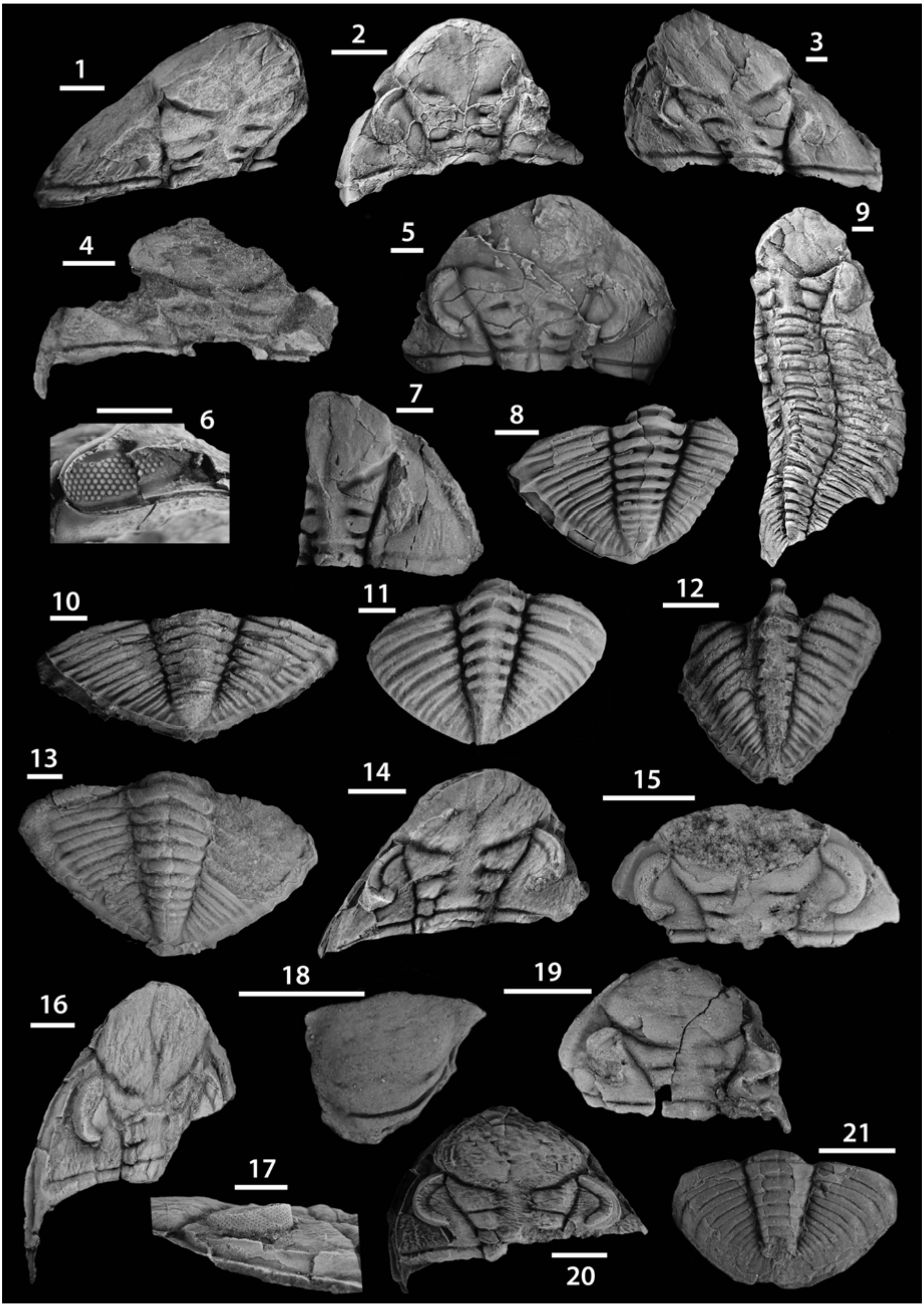
Figures 1-8, 10-13. *Delops obtusicaudatus* (Salter, 1849). **1.** lectotype, cephalon SM A38682, original of Salter (1851, pl. 1G, fig. 15); dorsal view, Coldwell Formation, High Cross Member, Coldwell, Westmoreland. **2.** cephalon NHM I 4234; dorsal view, Builth Formation, unknown locality, photographed by Phill Crabb. **3.** cephalon BGS GSM19261; dorsal view, Coldwell Formation, High Cross Member, Coldwell, Westmoreland. **4.** cephalon SM A41018; dorsal view, High Cross Member, Coldwell Formation, W of Hundreds Road, nr Skelgill, Westmoreland. **5-6.** cephalon BU4741; dorsal and lateral views, Randy Pike Member, Coldwell Formation, locality RR. **7.** cephalon NMW 2010.10G1; dorsal view, Builth Mudstones Formation, burrow mottled mudstones (*nassa-ludensis* biozones), east bank of River Irfon, south of Irfon Bridge, Builth Wells. **8.** pygidium OUM C.28109. **10.** pygidium NMW 2003.24G1; dorsal view, Coldwell Formation, Randy Pike Member, N Side of the most easterly crag of High Crag [NY 3547 0090], 3 km SW of Ambleside, Cumbria. **11.** pygidium NHM 59195, original of Salter (1865, text-fig. 23); dorsal view, Builth Mudstones Formation, Glan Wye, 3.2 km NW of Builth Wells, Powys. **12.** pygidium SM A38680; dorsal view, Builth Mudstones Formation, Builth, Builth Wells, Powys. **13.** pygidium NMW 62.24.G258; dorsal view, Builth Mudstones Formation, Belan, 3.5 km SW Welshpool, Powys. Scale bars represent 5 mm.

Figure 9. *Delops* cf. *obtusicaudatus*. Almost complete specimen NHM I 4233; dorsal view, Builth Mudstones Formation, unknown locality, photographed by Phill Crabb. Scale bar represents 5 mm.

Figures 14-21. *Struveria simrica* (Hede, 1915). 14-20 are from the Coldwell Formation, Randy Pike Member, Howgill Fells; fig. 21 is from the Colonus Shale, Smedstorp, Sweden. **14.** cephalon BU 4739; dorsal view, locality RR. **15.** cephalon BU 4748; dorsal view, locality CKF. **16-17.** cephalon BU 4740; dorsal and lateral view, locality RR. **18.** Hypostome BU 4750; ventral view, locality RR. **19.** cephalon BU 4749; dorsal view, locality CKF. **20.** cranidium SM X.22194a; dorsal view, SM X.22194b figured by Rickards (1965, pl. 85, fig. 1). **21.** lectotype, pygidium LO 2830t, original of Hede (1915, pl. 4, fig. 9); dorsal view. Scale bars represent 5 mm.

All scale bars represent 5 mm.

PLATE 3



EXPLANATION OF PLATE 4

Figures 1-3. *Struveria simrica* (Hede, 1915). 1 is from the Colonus Shale, Smedstorp, Sweden; 2 and 3 are from the Coldwell Formation, Randy Pike Member, locality RR. **1.** paralectotype, pygidium LO 2831t, original of Hede (1915, pl. 4, fig. 10); dorsal view. **2.** pygidium BU 4751; dorsal view, locality RR. **3.** latex cast of external mould of pygidium BU 4752; dorsal view, locality CKF. Scale bars represent 5 mm.

Figure 4. *Calymene* sp. pygidium SM A38676; dorsal view, Tranearth Group, Helms Knott, Howgill Fells. Scale bar represent 5 mm.

Figures 5-7. Cheirurinae indet. from the Coldwell Formation, Randy Pike Member. **5.** latex cast of external mould of cranidium BU 4753a; dorsal view, locality WH. **6.** Hypostome BU 4776; ventral view, locality RR. **7.** pygidium BU 4754; dorsal view, locality RR. Scale bars represent 5mm for figures 5-6, 2 mm for figure 7.

Figure 8. *Sphaerocoryphe* sp. latex cast of external mould of pygidium BU 4757a; dorsal view, Coldwell Formation, Randy Pike Member, locality CKF. Scale bar represents 2 mm.

Figure 9. ?Encrinuridae indet. pygidium SM A38992; dorsal view, Coldwell Formation, Randy Pike Member, locality RR. Scale bar represents 2 mm.

Figure 10. *Ktenoura postrema* (Lane, 1971). Holotype cephalon SM A38677, dorsal view, Tranearth Group, Helms Knott, near Dent. Scale bar represents 5 mm.

Figures 11-18 *Decoroproetus scrobiculatus scrobiculatus* Owens, 1973 from the Coldwell Formation. 11, 13-18 are from the Randy Pike Member. **11.** Holotype, cranidium NMW 71.6G.512a, dorsal view, locality CKF. **12.** cranidium SM A38688; dorsal view; High Cross Member, N side of Helms Knott. **13.** cranidium BU 4760; dorsal view, locality RR. **14.** cranidium BU 4759; dorsal view, locality RR. **15.** librigena BU 4761; dorsal view, locality RR. **16.** partial pygidium BU 4764; dorsal view. **17.** pygidium BU 4762; dorsal view, locality RR. **18.** pygidium BU 4763; dorsal view, locality RR. Scale bars represent 2 mm.

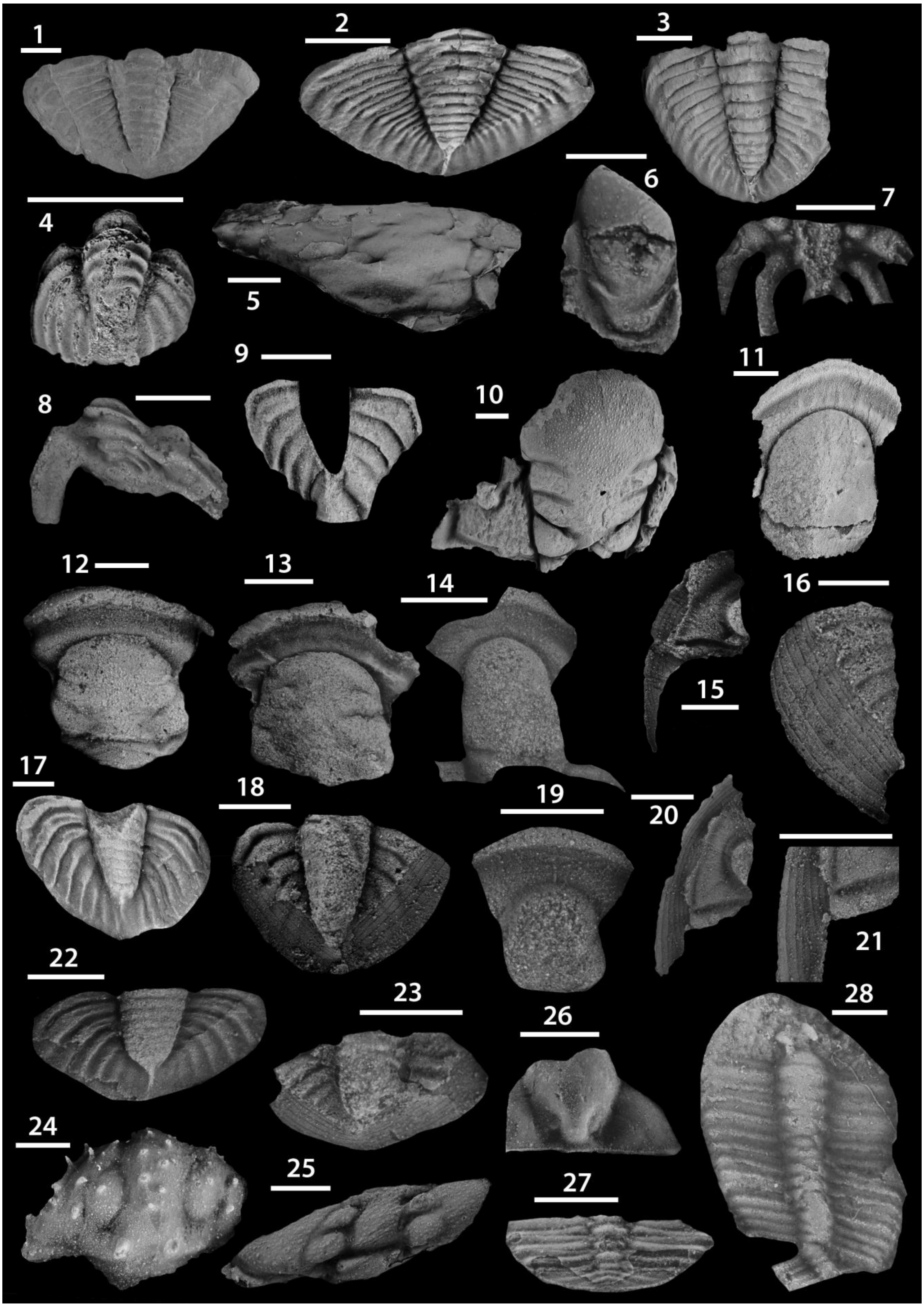
Figures 19-23. *Decoroproetus* sp. nov? from the Coldwell Formation, Randy Pike Member, locality RR. **19.** cranidium BU 4765; dorsal view. **20-21.** librigena BU 4769; dorsal view. **22.** pygidium BU 4766; dorsal view. **23.** pygidium BU 4767; dorsal view. Scale bars represent 2 mm.

Figures 24-25. *Miraspis* sp. from the Coldwell Formation. **24.** Latex cast of external mould of cephalon BU 4755; dorsal view, locality RR. **25.** cephalon BU 4756; dorsal view, locality WH. Scale bars represent 2 mm.

Figures 26-27. *Raphiophorus parvulus* from the Colonus Shale, Smedstorp, Sweden. **26.** cranidium LO 2822t; dorsal view. **27.** pygidium LO 2823t; dorsal view. Scale bars represent 2 mm.

Figure 28. ?*Scotoharpes* sp. from the Coldwell Formation, Randy Pike Member, locality CKF. Latex cast of external mould of almost complete specimen BU 4758; dorsal view. Scale bar represents 2 mm.

PLATE 4



CHAPTER THREE

TRILOBITE ASSOCIATIONS FROM THE LATE SILURIAN SHELF SEQUENCES OF ENGLAND AND WALES

3.1 INTRODUCTION

ALTHOUGH several trilobite taxa are known from basinal settings in the Silurian, these are the exception, for the majority of trilobites were then restricted to the shelf. The late Silurian shelf sequences of England and Wales contain an abundant and varied fauna, often dominated by brachiopods, but also containing numerous other invertebrate fossil groups that include trilobites, bivalves, bryozoans, ostracods, and crinoids. Several of the trilobite taxa occurring in the shelf facies of England and Wales were identified by König 1825, Murchison (1839), Salter (1853, 1864), Reed (1920, 1925), and Shirley (1962) and some of these were revised by later authors (Owens 1973, Shergold 1966, 1967, Siveter 1983, Tripp *et al*. 1977*b*, and Thomas 1978). Many of the trilobite species that occur in the late Silurian of Britain have not been revised in over 150 years, however.

Based on new collections amassed as part of the present study and a comprehensive museum survey, the systematics and stratigraphical ranges of trilobites occurring in the British Ludlow have been revised. In this chapter a total of 29 genera and 46 species of trilobite are documented from British late Silurian shelf settings. Sixteen species are recognised for the first time, but at present only three of these can be confidently assigned to new species and formally diagnosed. *Ananaspis*? *nuda* (Salter, 1864), *Richterarges bucklandii* (Milne-Edwards, 1840), *Trimerus* (*Trimerus*) *johannis* (Salter, 1865) and possibly *Acastella spinosa* (Salter, 1864), have a longer stratigraphical range than previously recognised. *Acaste downingiae* (Murchison, 1839) and *Dalmanites myops* (König, 1825), which were previously thought to occur in the Ludlow, are regarded here as being restricted to the Wenlock. The type material belonging to *Dalmanites nexilis* (Salter, 1864), *Homalonotus knightii* König, 1825, *Trimerus* (*Trimerus*) *johannis* (Salter, 1865), and *Trimerus* (?*Ramiotis*) *salteri* (Morris, 1988) are figured photographically here for the first time.

The term association is used here rather than community and assemblage, both of which have been described by previous authors (see section 3.5.1 for a discussion). Various fossil associations occurring in the British Ludlow have been recognised by previous authors (Watkins 1979, and papers in Boucot and Lawson 1999), and these are based on commonly co-occurring taxa related to a particular lithofacies. Thomas and Lane (1999) and others have shown that the composition of trilobite faunas has environmental significance. Numerous trilobite associations have been documented from the Llandovery and Wenlock, but few from the Ludlow. The majority of associations in the British Ludlow described thus far are based primarily on their brachiopod or other shelly fossil constituents but little emphasis has been given to trilobites. Watkins (1979) listed several of the trilobite species that occurred his brachiopod associations, but these are based on taxa that have not been revised in many years, and only include part of the trilobite fauna. In addition Cherns (1988) described the fauna from the Leintwardine Group, which included a list of several trilobite species. Based on the systematic revision of the trilobite species in this chapter the trilobite faunas occurring in the British Ludlow shelf are outlined.

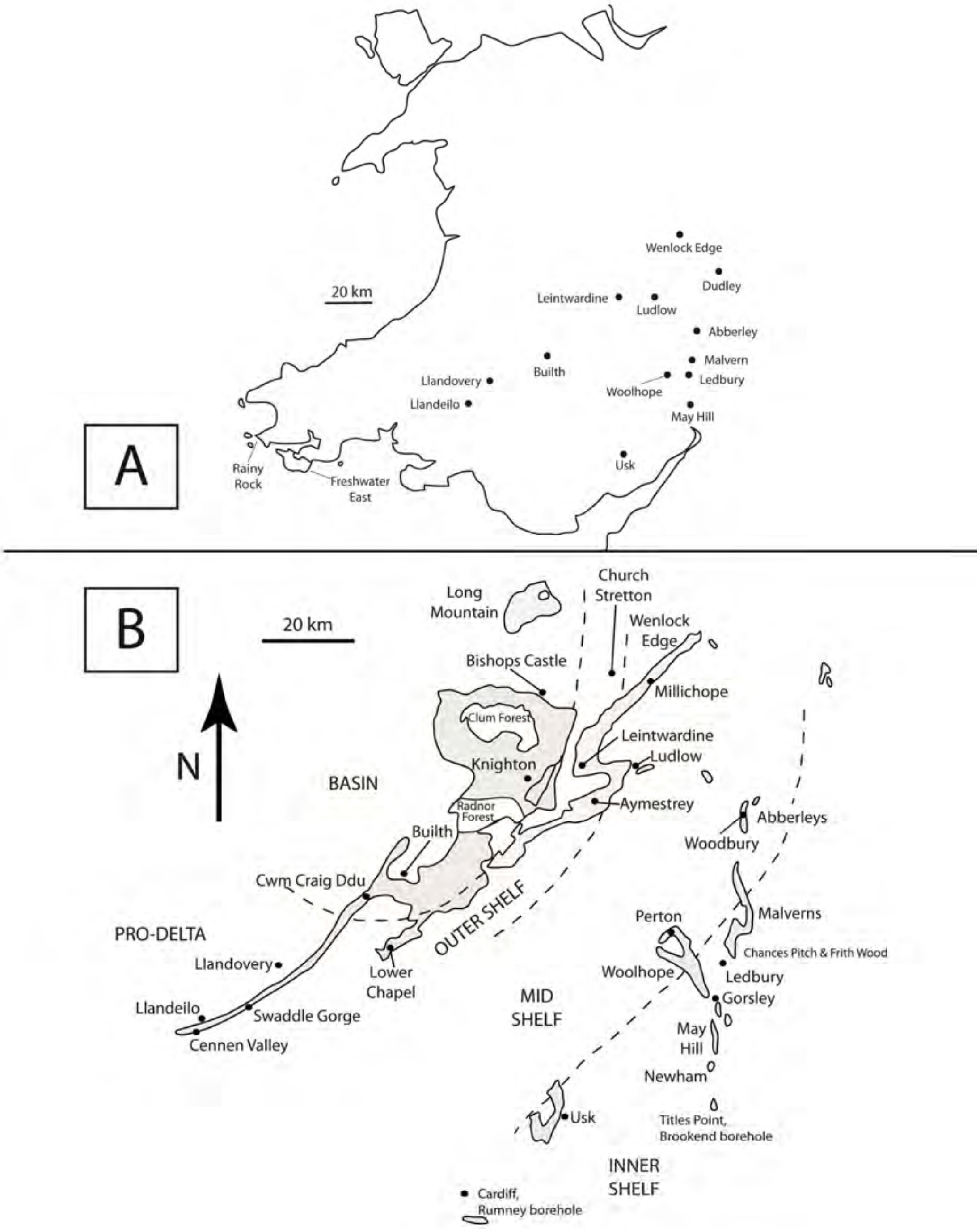
The sedimentology of the Elton, Bringewood, Leintwardine, and Whitcliffe groups have been described in detail by Holland *et al.* (1963), White and Lawson (1978), and

Watkins (1979), and Cherns (1988). A review is presented in Aldridge *et al.* (2000). The sequence from the Elton to Whitcliffe groups is regressive overall, and reflects conditions from the deep to shallow parts of the Ludlow shelf (Mikulic and Watkins 1981). The various palaeoenvironments represented are characterised by distinctive trilobite associations, documented herein. These associations are described in full, and their changes in species content and relative abundance are compared with changes in lithofacies. Silurian seas continued to shallow into the Přídolí, which is largely represented by marginal marine or non-marine facies in Britain (Thomas *et al.* 1984, Aldridge *et al.* 2000). As a result, trilobites occurring in the Přídolí are few in number and are not sufficiently abundant to systematize them into distinct associations.

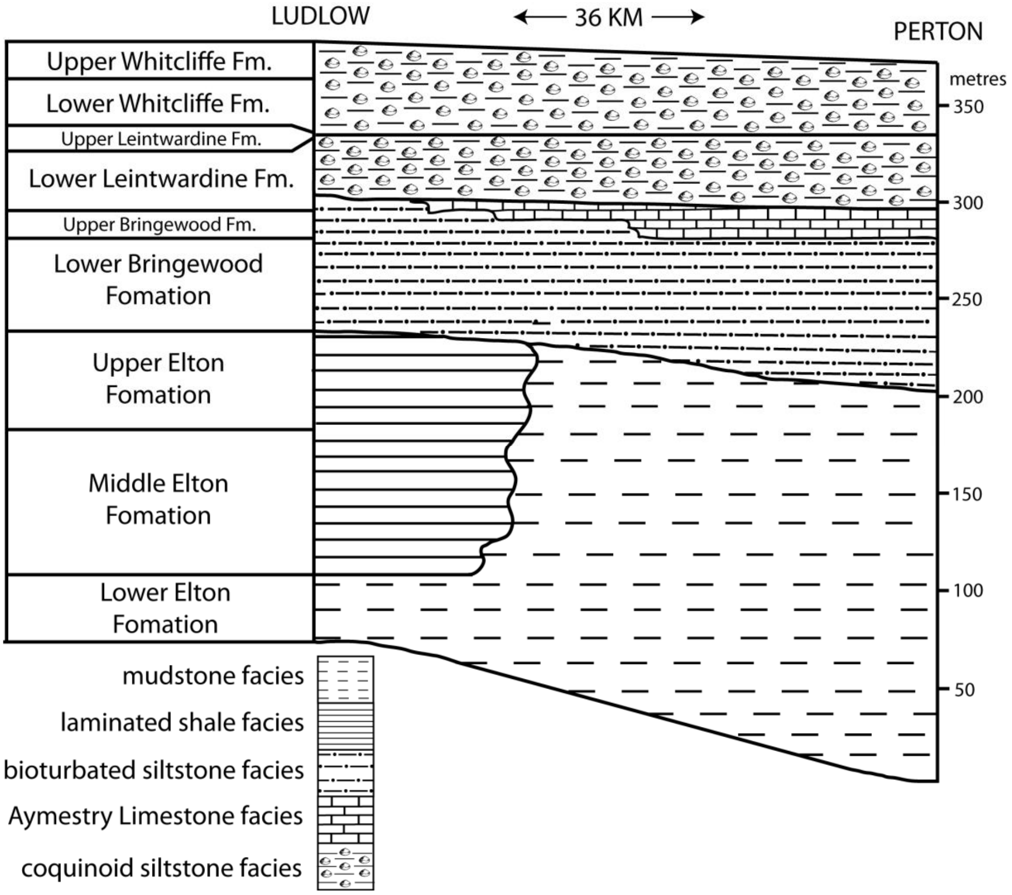
3.2 GEOLOGICAL AND PALAEOENVIRONMENTAL SETTING

In Britain rocks of Ludlow age are known from Wales, the English Midlands (Text-Figure 3.1A), and the Lake District Basin, and possibly south Scotland (Aldridge *et al.* 2000, p. 16). The main Ludlow outcrop area extends from the Welsh Borderlands to central Wales (Text-Figure 3.1B), which then formed the inner, middle, and outer sections of the shelf. A eustatic transgression in the early Ludlow resulted in a shift from widespread Wenlock shelf reef carbonates to fine siliclastic facies (Cherns *et al.* 2007). The Ludlow shelf sequences in Britain are less than 500 metres thick, and they comprise three main lithologies: mudstone, bioturbated calcareous siltstone, and coquinoid siltstone (Text-Figure 3.2). Clay-rich mudstone facies form the majority of the Elton Group, with nodules of limestone scattered throughout (White and Lawson 1978). In the Ludlow area the shale facies of the Middle and Upper Elton formations are laminated. The Bringewood Group is predominantly composed of bioturbated siltstone, but in the Ledbury and Pearton areas the

Upper Bringewood Formation and the base of the Lower Leintwardine Formation are represented by a 15 metre thick limestone unit, the Aymestry Limestone (Watkins 1979). Coquinoid siltstone facies primarily comprise the Leintwardine and Whitcliffe groups, as they are principally composed of silt and shelly material.



Text-Figure 3.1. A map of the localities mentioned in the text from Wales and the Welsh Borderlands are shown (A), with an enlargement of the main outcrops (B). Ludlow rock is indicated by grey shading. Modified from Lawson (1999*a*, p. 358).



Text-Figure 3.2. Sedimentology of the Elton to Whitcliffe groups (adapted from Watkins 1979).

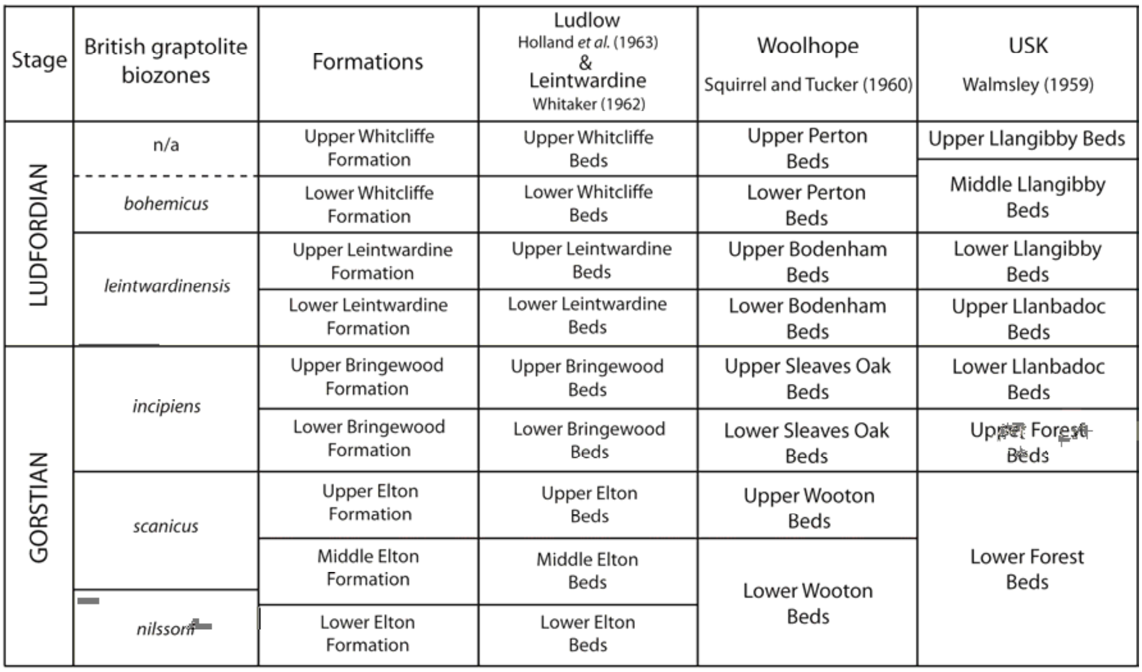
Following a transgression in the early Ludlow, the succession from the Elton to Whitcliffe groups reflect a progressive shallowing of the sea during the Ludlow. The mudstone facies of the Elton Group represents a quiet, distal shelf environment whereas the coquinoid facies of the Leintwardine and Whitcliffe groups suggests a proximal shelf setting with high sedimentation rates (Watkins 1979). As a result of continuing shallowing the majority of rock in the Přídolí represents marine or non-marine environments.

3.3 STRATIGRAPHICAL SETTING

The earliest reference to the term Silurian was by Murchison (1835) but it was not until five years later that in *The Silurian System* (Murchison 1839) the first detailed description of the Silurian rocks in Britain was documented. The history of Silurian stratigraphy and nomenclature, including that of Britain, has been reviewed by numerous authors including Whittard (1961), Cocks *et al.* (1971), Holland (1984), Holland and Bassett (1989), Cocks *et al.* (1992), and Aldridge *et al.* (2000).

Murchison (1835, 1839) recognised three rock units occurring in the Ludlow Series: the ‘Lower Ludlow Rock’, the ‘Aymestry and Sedgeley Limestone’, and the ‘Upper Ludlow Rock’. This terminology was supplemented by later works including Murchison (1853, 1857, 1872), Egerton (1857), Harley (1861), Marston (1870), Marr (1883), La Touche (1884), Wood (1900), and Elles and Salter (1906). The Ludlow rocks were later remapped and new classification schemes were proposed for several areas across Wales and the Welsh Borderlands. These included the areas of Bucknell (Stamp 1919), Builth (Straw 1937), Cwm Craig Ddu (Straw 1953), Gorsley (Lawson 1954), May Hill (Lawson 1955), Usk (Walmsley 1959), Knighton (Holland 1959), Ludlow (Holland *et al.* 1959), Woolhope (Squirrel and Tucker 1960), and Leintwardine (Whitaker 1962).

The classification scheme for the Ludlow area proposed by Holland *et al.* (1959) was described in detail by Holland *et al.* (1963). Holland *et al.* (1959) divided the Ludlow succession into nine units based largely on their palaeontology and lithology: the Elton (Lower, Middle, and Upper), Bringewood (Lower and Upper), Leintwardine (Lower and Upper), and the Whitcliffe beds (Lower and Upper). The units originally described by Holland *et al.* (1959) are now regarded as distinct and widespread formations belonging to the Elton, Bringewood, Leintwardine, and Whitcliffe Groups (Holland 1984). They are the same as coeval units described by previous authors across the Ludlow shelf (see Holland *et al.* 1963, p. 148-151, and Text-Figure 3.3).

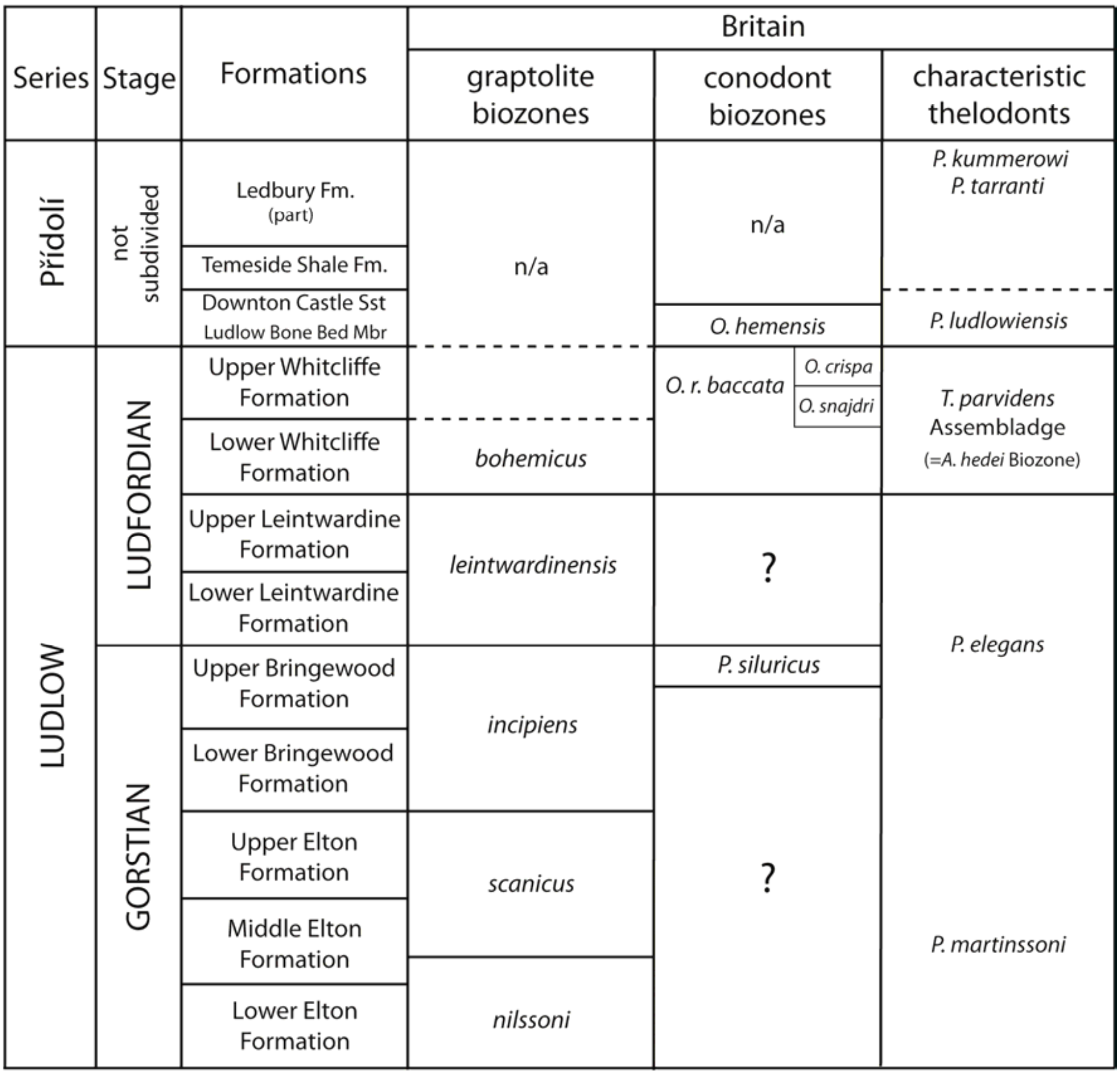


Stage	British graptolite biozones	Formations	Ludlow Holland *et al.* (1963) & Leintwardine Whitaker (1962)	Woolhope Squirrel and Tucker (1960)	USK Walmsley (1959)
LUDFORDIAN	n/a	Upper Whitcliffe Formation	Upper Whitcliffe Beds	Upper Perton Beds	Upper Llangibby Beds
	bohemicus	Lower Whitcliffe Formation	Lower Whitcliffe Beds	Lower Perton Beds	Middle Llangibby Beds
	leintwardinensis	Upper Leintwardine Formation	Upper Leintwardine Beds	Upper Bodenham Beds	Lower Llangibby Beds
		Lower Leintwardine Formation	Lower Leintwardine Beds	Lower Bodenham Beds	Upper Llanbadoc Beds
GORSTIAN	*incipiens*	Upper Bringewood Formation	Upper Bringewood Beds	Upper Sleaves Oak Beds	Lower Llanbadoc Beds
		Lower Bringewood Formation	Lower Bringewood Beds	Lower Sleaves Oak Beds	Upper Forest Beds
	scanicus	Upper Elton Formation	Upper Elton Beds	Upper Wooton Beds	Lower Forest Beds
		Middle Elton Formation	Middle Elton Beds	Lower Wooton Beds	
	nilssoni	Lower Elton Formation	Lower Elton Beds		

Text-Figure 3.3. Correlation of the Elton to Whitcliffe groups from the Ludlow and Leintwardine districts compared with equivalent units at Woolhope and Usk. The districts included are those collected from as part of the present study. Based on Holland *et al.* (1963) and Holland (1984).

Details of exposures and localities of the Ludlow of the Welsh Borderland are given in Holland *et al.* (1963), supplemented by Lawson (1973) and White and Lawson (1978) for the type area.

The Elton to Whitcliffe groups represent a continuous sequence through the Ludlow and contain graptolites from the *nilssoni* to *bohemicus* biozones (Text-Figure 3.4).



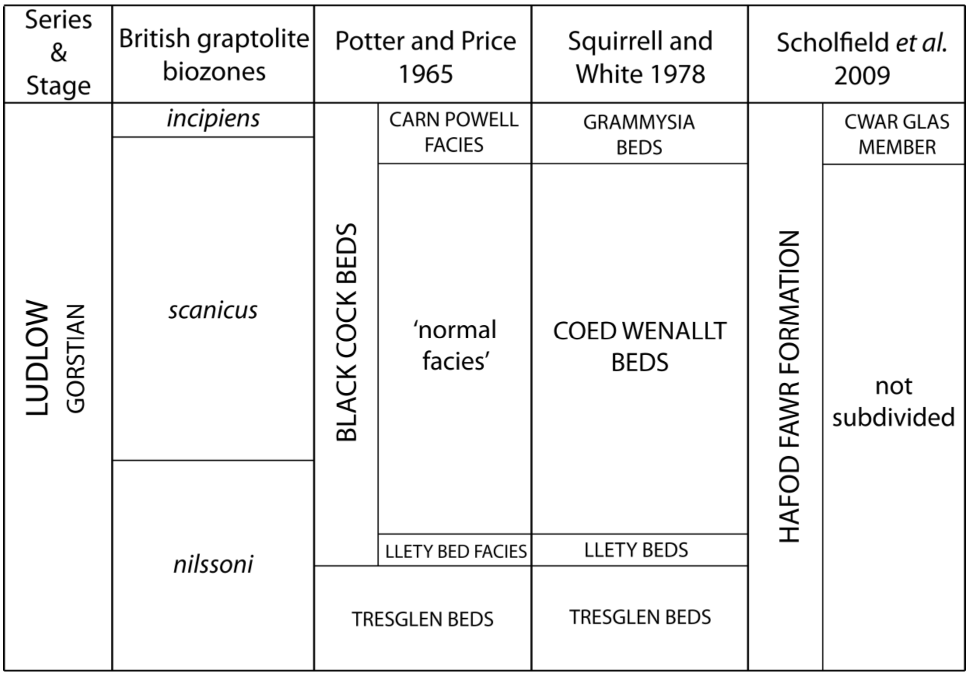
Series	Stage	Formations	Britain		
			graptolite biozones	conodont biozones	characteristic thelodonts
Přídolí	not subdivided	Ledbury Fm. (part)	n/a	n/a	*P. kummerowi* *P. tarranti*
		Temeside Shale Fm.			
		Downton Castle Sst Ludlow Bone Bed Mbr		*O. hemensis*	*P. ludlowiensis*
LUDLOW	LUDFORDIAN	Upper Whitcliffe Formation		*O. r. baccata* *O. crispa* *O. snajdri*	*T. parvidens* Assembladge (=*A. hedei* Biozone)
		Lower Whitcliffe Formation	*bohemicus*		
		Upper Leintwardine Formation	*leintwardinensis*	?	*P. elegans*
		Lower Leintwardine Formation			
	GORSTIAN	Upper Bringewood Formation	*incipiens*	*P. siluricus*	
		Lower Bringewood Formation		?	
		Upper Elton Formation	*scanicus*		
		Middle Elton Formation			*P. martinssoni*
		Lower Elton Formation	*nilssoni*		

Text-Figure 3.4. Correlation scheme showing graptolites, conodonts, and thelodonts for the Ludlow and Přídolí series' of the Ludlow area. Based on Holland *et al.* (1963) and Holland (1984), Siveter *et al.* (1989), and Märss and Miller (2004).

Conodont and thelodont faunas have also been described from the British Ludlow (Aldridge 1985, Aldridge and Schönlaub 1989, Miller and Aldridge 1997, Jeppsson and Aldridge 2000, Märss and Miller 2004) but these typically represent longer ranging intervals (compared with graptolite biozones), and there have been problems correlating the conodont and thelodont faunas of the British Silurian with those of Europe (see Märss and Miller 2004). The conodont *Ancoradella ploeckensis*, an index species of the Gorstian and early Ludfordian, does not occur in the British Ludlow (Aldridge and Schönlaub 1989), and the *Polygnathoides siluricus* biozone occurs in the upper part of the Upper Bringewood Formation, but in Europe it represents an early Ludfordian age (Jeppsson and Aldridge 2000). Märss and Miller (2004) recognised thelodonts indicative of the *Paralogania martinssoni* Biozone in the Middle Elton Formation, the *Paralogania elegens* Biozone in the Upper Bringewood and Lower Leintwardine formations, and the *Phlebolepis elegans* Biozone in the early Whitcliffe Group. The *Phlebolepis ornata* Biozone, which occurs between the *P. martinssoni* and *P. elegans* biozones, has not been recognised from the British Ludlow (Märss and Miller 2004).

Graptolites are not known in Britain after the *bohemicus* Biozone making it difficult to correlate the British latest Ludfordian and Přídolí rocks with those elsewhere. Conodonts of the *O. snajdri* Biozone occur at the top of the Lower Whitcliffe Formation which extends into the Upper Whitcliffe Formation, and it is succeeded by the *O. crispa* Biozone (Miller 1995). The index species *Ozarkodina remscheidensis baccata* occurs in the Upper Whitcliffe Formation too and appears just above the base. Märss and Miller (2004) commented that it is difficult to be sure about the earliest occurrences of *O. remscheidensis baccata* and several of the thelodont species, and in the case of the former it may extend down to the Lower Whitcliffe Formation. The *O. snajdri* and *O. crispa* biozones are probably equivalent to the upper *bohemicus* and *formosus* graptolite biozones respectively (Sadler *et al.* 2009). Trilobite species are rare in the Upper Whitcliffe Formation and it is uncertain which conodont biozones they occur in, and they are informally referred to in this chapter as occurring in the '*O. snajdri-O. crispa* Biozone'. Trilobites in the Whitcliffe Group, such as *Homalonotus knightii* and *Acastella spinosa* occur in the *formosus* biozone of Poland (see Tomczykowa 1991), and in Britain they probably span both the *O. snajdri* and *O. crispa* biozones.

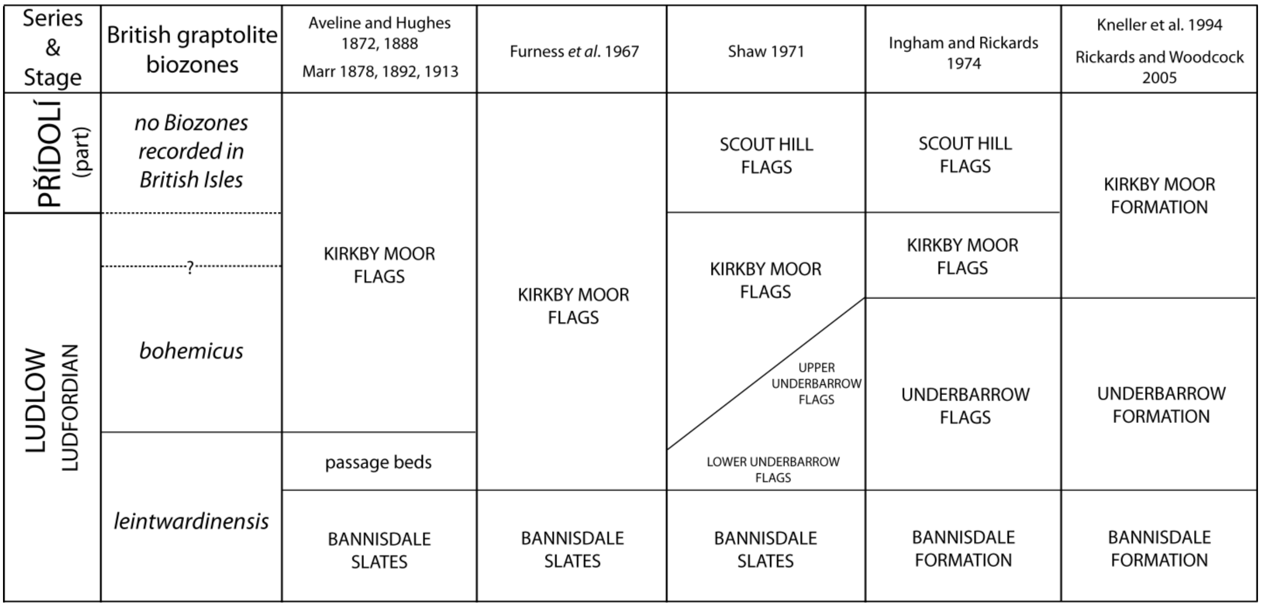
The trilobite fauna of the Hafod Fawr Formation (of Schofield *et al*. 2009) described in this chapter comprises the Black Cock and Tresglen beds of Potter and Price (1965), and the Coed Wenallt and *Grammysia* beds of Squirrel and White (1978). The latter unit equates with the Cwar Glas Member of the Hafod Fawr Formation. The Coed Wenallt Beds are the 'normal facies' of Potter and Price (1965), and these belong to an unnamed member of the Hafod Fawr Formation (R.A.Waters, personal communication 2011, Text-Figure 3.5).



Text-Figure 3.5. Correlation of the Hafod Fawr Formation of Schofield *et al.* (2009) with the units of Squirrell and White (1978) and Potter and Price (1965) for the Llandovery area. The graptolite biozone ages are approximate.

Several of the trilobite species described in this chapter occur in the Kendal Group of the

Lake District, northwestern England. The classification of the Kendal Group is reviewed in Kneller *et al.* (1994), Aldridge *et al.* (2000, p. 422), and Rickards and Woodcock (2005). The Kendal Group spans the late Ludlow to early Přídolí series' (Text-Figure 3.6), and comprises the Bannisdale, Underbarrow, and Kirkby Moor formations.



Text-Figure 3.6. Correlation of the Kendal Group reported in key publications since 1872. Based on Shaw (1971) and Rickards and Woodcock (2005).

Occurring at the base of the Kendal Group, the Bannisdale Formation is associated with graptolites of a *leintwardinensis* Biozone age (Rickards and Woodcock 2005). Based on a comparison of the benthic fauna in the Kendal Group, with those on the Ludlow shelf Shaw (1971) correlated the 'Lower Underbarrow Flags' (=basal Underbarrow Formation) with the Upper Leintwardine Formation, the 'Upper Underbarrow Flags' (=upper part of the Underbarrow Formation) with the Lower Whitcliffe Formation, and the 'Kirkby More Flags' (=lower part of the Kirkby Moor Formation) with the Upper Whitcliffe Formation. The lower part of the Kirkby Moor Formation is diachronous (Shaw 1971, Aldridge *et al.*

2000), representing an early Ludfordian (*leintwardinensis* Biozone) age in the north of the Lake District near Kentmere, and a late Ludfordian (*bohemicus* Biozone) age to the south at Underbarrow and southeast at Benson Knott (SD 5470 9414) near Kendal, and Hills Quarry (SD 5960 8803) near Killington.

A list of trilobite species in the late Silurian of England and Wales, and their straitgraphical and geographical distribution, is presented in table 3.1.

Species	Stratigraphical and geographical distribution
Acaste inflata	LEF (Shadwell Quarry near Much Wenlock)
Acaste cf. *subcaudata*	HFFCGM (43-45, 46A, C)
Acastella spinosa	LLF (Usk), ULF (Usk, Woolhope),ULF (Ledbury), UWF (Whitcliffe Chase, Ludlow)
Acastella cf. *spinosa*	IrF (47B-C, G)
Acastella macrocentra	Ludfordian (Prior's Frome, Hereford and Worcester), UWF (Shucknall Inlier, Hereford and Worcester)
Acastella minor	KMF (Benson Knot, near Kendal), ?Rushall Beds, Herefordshire
Acastella prima	KMF (Kendal and Kirkby Lonsdale regions)
Acastocephala? spp.	LEF (15), LLF (Usk), HFFU (48), Tresglen Formation (Golden Glove, Carmarthenshire)
Acidaspis brightii	Gorstian, Malvern
Alcymene lawsoni	UBF (Woolhope), LLF (Leintwardine and Ludlow areas), ULF (Wenlock Edge), Whitcliffe Group (Whitcliffe)
Alcymene cf. *lawsoni*	early Ludlow (Denbighshire)
Alcymene (s.l.) aff. *A. lawsoni*	LEF (27), MEF (Wenlock Edge), CWB (46A), IrF (47D, G), basal HFFU (48)
Alcymene neointermedia	British occurrence doubtful
Alcymene puellaris	LLF (22, 24, Usk, Gloucestershire, Woolhope) ULF (52, Gloucestershire), LWF (40), Kirkby Moor Formation (Lake District)
Alcymene cf. *puellaris*	Bannisdale Formation (Lake District)
Ananaspis? *nuda*	MEF (3-4, 7, Wenlock Edge), MEF (30), IrF (47D-E), early Ludlow (Ledbury)
Balizoma obtusus rosensteinae	LBF (10, 50), UBF (Ludlow), LLF (22), ULF (Ludlow), ALF (Wenlock Edge), LWF (Ludlow)
Balizoma variolaris	LEF (Ludlow)
Calymene oliveae sp. nov.	LEF (36), MEF (1, 11), UEF (51), IrF (47A, C)
Cheirurinae indet. spp.	LEF (15), Elton Group (42),
Cryphina? *gdoumontensis*	Přídolí (Little Missenden Borehole, Buckinghamshire)
Cyphaspis elachopos	?LEF (Dudley, Malvern, Walsall)
Cyphaspis sp.	UEF (51), LLF (19), Elton Group (Much Wenlock and Gwent)
Dalmanites nexilis	LEF (15, 27), MEF (1, 3-5, 11, 14, 29, 30, 33, 51), UEF (17), LBF, UBF (Ludlow), IrF (47C), LLF (31), ULF (52)

Dalmanites aff. *nexilis*	LEF (31), MEF (1, 3-4, 11, 14, 30), UEF (18, 51)
Dalmanites obtusus	MEF (26), UEF (51), LBF (10, 38, 50)
Dalmanites tuberculatocaudatus	LEF (36), MEF (2-4, 14), CWB (46A, C)
Diacalymene? sp.	CWB (46A)
Dicranopeltis salteri	?Gorstian of Sedgley
Encrinurus stubblefieldi	LLF (21-22, 24-25), HFFU (48). LBF, UBF, LLF, ULF, and LWF (Ludlow district)
Exallaspis coronata	MEF (1, 3-5, 14, 30), UEF (17, 51), ULF (52) IrF (47C-D, G). LEF-UBF (Wenlock Edge), Gorstian (Vinnal Hill)
Falcatoproetus falcatus	early Ludlow? (Dudley)
Homalonotus knightii	?UEF (33), CWB (46A), HFFCGM (45), LWF-UWF (Whitcliffe)
Kosovopeltis? *signata*	ALF (Aymestrey)
Kosovopeltis? sp.	Ludlow age, exact horizon and locality unknown
Maurotarion lanei sp. nov.	UEF (16), LLF (19), HFFCGM (44), Elton Group (Mortimer Forest)
Maurotarion cf. *lanei*	early Ludlow (Ludlow), Bailey Hill Fm (Bishops Castle)
Odontopleura ovata	Gorstian, Lake District and north Wales
Plesiowensus obconicus	LEF (15), UEF (33), LLF (20, 22, 24). LBF, UBF, LLF, ULF (across Welsh borderland and central Wales)
Plesiowensus aff. *obconicus*	UBF (13)
Plesiowensus raymondi sp. nov.	LLF (22, 24)
Platylichas (*Rontrippa*) *grayii*	?Gorstian of Sedgley
Proetus concinnus	LEF (Wenlock Edge, 36)
Proetus cf. *concinnus*	LEF (9, 15, 27), UEF (33)
Proetus (s.l.) *astringens*	MEF (30), UEF and LBF (across Welsh Borderland)
Raphiophorus parvulus	LEF (Abberley Hills), MEF (1, 4-6, 8, 30), UEF (16, 17), early Ludlow (High Vinnals)
Richterarges bucklandii	LEF (15), LBF (Ludlow District), LLF (Mortimer Forest)
Scharyia siceripotrix	LEF (35)
Scutelluidae indet.	LEF (27)
Trimerus (?*Ramiotis*) *salteri*	Whitcliffe Group (Whitcliffe)
Trimerus (*T.*) *johannis*	early Ludlow (Rainy Rock, Pembrokeshire), ?early Ludlow (Golden Grove, Llandeilo)
Warburgella (*Owensella*) *ludlowensis*	LLF, ULF (across welsh borderlands and central Wales). Bailey Hill Formation (Powys)
Warburgella (*W.*) aff. *baltica*	LEF (15)

Table 3.1. Table summarising the stratigraphical and geographical distribution of trilobite species from the late Silurian of England and Wales. Formation prefixes follows that of Section 3.4.1 in addition to ALF (Aymestry Limestone Formation), IrF (?Irfon Formation) and KMF (Kirkby Moor Formation).

3.4 SYSTEMATIC PALAEONTOLOGY

3.4.1 *Material, Localities, and Methods*

Large collections of Ludlow trilobite material are housed in several museums around the UK. As part of the present study, a complete survey of late Silurian trilobite collections in the British Geological Survey (Keyworth), the Natural History Museum (London), the National Museum of Wales (Cardiff), the Oxford University Museum, the Sedgwick Museum (University of Cambridge), the Lapworth Museum of Geology (Birmingham), and the Ludlow Museum (Shropshire) has been made. Type material of Ludlow trilobites in the Naturhistoriska Riksmuseet (The Swedish Museum of Natural History, Stockholm) was also studied. Institutions are mentioned throughout the systematics and are represented by a two or three letter institution code (Table 3.2), and are often followed by a specimen number.

Institution	Institution\Collection Code (specimen prefix)
British Geological Survey, Keyworth	BGS (GSM, HN, Zg, Zp, DEX) [formally GSL, GSM, IGS, GSa, GSb, GSc, Gsd]
Humboldt Museum, Berlin	HUK
Natural History Museum, London	NHM (It) [formally BM]
National Museum of Ireland	NMI
Narodní Museum, Prague	NMP
National Museum of Wales, Cardiff	NMW
Naturhistoriska riksmuseet, Stockholm	RM (Ar)

(Swedish National Museum of Natural History)	
Lapworth Museum of Geology, University of Birmingham	BU (BU, BIRUG)
Ludlow Museum, Shropshire	LM
Oxford University Museum	OUM (C.)
Sedgwick Museum, Cambridge	SM (A), HUD for several specimens formally at Hull
Senckenberg Museum Frankfurt	SMF
Sveriges Geologiska Undersökning, Uppsala (Geological Survey of Sweden)	SGU
Trinity College Dublin	TCD

Table 3.2: Table of institution codes used in this chapter. Former institution codes used in older publications are included in the table in brackets if different. The prefixes for specimen numbers are in brackets if different from the institution codes.

Additional material has been provided by supervisors A.T. Thomas and P. D. Lane, based on collections amassed over the last 40 years; this has been deposited in the Lapworth Museum of Geology, University of Birmingham. The bulk of the material is from the Elton, Bringewood, and Leintwardine groups although smaller collections are from the Whitcliffe Group, the Hafod Fawr Formation, and rock possibly belonging to the Irfon Formation (of Schofield *et al.* 2004). Material was collected from 53 localities comprising the areas around Ludlow, Woolhope, Malvern, Ledbury, Llandeilo, Llandovery, Builth, and Usk. A full list of localities is provided below.

For stratigraphical terminology the following prefixes are used:

MWLF: Much Wenlock Limestone Formation (Homerian)

LEF: Lower Elton Formation (*nilssoni* Biozone)

MEF: Middle Elton Formation (*nilssoni-scanicus* biozones)

UEF: Upper Elton Formation (*scanicus* Biozone)

LBF: Lower Bringewood Formation (*incipiens* Biozone)

UBF: Upper Bringewood Formation (*incipiens* Biozone)

LLF: Lower Leintwardine Formation (*leintwardinensis* Biozone)

ULF: Upper Leintwardine Formation (*leintwardinensis* Biozone)

LWF: Lower Whitcliffe Formation (*bohemicus* Biozone)

HFFU: Hafod Fawr Formation (unnamed member of the Hafod Fawr Formation, *nilssoni* to *scanicus* biozones). Underlies the HFFCGM. The Tresglen Beds (*nilssoni* Biozone) of Potter and Price (1965) has been replaced with the Hafod Fawr Formation in the Llandovery district (R.A. Waters, personal communication 2011)

CWB: Coed Wenallt Beds (=‘normal facies’ of the Black Cock Beds in Potter and Price 1965). The term Coed Wenallt Beds (*nilssoni* to *scanicus* biozones) of Squirrel and White (1978) has not been formally replaced in the literature but it now comprises part of the HFFU (R.A. Waters, personal communication 2011). Since this unit helps to better confine the age of the trilobite fauna at several localities it is listed separately and it is informally referred to herein as the Coed Wenallt Beds.

HFFCGM: Hafod Fawr Formation, Cwar Glas Member (=Carn Powell Facies of the Black Cock Beds of Potter and Price (1965), and the Grammysia Beds of Squirrell and White (1978). *scanicus* to *incipiens* biozones. Overlies HFFU.

Lawson’s locality numbers are included for the Ludlow district where appropriate, the precise location of these outcrops can be found in Lawson (1973). Details of localities 12 and 13 can be found in Lawson (1977).

List of sections where fossils were collected:

Ludlow District (1-25)

1. Lawson 69- cutting on S side trackway.
2. Lawson 69\1- in 1st cutting NW Lawson 69.
3. Lawson 69\1A.
4. Lawson 69\1B.
5. Lawson 69\2A- 2nd cutting NW Lawson 69.
6. Lawson 69\2D (in c. 20cms below bentonite).
7. Lawson 69\2C.
8. Lawson 69\2B.

All MEF- these are just above LEF and are most likely of *nilssoni* Biozone age.

9. Lawson 69\3- 3rd cutting NW (LEF).
10. Lawson 31 (LBF).
11. Ludlow above woodyard, exact locality unknown (MEF).
12. Exposure 260 m up forestry track, near Wigmore Road, East of Gorsty. =locality 5 of Lawson (1977). (UEF).
13. Exposure on the south side of Wigmore Road, 465 metres east of Mary Knoll House. = locality 7 of Lawson (1977). (UBF)

14. Mortimer Forest, locality 4 of Lawson (1977). (MEF).

15. Lawson 66. Cut above MWLF at Goggin Lane (LEF).

16. Goggin Section: between Lawson 70 and 46 (UEF).

17. Goggin Section: Lawson 73 (UEF).

18. Haye Park Valley. Lawson 53 (UEF).

19. Sunnyhill Section, Mary Knoll Valley: 7 m stratigraphically above base of section (LLF).

20. Sunnyhill Section, Mary Knoll Valley: 10 m stratigraphically above base of section (LLF).

21. Sunnyhill Section, Mary Knoll Valley: 17.5 m stratigraphically above base of section (LLF).

22. Sunnyhill Section, Mary Knoll Valley: 19 m stratigraphically above base of section (LLF).

23. Sunnyhill Section, Mary Knoll Valley: 20 m stratigraphically above base of section (LLF).

24. Sunnyhill Section, Mary Knoll Valley: 21 m stratigraphically above base of section (LLF).

25. Sunnyhill Section, Mary Knoll Valley: 23 m stratigraphically above base of section (LLF).

Woolhope (26-31)

26. SO 5809 3852. Exposure on north side of sunken Lane, immediately south of minor road at Cockshot (High MEF).

27. SO 5813 3516. Old quarry on south side of road, opposite entrance to trackway

leading to Nupend Farm (Basal LEF).

28. SO 6573 2845. Exposure in E bank of stream approx. 375 m slightly west of north of Upborn Court. (Topmost LWF).

29. SO 5925 3950. Exposure on southeast side of bend in trackway, *c.* 320 m north of locality 30 (UEF).

30. SO 5922 3918. Exposure in west bank of bend in trackway, *c.* 1.57 km east of Priors Frome (MEF).

31. SO 6505 3105. Old quarry 200 m southwest of Bodenham Farm. LLF.

Localities 29 and 30 are near the hamlet Perton (*non* Perton Staffordshire), Herefordshire, and where originally surveyed by Mikulic and Watkins(1981, figure 4.4).

Malvern, and Ledbury districts (32-42)

32. SO 7189 3804. Exposure on S side of forestry track leading east from entrance to Conygree Wood (LEF).

33. SO 7179 3933. Exposure on W side of forestry track 400 m east-southeast of Upper Mitchell Farm (UEF).

34. SO 7180 3934. Exposure on west side of Junction in forestry track, approx. 10 m north of 33 and approx. 3 m stratigraphically below it (UEF).

35. SO 7572 4052. Exposure in north bank of sunken lane c. 300 m east-southeast of Oldcastle Farm. Distance measured from fence junction at SO 7567 4051 (LEF).

36. SO 7152 3856. Exposure on north side of Cut Throat Lane, 208 m northwest of Upper Hall Farm (LEF).

37. SO 7478 4021. Exposure on N side of road (A449) at Chance’s Pitch, 155 m

southwest of minor junction and c. 3 m up face (LLF).

38. SO 7177 3924. Exposure on west side of forestry track, at bend 110 m south of locality 33 (LBF).

39. SO 7236 4035. Section in forestry track in Frith Wood: at bend in track by junction of ‘Godwins Rise’ and ‘Top Walk’ (UBF).

40. Trackside 28.8 m, southwest of locality 39. SO 723 403. (LWF).

41. Trackside 82 m southwest of locality 40. (LLF).

42. SO 7434 4831. Exposure on southeast side of road (A4 103), northeast of Brook House Farm (Elton Group, formation unknown).

Llandeilo, Llandovery, and Builth districts (43-48)

43. SN 7264 2483. 5 cm bed exposed in north face of north quarry at Cwâr Glas (HFFCGM)

44. Loose blocks from c. 5 m of beds overlying locality 43 (HFFCGM).

45. SN 6655 2100. Loose (c. 15 cm) block of rottenstone at west end of old quarry on north side of road, approx. 175 m southeast of Hafod Farm (HFFCGM).

46. Exposure in road (A476); cuttings on west side, north of junction at SN 6103 1903, around 3.92 km southwest of Llandeilo, Carmarthenshire (A476 a-d). All CWB (Squirrell and White 1978).
    a. 109 m north of junction; 10 cm sandstone bed with central rottenstone (about the junction of the CWB and *Grammysia* Beds of Squirrell and White 1978, around *scanicus* Biozone).
    b. 41.5 m north of a). 10 cm rottenstone (upper part of CWB, around *scanicus* Biozone).

c. 55 m north of b). 30 cm siltstone/sandstone (middle part of CWB, *nilssoni* Biozone).

d. 14 m south of c). 5 cm siltstone/sandstone (middle part of CWB *nilssoni* Biozone).

47. Localities in forestry track in Crychan Forest, Cwm Dyfnant. Measured from drain at road junction (SN 9038 4290) in a south-easterly direction. The exact age of the fauna is unknown. It may be from the top of the Wenlock Tirabad Formation (R.A. Waters, personal communication 2011) but the trilobite fauna indicates a Ludlow age. Material from these localities probably belong to ‘mudstones that equate with the Middle Elton Formation’ (locality 14.14b of Siveter *et al.* 1989, p. 83), and in this case it would belong to the Irfon Formation (Schofield *et al.* 2004, p. 20).

a) 56 m along bank- PDL LRG/4.
b) 49 m along bank from a).
c) 40 m along bank from b) PDL LRG/4 ½.
d) 4 m along bank from c) and 2.5 stratigraphically above it.
e) 17.5 m along bank from e) and 12m stratigraphically above it.
f) 3 m along bank from e) and 2.5m stratigraphically above it.
g) 15 m along bank from f).

48. SN 837 333. Upper quarry in Halfway Forest 7 km east of Llandovery, Carmarthenshire. Tresglen Beds (=HFFU, *nilssoni* Biozone).

Usk (49-53)

49. ST 3580 9780. Old quarry on southwest side of road at Porth-Llong (LBF).

50. ST 3275 9854. Cutting on southwest side of road at Sand Llandegfedd Reservoir (LBF).

51. ST 3653 9525. Section in south side of trackway about 1.8 km north-northwest of Llangybi (UEF).

52. ST 3680 9829. Old quarry on north side of trackway, about 300 m east of locality 51 (ULF).

53. SO 3275 0240. Section is south side of sunken lane at Little Mill, around 900 m northwest of Glascoed. (formation unknown.).

The practical methods and used in this chapter are as given in Chapter Two (2.4.1). Morphological terms follow Chapter Two (2.4.1), and additionally Owens (1973) for the proetids, Sandford (2005) for the homalonotids, Holloway and Lane (1998) for the scuetuluids, Siveter (1983) for the calymenids, Tripp (1962) and Ramsköld (1986) for the encrinurids, and Ramsköld (1985) for the dalmanitids. For a discussion on the use of subgenera and subspecies see Chapter Two (2.4.2).

Order CORYNEXOCHIDA Kobayashi, 1935

3.4.2 Family SCUTELLUIDAE Richter and Richter, 1955

Genus *Kosovopeltis* Šnajdr, 1958

Type species. By original designation; *Kosovopeltis svobodai* Šnajdr, 1958, p. 178 from the Kopanina Formation (Ludlow) of Kosov, near Králův Dvůr, Czech Republic.

Kosovopeltis? *signata* (Phillips, 1841)

. 1839 *Asaphus* (*Olenus*) *flabellifer*? Steininger; Murchison, p. 654.
*1841 *Bronteus signatus* Phillips, p. 131, pl. 57, fig. 255.
. 1928 *Bronteus signatus* Phillips; Reed, p. 52.
. 1988 *Kosovopeltis signata* (Phillips, 1841); Morris, p. 122 [with synonymy].

Type material. Holotype, by monotypy, appears to be from the Aymestry Limestone Formation (Gorstian; *incipiens* Biozone), Aymestrey, Shropshire. Morris (1998) noted that the holotype is housed in the Ludlow Museum (Lloyd Collection) but gave no specimen number. The specimen has never been traced.

Remarks. This species is only noted here. Based on the illustration in Phillips (1841, pl. 57, fig. 255) the axis is not longitudinally trilobed and it is relatively a little longer than that seen in *Kosovopeltis* species, indicating that the current generic assignment is unlikely. A revision of this species awaits the rediscovery of the holotype. The claim, by Reed (1928, p. 52), that this species is from Dudley, West Midlands, is in error (Morris 1988).

Occurrence. This species is only known from the type locality.

Stratigraphical range. Ludlow (Gorstian; *incipiens* Biozone).

Kosovopeltis? sp.

Plate 5, figure 1

Material. A pygidium (BGS GSM 36744) from the Ludlow of Ledbury (exact horizon and locality unknown).

Remarks. This taxon is known from a poorly preserved and incomplete pygidium only. It resembles *Kosovopeltis* but differs in possessing a bell-shaped and non longitudinal trilobed axis and is unlike anything seen in any described *Kosovopeltis* species. In addition the specimen is large for *Kosovopeltis* with a sagittal length of around 24 mm. P. D. Lane comments (personal communication, 2011) that he has not seen and does not know of any *Kosovopeltis* pygidium with a sagittal length of over 13 mm. The bell-shaped axis of this species is different from the subtriangular axis of *Kosovopeltis signata* (Phillips, 1841), and almost certainly represents a different species.

Scutelluidae indet.

Plate 5, figure 2

Material. A cephalon (BU 4777) from the Lower Elton Formation, (Gorstian; *nilssoni* Biozone) at locality 27.

Remarks. This taxon is known from a poorly preserved cephalon only and cannot be identified at the generic level. The anteriorly placed indentation may be an omphalus (see Holloway and Lane 1998), in which case it would indicate reference to *Bumastus* Murchison, 1839. Due to preservation it is difficult to be sure, however. The lack of an anterior border suggests that this does not belong to the genus *Cybantyx* Lane and Thomas, 1978.

Order LICHIDA Harrington *et al.*, 1959

3.4.3 Family LICHIDAE Hawle and Corda, 1847

Genus DICRANOPELTIS Hawle and Corda, 1847

Type species. Designation of Reed (1902, p. 61); *Lichas scabra* Beyrich, 1845, p. 28, Liteň Formation (Wenlock Series), Svatŷ Jan, near Beroun, Czech Republic.

Dicranopeltis salteri (Fletcher, 1850*a*)

*v**1850*a* *Lichas Salteri* Fletcher, p. 237, pl. 27, figs 9, 9a; pl. 27, fig. 4.

v. 1981 *Dicranopeltis salteri* (Fletcher, 1850); Thomas p. 68, pl. 19, figs 4-12 [with synonymy].

. 1984 *Dicranopeltis salteri* (Fletcher); Thomas *et al*., pp. 53, 56.

. 1988 *Dicranopeltis salteri* (Fletcher, 1850); Morris, p. 77 [with synonymy].

Type material. Lectotype selected by Thomas (1981, p. 68); SM A10261, original of Fletcher 1850*a*, pl. 27, figs 9, 9a, Much Wenlock Limestone Formation, Wenlock Series (Homerian), Dudley, West Midlands, England.

Other material. Numerous specimens that belong to this species are housed at NHM, BU, BGS, and NMW.

Diagnosis and description. See Thomas (1981, p. 68).

Remarks. An incomplete cranidium with hypostome (BU 12727) is the only possible record of *D. salteri* from the Ludlow Series of England and Wales (figured Thomas 1981, pl. 19, fig. 10a-b). Siveter (1989, p. 152) noted several specimens from the early Ludlow (*nilssoni* Biozone) of the Annascaul Formation, Ballynane Member, Dingle Peninsula, Ireland that may belong to this species. No new material belonging to this species has been found as part of the present study.

Stratigraphical range. Wenlock (Sheinwoodian; *riccartonensis* Biozone) to ?Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. This species is known from the Much Wenlock Limestone Formation (Homerian) of Dudley, the Coalbrookdale Formation (Sheinwoodian) of the Malvern District, the late Wenlock of Penylan, Cardiff (exact horizon unknown), and the early ?Gorstian of Sedgley (exact horizon unknown).

Genus RICHTERARGES Phleger, 1936

Type species. By original designation; *Lichas* (*Dicranogmus*) *ptyonurus* Hall and Clarke, 1888, p. 86, from the Cobleskill Limestone (late Přídolí), New York.

Richterarges bucklandii (Milne-Edwards, 1840)

Plate 5, figures 3-10

*1840 *Peltoura Bucklandii* Milne-Edwards, p. 345, pl. 34, fig. 12.

v. 1903 *Lichas* (*Corydocephalus*) *anglicus wenlockensis* Reed, p. 3, pl. 1, fig. 1.

v. 1903 *Lichas* (*Corydocephalus*) *anglicus obtusicaudatus* Reed, p. 4, pl. 1, fig. 2.

. 1981 *Hemiarges* sp.; Mikulic and Watkins, fig. ‘4-9’, F.

v. 1981 *Hemiarges bucklandii* (Milne Edwards); Thomas, p. 74, pl. 20, figs 18-20, 22-28 [with synonymy].

. 1984 *Hemiarges bucklandii* (Milne Edwards); Thomas *et al.*, p. 53.

. 1988 *Hemiarges bucklandii* (Milne Edwards, 1840); Morris, p. 107 [with synonymy].

. 1988 *Richterarges bucklandii* (Milne Edwards, 1840); Thomas and Holloway, pp.

236-237, 251, pl. 15, figs 318-21, 324 [with synonymy].

Type material. Holotype (not traced) is a complete specimen (figured by Milne-Edwards 1840, pl. 34, fig. 12) from the Much Wenlock Limestone Formation (Homerian), Dudley, West Midlands, England.

Other material. 2 pygidia (BU 4778-4779) from locality 15. The syntypes of *wenlockensis* are SM A10268-69, and those of *obtusicaudatus* are SM A10270-71. SM, NMW, and NHM contain numerous specimens belonging to this species.

Diagnosis and description. See Thomas (1981, p. 74).

Remarks. This species occurs commonly in the Wenlock but it is rare in the Ludlow. A single pygidium (LM G9554) is known from the early Ludfordian implying a relatively long stratigraphical range.

Stratigraphical range. Wenlock (Sheinwoodian; *riccartonensis* Biozone) to Ludlow (Ludfordian; *leintwardinensis* Biozone).

Occurrence. This species occurs in the Coalbrookdale Formation (Sheinwoodian) of Dudley and Malvern; the Much Wenlock Limestone Formation (Homerian) of Dudley, West Midlands, and of Hayes Quarry, 2.4 km SW of Much Wenlock, Shropshire; the early Ludlow of Moel Fodiar, Denbighshire (exact horizon unknown); the Lower Elton Formation of an old quarry near Monkswood, Usk Inlier, Gwent (SO 3334 0155); locality

15; the Lower Bringewood Formation of the Ludlow District; and the Lower Leintwardine Formation of Haye Park, Mortimer Forest.

Genus PLATYLICHAS Gűrich, 1901

Type species. By original designation; *Lichas margaritifer* Nieszkowski, 1857, p. 568, Porkuni Limestone (late Ashgill), Estonia.

Subgenus RONTRIPPIA Thomas and Holloway, 1988

Type species. Lichas grayii Fletcher, 1850*a* from the Much Wenlock Limestone Formation (Homerian) of Dudley, West Midlands.

Platylichas (*Rontrippa*) *grayii* (Fletcher, 1850*a*)

*v**1850*a* *Lichas Grayii* Fletcher, p. 237, pl. 27, fig. 8; pl. 27 *bis,* figs 3-3b.

v. 1981 *Platylichas grayii* (Fletcher); Thomas, p. 78, pl. 21, figs 6, 10-20 [with full synonymy].

. 1984 *Platylichas grayii* (Fletcher); Thomas *et al.*, pp. 53, 56.

. 1988 *Platylichas grayii* (Fletcher, 1850); Morris, p. 179 [with synonymy].

. 1988 *Platylichas (Rontrippa) grayii* (Fletcher, 1850); Thomas and Holloway, p. 213, pl. 9, figs 182, 184, 187.

Type material. Lectotype selected by Thomas (1981, p. 79) as SM A10258, original of Fletcher 1850*a*, pl. 27, fig. 8, refigured Thomas 1981, pl. 2, fig. 11 from the Much Wenlock Limestone Formation (Homerian) of Dudley, West Midlands, England.

Diagnosis and description. See Thomas (1981, p. 79).

Remarks. P. grayii was noted by Thomas (1981, p. 79) to occur in the basal ?Ludlow of Sedgley, and remains the only possible Ludlow record of this species to date. In Gotland this species occurs in the Wenlock only, suggesting that the latter is more likely.

Stratigraphical range. Wenlock (Sheinwoodian; *riccartonensis* Biozone) to ?Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. This species is known from the Much Wenlock Limestone Formation (Homerian) of Hurst Hill, Wenlock Edge and the Ledbury district; the Coalbrookdale Formation, Malvern district; the late Wenlock of Penylan, Cardiff (exact horizon unknown); and the early Ludlow of Sedgley (exact horizon unknown). This species is also known from the Wenlock of Gotland.

3.4.4 Family ODONTOPLEURIDAE Burmeister, 1843

Genus ACIDASPIS Murchison, 1839

Type species. By monotypy; *Acidaspis Brightii* Murchison, 1839, p. 658 from the Much

Wenlock Limestone Formation (Homerian; *ludensis* Biozone) of the Malvern Hill, Hereford and Worcester, England.

Diagnosis. See Whittington (1956*b*, p. 232).

Acidaspis brightii Murchison, 1839

Plate 5, figures 11-12

* 1839 *Acidaspis Brightii* Murchison, p. 658, pl. 14, fig. 15.

. 1956*a* *Acidaspis brightii* Murchison, 1839; Whittington, p. 510, pl. 58, figs 8, 12; text-fig. 1A-C.

1956*b* *Acidaspis brightii* Murchison, 1839; Whittington, p. 232, text-fig. 13A-C [copy Whittington 1956a, text-fig. 1A-C].

v. 1981 *Acidaspis brightii* Murchison; Thomas, p. 81, pl. 22, figs 4-5, 7-8, 10-12, 17 [with full synonymy].

. 1984 *Acidaspis brightii* Murchison; Thomas, *et al*., pp. 53, 56.

. 1988 *Acidaspis brightii* Murchison, 1839; Morris, p. 12 [with synonymy].

Type material. The holotype is a cephalon (Murchison 1839, pl. 14, fig. 15) from the Much Wenlock Limestone Formation (Homerian; *ludensis* Biozone) of the Malvern Hills, Hereford and Worcester (exact locality unknown). The current whereabouts of the holotype specimen is unknown.

Other material. This species is well represented in the collections at BU, BGS, and NHM.

Diagnosis and description. See Thomas (1981, p. 82).

Remarks. A. brightii is most like *A. grayi* Barrande, 1852 from the Motol Formation (Homerian, *testis* Biozone) of the Liteň Group, Bohemia, but differs from it in the narrower medial part of the occipital ring which is more strongly separated from the median lobe, a longer genal spine, and coarser granulation (Bruton 1968, p. 34).

Stratigraphical range. Wenlock (Homerian; *lundgreni* Biozone) to Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. This species occurs in the Much Wenlock Limestone Formation (Homerian; *ludensis* Biozone), Malvern Hills; the Coalbrookdale (Homerian; *lundgreni* Biozone) and Much Wenlock Limestone (Homerian; *ludensis* Biozone) formations of Dudley; and the early Ludlow of the Wych, near Malvern.

Genus EXALLASPIS Ramsköld and Chatterton, 1991

Type species. Leonaspis bufo Ramsköld, 1984 from the Mulde Beds, Wenlock Series (Homerian), Gotland, Sweden.

Diagnosis. From Ramsköld and Chatterton (1991, p. 362): acidaspidine with conical cheek border spines; one pair of lateral pygidial and two pairs of medial pygidial border spines.

Exallaspis coronata (Salter, 1853)

Plate 5, figures 13-18; Plate 6, figures 1-10

*v**1853 *Acidaspis coronatus* Salter, dec. 7, p. 7 of pl. 6.

1857 *Acidaspis coronatus* sp. nov.; Salter, p. 210.

1938 *Leonaspis coronata* (Salter); Stubblefield, p. 37.

1956*c* *Leonaspis coronata* (Salter); Whittington, p. 506, pl. 59, fig. 12.

1969 *Leonaspis coronata* (Salter); Clarkson, p. 334, fig. 4B.

1970 *Leonaspis coronata* (Salter); Shergold and Bassett, pp. 131, 138.

. 1977*a* *Acidaspis coronata* Salter; Thomas, p. 92.

v. 1981 *Leonaspis coronata* (Salter); Thomas (*pars*), p. 88, pl. 23, figs 12-14; *non* figs 10, 16-18, 20, 22, 23-26 [= *E. quadrimucronata* (Murchison, 1839)].

1982 *Leonaspis coronata* (Salter); Rushton, p. 181.

non 1984 *Leonaspis coronata* (Salter); Thomas *et al*., p. 53 [=*E. quadrimucronata* (Murchison, 1839)].

. 1984 *Leonaspis coronata* (Salter); Thomas *et al*., p. 56.

. 1988 *Leonaspis coronata* (Salter, 1853); Morris, p. 124.

. 1991 *Exallaspis coronata* (Salter) gen. nov.; Ramsköld and Chatterton, p. 362.

Type material. Lectotype selected by Whittard (1938, p. 109) as a cephalon (BGS GSM 36734), from the Ludlow (Gorstian) of Vinnal Hill, near Ludlow, Hereford and Worcester. The paralectotypes are a cranidium (BGS GSM 36738) and a pygidium (BGS GSM 36735) from the same locality.

Other material. Material collected as part of the present study comprises a complete specimen, 14 cephala, 10 librigena, and 7 pygidia, and are housed at BU. Specimens belonging to this species were collected from localities 1, 3-5, 14, 17, 47 (C, D, G), 51, and 52.

Diagnosis. Genal spine long; most posterior end of eye positioned just anterior to base of L1; genal field wide, only a little narrower (sag.) than glabellar width at L1; 13 spines on border of librigena; pygidial pleural ridge weak.

Description. Glabella convex (sag.) around 0.77-0.86 times as wide as long. Posterior margin of occipital lobe curving strongly posteriorly, resulting in semicircular outline. Occipital lobe around one-quarter as long as rest of glabella, narrowing to 0.40-0.45 times its length behind L1. L1 suboval in outline, a little longer than occipital lobe. S1 deep and wide around one-quarter to one-third the width of L1, becoming fainter and narrower posteriorly. Median glabellar lobe expanding (tr.) slightly anteriorly, separated from lateral glabellar lobes by shallow furrow. L2 subquadrate, around 0.71 times length of L1. S2 almost extending as close to a sagittal line as S1, becoming fainter posteriorly. Anterior border transverse, raised above convex (sag., tr.) frontal lobe. Axial furrows approximately equal in depth and width to glabellar furrows. Anterior sutural ridge straight, then at a position opposite base of L2 curves gently adaxially towards anterior border. Palpebral area wide, about one-third width of glabella at L1. Cephalon with coarse tubercles, most densely packed and almost touching in medial part of glabellar frontal lobe. Less numerous smaller tubercles often spaced between larger ones.

Librigena convex (tr.). Genal spine 1.5 times longer than genal field, running generally straight from genal field then curves gently downwards from most posterior border spine. Genal spine tapers sharply backwards, 5 times as wide proximally as distally. Eye 0.32 times length of librigenal field. Spines on border of librigena subtriangular, decrease in length anteriorly.

Pygidium, excluding spines, subrectangular in outline, three times as wide as long. Pygidial axis with 2 rings and a weakly defined terminal piece; first ring prominent, better defined and raised above rest. A weak pygidial pleural ridge merges with most anterior axial ring and prominent pair of pygidial border spines. Four medial pygidial border spines slender, parallel to sagittal line, around two-thirds as long as most prominent pair of spines. Most prominent pair of pygidial border spines gently curving adaxially downwards, the lateral most pair curving only slightly adaxially. Prominent tubercles arranged in a row parallel to sagittal line on the pygidial border spines and transversally on axial rings. Smaller tubercles arranged more randomly on the pygidium but are much less common. Prominent tubercle at most anterior end of pygidial border spines parallel to each other along a transverse plane. Few tubercles occur in areas of the pygidium other than the axial rings and pygidial border spines.

Remarks. This species was described by Thomas (1981), but it was largely based on material that is now thought to belong to *E. quadrimucronata*. A new description is given here for the Ludlow material only.

Thomas (1977*a*, 1981) regarded *E. coronata* and *E. quadrimucronata* (Murchison, 1839) as conspecific. The holotype of *E. quadrimucronata* is a lost articulated thorax and pygidium from Dudley. Numerous specimens previously assigned to *E. coronata* from the Much Wenlock Limestone Formation of Dudley differ from that species in many respects (see below) and were reassigned to *E. quadrimucronata* by Ramsköld and Chatterton (1991). Assuming that the illustration of the holotype by Murchison is accurate the pleural ridge is strong (rather than weak in *E. coronata*) and it is consistent with the *Exallaspis* material from the Much Wenlock Limestone of Dudley. Given that the holotype of *E. quadrimucronata* was collected from the same locality is seems likely that it is synonymous with the Wenlock material formerly assigned to *E. coronata.*

Ramsköld and Chatterton (1991) noted that the type material of *E. coronata* (Ludlow) differs from *E. quadrimucronata* (Wenlock) in possessing more anteriorly placed eyes that are distant from the posterior border furrow (rather than in contact with it), a wider palpebral area and area of genal field between suture and posterior border furrow, a weaker lateral border furrow, a longer genal spine, and a weak pygidial pleural ridge (rather than strong). In addition *E. coronata* possesses 13 spines on the border of the librigena (*E. quadrimucronata* typically has 11), and the largest (sag., tr.) pair of pleural ribs are not as convex and are less strongly curved adaxially downwards compared to *E. quadrimucronata*. Features recognized by Thomas (1977*a*, 1981), present in both *E. coronata* and *E. quadrimucronata* (such as the two pairs of secondary spines) are distinctive of the genus, rather than supporting a synonymy between the two species. I am in agreement with Ramsköld and Chatterton (1991) that *E. quadrimucronata* is a distinct species, and that it includes of specimens from the Wenlock of England and Wales previously assigned to *E. coronata*. It seems, therefore, that *E. coronata* is restricted to the Ludlow Series. Material collected as part of the present study mostly comprises disarticulated specimens. Even though the cranidia of *E. coronata* and *E. quadrimucronata* cannot be easily distinguished there can be no doubt about the affinity of the present material, as the associated pygidia and librigena are of the *E. coronata* type.

In the event that *E. coronata* and *E. quadrimucronata* are regarded as synonymous, then *E. coronata* is deemed to be the senior name (see Thomas 1977*a*).

Stratigraphical range. Ludlow (Gorstian; *nilssoni* Biozone to Ludfordian; *leintwardinensis* Biozone).

Occurrence. This species occurs in the Middle Elton Formation of the Ludlow district (localities 1, 3-5, 14) and near Perton (locality 30), the Upper Elton Formation of the Ludlow district (locality 17) and Usk (locality 51), the whole Elton and Bringewood groups of Wenlock Edge, Shropshire, the ?Irfon Formation (localities 47C-D, G) of Cwm Dyfnant, and the Upper Leintwardine Formation of Usk (locality 52).

Genus ODONTOPLEURA Emmrich, 1839

Type Species. By monotypy; *Odontopleura ovata* Emmrich, 1839, p. 53, Wenlock or early Ludlow erratic of Silesia, Poland.

Diagnosis. See Thomas (1981, p. 80).

Odontopleura ovata Emmrich, 1839

*1839 *Odontopleura ovata* Emmrich, 1839, p. 53, pl. 1, fig. 3.

v. 1873 *Acidaspis Hughesii* Salter, p. 93.

1967 *Odontopleura ovata* Emmrich; Bruton, p. 216, pl. 30, fig. 1 [with synonymy].

. 1968 *Odontopleura ovata* Emmrich, 1839; Bruton, p. 8, pl. 1, figs 1-4, 6-7.

1981 *Odontopleura ovata* Emmrich; Thomas, p. 80, pl. 22, figs 1-3.

. 1984 *Odontopleura ovata* Emmrich; Thomas, *et al.*, pp. 52, 56.

. 1988 *Odontopleura ovata* Emmrich, 1839; Morris, p. 150.

. 1989 *Odontopleura (Odontopleura) ovata* Emmrich, 1839; Siveter, p. 138, pl. 20, figs 1-7, 11-21; pl. 21, figs 1, 3- 4, 8 [with synonymy].

. 1991 *Odontopleura (Odontopleura) ovata* Emmrich, 1839; Tomczykowa, p. 49, pl. 16, figs 14-15.

Type material. Holotype by monotypy; HUK 162, original of Emmrich 1839, pl. 1, fig. 3, from an erratic, late Wenlock or early Ludlow (Graptolithengestein), Kujakowice Dolne (formerly Nieder-Kunzendorf), near Kluczbork, Silesia, Poland.

Other material. The holotype of *O. hughesii* Salter, 1873 is SM A37135 from Casterton Low Fell (Ludlow Series), Cumbria, England.

Description. See Bruton (1967, p. 217).

Stratigraphical range. Wenlock (Sheinwoodian; *murchisoni* Biozone) to Ludlow (Gorstian: *scanicus* Biozone).

Occurrence. O. ovata is known from the early Ludlow (*nilssoni* and *scanicus* biozones) of the Lake District and north Wales; Dolyhir & Nash Scar Limestone (Sheinwoodian; *murchisoni* to *riccartonensis* biozones), Powys, Wales; the Annascaul Formation, Ballynane Member (early ?Ludlow), Annascaul inlier, Dingle Peninsula, County Kerry, Ireland. This species is also known from several Wenlock and Ludlow localities in Europe including Bohemia and Poland, and the Wenlock of Canada.

Order PHACOPIDA Salter, 1864

3.4.5 Family HOMALONOTIDAE Chapman, 1890

Genus HOMALONOTUS König, 1825

Type species. By monotypy; *Homalonotus knightii* König, 1825 from the Ludlow Series (Ludfordian) of Hereford and Worcester, England.

Diagnosis. See Sandford (2005, p. 14)

Homalonotus knightii König, 1825

Plate 6, figures 11-16; Plate 7, figures 1-3, ?4, 5-10

*v**1825 *Homalonotus Knightii* König, p. 4, pl. 7, fig. 85.

1839 *Homalonotus Ludensis* Murchison, p. 651, pl. 7, figs 3-4.

1839 *Homalonotus Knightii*, König; Murchison, p. 651, pl. 7, figs 1-2.

v. 1865 *Homalonotus Knightii* König; Salter, p. 119, pl. 12, figs 2-10; pl. 13, fig. 8; text-fig. 29.

non 1865 *Homalonotus ludensis*, n. sp., Salter, p. 121, pl. 12, fig. 1 [=*Dipleura salteri*].

non 1884 *H. Ludensis*; La Touche, p. 76 [= *Dipleura salteri*].

non 1901 *Homalonotus Knighti* [*sic*] König; Lindström, p. 57 [pars], pl. 4, figs 20-21 (=*H. rhinotropis*).

non 1909 *Homalonotus Knighti* [*sic*], Kön. var. *rhinotropis* Ang.; Moberg and Grønwall, pp. 72-77, pl. 5, figs. 1-4, (= *H. rhinotropis*).

. 1975 *Homalonotus knighti* [*sic*] König; Tomczykowa, p. 5, 18-20; text-fig. 3a; tables 2-5, pl. 1, figs 1-11.

. 1984 *Homalonotus knightii* König; Thomas *et al.*, p. 56.

1988 *Homalonotus knightii* König, 1825; Morris, p. 111 [with synonymy].

. 1991 *Homalonotus knightii* König; Tomczykowa, p. 8 [table 1].

Type material. The holotype is a partially exfoliated incomplete thorax and pygidium BM 42175, figured by König (1825, pl. 7, fig. 85) and refigured by Salter (1865, pl. 13, fig. 8) from the Ludlow Series, probably of Powys, Wales.

Other material. 3 cephala and 13 pygidia were collected from localities 45, and 46A and are stored at BU. A partial thorax (BU 4780) collected from locality 33 most likely belongs to this species. 2 thoracopygidia (LM G11738, 2813) from the Lower Whitcliffe Formation of the Ludlow District. Numerous specimens belonging to this species are housed at BGS, NHM, and OUM.

Diagnosis. Paraglabellar area around 0.41 times length (sag.) of preoccipital part of glabella; preglabellar furrow and anterior margin of glabella transverse; preglabellar furrows shallow to moderately impressed; hypostome length (sag.) 0.81 times that of width (tr.); hypostomal suture 'wavy', pointing forwards medially, trilobation of thorax and pygidium indistinct.

Description. Cephalon semicircular in outline. Glabella gently convex, 0.86-0.90 times as long as wide, tapering forwards so that frontal lobe is 0.76 times narrower (tr.) than occipital lobe. Preoccipital area of glabella trapezoid in outline. Occipital lobe 0.15-0.18 times glabellar length, occipital furrow deep and wide. Axial furrows indistinct, parallel to a sagittal line from base of glabella to position opposite eye, then converge adaxially. Trilobation recognised by independent convexity of glabella, and concave area of axial furrows. Glabellar furrows barely perceptible. S1 widening slightly adaxially from axial furrows, then narrowing and curving downwards at a position below distal end of S2. L1 around 0.35 times glabellar length. L2 around one-third times length of L1, only a little longer than L3. S2 and S3 shorter than S1, consistent in depth and width adaxially, both terminate at an equal distance from sagittal line. Librigenal field gently convex (tr.), steeply inclined. Eye with a length around 0.18 times preoccipital part of glabellar length, anterior end around 87 per cent towards anterior margin. Palpebral lobe around 0.35-0.37 times glabella width at L1. Posterior border furrow shallow, wide, widening abaxially.

Hypostome with very faint macula and lateral border furrow, middle furrow barely perceptible. Posterior border furrow faint, curving inwards opposite posterior border lobe.

Thorax composed of 11 segments. Trilobation faint, but perceptible based on very weak axial furrows, independent convexity of axis, and depressed region at proximal ends of pleurae. Thoracic segmentation well defined by deep inter-ring, articulating, and pleural furrows. Axial rings gently arched anteriorly, straightening (tr.) posteriorly.

Pygidium triangular in outline. Height of pygidium in lateral view 0.66 times the length. Axial furrow indistinct, weak trilobation evident by raised axis. 8-9 pygidial axial rings with distinct furrows, most posterior 1-2 very faint. Axial ring furrows, apart from most posterior 3, confluent with interpleural furrows, equal in width and depth. Terminal axial piece unsegmented, together with terminal pygidial spine around 0.40 times pygidial length. 8-9 pleural ribs, narrowing posteriorly. Interpleural furrows becoming faint just before pygidial margin.

Remarks. The closest species described to *H. knightii* is *H. rhinotropis* Angelin, 1872, from the Ludlow of Gotland; they were regarded as synonymous by Salter (1865) and Lindström (1885). Later, Moberg and Grønwall (1909) separated *H. knightii* and *H. rhinotropis* at the subspecific level only. *H. knightii* differs from *H. rhinotropis* in the more distinct trilobation on the thorax and pygidium, the transverse (rather than curved) glabellar anterior margin and preglabellar furrows, the eyes are more anteriorly placed, the length of the hypostome is around 0.81 times that of the width (1.10 in *H. rhinotropis*); the projections of the posterior margin of the hypostome are longer (sag.). The differences between *H. knightii* and *H. rhinotropis*, are considered here to be sufficient to separate them at the specific level.

Stratigraphical range. Ludlow (Gorstian; *scanicus* Biozone) to Přídolí (*transgrediens* Biozone).

Occurrence. In Britain this species is known from the Cwar Glas Member of the Hafod Fawr Formation (locality 45); the Coed Wenallt Beds of Llandovery (locality 46A); and possibly the Upper Elton Formation of locality 33; undifferentiated Ludfordian rocks of Ludlow Castle (Shropshire), Presteign Clwyd (Powys), and Malvern (Worcestershire); and the Lower and Upper Whitcliffe Formation of Whitcliffe, Ludlow, Shropshire. Outside Britain this species is known from the Ludfordian of Nova Scotia (Canada), and the Ludfordian (*formosus* Biozone) to Přídolí (*transgrediens* Biozone) of Poland (see Tomczykowa 1991,Teller and Boucot 1999, Kozłowski 2003).

Genus TRIMERUS Green, 1832

Type species. By monotypy; *Trimerus delphinocephalus* Green, 1832 from the Wenlock Rochester Shale, New York State.

Diagnosis. See Sandford (2005, p. 33).

Remarks. Trimerus is similar to *Homalonotus*, and Reed (1918) regarded *H. knightii* and *T. johannis* to form a close relationship based on the anteriorly tricuspid rostral plate. *Trimerus* differs from *Homalonotus* mainly in possessing a subtriangular cephalon (rather than semicircular), a longer preglabellar field, more distinct trilobation (in particular on the pygidium), and a narrower pygidial axis.

Subgenus TRIMERUS Green, 1832

Trimerus (*Trimerus*) *johannis* (Salter, 1865)

Plate 7, figures 11-15; Plate 8, figures 1-4

*v**1865 *Homalonotus Johannis* n. sp.; Salter, p. 117, pl. 12, fig. 11; pl. 13, figs 1-7.

v. 1869 *Homalonotus Johannis* Salter; Salter, p. 241, pl. 5.

. 1977*b* *T. johannis*; Thomas, p. 172.

. 1984 *T. johannis* Salter; Thomas *et al.*, p. 53.

. 1988 *Trimerus johannis* (Salter, 1865); Morris, p. 234 [with synonymy].

Type material. Lectotype selected by Morris (1988, p. 234) as NHM It14521, original of Salter 1867 (pl. 13, figs 5, 7; ?2). The paralectotypes are NHM It14522 (Salter 1867, pl. 1, fig. 3), NHM It14523 (Salter 1867, pl. 13, fig. 1) and NHM It14525 (Salter 1867, pl. 13, fig. 6). All are from the Coalbrookdale Formation (Homerian) of Craig y Garcyd, near the River Usk, Gwent, Wales.

Other material. Two cephala (BGS GSM36147, 36149), and a pygidium (BGS GSM36150) from the Coalbrookdale Formation (Homerian), Garcoed, Usk; a pygidium (BGS GSM1387) from the early Ludlow of Rainy Rock, Wooltack Bay, Pembrokeshire (exact horizon unknown), and a thorax and pygidium (BGS GSM36743) from the ?early Ludlow of Golden Grove, Llandeilo, Carmarthenshire, Wales.

Diagnosis. Glabella raised, bulging very strongly laterally at L1; preglabellar area 0.31-0.34 times cranidial length; glabellar furrows very faintly impressed; S2 and S3 indistinct; anterior margin of cephalon tricuspid, dorsal section of rostral plate concave; axial and interpleural furrows of thorax and pygidium confluent, equal in depth and width; most anterior 4 pygidial axial rings strongly arched forwards; pygidial axial rings long posteriorly; pygidial axis projecting beyond pygidial margin, ending as an acute tip.

Description. Cephalon triangular in outline, around 0.70-0.77 times as long as wide. Preoccipital part of glabella bell-shaped, curving from base to S2, then parallel to a sagittal line. Glabella gently convex (tr.), a little longer than wide, tapering strongly forwards so that frontal lobe is around half glabellar width at L1. Medial part of glabellar indented (sag.) at base and top, most noticeable at base. Occipital ring curving forwards slightly at lateral ends, 0.13-0.15 times glabella length, bound by well defined occipital furrow. Axial furrows weak, but raised glabella results in well defined trilobation. L1 around 0.40 times length of glabella, with faint muscle scar beneath S1. Glabellar furrows short. S1 and S2 curving posteriorly but shallowing rapidly before dying out. S2 and S3 faint. Preglabellar furrow generally straight (tr.) but curving slightly downwards, following median indentation. Preglabellar field short, only a little longer than width of preglabellar furrow. Rostral suture straight (tr.). Dorsal section of connective sutures diverging from rostral suture resulting in anterior expansion (tr.) of rostral plate. Posterior border deep and wide, widening adaxially. At its widest point genal field around 1.20 times length of preglabellar area. Eye extending from a position opposite most anterior end of L1 to most anterior end of L2. Palpebral area around 0.35-0.39 width of glabella at L2. Preglabellar area wide, extending close to posterior end of eye. Posterior branch of facial suture near oblique initially, then curving gently downwards to lateral border furrow. Anterior branch of facial suture oriented at around 60 degrees anteriorly, then straightening just before reaching rostral suture. Large tubercles occur on cephalon concentrated on preocular fixigenal field, posterior border, and the dorsal section of the rostral plate. Anterior end of rostral plate tricuspid. Smaller (sag., tr.) tubercles in between larger (sag., tr.) ones.

Thorax gently convex (tr.), with 12 segments showing faint trilobation, axis distinguished from pleural areas by faint axial furrows; slightly higher convexity than pleura, and a slightly depressed area at most proximal end of pleurae. Articulating half-ring as deep and wide as interpleural furrows. Pleural tips and articulating facet of thoracic segments, due to incompleteness, not known.

Complete pygidium not known, triangular. Clear trilobation evident on most specimens depending on preservation. Axis with 10 rings, and a terminal piece. Axial ring furrows become fainter posteriorly, most posterior 3 very faint near axial furrows. Terminal axial piece 3 times longer than axial ring anterior. Most anterior axial ring raised slightly above rest. 7-8 pygidial pleurae, narrowing posteriorly, eighth pleural rib very narrow or absent.

Remarks. T. (*T.*) *johannis* is most similar to *T.* (*T.*) *vomer* (Chapman, 1912), from the Yan Yean Formation (Wenlock, Homerian) of Australia, but differs in the more posteriorly positioned eyes, the eye ridges are indistinct, the glabella bulges laterally at L1 less, the glabellar and axial furrows are faintly impressed, the S1 lacks an apodemal pit, shallower S2 and S3, a shorter and subtriangular preglabellar field, and straight pygidial axial furrows (rather than diverging anteriorly one-third from posterior end).

Stratigraphical range. Wenlock (Homerian; *lundgreni* Biozone) to Ludlow (Gorstian;

exact biozone age unknown).

Subgenus RAMIOTIS Sandford, 2005

Type species. By original designation, *Trimerus* (*Ramiotis*) *rickardsi* Sandford, 2005 from the late Llandovery (Telychian; *crenulata* Biozone) Chintin Formation, central Victoria, Australia.

Diagnosis. See Sandford (2005, p. 43).

Trimerus (?*Ramiotis*) *salteri* (Morris, 1988)

Plate 8, figure 5

non 1839 *Homalonotus Ludensis* Murchison, p. 651, pl. 7, figs 3-4 [= *H. knightii*].

non 1843 *Homalonotus Ludensis*, Murchison; Goldfuss, p. 559 [=*H. knightii*].

non 1846 *Homal. Ludensis* Murchison; Burmeister, p. 86 [=*H. knightii*].

non 1868 *Homalonotus Ludensis* Murch; Bigsby, p. 53 [=*H. knightii*].

. 1884 *H. Ludensis*; La Touche, p. 76.

. 1975 *Dipleura*? *Ludensis*; Tomczykowa, pp. 6, 9, 11, 20.

. 1984 *Dipleura ludensis* Salter; Thomas *et al*., p. 57.

*v**1988 *Dipleura salteri* nom. nov.; Morris, p. 81 [with synonymy].

. 2005 *Dipleura salteri* Morris, 1988; Sandford, p. 43 [tentatively assigned to the subgenus *Ramiotis*].

Type material. The holotype is an internal mould of cranidium BGS GSM 36855, figured by Salter (1865, pl. 12, fig. 1) from the Whitcliffe Group (formation unknown), Whitcliffe, Ludlow, Shropshire.

Diagnosis. A *Trimerus* (?*Ramiotis*) species with a very strongly tapered glabellar outline; preglabellar furrow and anterior border gently rounded; preoccipital part of glabella around 1.34 times as wide as long.

Description. Glabella convex (sag., tr.), trapezoid in outline, 1.04 times as wide as long, narrowing forwards so that frontal lobe is around 0.57 times narrower than occipital ring. Occipital ring 0.15 times as long as glabella, curving forwards slightly laterally. Occipital ring furrows deep, well defined, equal in width to posterior border furrows. Axial furrows poorly developed resulting in faint trilobation. Glabellar furrows not perceptible. Anterior border flat, around 0.24 times as long (sag.) as glabella. Genal field narrower than glabella. Posterior end of eye at a position around 40 per cent glabellar length, most anterior end at a position around 76 per cent of glabellar length.

Remarks. Tomczykowa (1975) and Morris (1988) assigned this species to *Dipleura*. Sandford (2005, p. 44) noted that the anteriorly placed eyes and the nature of the facial suture are consistent with *Trimerus* and this species was reassigned by him to that genus. The assignment by Sandford (2005) to the subgenus *Ramiotis* remains tentative. The strongly tapering glabella, for instance, is similar to that of *Trimerus* (*Trimerus*). This species lacks other features characteristic of *Trimerus* (*T.*), however, such as the distinct lobration (tr.) and the glabella does not bulge laterally at L1. In all other respects *T.* (?*R.*) *salteri* is consistent with *Ramiotis*. The strong tapering of the glabella is, therefore, most likely a diagnostic feature at the specific level, although this has been accentuated by compression.

The description and diagnosis given here are preliminary and are limited to the single compressed specimen. A more detailed and revised account awaits further material.

Homalonotus ludensis Salter, 1865 is a junior primary homonym of *Homalonotus ludensis* Murchison, 1839 (=*H. knightii*). *Homalonotus ludensis* is a permanently invalid name, replaced by a *nomen novum* by Morris (1988, p. 81).

Stratigraphical range. Ludlow (late Ludfordian; the exact biozone age is unknown).

3.4.6 Family CALYMENIDAE Burmeister, 1843

[=Calymmenidae Angelin, 1854]

Genus CALYMENE Brongniart, 1822

Type species. Calymena [*sic*] *Blumenbachii* [Brong. MS] Desmarest, 1817, p. 517 from the Much Wenlock Limestone Formation (Wenlock; Homerian), Dudley, West Midlands, England.

Other species. There are numerous species referred to this genus. British Silurian species are listed here; question marks denote species assigned tentatively to this genus. *C. aspera*

(Shirley, 1936) from the Coalbrookdale and Much Wenlock Limestone formations (Wenlock, Homerian) of Dudley; *C*? *frontosa* Lindström, 1885 from the Wether Law Linn, Ree Burn, and Knockgardner formations (Llandovery) of Girvan; *C. fuliginata* Siveter, 1996 from the Coalbrookdale and Much Wenlock Limestone formations (Wenlock; Homerian) at Dudley; *C*? *hadyardensis* Lamont, 1949 from the Wood Burn Formation (Llandovery) of Girvan; *C. neotuberculata* Schrank, 1970 from the Coalbrookdale and Woolhope formations (Wenlock; Sheinwoodian) of Walsall and West Midlands; *C. oliveae* sp. nov.; *C. replicata* Shirley, 1936 (= *C. ubquitosus* Howells, 1982) from the Rhydings (Llandovery; late Aeronian) and Crychan (Llandovery; Telychian) formations of the Llandovery area, Bog Quartzite (Llandovery), Shropshire, and the Damery Beds (Llandovery; Telychian) of Gloucestershire; and *C. tuberculosa* Dalman, 1827 from the Much Wenlock Limestone Formation (Wenlock; Homerian), of Wenlock Edge, Shropshire.

Diagnosis. Emended diagnosis from Harrington *et al.* (1959). Occipital lobe equal in length to most distal end of posterior border; L1 and L2 bulging strongly laterally, width of glabella at L1 almost equal to glabellar length; posterior end of eye opposite base of L2; intermediate lobe between L1 and L2 well defined to weak; glabella very convex (sag.), raised well above palpebral lobe, anterior border lower than height of frontal lobe; well defined tubercles at lateral ends of thoracic axial rings; tubercles often occurring at lateral ends of pygidial axial rings but typically less distinct than thorax, pygidial axis with high degree of convexity.

Remarks. Siveter (1985) revised the type species, *C. blumenbachii*, but gave no generic diagnosis. A diagnosis for *Calymene* is presented here. The palpilette L2, where a swollen projection (buttress) extends from the fixigena and joins the L2 occurs in many other calymenid genera (for example *Alcymene*) and it is, therefore, not a reliable character to separate taxa at the generic level. The low anterior border, very convex (sag.) glabella, well-defined tubercles at lateral ends of thoracic axial rings seem to be distinctive of this genus. The convex glabella elevated well above the fixigenal field is a feature shared with *Dekalymene* Curtis and Lane, 1998.

Calymene oliveae sp. nov.

Plate 8, figures 6-16; plate 9, figures 1-5

Derivation of name. After my late grandmother Olive Storey.

Type material. The holotype is a cephalon (BU 4781) from the Middle Elton Formation of locality 1. The paratypes are 15 cephala (BU 4782-4796), 7 pygidia (BU 4798-4804), a thoracopygidium (BU 4805), a partial thoracic segment (BU 4806), and a librigena (BU 4797). This species was collected from localities 1, 11, 36, 47A, 47C, and 51.

Diagnosis. Genal field wide, 0.81-0.85 times as wide as glabella at L1; axial furrows wide around L1, much wider than preglabellar furrow; glabella very convex (sag.), L2 raised well above palpebral lobe; intermediate lobe lacking; L3 short, poorly defined; buttress prominent; pygidial axis tapers rapidly posteriorly, terminating close to pygidial margin; pleural furrows indistinct, only perceptible at proximal end.

Description. Cephalon subsemicircular in outline, around 2.3 times as wide as long.

Glabella bell-shaped, 0.85-0.88 times as wide as long. From a position of S2 glabella curves strongly downwards towards preglabellar field so that anterior end is oblique in lateral view. Occipital ring convex, higher than rest of glabella. Occipital ring 0.18-0.23 times glabellar length, decreasing behind L1 to 0.37-0.40 times its maximum length. L0 poorly defined. L1 subrounded to suboval in outline, bulging transversely and sagittally, 1.21-1.30 times length of occipital ring. S2 oval 0.60-0.74 times length of L1. S1 and S2 as deep as axial furrows, consistent in width, curving gently from an oblique line adaxially. S1 terminating around one-third between anterior end of L1 and occipital furrow, extending around 1.5 times closer than S2 to sagittal line. L3 oval, around 0.45 times length of L2, deflecting slightly posteriorly. S3 shallow, generally transverse, curving very gently around anterior part of L3, extending about two-thirds as close to sagittal line as S2. L4 poorly defined, very weak S4 where impressed parallel to S3. Preglabellar furrow, narrower than axial furrows, curving forwards strongly resulting in semicircular frontal lobe. Preglabellar area 0.16 times glabellar length, curving forwards strongly. Posterior border curving and widening gently downwards abaxially until reaches position below eye then curves and widens more strongly towards anterolateral border, distal end around 3 times longer than most proximal end. Posterior border furrow narrow, transverse, widening slightly abaxially. Fixigenal field gently convex adaxially, the highest point immediately opposite axial furrows. Width across palpebral area around one-third glabella width at L1. Eye only a little longer than L2. Tubercles randomly distributed across the cephalon but more concentrated on the glabella.

Thoracic axial rings arched gently forwards at lateral ends, which contains a distinct well rounded tubercle. Tubercles decreasing in size posteriorly, the anterior ones around twice as large (sag., tr.) as those at the posterior end.

Pygidial axis around 0.36-0.40 times pygidial width. 6-8 axial rings, most anterior ring raised above rest. 5 pleural ribs, straightening (sag.) posteriorly, 4th and 5th pleural ribs sub-parallel and parallel respectively to a sagittal line.

Remarks. Calymene oliveae sp. nov. differs from the type species in possessing a wider genal field, deeper axial furrows (in particular around L1), a wider palpebral area, a less well developed intermediate lobe between L1 and L2, a shorter posterior border, a generally narrower pygidial axis, fainter interpleural furrows, and a longer pygidial axis that tapers backwards more strongly. This species is most similar to *C. fuliginata* Siveter, 1996 but differs in the more convex glabella which is more highly elevated above the palpebral lobe, a less well-developed intermediate lobe between L1 and L2, laterally placed tubercles on the thorax axial rings are more prominent, more pygidial axial rings, and a slightly wider and longer pygidial axis.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* to *scanicus* biozones).

Occurrence. This species is known from the Lower Elton Formation of Ledbury, Herefordshire (locality 36); the Middle Elton Formation of the Ludlow District, Shropshire (localities 1 and 11), the Upper Elton Formation of Usk, Gwent, Wales (locality 51); and the ?Irfon Formation of Cwm Dyfnant (locality 47A,C), Wales.

Genus ALCYMENE Ramsköld *et al.*, 1994

Type species. Calymene neointermedia Richter and Richter, 1954, Hemse Beds, Ludlow

Series (early Gorstian), Petesvik, Hablingbo parish, Gotland, Sweden.

Other species. A. alveus Ramsköld *et al.* (1994), *A.* (s.l.) *beyeri* (Richter and Richter, 1954), *A. lawsoni* (Shirley, 1962), *A. lindstroemi* Ramsköld *et al.*, 1994, *A. puellaris* (Reed, 1920).

Diagnosis. Modified from Ramsköld *et al.* (1994, p. 557). Cranidial anterior border of even length (sag., exsag.) laterally and medially; glabella flattened or weakly convex (sag.); fixigenal field opposite axial furrows highly elevated medially, outline follows that of a wide inverted 'v' in profile, above height of L2 and about equal to or a little higher than maximum height of glabella; preglabellar furrow approximately transverse to gently convex forwards; lateral nodes on thoracic axis subdued to absent; distinct paired tubercles on posterolateral region of median glabellar lobe and at position of intermediate lobe; transverse rows of subdued tubercles on rings and posterior occipital ring, row on cranidial posterior border, thoracic axial rings and posterior pleural bands; intermediate lobe weak to lacking.

Remarks. Many of the species assigned to this genus were previously assigned to *Calymene*. *Alcymene* (s.s.) species differ from *Calymene* principally in the intermediate lobe never being well developed, having distinct paired tubercles on the glabella, a flattened or very weakly convex (sag.) glabella, the glabella tapers forwards more strongly, the fixigenal field directly opposite the axial furrows are highly elevated medially following an outline of a wide inverted 'v', the preglabellar field is longer, the anterior border is raised above the frontal lobe, and tubercles on lateral ends of the thoracic and pygidial axis are indistinct or absent.

Calymene beyeri Richter and Richter, 1954, from the Köbbinghausen Formation (Ludfordian) of Germany, probably belongs to this genus based on the relatively flat (sag.) glabella, the palpebral lobe being much higher than that of glabella, and the transverse preglabellar furrow. It differs from other *Alcymene* species in the anterior border narrowing slightly medially, and the lack of distinct paired tubercles and is assigned here to *Alcymene* (s.l.). *Calymene endemopsis* Siveter, 1989, from the Ballynane Member (?Gorstian; *nilssoni* Biozone) of the Annascaul Formation (Dingle Peninsular, Ireland), possibly belongs to this genus also based on the flattened glabella, the anterior border is raised above the frontal lobe and is consistent in length laterally, and the fixigenal field opposite the axial furrows is raised above the glabella.

Alcymene neointermedia (Richter and Richter, 1954)

Plate 9, figures 6-8

v. 1885 *Calymene intermedia* n.; Lindström, p. 71, pl. 15, figs 8-12; ?figs 5-7.

*1954 *Calymene (Calymene) neointermedia* n.n; Richter and Richter, p. 19.

v. 1983 *Calymene neointermedia* R. and E. Richter, 1954; Siveter, p. 74, pl. 8, figs 7, 12, 16-17; pl. 9, figs 1-3, 8, 10, 13 [with synonymy].

. 1984 *Calymene neointermedia* Richter & Richter; Thomas *et al.*, p. 57.

. 1988 *Calymene neointermedia* Richter & Richter, 1954, Morris p. 45.

. 1994 *Alcymene neointermedia* Richter and Richter n. gen., 1954; Ramsköld *et al.*, pp. 557-560, fig. 2.1-6, fig. 5.15.

Type material. Holotype is a damaged, enrolled specimen RM Ar6225; figured Lindström (1885, pl. 15, figs 11-12); Shirley (1933, pl. 1, fig. 16); Schrank (1970, pl. 1, fig. 4); Siveter (1983, pl. 8, figs 12, 16-17).

Diagnosis and discussion. See Siveter (1983, p. 75).

Remarks. This species has been reported by several authors from the Ludlow Series of Britain and was often used as stratigraphical indicator of the early Ludfordian. As noted by Siveter (1983) *A. neointermedia* does not occur in the British Ludlow, and specimens assigned to this species belong to *A. puellaris* (see remarks on *A. puellaris* for a comparison). There is one possible occurrence of this species in Britain: a complete specimen and a cephalon NHM It9145 (figured Siveter 1983, pl. 9, figs 1-2, 8, 10, 13; pl. 8, fig 7), recorded at NHM from an old museum label 'Wenlock Limestone, Malvern'; its history is unknown. An analysis of the ostracods, acritarchs, and chitinozoa from the matrix of NHM It19145 suggests that it derived from the early Ludlow of Gotland (see Siveter 1983, p. 78-80 for a full discussion). Given that *A. neointermedia* is abundant in the Gorstian of Gotland and that no British material has been found since, including collections for the present study, it seems likely that the museum label for NHM It9145 is in error.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* Biozone) to Ludfordian (*kozolwskii* Biozone).

Occurrence. This species is common in the Hemse Group, Petesvik, Hablingbo Parish, Gotland, Sweden with associated graptolite faunas (*Saetograptus chimaera* and *Neodiversograptus nilssoni*), early Gorstian age. According to Manten (1971) this species also occurs in the Eke Formation (Ludfordian, *kozlowskii* Biozone) of Gotland.

Alcymene lawsoni (Shirley, 1962)

Plate 9, figures 9-15

*1962 *Calymene lawsoni* Shirley, p. 237.

? 1967 *Calymene* cf. *beyeri* Richter; Phipps and Reeve, pp. 345, 367.

v. 1983 *Calymene lawsoni* Shirley, 1962; Siveter, p. 70, pl. 7, figs 1-18; pl. 8, figs 1-6, 10, 14, 18-19 [with synonymy].

. 1984 *Calymene lawsoni* Shirley; Thomas *et al.*, p. 56.

. 1988 *Calymene lawsoni* Shirley, 1962; Morris, p. 45 [with synonymy].

. 1994 *Alcymene lawsoni* Shirley n. gen.; Ramsköld *et al.*, pp. 557-560.

Type material. Lectotype selected by Siveter (1983, p. 70, pl. 7; fig. 14) as cranidium NHM It16000 from the Lower Leintwardine Formation (Ludfordian), from the south side of Tatteridge Hill [SO 4209 7259], near Leintwardine, Shropshire, England.

Other material. In addition to material listed by Siveter (1983, p. 70): a cephalon (BGS GSM 19685) and pygidium (BGS GSM 19683) from the Leintwardine Group (exact horizon unknown) of Leintwardine, Herefordshire. Two pygidia (BGS GSM 19698, 19694) from the Whitcliffe Group (exact horizon unknown) of Whitcliffe, Ludlow, Shropshire.

Diagnosis. Modified from Siveter (1983, p. 70). L1 longer than occipital ring; lateral and posterior border furrows continuous across facial suture. Preglabellar furrow and anterior border transverse, preglabellar area fairly short, around 0.12 to 0.20 times as long as glabella; anterior border short, low, sharply raised convex to subangular rim; glabella flattened (sag.) to very gently convex; pygidial axis 0.3-0.33 times as wide as pygidium; 6-8 pygidial axial rings, 5 pleural ribs.

Description. See Siveter (1983, p. 71).

Remarks. This species is similar to *A. puellaris* but differs mainly in possessing a longer L1, a shorter preglabellar area, the preglabellar furrow and the anterior border is transverse to very gently curved forwards (rather than strongly curved forwards), the anterior border and palpebral lobe are not as highly elevated, the paired larger granules on the posterior part of the median glabella lobe are more distinct, the lateral and posterior border furrows are continuous across the facial suture; and the pygidial axis is narrower.

A. lawsoni was considered the most basal member of the genus by Ramsköld *et al.* (1994, fig. 7) as demonstrated by their cladistic analysis. The continuous border furrows across the facial suture and the longer L1 in *A. lawsoni* separate this species from all other *Alcymene* s.s. species.

Stratigraphical range. Ludlow (Gorstian; *incipiens* Biozone to late Ludfordian; exact biozone unknown).

Occurrence. This species is known from the Upper Bringewood Formation of Woolhope, the Lower Leintwardine Formation of Leintwardine and Ludlow areas, the Upper Leintwardine Formation of Wenlock Edge, and the Whitcliffe Group of Whitcliffe, Ludlow, Shropshire. *A. lawsoni* is confined to Britain.

Alcymene cf. *lawsoni* (Shirley, 1962)

Plate 9, figure 16; Plate 10, figures 1-2

Material. Two cranidia (BGS RK3991-3992) and a partial pygidium (BGS RK3988) from the early Ludlow of Bach-y-Craig (SH 8615 6225), Denbighshire, Wales.

Remarks. This species closely resembles *A. lawsoni* but is distinguished by a convex fixigena opposite the anterior half of glabella. Due to the high convexity of the fixigena the buttress overhangs L2. More material is needed to better compare this species with *A. lawsoni*.

Stratigraphical range. Ludlow (Gorstian; biozone age unknown).

Alcymene (s.l.) aff. *A. lawsoni*

Plate 10, figures 3-12

v. 1983 *Calymene* aff. *C. lawsoni* Shirley, 1962; Siveter, p. 74, pl. 8, figs 8-9, 11, 13, 15.

Material. Two cranidia (LM 2859 and BM It 16045) and one pygidium (BM It 16046) from the Middle Elton Formation, Upper Millichope, Wenlock Edge, Shropshire. LM 2859 is missing. Specimens belonging to this species, as part of the present study, were collected from localities 27, 46A, 47D, 47G, and 48, and comprise 11 cephala, 5 cranidia, 2 librigena, and 7 pygidia (stored at BU).

Remarks. Siveter (1983) noted several specimens resembling *A. lawsoni* but differing in a shallower posterior border furrow not expanding as much laterally, a convex fixigena, the paired arrangement of tubercles are absent, and the pygidial pleural furrows are longer. In addition this species has a more convex glabella, and the anterior border is more strongly curved forwards in comparison to *A. lawsoni*. Due to the more convex glabella and the lack of paired tubercles on the cephalon this species is here assigned to *Alcymene sensu lato*.

Occurrence. This species is known from the basal Lower Elton Formation of Woolhope, Herefordshire (locality 27); the Middle Elton Formation of Wenlock Edge, Shropshire; the uppermost Coed Wenallt Beds near Llandeilo, Carmarthenshire (locality 46A); the ?Irfon Formation in Crychan Forest, Cwm Dyfnant (localities 47D and G); and from the lower part of the Hafod Fawr Formation, Halfway Forest, near Llandovery, Carmarthenshire (locality 48).

Stratigraphical range. Ludlow (Gorstian; *nilssoni* to *scanicus* biozones).

Alcymene puellaris (Reed, 1920)

Plate 10, figures 13-15; Plate 11, figures 1-8

. 1848 *Calymene tuberculosa*, Salter [*pars*] *in* Phillips and Salter, p. 342, *non* pl. 12, figs 1-5.

. 1849 *Calymene tuberculosa*; Salter [*pars*], pl. 8, p. 1, figs 8; *non* figs 1-7.

*v**1920 *Calymene papillata,* var. Nov, *puellaris;* Reed *in* Gardiner, pp. 207, 218, 221, unnumbered text-fig on bottom left hand side of p. 221.

v. 1933 *Calymene* cf. *intermedia* Lindström; Shirley, p. 63, pl. 1, fig. 15 [holotype of *A. puellaris*].

v. 1963 *Calymene neointermedia* (R. and E. Richter); Holland *et al*. pp. 117, 145, 147, pl. 6, figs ?4, 7.

v. 1983 *Calymene puellaris* Reed; Siveter, p. 80, pl. 9, figs 4, 6-7, 9, 15-16; pl. 10, figs 1-16, 18-20 [with synonymy].

. 1984 *Calymene puellaris* Reed; Thomas *et al*., p. 56.

. 1988 *Calymene puellaris* Reed, 1920; Morris, p. 45 [with synonymy].

. 1994 *Alcymene puellaris* Reed n. gen.; Ramsköld *et al.,* p. 557.

Type material. Holotype is complete specimen SM A3320, original of Reed (1920, text-fig on bottom left hand side on p. 221) from the lower Longhope Beds?, (see Siveter 1983, p. 82 for discussion) Ludfordian Stage, small quarry 410 m E of Longhope Church, Gloucestershire, England.

Other material. 8 cephala, 3 cranidia, a thorax, 2 pygidia, a cephalothorax, and a complete enrolled specimen housed at BU. As part of the present study this species was collected from localities 22, 24, 40, and 52. A cranidium (BGS DEX 873) from the Lower Leintwardine Formation of an old quarry near Newnham, Gloucestershire (SO 680107). Three cephala are known from the Upper Leintwardine Formation, near Coed-y-Paen Church, Monmouthshire: BGS DEW 4640 from 1.44 km west of Llangybi (ST 35789651), BGS DEW 6176 from an old quarry SW of the Church (ST33409593), BGS DEW 4025 from a lane section 1.74 km S28ºE of the Church (ST 34309698). Specimens from the Leintwardine Group of Usk Monmouthshire are three complete specimens BGS GSM 19688-19690, a cranidium (BGS GSM 19691), and a cephalothorax (BGS GSM 19692). Numerous specimens belonging to this species occur in the NHM, NMW, and SM.

Diagnosis. Modified from Siveter (1983, p. 82). Posterior border furrow tapers sharply towards genal angle; main field of free cheek between eye and lateral border furrow subangular in profile; posterior margins of palpebral lobes are 2.0 to 2.3 times as wide as L2; L2 only a little shorter (sag.) than L1; preglabellar area 0.25-0.4 times as long as glabella, curving forward; anterior border highly elevated. 12 thoracic segments.

Description. Glabella gently convex sagittally, 0.75-0.83 times as wide as long. Occipital ring 0.16-0.20 times as long as glabella, narrowing to around one-half its maximum length behind L1. L1 oval in outline, around the same length as occipital ring. Intermediate lobe between L1 and L2 lacking. L2 subrounded 0.80-0.90 as long as L1, not quite touching distinct buttress projecting from fixigenal field. S1 and S2 as deep as axial furrows, S1 extending a little closer than S2 to sagittal line. S1 twice as long as S2, curving and sagittally expanding posteriorly. Deepest part of S1 opposite posterior end of eye, faintly extending downwards beyond this point isolating L1. S2 generally transverse, but curving downwards slightly at most distal end. L3 node-like, elongate, around 0.50-0.66 times length of L2. S3 generally straight (tr.), narrow, extending almost as close to sagittal line as S2. L4 poorly defined, very weak S4 seen on only a few specimens. Frontal lobe subrectangular with forwardly convex anterior margin. Anterior border strongly arched anteriorly, only a little longer than occipital lobe, around twice as high as frontal lobe. Posterior border at proximal end equal to length of occipital ring behind L1, increasing in length abaxially to 3 times longer at most distal end. Margin of posterior border transverse from occipital ring to a position below eye then oblique before curving around to join lateral border. Posterior border furrow longest medially, becoming shorter towards librigena and occipital ring, equal in length to occipital furrow near occipital ring. Fixigenal field convex, curving upwards towards glabella. Anterior branch of facial suture roughly parallel to an exsagittal line, curving slightly adaxially on anterior border. Posterior branch of facial suture gently curving backwards until anterolateral border reached then curves strongly posteriorly. Posterior and lateral borders do not cross posterior branch of facial suture.

Thoracic axial rings with deep furrows, Very weak lateral nodes on axis seen on a few specimens only. Thoracic segments of normal calymenid type.

Pygidial axis 0.37-0.42 times pygidial width, tapering gently backwards, posterior end poorly defined. Six axial rings and a terminal piece present, ring furrows deeper laterally than medially. Most posterior two axial rings with incomplete ring furrows, furrows absent medially and not reaching axis. Five pleural ribs, pleural furrows better defined anteriorly than posteriorly, not reaching pygidial margin. Interpleural furrows faint, not reaching pygidial margin, less well defined adaxially.

Remarks. A. puellaris is most similar to *A. neointermedia* and has often been mistaken for that species. The former differs from *A. neointermedia* in possessing a longer posterior border furrow that is longest medially, a more strongly upturned preglabellar area elevated well above the frontal lobe, L1 and L2 similar in length, the anterolateral border furrow extends closer to the posterior branch of the facial suture, wider palpebral lobes, and 12 thoracic segments (rather than 13).

Stratigraphical range. Ludlow (Ludfordian; *leintwardinensis* to *bohemograptus* biozones).

Occurrence. This species occurs in the Lower and Upper Leintwardine Formation of the Usk Inlier and Gloucestershire; the Upper Bodenham Beds (=Upper Leintwardine Formation) at Woolhope; the Lower Longhope Beds (=Leintwardine Group) of Gloucestershire, the Lower Llangibby Beds (=Lower Leintwardine Formation) of the Usk Inlier, the base of the Kirkby Moor Formation (late Ludfordian) of the Lake District, the Lower Leintwardine Formation of the Ludlow Anticline, the Lower Whitcliffe Formation near Ledbury; the Derrymore Glen Formation of the Dingle Peninsula (south-western Ireland). Siveter (1983, p. 87) noted that this species occurs abroad in the ‘high Hemse’ (=Etelhem Formation), Ludfordian (*leintwardinensis* Biozone), and the ‘lower Eke beds’ (=Eke Formation), Ludfordian (*bohemicus* Biozone) of Gotland (Jeppsson *et al.* 2006).

Alcymene cf. *puellaris* (Reed, 1920)

Plate 11, figure 9

v. 1983 *Calymene* cf. *puellaris*, Siveter, pl. 10, fig. 15.

Material. A complete distorted specimen BGS GSM 104357, Bannisdale Formation (Ludfordian; *leintwardinensis* Biozone), Crook of Lune Flag Quarry, 5 km northwest of Sedbergh, Lake District, Cumbria, England.

Remarks. This species bears strong resemblance to *A. puellaris* based on characters such as the short L1 and the strongly upturned preglabellar area. The short and sharply impressed posterior border furrow and the presence of weak nodes at the lateral ends of the thoracic axial rings are uncharacteristic of *A. puellaris*, however.

Stratigraphical range. Ludlow (Ludfordian; *leintwardinensis* Biozone).

Genus DIACALYMENE Kegel, 1927

Type species. Calymene diademata Barrande, 1846 from the Motol Formation (Wenlock Series), Svatŷ Jan pod Skalou, Czech Republic.

Diacalymene? sp.

Plate 11, figure 10

Material. A single cranidium (BU 4949) from the uppermost Coed Wenallt Beds (Gorstian; *scanicus* Biozone) of locality 46A.

Remarks. This species is known from a single poorly preserved cranidium only. The flattened glabella and the raised anterior border and fixigena suggest that this species does not belong to *Calymene*. The cranium bears resemblance to *A.* (sl.) aff. *lawsoni* but differs in that the anterior border is longer and is not consistent in length laterally, the preglabellar furrow is shorter and consistent in length laterally, the S1 dies out before the occipital furrow is reached, and the glabella narrows significantly at L2 so that the distal end is at a position half-way between S1 and the axial furrows. Both the axial furrows and the fixigena converge strongly towards L2 as a result of the latter. This species resembles *Diacalymene* and the contraction of the glabella at L2 is consistent with *Diacalymene allportiana* (Salter, 1865) from the Wenlock Coalbrookdale Formation, Shropshire. The species described here differs from *Diacalymene* in the lower anterior border, an apparent lack of an intermediate lobe between L1 and L2, and a lack of a well defined L3. The absence of these features may be preservational, but until better material is found the present author prefers to keep the generic assignment in question.

3.4.7 Family DALMANITIDAE Vogdes, 1890

Subfamily DALMANITINAE Vogdes, 1890

Genus DALMANITES Barrande, 1852

[*Synonyms: Heliocephalus* Delo, 1936; *Ommokris* Holloway, 1981].

Type species. By original designation; *Trilobus caudatus* Brünnich, 1781 from the Coalbrookdale Formation (Wenlock), Ironbridge power station, Shropshire, England. Topotype material belonging to *D. caudatus* is figured here on Plate 11, figures 11-13; Plate 12, figures 1-3.

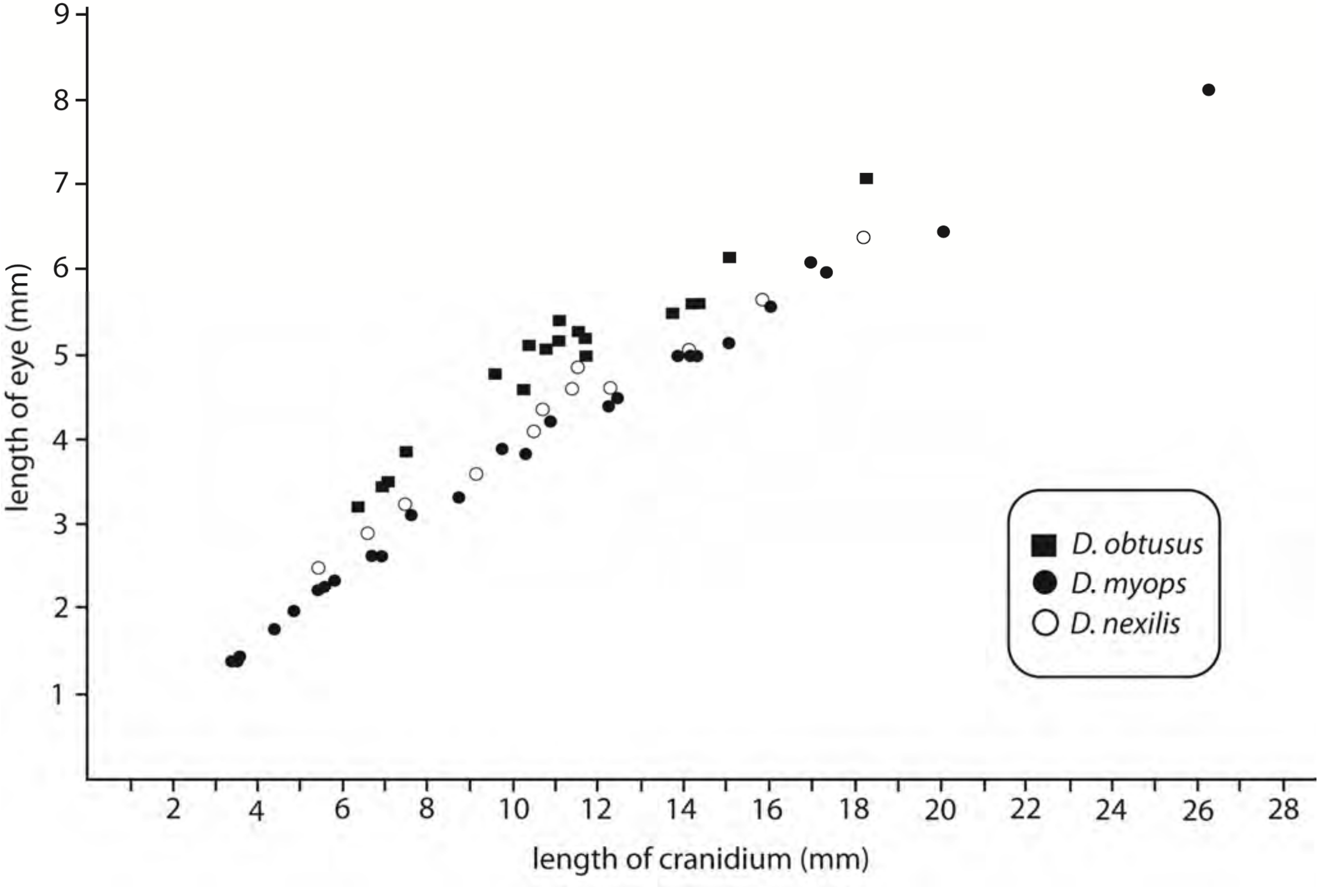
Diagnosis. Revised from Harrington *et al.* (1959, p. 468). Eye with a maximum length extending from close to posterior border furrow to most anterior end of L3, distant from lateral border; anterior extent of facial suture reaches frontal lobe at anterior border furrow, glabella expanding forwards strongly; hypostome subtriangular, slightly wider than long, posterior border of hypostome around 22-25 per cent length of hypostome; 11 thoracic segments; pygidium subtriangular; pygidial axis terminating close to or reaching border furrow; pygidial border distinct with distinct border furrow, pleural ribs terminate at border furrow; 11-16 pygidial axial rings, 6-10 pleural ribs.

Remarks. Ramsköld commented (1985, p. 34) that there was then no useful diagnosis for *Dalmanites*, and one has not been made until now. A diagnosis is attempted here, but this may require some modification following a full revision of *Odontochile* and allied genera. Ramsköld (1985), Morris (1988), and others indicated that *Odontochile* may be better placed as a subgenus of *Dalmanites*. The type species of *Odontochile, O. hausmanni* (Brongniart, 1822), from the Dvorce-Prokop Limestone (Early Devonian; Pragian) of Czech Republic, differs from *Dalmanites* in several respects including the position of the eye close to the lateral border, anterior extent of facial suture in front of frontal lobe on anterior border; a more elongate hypostome (length greater than the width), a larger posterior border of the hypostome (see Budil *et al.* 2008 for discussion), a wider pygidium, a shorter pygidial axis, a less distinct pygidial border, pleural furrows extending onto border, a greater number of pygidial and axial rings, and a wider doublure. *Odontochile* is, therefore, regarded here as separate. *Dalmanites puticlifrons* Whittington and Campbell, 1967, from the Hardwood Mountain Formation (late Wenlock/early Ludlow) of Maine (USA), shows similarities to *Dalmanites* and *Odontochile*. *D. puticlifrons* would probably be best placed in *Odontochile* based on the separation of the anterior facial suture and frontal lobe on the anterior border, the lack of a distinct pygidial border and furrow, and pleural ribs extending onto the pygidial border.

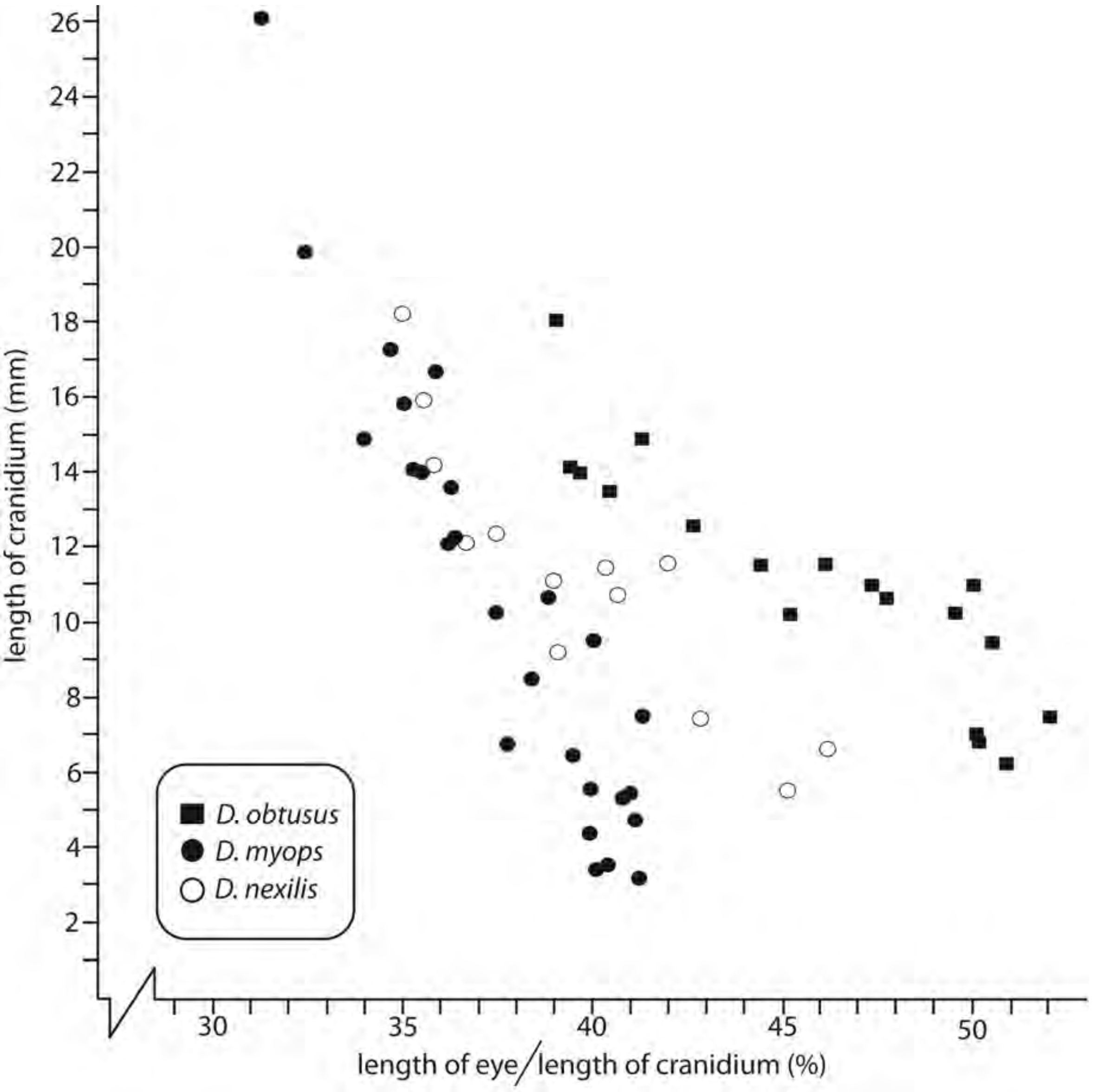
Ommokris Holloway, 1981 was regarded by Ramsköld (1985, p. 34) as synonymous with *Dalmanites* and that is accepted here. *Ommokris* species differ from species of *Dalmanites* in possessing highly elevated eyes, a shorter L1, and a longer and convex anterior process. The pygidia of *Ommokris* and *Dalmanites* species are not different, and the 10 pleural furrows recognised by (Holloway 1981) in the former occurs in *D. imbricatulus* (Angelin, 1851).

Ramsköld (1985) showed that *Dalmanites* species can be discriminated on the basis of the length of the eye as a percentage of the length of the cranidium. The relative eye size decreases with growth at a greater rate in *D. obtusus* than in *D. myops* and the size of the specimen should, therefore, be taken into account when comparing relative eye sizes. The length of eye relative to length of cranidium is illustrated in Text-Figure 3.7; the relative eye size is shown in Text-Figure 3.8.

The eye length in *D. obtusus* can be distinguished from *D. myops* (Ramsköld 1985, fig. 8) in that it is 50-52 per cent of a cranidial length of 7mm (37-41 per cent in *D. myops*) and 38-40 per cent of a cranidial length of 17mm (33-36 per cent in *D. myops*). As part of the present study several species in the British Ludlow show a relative eye size that overlaps with the variation seen in *D. myops*. For example *D. nexilis* in small specimens the eye size is between *D. obtusus* and *D. myops* but in larger specimens it fits within the variation of *D. myops*. It seems that for larger specimens (those with a cranidial length above 10 mm) it becomes increasingly difficult to differentiate between species. A combination of the position of the eye relative to the posterior border furrow, the width of the genal area compared to L3, anterior process, the width of the anterolateral border, and the width of the axis relative to the pygidium seem to be more reliable characters in differentiating between species of *Dalmanites*.



Text-Figure 3.7. Length of eye relative to length of cranidium in *Dalmanites nexilis*, *D. myops*, and *D. obtusus*. Adapted from Ramsköld (1985, fig. 7) to include *D. nexilis*, based on material of the present study.



Text-Figure 3.8. Length of cranidium in relation to relative eye size for *Dalmanites nexilis*, *D. myops*, and *D. obtusus*. Adapted from Ramsköld (1985, fig. 8) to include *D. nexilis*, based on material of the present study.

Dalmanites myops (König, 1825)

Plate 12, figures 4-8

*v** 1825 *Asaphus myops* König, pl. 4, fig. 53.

v. 1864 *Ph.* (*Odontochile*) *caudatus* Var. α, *vulgaris*; Salter, p. 49, pl. 3, figs 4-5, 7-9, 13-17; text-figs 11-12.

v. 1864 *Phacops caudatus*, junior, Salter, pl. 4, fig. 2.

v. 1900 *Phacops* (*Dalmania*) *coronatus* Thomas, p. 616, pl. 35, figs 1-4.

non 1981 *Dalmanites myops*; Mikulic and Watkins, ‘fig. 4-8, B, F’ [=*D. nexilis*], ‘fig. 4-9, A, D’ [=*D. obtusus*].

. 1984 *Dalmanites myops* (König); Thomas *et al*., p. 53 [Wenlock only, *non* p. 56].

v. 1985 *Dalmanites myops* (König); Ramsköld, p. 45, pl. 10, figs 1-3, 5-13; pl. 12, figs 7-11.

. 1988 *Dalmanites myops* (König, 1825); Morris, p. 69 [with synonymy].

. 2008 *Dalmanites myops* (König, 1825); Budil *et al*., fig. 4a-c, fig. 5c.

Type material. The holotype is BM In54865 the original of König 1825, pl. 4, fig. 53 and Salter 1864, pl. 3, fig. 13 from the Much Wenlock Limestone Formation (Homerian) of Dudley, West Midlands, England.

Other material. The lectotype of *vulgaris* selected by Dean (1960, p. 280) is also BM In54865. Morris (1988, p. 69) selected the original of Thomas (1900, pl. 35, figs 2-3)

OUM C35 as the lectotype of *coronatus*, from the Coalbrookdale Formation (Wenlock Series), of the Malvern rail tunnel, near Malvern, Hereford and Worcester, England. There are numerous specimens belonging to *D. myops* at BU, BGS, OUM, and SM.

Diagnosis. Revised from Ramsköld (1985, p. 46). Posterior border furrow wide; occipital ring with median node; eye extends from position opposite occipital ring and S1 to half way or three-quarters towards anterior most end of L3; L3 bulging strongly laterally; pygidial axis broad, first axial ring around 0.31-0.33 times pygidial width.

Description. In addition to Ramsköld (1985, p. 46). Anterolateral border narrow, at its widest point around 0.22-0.27 times width of genal field. Length of eye decreases from 37-47 per cent of glabellar length of 7mm to 33-36 per cent of a glabellar length of 17 mm (Text-Figure 3.8) Genal field beneath eye equal to or narrower than width of glabella at L3. Pygidial axis reaches border furrow.

Remarks. Dalmanites myops was described by several authors as occurring in the Ludlow of England (Mikulic and Watkins 1981; Shergold and Bassett 1970). Three *Dalmanites* species are recognised here from the British Ludlow; *D. nexilis*, *D. obtusus*, *D. tuberculatocaudatus*. They are similar to, but lack features typical of, the Wenlock *D. myops* (see under remarks for each). It would appear, therefore, that *D. myops* is restricted to the Wenlock Series.

Stratigraphical range. Wenlock (Sheinwoodian; *riccartonensis* Biozone to Homerian; *ludensis* Biozone).

Occurrence. This species is known from the Coalbrookdale Formation (Sheinwoodian; *riccartonensis* Biozone to Homerian), Hereford and Worcester, England, and the Much Wenlock Limestone Formation (Homerian) of England. In Gotland this species was noted by Ramsköld (1985) to occur in the 'Mulde Beds' (=Halla Formation), and stratigraphical equivalents of the 'Halla Beds' (Homerian).

Dalmanites nexilis (Salter, 1864)

Plate 12, figures 9-15; Plate 13, figures 1-15; Plate 14, figures 1-6

v. 1849 *Phacops caudatus*; Salter, p. 2, pl. 1, figs 10-11 only.
v. 1864 *Phacops* (*Odontochile*) *caudatus* var. γ *nexilis* Salter, pl. 4, figs 3-5; text-fig. 13.
. 1981 *Dalmanites myops*; Mikulic and Watkins, 'fig. 4-8, B, F'.
. 1984 *Dalmanites nexilis* (Salter); Thomas *et al*., p. 56.
. 1988 *Dalmanites nexilis* (Salter, 1864); Morris, p. 69.

Type material. The lectotype is selected here as complete specimen BGS GSM 19371 (original of Salter 1864, p. 54, text-fig. 13) from the early Ludlow near Ledbury. The paralectotypes are pygidium BGS GSM 19368, BGS GSM 19369 (cephalon), and BGS GSM 19370 (incomplete cephalon). The paralectotypes are from the Bringewood Group (Gorstian; *incipiens* Biozone) of Vinnal Hill near Ludlow, Hereford and Worcester, England.

Other material. 65 cephala, 2 librigenae, 2 hypostomes, and 75 pygidia in BU. This species was collected from localities 1, 3-5, 11, 14-15, 17, 27, 30, 33, 47.C, 51-52, and 53.There are many specimens belonging to this species at BGS.

Diagnosis. Genal field beneath eye broad, around 1.12-1.33 times as wide as glabellar width at L3; posterior border furrow decreasing in width only slightly abaxially, consistent in width from a position below eye to occipital ring; eye extends opposite from between occipital ring and S1 to most anterior end of L3; occipital ring short, equal in length to 1.3 times longer than L1; pygidial axis narrow, first axial ring around 0.19-0.24 times pygidial width, strongly tapering posteriorly.

Description. Frontal lobe wide, around 0.82-0.88 times glabellar length, with evenly rounded anterior margin. Anterior process short, poorly developed. Anterolateral border at its widest point around 0.33-0.36 times width of genal field. Length of eye decreasing from 43-44 per cent of a glabellar length of 7 mm to 35 per cent of a glabellar length of 18 mm (Text-Figure 3.8). L2 approximately equal in length to L1 in most specimens, but up to 1.28 times longer than L1 in some. L3 1.8-3 times longer than L2. L3 expanding laterally, 1.31-1.37 times wider than L2. S1 and S2 transverse, weakly joining axial furrows. Glabella smooth or with sparse tubercles. Anterior branch of facial suture runs almost parallel to an exsagittal line opposite frontal lobe leaving a narrow strip of cheek between it and frontal lobe, curving anteriorly around frontal lobe near anterior border furrow. Most anterior end of eye not quite reaching axial furrow. Genal spine behind posterior border around 0.80 times length of cephalon. Hypostome granulate, including anterior wings 0.89 times as wide as long. Middle body transversally elliptical in outline, bounded by a thin shoulder. Middle furrow deep.

Thorax without tubercles, but with distinct nodes at lateral ends of axial rings which are arched strongly forwards, 0.28 of thoracic width.

Pygidium broad and rounded with a length to width ratio of 0.56-0.68 (excluding posterior spine). Pygidium composed of 7 pleural ribs, 10-11 complete and 4-5 incomplete axial rings. Postaxial ridge distinct until pygidial border furrow reached, then extends faintly onto posterior spine. Posterior spine 0.26-0.33 times length of pygidium.

Remarks. Salter (1849) originally figured this species from a partial cephalon BGS GSM 19370 (Salter 1849, pl. 1, fig. 10) and a pygidium BGS GSM 19369 (Salter 1849, pl. 1, fig. 11) from the Ludlow of Vinnal Hill under *D. caudatus*, but noted then the rather narrow pygidial axis. In 1864 Salter figured BGS GSM 19369 (Salter 1864, pl. 1, fig. 5) and BGS 19370 (Salter 1864m pl. 4, fig. 4) again with a complete specimen BGS GSM 19371 (Salter 1864, p. 54), and a cephalon (Salter 1864, pl. 1, fig. 3), and named this species *Phacops* (*Odontochile*) *caudatus* var. γ *nexilis*. *D. nexilis* is recognised here as a valid species.

D. nexilis is the most common species of *Dalmanites* in the British Ludlow. In smaller specimens its relative eye size (compared to glabellar length) is between those of *D. myops* and *D. obtusus* (Text-Figure 3.8) but in larger specimens fits within the variation of *D. myops*. The broader genal field beneath the eye, a broader anterolateral border, shorter occipital ring, no tubercle on occipital ring, a narrower posterior border furrow not narrowing significantly towards occipital ring, a narrower pygidial axis, and a longer pygidial posterior spine distinguishes this species from *D. myops*. *D. nexilis* differs from *D. obtusus* primarily in the eyes not extending as close to posterior border furrow; a shorter occipital ring, and a narrower pygidial axis. *D. caudatus* is the closest species to *D. nexilis* in possessing a broad genal field and a relatively narrow pygidial axis. *D. nexilis* differs from *D. caudatus* mainly in possessing shorter eyes, a shorter occipital ring, a shorter anterior border, a narrower posterior border that does not narrow adaxially from a position below the eye, a shorter and less well developed anterior process, and a much shorter pygidial posterior spine.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* Biozone to Ludfordian; *bohemicus* Biozone).

Occurrence. This species is known from the ?Irfon Formation (locality 47.C), Crychan Forest, Cwm Dyfnant; the Lower Elton Formation at Ludlow (locality 15) and Woolhope (locality 27); the Middle Elton Formation at Ludlow (localities 1, 3-5, 11, 14), Wenlock Edge, near Perton (locality 30), Ledbury (locality 33), and Usk (51); the Upper Elton Formation (locality 17); the Bringewood Group of Vinnal Hill; the Lower Leintwardine Formation at Woolhope (locality 31); and the Upper Leintwardine Formation at Usk (locality 52). Abroad this species has been noted by Kozłowski and Tomczykowa (1999) to occur in the Niewachlów Beds (*bohemicus* Biozone) from the Holy Cross Mountains of Poland.

Dalmanites aff. *nexilis* (Salter, 1864)

Plate 14, figures 7-13

Material. 8 cephala and 5 pygidia, from the Elton Group, housed at BU. This species was collected from localities 1, 3-4, 11, 14, 18, 30, 32, 51. A cephalon OUM C. 20988 and a pygidium OUM C.20984 from the late Ludlow of Halesend, north of Cradley, Herefordshire (exact horizon unknown) housed at OUM.

Remarks. This species is similar to *D. nexilis* but differs in possessing a rounded and narrow frontal lobe that has a width 0.72-0.76 (rather than 0.82-0.88) times that of the cranidial length, a more convex glabella (sag., tr.), and a longer L2 that is 1.5 times longer than L1 (rather than approximately equal). Pygidia associated with this taxon have a slightly wider axis than *D. nexilis* that is 0.25 times the pygidial width (rather than 0.19-0.24), 6 pleural ribs (rather than 7), and a shorter axis.

Occurrence. This taxon occurs in the Lower Elton Formation near Ledbury (locality 32), Middle Elton Formation of Ludlow (localities 1, 3-4, 11, 14) and Woolhope (locality 30), and the Upper Elton Formation of Ludlow (locality 18) and Usk (locality 51).

Stratigraphical range. Ludlow (Gorstian; *nilssoni* Biozone) to Ludfordian (biozone age unknown).

Dalmanites obtusus (Lindström, 1885)

Plate 15, figures 1-9

*v**1885 *Phacops obtusa*; Lindström, p. 41, pl. 12, figs 3-4, 7-8; pl. 13, fig 1.

v. 1901 *Dalmanites obtusus* Lindström; Lindström, p. 53, pl. 3, figs 45-46.

. 1981 *Dalmanites myops*; Mikulic and Watkins, ‘fig. 4-9, A, D’.

? 1984 *Dalmanites myops* (König); Thomas *et al*., p. 56 [Ludlow only, *non* p. 53].

v. 1985 *Dalmanites obtusus* (Lindström, 1885); Ramsköld, p. 52, pl. 11, figs 1-11; pl. 12, figs 1-2 [with synonymy].

. 1988 *Dalmanites obtusus* (Lindström, 1885); Morris, p. 70 [with synonymy].

Type material. Lectotype, selected by Ramsköld (1985, p. 52); an incomplete cephalon NRM Ar31404, figured by Lindström (1885, pl. 12, fig. 3), and Ramsköld (1985, pl. 11, fig. 11a-b), from Petesvik, Hablingbo parish, ‘lower Hemse Marl’ (=Levide Formation, Gorstian).

Other material. 7 cephala and 10 pygidia in BU. Several specimens belonging to this species are also housed at BGS (the formations are unknown); there are 2 complete specimens from the early Ludlow northeast of Leintwardine (BGS GSM 19365) and early Ludlow of Ledbury (BGS GSM 19400), a near complete specimen (BGS GSM 19399) from the early Ludlow of Leintwardine, 2 pygidia (BGS GSM 13991-2) from the early Ludlow of Vinnal Hill, a pygidium (BGS GSM Zp 3473) from the early Ludlow of Denbighshire, and a pygidium (BGS GSM 19291) from the Much Wenlock Limestone Formation of Ledbury (Homerian; *ludensis* Biozone). 11 Cephala and 9 pygidia were collected as part of the present study from localities 10, 26, 38, 47.G, 50, 51, 53, and are housed at BM.

Diagnosis. Revised from Ramsköld (1985, p. 52). Eye large, extending from a position close to posterior border to a position opposite most anterior end of L3; first pygidial axial ring 27-30 per cent of pygidial width, typically 8 but sometimes 7 pleural ribs.

Description. In addition to Ramsköld (1985, p. 53) at its widest point anterolateral border 0.33-0.37 times as wide as genal field. Length of eye decreases from 50-52 per cent of a glabellar length of 7 mm to 38-40 per cent of a glabellar length of 17 mm (Text-Figure 3.8). Occipital lobe 1.5-2 times longer than L1. Glabellar lobes increasing in size gradually, L2 1.25-1.33 times longer than L1, L3 1.5-2 times longer than L2. Anterior process curved forwards. Anterior and lateral border with fine granules densely packed. Axis terminates just anterior to pygidial border furrow.

Remarks. D. obtusus more closely resembles *D. tuberculatocaudatus* (Murchison, 1839) than any other species. Similarities with *D. tuberculatocaudatus* include the transverse S1, a well-developed anterior process, a relatively wide anterolateral border, width of frontal lobe, and axis not quite reaching pygidial border furrow. *D. obtusus* differs from *D. tuberculatocaudatus* in possessing longer eyes extending closer to posterior border furrow, a shorter genal spine, a shorter and curved anterior process (rather than pointed), a narrower posterior border furrow, even narrower lateral and anterior border, a slightly wider axis, 8 pleural ribs (rather than 7), and a narrower pygidial posterior spine. *D. obtusus* also resembles *D. myops* but differs from the latter in possessing longer eyes; the genal field beneath eye is equal to or slightly wider than the glabellar width at L3 (in *D. myops* the genal field is equal to or slightly smaller than glabellar width at L3), a longer anterior process, a broader anterolateral border, a narrower pygidial axis, the pygidial axis does not quite reach the border furrow, and an extra pleural rib.

Stratigraphical range. Wenlock (Homerian; *ludensis* Biozone) to Ludlow (Gorstian; *incipiens* Biozone).

Occurrence. This species is rare in Britain but occurs in the Much Wenlock Limestone Formation, near Ledbury, Herefordshire and possibly at Dudley, West Midlands; the Middle Elton Formation at Woolhope (locality 26); the Upper Elton Formation at Usk (locality 51); the Lower Bringewood Formation at Ludlow (locality 10), Ledbury (locality 38), and Usk (locality 50). In Gotland this species was noted by Ramsköld (1985) to occur in the Ludlow (Gorstian) uppermost ‘Klintberg Beds’ (=Klintberg Formation) and the lower part of the Ludlow (Gorstian) ‘Hemse Marl’ (=Levide and possibly Petes formations).

Dalmanites tuberculatocaudatus (Murchison, 1839)

Plate 16, figures 1-4; Appendix B11

*	1839	*Asaphus tuberculato-caudatus*, Murchison, p. 654, pl. 7, fig. 8a-b.
v.	1864	*Phacops* (*Odontochile*) caudatus var. β, *tuberculato-caudatus* Murchison; Salter, p. 53, pl. 4, fig. 1.
.	1988	*Dalmanites tuberculatocaudatus* (Murchison, 1839); Morris, p. 70 [with synonymy].

Type material. Holotype, by monotypy, is a missing specimen (original of Murchison 1839, pl. 7, fig. 8b) from Dudley, West Midlands, England. Murchison did not specify which horizon the holotype was collected from.

Other material. 7 cephala, 1 cephalon and part thorax, and 6 pygidia are housed in BU. Specimens belonging to this species were collected from localities 2-4, 14, 36, and 46A, C. A complete specimen (OUM C.11) is from the Ludlow (Gorstian) of Ledbury Tunnel, Malvern, Hereford and Worcester, England (original of Salter 1864, pl. 4, fig. 1).

Diagnosis. Eye extends from opposite half-way between occipital ring and S1 to three-quarters towards anterior of L3, broad anterior and lateral border, at its widest point anterolateral border 0.43-0.45 times as wide as genal field; anterior process relatively long and concave dorsally, subtriangular.

Description. Cephalon semicircular. Genal spine behind posterior border furrow slightly longer than cranidium. Genal field beneath eye equal in size to around 1.10 times wider than glabella at L3. Posterior border furrows deep and long (sag.), narrowing adaxially. Occipital ring without sagittal tubercle, around 1.66-1.72 times longer than L1. Glabellar lobes increase in size gradually anteriorly, L2 around 1.3-1.5 times longer than L1, L3 around 1.6-2.2 times longer than L2. L3 bulging weakly abaxially. Frontal lobe width 0.81-0.87 times glabellar length. Eye with a length 35 per cent of glabella for a glabellar length of 11.5 mm and 34 per cent for a glabellar length of 14.7 mm, and 35 per cent for a glabella length of 21 mm (n=3). Anterior process concave, well developed. Cephalon bears coarse tubercles. Densely spaced granules ornament anterior and lateral border.

Axis with a maximum width almost one-third that of thorax. Four tubercles arranged laterally on thoracic axial rings, one at each end near pleural ribs, and a faint pair close to centre of axis.

Pygidium triangular, with a broad pygidial border. 7 pleural ribs, the axis around 25-26 per cent width of pygidium. Faint postaxial ridge extends onto caudal spine. Posterior spine wide, around 0.42 times width of pygidium. Axis terminates just anterior to pygidial border furrow. Central pair of tubercles on first and fourth axial rings.

Remarks. D. tuberculatocaudatus was originally described by Murchison (1839) from Dudley, and later by Salter (1864) from the early Ludlow of Malvern. Both authors figured a single complete specimen only. Salter (1864, p. 54) was unable to locate the original of Murchison and it was not listed in the first catalogue of fossils in the Museum of Practical Geology (Huxley and Etheridge 1865) with Murchison's other specimens. The holotype specimen has not been located in any of the main museum collections in England. Based on the description and illustration of the holotype (Murchison 1839, pl. 7, fig. 8b) there is no noticeable difference between this and that described by Salter (OUM C.11). In the absence of the holotype, Salter's well preserved specimen (OUM C.11) is used in this study to compare *D. tuberculatocaudatus* to other *Dalmanites* species.

Material collected as part of the present study is poorly preserved and is similar to *D. myops* but shows a broad anterior border, and a wide pygidial spine. In these respects the material described here and OUM C.11 differ from other known *Dalmanites* species. The newly collected material is therefore assigned to *D. tuberculatocaudatus*.

This species is similar to *D. myops* with respect to eye size, general shape of the pygidium, and the number of pleural ribs but differs from *D. myops* in the L3 not bulging as strongly laterally, lacking a central tubercle on the occipital ring, broader anterior and lateral border, a longer anterior process, narrower posterior border furrow and pygidial axis, and a broad pygidial posterior spine.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* to *scanicus* biozones).

Occurrence. This species is rare and was originally described from an unspecified horizon (?Ludlow) of Dudley, West Midlands, England. This species is also known from the Gorstian of Ledbury Tunnel near Malvern, from the Lower Elton Formation near Ledbury (locality 36), the Middle Elton Formation of Ludlow (localities 2-4, 14, and from the Coed Wenallt Beds (=Hafod Fawr Formation) of Llandeilo (localities 46A, C).

Discussion.

Species around *D. caudatus* (Brünnich, 1781) including *D. corrugatus* (Reed, 1901), *D. limulurus* (Green, 1832), *D. nexilis* (Salter, 1864), *D. myops* (König, 1825), *D. obtusus* (Lindström, 1885), *D. platycaudatus* Weller, 1907, and *D. tuberculatocaudatus* (Murchison, 1839) form a closely related group from the Wenlock and Ludlow series of Europe and North America (see Ramsköld 1985, p. 34; Budil *et al.* 2008, p. 3). The group differs from other species of *Dalmanites* in the presence of a short anterior process and distinct lateral nodes on the thoracic axial rings. Another group consists of species close to *D. athalamus* Öpik, 1953, from the Wenlock Wapentake Formation of Costerfield, Australia, and is distinguished by a lack of anterior process, a flattened occipital ring, pygidial pleural ribs consistent in length (exsag.), long pleural furrows, and distally flattened pleural ribs (see Sandford and Holloway 2006, p. 238). Species formally assigned to *Ommokris*, i.e. those around the type species *O. bassleri* Ulrich and Delo *in* Delo 1940, from the St. Clair Limestone (Wenlock) of Arkansus (USA), form a third group and differ from other species of *Dalmanites* in possessing a long anterior process, highly elevated eyes and a short L1. The species around *D. caudatus* and *D. bassleri* both show a convex occipital lobe, pleural nodes on the pygidium, pleural ribs are curved distally, and short pleural furrows, and are probably more closely related than to species around *D. athalamus*. The differences between the three groups are not large and most likely reflect differences at the subgeneric level only. A complete revision of *Dalmanites* and allied genera is needed before these can be diagnosed formally.

3.4.8 Family ACASTIDAE Delo, 1935

Genus ACASTE Goldfuss, 1843

Type species. By subsequent designation of Burmeister, 1843; *Calymene? Downingiae* Murchison, 1839, from the Wenlock Series of the West Midlands, England.

Diagnosis. Revised from Tomczykowa (1991, p. 37). Cephalon anteriorly rounded; genal angle oblique; without spines in holaspid stage, genal projections or short spines sometimes present prior to holaspid stage; lateral margin gently curved anteriorly from anterior end of genal angle; posterior border furrow shallower and narrower than S1; axial furrows diverging gently anteriorly or swollen laterally (due to convex glabella) between occipital furrow and opposite base of L1, then straightens (sag.) becoming parallel to sagittal line; S1 deeper than S2 and S3; S3 oblique, curving only slightly downwards at distal end. Pygidium subtriangular in outline with distinct border; pygidial axis scarcely tapering posteriorly; margin entire; 7-9 pygidial axial rings, 5-7 pleural ribs.

Acaste downingiae (Murchison, 1839)

Plate 16, figures 5-6

v*1839 *Calymene? Downingiae* Murchison, p. 655, pl. 14, fig. 3a-b.

v. 1864 *Phacops (Acaste) Downingiae* (Murchison) var. α *vulgaris* Salter, p. 26, pl. 2, figs 17-23, 25 and unnumbered figure.

v. 1864 *Phacops (Acaste) Downingiae* (Murchison) var. γ *inflatus* Salter, p. 27, pl. 2, figs 31, 33.

v. 1954 *Acaste (Acaste) Downingiae* (Murchison); Richter and Richter, p. 16, pl. 3, figs 36-41.

. 1966 *Acaste downingiae* (Salter, 1864); Clarkson, p. 11, pl. 1, figs 1-9; pl. 2, figs 1-8; pl. 3, figs 1-3 [with synonymy].

v. 1966 *Acaste downingiae* (Murchison); Shergold, p. 187, pl. 28, figs 1-18; pl. 29, figs 1-8 [with synonymy].

1970 *Acaste downingiae* (Murchison); Shergold and Bassett, p. 138.

. 1984 *Acaste downingiae* (Murchison); Thomas *et al.*, p. 53 [Wenlock only, *non* p. 56.

. 1988 *Acaste downingiae* (Murchison, 1839); Morris, p. 9 [with synonymy].

. 1998 *A. downingiae*; Thomas, pp. 903, 905, 907.

Type material. Lectotype selected by Richter and Richter (1954, p. 17); BU 54, original of Murchison (1839, pl. 14, fig. 3a) from the Much Wenlock Limestone Formation

(Homerian), Wren's Nest, Dudley, West Midlands, England. The lectotype of '*vulgaris*', was selected by Morris (1988, p. 9) is also BU 54, original of Salter (1864, pl. 2, fig. 18).

Diagnosis and description. See Shergold (1966, p. 187).

Remarks. Thomas *et al*. (1984, p. 56) showed *A. downingiae* to range from the Wenlock to the Ludlow *leintwardinensis* Biozone, but they indicated (based on dashed line in their fig. 24) that the Ludlow occurrence is in doubt. Material collected for the present study, and a survey of British Ludlow trilobites in museum collections, has not yielded any material belonging to this species. It would appear, therefore, that *A. downingiae* is restricted to the Wenlock Series.

Stratigraphical range. Wenlock (Homerian; *lundgreni* to *ludensis* biozones).

Occurrence. Much Wenlock Limestone Formation (Homerian; *lundgreni* to *ludensis* biozones), Wren's Nest, Dudley, West Midlands, England.

Acaste inflata (Salter, 1864)

Plate 16, figures 7-10

v * 1864 *Phacops (Acaste) Downingiae* var. γ *inflatus* Salter, p. 27, pl. 2, fig. 30 only.

. 1966 *A. downingiae inflatus* (Salter); Clarkson, p. 11.

v. 1966 *Acaste inflata* (Salter, 1864); Shergold, p. 192, pl. 29, figs 9-16.

. 1984 *Acaste inflata* (Salter); Thomas *et al*., pp. 53, 56.

. 1988 *Acaste inflata* (Salter, 1864); Morris, p. 9.

. 1998 *Acaste inflata* Salter, 1864; Thomas, p. 904, pl. 1, figs 6, 9-11, text-fig. 5.

Type material. Lectotype selected by Shergold (1966, p. 192); OUM C9, from the Much Wenlock Limestone Formation (Homerian), Ledbury Railway Tunnel, Ledbury, Hereford and Worcester, England (exact locality unknown).

Other material. A list of Wenlock specimens can be found in Shergold (1966, p. 194). Material identified here from the Ludlow is represented by a cranidium (OUM C.28807) and a pygidium only (C.28808), from the Lower Elton Formation of Shadwell Quarry, Much Wenlock, Shropshire.

Diagnosis and description. See Shergold (1966, p. 192).

Remarks. A. inflata differs from the type species mainly in possessing more convex glabellar lobes, in particular L2 which overhangs L1 more; S3 terminates closer to S2; the eye contains fewer lens files; and the eye extends a little closer to the posterior border furrow. The convex frontal lobe and L1 (tr.) are evident on OUM C.288807. The closest species to *A. inflata*, as noted by Shergold (1966, p. 194), is *A. dayiana* Richter and Richter, 1954, from the Köbbinghauser *Dayia-Schichten* (mid Ludlow). *A. inflata* differs from *A. dayiana* in possessing a less convex (sag.) glabella, the eye has 6-7 rows of lenses (rather than 5-6), and the pygidium is subtriangular (rather than subsemicircular) and is a little narrower.

Stratigraphical range. Wenlock (Homerian; *lundgreni* Biozone) to Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. A. inflata is known from the Much Wenlock Limestone Formation (Homerian; *lundgreni* to *ludensis* biozones) of the Welsh Borderlands and West Midlands. The Lower Elton Formation of Shadwell Quarry, Much Wenlock, Shropshire has yielded the only recorded Ludlow occurrence of this species.

Acaste cf. *subcaudata* (Murchison, 1839)

Plate 17, figures 1-9

v. 1978 *Acaste* cf. *subcaudata* (Murchison); Squirrell and White, p. 44, pl. 5, figs 9-12.

Material. All specimens belonging to this species are from the Hafod Fawr Formation (Coed Wenallt Beds and Cwar Glas Member) in Wales. Specimens collected as part of the present study total 25 cephala and 23 pygidia from localities 43-45, 46A, and 46C, and are housed at BU. Additionally a pygidium (BGS HC 1091) from Lan Quarry, Rhondda Cynon Taff (SN 6599 2063), a pygidium (BGS TCC 384) from Hafod Quarry (SN 6648 2095, locality 45 herein), Hafod, a cephalon (BGS HC 1773) and a pygidium (BGS HC 1774) from Caeth-argoed-uchaf (SN 6005 1906).

Remarks. Acaste subcaudata occurs in the Gray Sandstone Group (Wenlock) of Freshwater East (Pembrokeshire, Wales), which was previously thought to have been of Ludlow age (Shergold 1966, p. 197). The only possible Ludlow occurrence of *A. subcaudata* is the poorly preserved material from the Hafod Fawr Formation of Hafod and Cwâr Glas. Specimens from those localities show a more convex frontal lobe (sag.) than *A. downingiae* but not to same degree as in *A. inflata*. The L1 is convex medially like that of *A. inflata* but the L2 does not overhang L1 as much. The *Acaste* specimens from the Hafod Fawr Formation appear to closely resemble *A. subcaudata* and are consistent with that species regarding the convexity of the glabella, relatively shallow S3, and the number of pygidial axing rings and pleural ribs. The number of lens rows at the maximum height of the eye is a useful feature when separating species of *Acaste* (*A. subcaudata* has 5-6), but unfortunately the visual surface is not preserved on any of the specimens here. The *Acaste* specimens here differ from *A. subcaudata* in a slightly shorter eye and pygidial axis (sag.) only. Although these differences are small refer to this species is referred to herein as *Acaste* cf. *subcaudata*, until better preserved material is available.

A. subcaudata was assigned with question to *Scotiella* Delo, 1935, type species *S. logani* (Hall, 1860) from the Stonehouse Formation (Přídolí) of Nova Scotia (Canada), by Tomczykowa (1991, p. 35) without explanation, but presumably due to the faint S2 and S3. The material of *Scotiella* is limited and the genus is not as well known as *Acaste*. The S3 and S2 seen in *A. subcaudata* and *A.* cf. *subcaudata* vary a little in depth from very shallow and faint (sometimes absent on internal moulds due to preservation) to deeper and better defined. Although the S2 and S3 in *A. subcaudata* are relatively faint compared to other *Acaste* species it is still considerably deeper than *Scotiella*. The smaller (exsag.) eyes, and the stronger backward curvature of S2 in *A. subcaudata* also serve to distinguish this species from *Scotiella*.

Stratigraphical range. Ludlow (Gorstian; *scanicus* Biozone).

Genus ACASTELLA Reed, 1925

Type species. By original designation; *Phacops (Acaste) Downingiae* var? δ *spinosus* Salter 1864, by Reed (1925, p. 75), from the Upper Whitcliffe Formation (Ludfordian) of Whitcliffe Chase, Ludlow, Shropshire, England.

A. macrocentra Reed, 1925, is not the type species of this genus as stated by Morris (1988, p. 9), but it is *A. spinosa* (Salter, 1864) as originally stated by Reed (1925, p. 75).

Diagnosis. Revised from Tomczykowa (1991, p. 42). Cephalon rounded or subtriangular anteriorly; lateral margin straight between base of genal spine to posterior branch of facial suture, then tightly curves anteriorly; genal spines present; posterior border furrow roughly as deep and wide as S1; Axial furrows diverging anteriorly, sometimes straightening (sag.) opposite anterior end of L3; S1 deep, subparallel to S2, equally wide, and of similar depth; S3 narrower than S1 and S2, curving markedly downwards at distal end terminating close to S2; anterior border distinct, pointed or rounded; hypostome with maculae near margin. Pygidium triangular in outline; pygidial border showing weak denticulation or entire; axis convex with 7-10 rings; 4-5 pleural ribs; posterior spine present.

Remarks. Acastella is similar to *Acaste* but differs in that the lateral margin is more strongly curved anteriorly from the posterior branch of the facial suture; the genal spine is present in larger specimens; the axial furrows diverge more strongly anteriorly; the glabella is more convex (sag.); the posterior border furrow and S2 are about as deep and long as S1 (rather than S1 deeper and longer); S3 is more sharply defined being narrower than S1 and S2, S2 is transverse to curving very gently posteriorly; S3 curves more strongly at the distal end extending closer to S2; the preglabellar furrow is deep and well defined, and the pygidial border is sometimes shows weak denticulation.

Acastella spinosa (Salter, 1864)

Plate 17, figures 10-14; Plate 18, figure 1

*v**1864 *Phacops (Acaste) Downingiae* var? δ *spinosus* Salter, p. 27, text-fig. 7.

non 1925 *Acaste (Acastella) macrocentrus* Reed, p. 73, pl. 2, figs 4, 4a.

v. 1967 *Acastella spinosa* (Salter); Shergold, p. 176, pl. 24, figs 1-8; pl. 25, figs 6-12 [with synonymy].

. 1984 *Acastella spinosa* (Salter); Thomas *et al.*, p. 56.

. 1988 *Acastella spinosa* (Salter, 1864); Morris, p. 9 [with synonymy].

. 1991 *Acastella spinosa* (Salter, 1864); Tomczykowa, p. 43, pl. 8, figs 1-7, p. 8 [table 1].

Type material. Holotype by monotypy; BGS GSM 19412 (Salter 1864, text-fig. 7) from the Upper Whitcliffe Formation (Ludfordian) of Whitcliffe Chase, Ludlow, Shropshire, England.

Other material. In addition to the material listed by Shergold (1967, p. 181) a cephalon (NMW 78.52G.128) and cranidium (NMW unnumbered) from the Lower Llangibby Formation (=Lower Leintwardine Formation) from a temporary trench west of Cwm-bwrwch Wood, southwest of Llandegledd Reservoir Dam, Usk, Gwent (ST 322 982 - ST 322 985).

Diagnosis. Modified from Shergold (1967, p. 177). Genal spines slender, curving gently adaxially. Occipital ring raised above lateral glabella lobes; axial furrows diverging at angles between 22-30 degrees; S2 straight (tr.) or curving gently backwards, weakly reaching axial furrows; L3 a little wider (tr.) than L2; frontal lobe moderately convex (sag.), anteriorly rounded or very slightly angled. Pygidium subtriangular in outline; 7-8 axial rings; 5 pleural ribs; margin entire but with slight lateral swellings; caudal mucronation comprises a short (sag.) projection from margin.

Description. See Shergold (1967, p. 177).

Remarks. For a comparison between this species and *A. macrocentra* and *A. prima* see the remarks for each.

Stratigraphical range. Ludlow (Ludfordian; *leintwardinensis*) to Přídolí (*transgrediens* Biozone).

Occurrence. In Britain this species occurs in the Upper Leintwardine Formation in a Quarry near Llandegfydd Hill (Usk, Monmouthshire), and from Woolhope; the Upper

Whitcliffe Formation from several localities between Norton Camp (Craven Arms) and Bourton (Much Wenlock); and from the Upper Whitcliffe Formation of Whitcliffe Chase, Ludlow; and a quarry at Cwm Colebatch Farm, Cefn Einion. In Poland this species is known from the Ludfordian and Přídolí of the Holy Cross Mountains (see Tomczykowa 1991, Teller and Boucot 1999, Kozłowski 2003).

Acastella cf. *spinosa* (Salter, 1864)

Plate 18, figures 2-3

Material. 2 poorly preserved cranidia and 4 pygidia from the ?Irfon Formation, locality 47 (B-C, G).

Remarks. This species differs from *A. spinosa* in possessing a slightly shorter (sag.) eye, and the caudal mucronation is a little wider (tr.) and not as clearly defined. Material belonging to this species is poorly preserved but resembles *A. spinosa* in all other respects, and these differences are most likely due to variation in the case of the eye and preservation with regards to the caudal projection. If this form belongs to *A. spinosa* it would be its oldest record.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* or *scanicus* biozone).

Acastella macrocentra Reed, 1925

*1925 *Acaste (Acastella) macrocentrus* Reed, p. 73, pl. 2, figs 4, 4a.

Type material. By monotypy; a pygidium SM A16539 (untraced) from the Ludfordian of Prior's Frome, Hereford and Worcester, England. There is no other material known of this species.

Remarks. This species was regarded as synonymous with *Acastella spinosa* by Shergold (1967). Tomczykowa (1991, p. 43) noted that the pygidium of *A. macrocentra* is "larger, more convex, has a thicker and longer posterior spine, and the axis extends to the very base of [the] caudal spine". The whereabouts of the holotype is currently unknown. Based on the illustration in Reed (1925, pl. 2, figs 4, 4a), the spine in this species seems longer than any other species of *Acastella,* it is well defined, convex, and curves upwards strongly. The pygidial border appears to be well defined and its margin is entire, and without lateral swellings. The pygidial features outlined above serve to distinguish this species from *A. spinosa*. The present author is in agreement with Tomczykowa (1991) in regarding *A. macrocentra* as a distinct species. *A. macrocentra* was recorded from the topmost Upper Perton Beds (=Upper Whitcliffe Formation) of the Shucknall Inlier, Hereford and Worcester, by Squirrel and Tucker (1960, p. 150). No material belonging to this species has been traced.

Stratigraphical range. Ludfordian (*O. snajdri-O. crispa* Biozone).

Acastella minor (M^{c}Coy, 1851)

Plate 18, figures 4-5

*v**1851 *Phacops (Odontochile) audate* var. *Minor* M'Coy, p. 161.

v. 1967 *Acastella? minor* (M'Coy 1851); Shergold, p. 184, pl. 25, figs 1-3 [with synonymy].

. 1984 *Acastella? minor* (McCoy); Thomas *et al*., p. 56.

. 1988 '*Acastella*' *minor* (McCoy, 1851); Morris, p. 9.

Type material. Lectotype; selected by Shergold (1967, p. 184); SM A37142, from the Kirkby Moor Formation (late Ludfordian) at Benson Knot, 3 km northeast of Kendal, Cumbria.

Other material. A cranidium SM A37195 from the Kirkby Moor Formation (late Ludfordian) at Benson Knot, near Kendal, Cumbria. A cephalon (BGS GSM 84723) from the Přídolí of Prior's Frome, Herefordshire; and an incomplete cephalothorax from the Bannisdale Formation (Ludfordian; *leintwardinensis*) of Underbarrow, Cumbria, possibly belong to this species.

Diagnosis and discussion. See Shergold (1967, p.184).

Remarks. Shergold (1967, p. 186) referred *Acastella conservatrix* (McLearn, 1924) to *Scotiella* Delo, 1935, and amended the diagnosis of the latter to include mesially interrupted posterior axial rings, and Shergold (1967) regarded *A. minor* and *A. conservatrix* to be closely related. Faint to barely perceptible S2 and S3 seem to be important diagnostic features of *Scotiella* (see Tomczykowa 1991, p. 35) and not the nature of the axial rings. The convexity (sag.) of the glabella, the relatively straight S2, the deep and wide S3 and S2, and the position of the eye of *A. minor* are like that of *A. spinosa*. *A.*

minor and *A. conservatrix* bear features which are consistent with *Acastella* and are regarded here as belonging to that genus.

Stratigraphical range. Ludlow (Ludfordian; *leintwardinensis* Biozone) to ?Přídolí.

Occurrence. A. minor s.s. is restricted to the Kirkby Moor Formation (late Ludfordian) near Kendal, Cumbria. Specimens occurring in the Bannisdale Formation (Ludfordian, *leintwardinensis* Biozone) and the Přídolí (?Rushall Beds) of Herefordshire possibly belong to this species (see Shergold 1967, p. 185 for discussion).

Acastella prima Tomczykowa, 1962*a*

Plate 18, figures 6-7

* 1962 *Acastella prima* Tomczykowa, p. 260, pl. 1, figs 2-7.

v. 1967 *Acastella prima* Tomczykowa; Shergold, p. 183, pl. 25, figs 4-5, 13-14 [with synonymy].

. 1984 *Acastella prima* Tomczykowa; Thomas et al., p. 56.

. 1988 *Acastella prima* Tomczykowa, 1962; Morris, p. 9 [with synonymy].

. 1991 *Acastella prima* Tomczykowa, 1962; Tomczykowa, p. 42, pl. 7, figs 5-13, p. 8 [table 1]. [with synonymy].

Type material. Holotype by original designation; original of Tomczykowa 1962, pl. 1, figs 2-4, from the upper part of the Siedlce Beds (Ludlow Series) of Lebork Borehole, N

Poland.

Other material. See Tomczykowa (1991) for a list Polish material. In Britain this species is represented by 2 cranidia (BGS TMcKH 1350, 1366) and 3 pygidia (BGS LCM 60.64 ME, BGS TMcKH 1023, 1336) from the Kirkby Moor Formation (late Ludfordian) of the Kendal and Kirkby Lonsdale regions. During the time of this study the cranidia could not be located at BGS.

Diagnosis. Genal spine occurs as a slight projection from gena; axial furrows diverging at 20 degrees; S2 curving backwards strongly; S3 and S2 bulging laterally so that they are wider (tr.) than L1. Pygidium subtriangular in outline; pygidial border entire, without lateral swelling; pygidial mucronation short (sag.), inflected, node-like; 7 axial rings, 5 pleural ribs.

Description. See Tomczykowa (1962, p. 261), and Shergold (1967, p. 183) for a translation.

Remarks. Acastella prima differs from the type species in possessing very small genal spines, the axial furrows diverge at a lower angle, the S2 curves backwards more strongly, the S3 and S2 bulge strongly laterally, the pygidial mucronation is much shorter (sag.), and there are fewer axial rings.

The British cranidia belonging to *Acastella prima* cannot be located in BGS, but they were figured in Shergold (1967) and undoubtedly belong to this species along with the associated pygidia. The age of the Polish material was revised and stated to be of Přídolí age by Tomczykowa (1991, p. 43).

Stratigraphical range. Ludlow (Ludfordian; *O. snajdri-O. crispa* Biozone) to Přídolí (*branikensis-lochkovensis* Biozone).

Occurrence. The British material is from the Kirkby Moor Formation (late Ludfordian) of the Kendal and Kirkby Lonsdale regions. This species also occurs in the Přídolí of Poland, from several boreholes including Lębork IG 1, Darżlubie IG 1, and Hel IG 1; and the Dzwinogorod Beds of Ukraine; both were noted in Tomczykowa (1991).

Genus ACASTOCEPHALA Shergold, 1966

Type species. By original designation; *Acastocephala macrops* (Salter, 1864) from the Coalbrookdale Formation (Wenlock) of Malvern, Worcestershire.

Diagnosis. See Shergold (1966, p. 199).

Remarks. *Acastocephala* is similar to *Acaste*. Shergold (1966, p. 199) stated that *Acastocephala* differs from *Acaste* in the following respects: a larger eye, extending closer to the posterior border; and containing a higher number of lens rows on the visual surface; the pygidium is less convex (tr.); and both the pleural and interpleural furrows are weaker. In addition to this the S2 is transverse in *Acastocephala* rather than curved backwards. The main differences between *Acastocephala* and *Acaste* are smaller than suggested by Shergold (1966) and they are probably conspecific. *Acastocephala macrops* has only one additional lens on the maximum height of the eye than *Acaste downingiae*, which itself has up to the same number of these compared to *Acastocephala dudleyensis*. There appears to be an overlap in the eye lens files between the genera and the differences between both type species is no greater than that between *Acaste downingiae* and *Acaste inflata*. The number of lens rows in the eye are not a reliable feature, therefore, to distinguish between *Acaste* and *Acastocephala*. The eye in *Acastocephala* extends close to the posterior border in the type species similar to that in *Acaste inflata*, but is unlike all *Acaste* species in that the anterior end of the eye extends above the confluence of S3 and the axial furrows. *Acastocephala dudleyensis* differs from species of *Acaste* in that the eye is in contact with the posterior border furrow, and the anterior end extends slightly farther by reaching a position opposite S3 (rather than terminating at a position posterior to S3). The convexity of the axis in *Acastocephala* does not seem that different to *Acaste subcaudata*, and the weaker pygidial and interpleural furrows are similar to those seen in *Acaste downingiae*; see OUM C.7. The main difference between *Acastocephala* and *Acaste* is, therefore, the nature of S2 and the position of the eye. Variation in eye length is not unusual in the Phacopida. *Dalmanites* shows an even larger variation in eye size, for example (compare *D. myops* with *D. obtusus*). *Acastocephala* could possibly, therefore, be regarded as a subgenus of *Acaste* along with the closely related genus *Acastava* Richter and Richter, 1954. All three genera are retained here as such a revision should follow a comprehensive revision of the Acastidae, and be supported by a phylogenetic analysis.

Acastocephala? sp. A

Plate 18, figures 8-9

v. 1978 *Acastocephala*? sp.; Squirrell and White, pl. 5, figs 1-2.

Material. 1 cephalon (BGS HC 801) and a pygidium (BGS DEX3120) from the Tresglen Formation (Gorstian, *nilssoni* Biozone), Berach Quarry, Golden Grove, Carmarthenshire.

Remarks. This form is distinguished from species B and C by a more convex (sag., tr.) glabella, deeper S2 and S3, a transverse S2, the S1 curves strongly forwards; a wider pygidial axis, and less impressed pygidial furrows.

Acastocephala? sp. B

Plate 18, figures 10-15

v. 1954 *Acaste* (*Acaste*?) sp.; Richter and Richter, p. 17, pl. 3, fig. 44.

Material. A cephalon (BGS GSM19043) from the Tresglen Formation (Gorstian, *nilssoni* Biozone), Berach Quarry, Golden Grove, Carmarthenshire; A cephalon and two pygidia from the Lower Elton Formation at locality 15; and 2 cephala and a pygidium from the lower part of the Hafod Fawr Formation at locality 48.

Remarks. This species differs from sp. A and C in possessing a glabella that is not as convex (tr.) as the others. The visual surface on the eye contains ten rows of lenses, like that of the type species. It differs from *A. macrops* in possessing less impressed S2 and S3, the S2 curves posteriorly (rather than transverse), and the furrows on the pygidium are deeper and better defined.

Acastocephala? sp. C

Plate 19, figures 1-6

Material. A single cranidium (NMW 78.52G) from the Lower Llangibby Formation (=Lower Leintwardine Formation) from a temporary trench west of Cwm-bwrwch Wood, southwest of Llandegledd Reservoir Dam, Usk, Gwent (ST 322 982- ST 322 985); 3 cephala and a pygidium from the Upper Leintwardine Formation, locality 52; a cephalon from the lower part of the Hafod Fawr Formation of locality 48; and possibly a pygidium from the Upper Elton Formation (Gorstian, *scanicus* Biozone) of locality 51.

Remarks. This species is distinguished from species A and B in possessing a slightly shorter eye, not extending anteriorly past the confluence of S3 and axial furrows; and the S2 and S3 curve more strongly backwards. The S2 curving backwards is similar to that of *Acastella spinosa* but is stronger. The very strong backwards curving S3 is stronger than any other *Acastella* species.

Discussion.

Acastocephala? sp. A, B and C seem to occupy an intermediate position between *Acastocephala* and *Acastella*. The large eye, the apparent lack of a genal spine, and relatively faint furrows on the pygidium are consistent with *Acastocephala*, but the very high degree of convexity on the glabella is closer to *Acastella spinosa*. The degree of convexity (tr.) in *Acastocephala*? sp. A and C is, however, even higher than that of *Acastella* species causing the L1 and L2 to bulge greatly laterally. The glabella rapidly tapers backwards in *Acastocephala*? sp. A and C as in *Acastella spinosa* but to a much stronger degree so that the gena is much wider (tr.) than the glabella at L1. The glabella in sp. B is not as convex as spp. A and C, but the gena is still wider than the glabella at L1. The eye in spp. A and B are consistent with *Acastocephala macrops* in extending from just above the confluence of S3 and the axial furrows to close to the posterior border furrow. The visual surface is also preserved in sp. B showing 10 rows of lenses as in the type species. *A*? Sp. C has a slightly smaller eye (sag.), but this is still relatively large extending from the confluence of S3 and the axial furrows to close to the posterior border furrow.

The *Acastocephala*? species presented here are assigned to that genus with question due to the following: in *A*? species A the glabella is very convex (sag., tr.) and the S1 curves strongly forwards; in species B the S2 and S3 are shallow, the S2 curves posteriorly, and the furrows on the pygidium are deeper; and in species C the glabella is very convex (tr.), and S2 and S3 curve strongly backwards. In addition species A, B and C all possess gena that is wider than the glabella at L1. Due to the differences between these species (outlined in the remarks) they probably all reflect distinct species, but the material is not of sufficient quantity to assess variation. The differences between *Acastocephala*? spp. identified here, in comparison to other members of the Acastidae in the British Ludlow, may well later form the basis of a new genus, but until these species are better known they are left under open nomenclature. Based on the apparent lack of a genal spine, very large (sag.) eyes, narrower frontal lobe, and relatively faint pleural furrows they are unlikely to belong to *Acastella*.

Genus CRYPHINA Oehlert, 1889

Type species. By original designation; *Cryphina andegavensis* Oehlert, 1889 from the Lower Devonian near Angers, Brittany, France.

Cryphina? *gdoumontensis* (Asselberghs, 1930)

Plate 19, figure 7

*1930 *Asteropyge gdoumontensis* Asselberghs, p. 60, pl. 6, figs 6-9.

. 1988 *Cryphina*? *gdoumontensis* (Asselberghs, 1930); Morris, p. 58 [with synonymy].

Type material. The syntypes are several specimens (unnumbered) in the Institut royal des Sciences naturelles de Belgique and are from Grès de Gdoumont (Devonian, late Gedinnian) of Gdoumont, Weismes, Belgium.

Remarks. In Britain this species is known only from two specimens (BGS GSM51871, GSM51886) from the Přídolí (see Thomas *et al.* 1984, p. 57 for discussion) of the Little Missenden Borehole (370 metres), Buckinghamshire (SU 902 982).

Stratigraphical range. Silurian (Přídolí) to Devonian (late Gedinnian).

3.4.9 Family PHACOPIDAE Hawle and Corda, 1847

Genus ANANASPIS Campbell, 1967

Type species. *Phacops fecundus* Barrande, 1846 from the middle part of the Kopanina Formation (Ludlow), Kolednik, near Beroun, Czech Republic.

Diagnosis. See Chulupáč (1977, p. 78).

Ananaspis? *nuda* (Salter, 1864)

Plate 19, figures 8-15; Plate 20, figures 1-2

*1864 *Phacops nudus*; Salter, p. 22, pl. 6, figs 19-20.

. 1984 *Ananaspis* sp.; Siveter *in* Thomas *et al.*, p. 55.

. 1988 *Ananaspis nuda* (Salter, 1864); Morris, p. 18.

. 1989 *Ananaspis* sp. aff. *stokesii* (Milne Edwards, 1840); Siveter, p. 133, pl. 19, figs 1-27; pl. 20, figs 8-10 [with synonymy].

. 1991 *Phacops nuda* Salter, 1864; Ramsköld and Werdelin, p. 73.

. 1998 *Ananaspis* aff. *stokesii* (=*A.* (s.l.) *nuda*) Salter, 1864; Thomas, p. 907.

Type material. The syntypes are B242, B243, housed in the Museum of Irish Industry, from the Annascaul Formation, Ballynane Member, (early ?Ludlow), west side of Cahirconree Mt., Dingle, Co. Kerry, Ireland.

Other material. Material collected by Siveter (1989) comprises 70 cephala, 3 hypostomes, and 20 pygidia from the Annascaul Formation, Ballynane Member, (early ?Ludlow), and are housed in TCD and UM. A complete specimen (BGS GSM 19405) from the early Ludlow of Cut Throat Lane, near Ledbury (exact horizon unknown), a cephalon (BGS GSM 19386) from the early Ludlow of Vinnal Hill, Ludlow. 2 cephala (LM 2875, G3064) are from the Middle Elton Formation of Upper Millichope (Wenlock Edge), and are housed at LM. 9 cephala, 2 cephalothoraxes, 3 pygidia were collected as part of the present study from localities 3-4, 7, and 47 (D-E), and are stored in BU.

Diagnosis. Eye with 17-20 lens files, 8-9 rows; lateral border curves around eye, not cutting posterior end, leaving a narrow strip of cheek subtriangular in outline between posterior end of eye and epiborder furrow; area of cheek between posterior end of eye and posterior border furrow a little shorter (sag.) than L1; L1 node pronounced, subrounded to suboval in outline. Granules on cephalon weak or absent.

Description. In addition to Siveter (1989, p. 133). Thorax composed of 11 segments. Axis around 0.29 times width of thorax, anterior 9 rings arched anteriorly at lateral ends, posterior 2 rings transverse. Anterior axial ring convex (tr.), raised slightly above rest. Pleurae adaxially transverse, then at around one-third distance becoming oblique, then finally curving forwards abaxially at end. Most anterior axial ring convex, raised well above rest. Second and third anterior axial rings also slightly raised, but less than first.

Remarks. A cladistic analysis by Ramsköld and Werdelin (1991) showed that *Ananaspis* was then paraphyletic, and that species close to the type species formed a separate clade

(*Ananaspis* s.s here) from species close to *A. guttulus* Campbell, 1967 (=*Kainops* Ramsköld and Werdelin, 1991), and '*A.' nuda, A.* cf. *stokesii*, and '*A.' amelangorum* Ramsköld 1985 (the last species name was corrected from *A. amelangi* by Ramsköld and Werdelin 1991, p. 70). The exact position of *A. nuda* and *A. amelangorum* was not resolved by Ramsköld and Werdelin (1991), since they formed a polytomy between the *Ananaspis* ss. clade and *Kainops*. Ramsköld and Werdelin (1991) did not revise the British Wenlock *A. stokesii*, due to the absence of the type material, and it occurred even more distant on their tree to the *Ananaspis s.s.* clade. *A. nuda, A. stokesii*, and *A. amelangorum* may well represent distinct genera, but a generic revision of these requires a full revision of specimens belonging to *A. stokesii* and a further phylogenetic analysis. These three species are assigned here to *Ananaspis*?.

A.? *nuda* is similar to *A.*? *amelangorum* Ramsköld, 1985 from the Mulde beds (Wenlock, Homerian) of Gotland, but differences include a much less convex glabella, the occipital ring lacks a medial node, the granulation on the cephalon is less prominent, the eye is situated farther from the posterior border furrow, subtriangular section of cheek present between posterior end of eye and epiborder, the eye is roughly consistent in height anteriorly to posteriorly, and the eye consists of fewer lens files (for additional similarities and differences see Ramsköld and Werdelin 1991). The type material of *A. stokesii* has yet to be located. Based on a study of topotype material at BGS *A.*? *nuda* is similar to *A.*? *stokesii* in having a flattened glabella, the absence of a node on the occipital ring, and a similar number of eye lens files, but differences include the eye not extending as close to the lateral border and epiborder furrows; there is a wider (tr.) strip of cheek, which is subtriangular in outline (rather than crescent shaped), between the posterior end of the eye and epiborder furrow, and is due to the lateral border not undercutting the posterior end of the eye abaxially, the lateral border furrow is wider and is not as sharply impressed, the posterior branch of S1 is better defined and more clearly bounds the L1 node, the L2 is longer (exsag.), the granulation on the cephalon is less distinctive, and the axial furrows are shallower.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* to *scanicus* biozones).

Occurrence. A.? *nuda* occurs in the Middle Elton Formation of the Ludlow District (localities 3-4, and 7), the Middle Elton Formation of Upper Millichope (near Wenlock Edge), the Middle Elton Formation near Perton (locality 30), and the ?Irfon Formation of Crychan Forest (locality 47D-E). Outside the UK this species is known from the Annascaul Formation (Ballynane Member), Dingle, Ireland.

3.4.10 Family CHEIRURIDAE Salter, 1864

Cheirurinae indet. A

Plate 20, figure 3

Material. A single cranidium and part thorax (BU 4807) from the Elton Group (Gorstian, exact formation and age unknown) from locality 42.

Remarks. The cranidium is incomplete and poorly preserved making identification beyond the family level difficult. The posterior end of the eye appears to lie at a position opposite the confluence of S1 and the axial furrow, although the anterior end is missing. The posterior extent of the eye indicates that it does not belong to *Didrepanon,* since the eye in that genus is more anteriorly placed. The S1 is oblique, rather than curved adaxially, and reaches the axial furrows. The specimen bears resemblance to *Cheirurus* with regards to the nature of the S1 which is consistent with *Cheirurus centralis* Salter, 1853, from the Wenlock of England and Wales. More material is needed even before a generic identification can made with any confidence, however.

Cheirurinae indet. B

Plate 20, figure 4

Material. A single pygidium (BU 4808) from the Lower Elton Formation (Gorstian, *nilssoni* Biozone) at locality 15.

Remarks. A poorly preserved pygidium resembling *Cheirurus*. The specimen bears a distinctive pair of nodes at the proximal end of the first pair of pleural ribs. Cheirurinae indet. B and Cheirurinae indet. A occur at different localities, thus the only link between them is their similar stratigraphical position and their apparent similarity to *Cheirurus*. To avoid the assumption that the pygidium must belong to the same species as the cranidium they are listed separately.

3.4.11 Family ENCRINURIDAE Angelin, 1854

Genus ENCRINURUS Emmrich, 1844

Type species. Designation of ICZN Opinion 537, (1959, p. 43); *Entomostracites punctatus* Wahlenberg, 1818, p. 32, pl. 2, fig 1, ?Hogklint Group (Wenlock Series), Gotland, Sweden.

Diagnosis. For a revised diagnosis see Ramsköld (1986, p. 532).

Encrinurus stubblefieldi Tripp, 1962

Plate 20, figures 5-13

*1962 *Encrinurus stubblefieldi* Tripp, p. 471, pl. 65, fig 12; pl. 67, figs 14-15; pl. 68, fig. 11.

. 1972 *Encrinurus* (*E.*) *stubblefieldi* TRIPP, 1962; Schrank, p. 42, pl. 12, figs 4-5 [with synonymy].

. 1984 *Encrinurus stubblefieldi* Tripp; Thomas *et al.*, p. 56.

. 1988 *Encrinurus stubblefieldi* Tripp, 1962; Morris, p. 89 [with synonymy].

v. 1986 *Encrinurus* (*Encrinurus*) *stubblefieldi* Tripp, 1962; Ramsköld, p. 554, pl. 45, figs ?12, ?14, ?15; pl. 46, figs 1-14 [with synonymy].

Type material. Holotype, by original designation; BGS GSM 36846 (untraced), original of Tripp 1962, pl. 65, fig. 12; pl. 67, fig. 15, ‘Upper Ludlow Shales’ (Ludfordian), Whitcliffe, Ludlow, Shropshire, England. The paratype is cephalothorax BGS GSM 36844, original of Tripp 1962, pl. 67, fig. 14, ‘Upper Ludlow Shales’, N.E. of Pillard’s Barn, Shropshire, England.

Other material. 3 partial cephala, 3 librigena, a thoracopygidium, and 11 pygidia in BU. This species was collected from localities 21-22, 24-25, and 48. Additional material of this species can be found at BGS, NRM, and SGU.

Diagnosis. Revised from Ramsköld (1986, p. 554). Glabella weakly convex, depressed posteriorly; axial furrows wide; L1 well developed, with subdued or no tubercles; eyes very low; genal field wide, 2-2.5 times wider than glabellar width at L1; genal spines very stout and long; glabella lacking tubercle row VI; eight tubercles on anterior border; free cheek with faint tuberculation only; lateral border furrow shallow. Pygidium with 16-24 axial rings, pleural tips poorly defined on lateral margin; R/P ratio 1.7-2.2; caudal spine at least as long as axis. All tuberculation of low relief.

Description. See Ramsköld (1986, p. 554).

Remarks. E. intersitus Ramsköld, 1986 seems to be the most closely related species to *E. stubblefieldi*.

Stratigraphical range. Gorstian (*nilssoni* Biozone) to Ludfordian (*bohemograptus* Biozone).

Occurrence. In Britain, *E. stubblefieldi* is known from the Bringewood and Leintwardine groups and the Lower Whitcliffe Formation of the Ludlow district. A single pygidium was collected from the lower part of the Hafod Fawr Formation, Halfway Forest (locality 48), Llandovery, which is the earliest record of this species. This species is known from the Ludlow of Germany, the Sokol and Bernovo subsuites (Ludlow) of Ukraine, and the Hemse Group (Gorstian to early Ludfordian) from several localities in Gotland (see Ramsköld 1986, p. 554 for a list).

Genus BALIZOMA Holloway, 1980

Type Species. By original designation; *Calymene variolaris* Brongniart, 1822, p. 14 from the Wenlock Series, Much Wenlock Limestone Formation, Dudley, West Midlands, England.

Diagnosis. See Ramsköld (1986, p. 560) for a revised diagnosis.

Remarks. For a discussion on this genus see Ramsköld (1986, p. 560).

Balizoma variolaris (Brongniart, 1822)

Plate 20, figures 14-15; Plate 21, figure 1

*1822 *Calymene variolaris* Brongniart, p. 14.

v. 1839 *Calymene variolaris* Brongniart; Murchison, p. 655, pl. 14, fig 1.

1853 *Encrinurus variolaris* Brongniart; Salter, dec. 7, p. 7 of pl. 4, figs 13-14.

v. 1962 *Encrinurus variolaris* (Brongniart); Tripp, pl. 65, figs 17-20.

. 1977*a* *Calymene variolaris* Brongniart, 1822; Tripp *et al.*, p. 250.

v. 1977*b* *Encrinurus variolaris* (Brongniart); Tripp *et al.*, p. 850, pl. 113; text-figs 1-2, 3B, 4A [with synonymy].

. 1984 *Encrinurus variolaris* (Brongniart); Thomas *et al.*, pp. 53, 56.

. 1988 *Balizoma variolaris* (Brongniart, 1822); Morris, p. 31 [with synonymy].

Type material. The neotype was selected by Tripp *et al.* (1977*b*); BU 55, original of Murchison 1839, pl. 14, fig. 1, from the Much Wenlock Limestone Formation (Homerian), Wenlock Series, Dudley, West Midlands, England.

Other material. The holotype of *E. magnituberculatus* is SM A16538 from the Much Wenlock Limestone Formation of Buckenhill Wood, near Woolhope, Hereford and Worcester, England. Numerous specimens belonging to this species can be found at BU, NHM, NMW, SM.

Diagnosis and description. See Tripp *et al.* (1977*b*, p. 850)

Remarks. This species was noted by *Tripp et al.* (1977*b*) to occur rarely in the Lower Elton Formation, but no new material was found as part of the present study.

Stratigraphical range. Wenlock (Sheinwoodian; *riccartonensis* biozone) to Ludlow (Gorstian; *nilssoni* biozone).

Occurrence. This species is most common in the Much Wenlock Limestone Formation (Homerian) of Dudley and Wenlock Edge, and occurs only rarely in the Coalbrookdale (Sheinwoodian) and Lower Elton formations.

Balizoma obtusus rosensteinae (Tripp *et al.*, 1977*b*)

Plate 21, figures 2-10

*v**1977*b* *Encrinurus rosensteinae;* Tripp *et al.*, p 860, pl. 115, figs 1-13, text-fig. 3c.

. 1984 *Encrinurus rosensteinae* (Tripp, Temple & Gass); Thomas *et al.*, p. 56.

v. 1986 *Balizoma obtusus* Form B; Ramsköld, p. 562, pl. 49, figs 1-10.

. 1988 *Balizoma rosensteinae* (Tripp, Temple & Gass); Morris, p. 31.

Type material. Holotype by original designation; pygidium BM It14139 from the Lower Bringewood Formation (Gorstian; *incipiens* Biozone) of Mortimer Forest, near Ludlow, Shropshire, England.

Other material. A complete specimen, a cranidium, and twelve pygidia were collected as part of the present study from localities 22 and 50 and are stored in BU. Other specimens belonging to this species include a pygidium (BGS FG 1533) from the Lower Bringewood Formation, from an exposure in a field 1140 metres from St Mary’s Church Llanfair Kilgeddin, Gwent (Wales); a pygidium (BGS GSM 36848) from the Lower Whitcliffe Formation, Whitcliffe, Ludlow; and a pygidium (SM A37.371) from the early Ludlow

(?Bringewood Group) of Ledbury. This species is well represented at NHM.

Diagnosis. Length of posterior border typically longer than distance between posterior border furrows and eye. 1-2 tubercles between axial furrow and palpebral lobe. Pygidium with relatively low convexity; axis narrow, tapering strongly backwards; 11-14 axial rings and typically 9-11 pleura; prominent sagittal tubercle absent on most anterior two axial rings.

Description. See Tripp *et al.* (1977*b*, p. 860).

Remarks. Ramsköld (1986) suggested that *B. rosensteinae* may be synonymous with *B. obtusus* (Angelin, 1851) from the Hemse Group of Gotland. Both species have one or two tubercles between the axial furrows and the palpebral lobe, a relatively narrow pygidial axis, the most anterior two pygidial axial rings lack a prominent sagittal tubercle, and the number of pygidial pleura and axial rings overlap between the two species. Ramsköld (1986) split his *B. obtusus* specimens into three forms (‘A’, ‘B’, and ‘C’) but based on the degree of variation in each he found it difficult to separate them as distinct species. Form A of Ramsköld (1986) includes the type specimen. British specimens formally referred to as *B. rosensteinae* are generally poorly preserved or distorted making comparisons with the better preserved Swedish material difficult. *B. rosensteinae* does appear to differ from *B. obtusus* form A, however, in having a more posteriorly positioned eye, an even narrower pygidial axis that tapers backwards strongly, no more than 9 pleural ribs (rather than 9-12), and prominent tubercles on each pleural rib (rather than being faint or absent). *B. rosensteinae* is very similar to *B. obtusus* form B of Ramsköld (1986), but it differs in the axis tapering backwards a little more strongly. In all other respects *B. rosensteinae* appears consistent with *B. obtusus* form B and they are regarded here as synonymous. *B. obtusus* form A and *B. rosensteinae* are distinguished on pygidial differences only, and are regarded as separate subspecies. *B. obtusus rosensteinae* can be reliably separated from *B. obtusus obtusus* in having a narrower axis, prominent tubercles on the pygidial pleura, and due to the lower convexity of the pygidium the pleural regions are not as highly elevated. Form C does not differ significantly from form A and they are regarded here as belonging to the same subspecies.

This species is most common in the Lower Bringewood Formation (Tripp *et al.* 1977*b*).

Stratigraphical range. Gorstian (*incipiens* biozone) to Ludfordian (*bohemograptus* Biozone).

Occurrence. This taxon is known from the Lower Bringewood Formation of Usk (locality 50), Mortimer Forest (locality 10), Ludlow, and Millichope Park, near Wenlock Edge; the Upper Bringewood Formation of Ludlow; the Lower (locality 22) and Upper Leintwardine Formation of the Ludlow district; the Ludlow of Ledbury, the Aymestry Limestone of Craven Arms, Shropshire; the Lower Whitcliffe Formation of Ludlow.

Order PROETIDA Fortey and Owens, 1975

3.4.12 Family PROETIDAE Salter, 1864

Genus PROETUS Steininger, 1831

Type species. By original designation; Steininger (1831), p. 29; *Calymmene concinna* Dalman, 1827, p. 234, ‘Mulde Beds’ (=Hala Formation), Wenlock Series (Homerian), Djupvik, Gotland, Sweden.

Diagnosis. Modified from Lieberman (1994, p. 20). Occipital lobe longer than anterior border; glabella parallel-sided; L0 prominent, bulging strongly laterally so that occipital ring is wider than preoccipital part of glabella; in profile preoccipital part of glabella flat at posterior end; frontal lobe quadrate in dorsal view; glabella often interrupts anterior border furrow; preglabellar field typically absent; terrace ridges on anterior border generally transverse but wavy and separated; pygidial border absent.

Remarks. Proetus has been subject to substantial and frequent revisions over the years. Notable publications include Přibyl (1946), Erben (1951), Richter and Richter (1952, 1956), Campbell (1967), Whittington and Campbell (1967), Owens (1973), Thomas (1978), Alberti (1970), Šnajdr (1980), Lütke (1990), and Lieberman (1994). For many years it was used to accommodate a large number of seemingly closely related proetid species that displayed a wide range of morphologies, but little consideration was then given to separating these at a generic level. Since the 1950’s a greater emphasis has been placed on restricting the diagnosis of *Proetus* and to identify species groups within it; see

Lieberman (1994) for a review. Owens (1973), for example, regarded *Lacunoporaspis* Yolkin, 1966 as a subgenus of *Proetus* and emended Yolkin's diagnosis to include the species *P. confossus* and *P. obconicus*. Several other species occurring in the British Silurian were thought by Owens (1973) to represent one or more additional subgenera, but were assigned to *Proetus sensu lato*: those occurring in the British Ludlow are *P.* (s.l.) *latifrons* and *P.* (s.l.) *falcatus*. Lütke (1990) reassigned the latter species to a new genus, *Falcatoproetus*. A cladistic analysis by Lieberman (1994) showed that *Proetus* was polyphyletic, and that *Proetus*, *Lacunoporaspis*, *Falcatoproetus*, and the species around *P. obconicus* all belonged to separate genera. Lieberman (1994) erected a new genus, *Plesiowensus*, to accommodate the last of these groups.

Proetus concinnus (Dalman, 1827)

Plate 21, figures 11-13

*1827 *Calymmene concinna* Dalman, p. 234, pl. 1, figs 5a-c.

v. 1854 *Forbesia concinna* (Dalman); Angelin, p. 22, pl. 17, fig. 5.

v. 1885 *Proetus concinnus* (Dalman); Lindström, p. 78.

v. 1973 *Proetus (Proetus) concinnus* Dalman; Owens, p. 12, pl. 2, figs 14-15; pl. 3, figs 1-9 [with synonymy].

v. 1973 *Warburgella (Warburgella) stokesii* (Murchison, 1839), Owens, [pars], pl. 13, fig. 10a-b only.

v. 1978 *Proetus (Proetus) concinnus* Dalman; Thomas, p. 36, pl. 9, figs 1-9 [with synonymy].

v. 1980 *Proetus (Proetus) concinnus* (Dalman); Thomas, p. 450, pl. 1, figs 3-4.

. 1984 *Proetus (P.) concinnus* Dalman; Thomas *et al.*, pp. 52, 56.

. 1988 *Proetus concinnus* (Dalman, 1827); Morris, p. 188 [with synonymy].

. 1994 *Proetus concinnus* (Dalman, 1827); Lieberman, p. 22.

Type material. Holotype by monotypy; Uppsala Pal. Inst. G 733, original of Dalman 1827, pl. 1, figs 5a-c, 'Mulde Beds' (=Hala Formation), Wenlock Series (Homerian), Djupvik, Gotland, Sweden.

Other material. A complete list of specimens belonging to *P. concinnus* are in Owens (1973, p. 12).

Diagnosis. Modified from Lieberman (1994, p. 22). Anterior branch of facial suture diverging from glabellar margin; posterior edge of L0 straight, parallel to posterior border furrow; pygidial axis wide, width of anterior most axial ring 36-39 per cent of pygidial width.

Description. See Owens (1973, p. 13).

Remarks. This species is most common in the Wenlock and occurs rarely in the early Ludlow. As part of the present study, material collected from the Lower Elton Formation closely resembles this species but is assigned here to *P.* cf. *concinnus*.

Stratigraphical range. Wenlock (Sheinwoodian; *centrifugus* Biozone) to Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. P. concinnus is known from many localities of the Coalbrookdale Formation Much Wenlock Limestone Formation (See Owens 1973, p. 12) and from the Lower Elton Formation of Wenlock Edge, Shropshire, and Cut-throat Lane (locality 36), Ledbury, Herefordshire. It also occurs in the Wenlock (Homerian) 'Mulde Beds' (=Hala Formation) of Gotland and from the Wenlock of Germany and Estonia.

Proetus cf. *concinnus* (Dalman, 1827)

Plate 22, figures 1-7

Material. 4 cranidia, a librigena, and 4 pygidia from the Lower Elton Formation (Gorstian, *nilssoni* Biozone), in BU, from localities 9, 15, and 27 and a cranidium from the Upper Elton Formation (Gorstian, *scanicus* Biozone) of locality 33.

Remarks. As part of the present study several poorly preserved pygidia have been found that strongly resemble *P. concinnus,* but several associated cephala differ from that species in possessing a very short preglabellar field. In addition an associated librigena bears an area of cheek between the eye and the lateral border that is a little wider than that seen in *P. concinnus*. These differences probably reflect variation within *P. concinnus* but the material is too poorly preserved to be certain of its specific assignment.

Proetus (s.l.) *astringens* Owens, 1973

Plate 22, figures 8-13

*v**1973 *Proetus* (s.l.) *astringens* sp. nov.; Owens, p. 25, pl. 2, figs 7, 11-12.

. 1984 *Proetus* (s.l.) *astringens* Owens; Thomas *et al*., p. 56.

. 1988 *Proetus* (s.l.) *astringens* Owens, 1973; Morris, p. 187.

Type material. Holotype by original designation; NMW 71.6G.494 from the Upper Elton Formation, exposure in ditch on south side of Worcester-Hereford road (A4103), near Storridge, Herefordshire, (SO 743 480).

Other material. Material belonging to this species is stored in the NMW. A complete list of specimens is noted in Owens (1973, p. 25).

Diagnosis. Modified from Owens (1973, p. 25). L0 large; Glabella pyriform, laterally constricted at about two-thirds of its length from anterior; glabella broad at posterior end, preoccipital part of glabella wider than long; no preglabellar field; free cheek with genal spine; pygidium without border, pygidial axis with 5-6 rings.

Description. In addition to Owens (1973, p. 25): L0 large, rounded, 18 per cent width of occipital ring. Occipital ring roughly equal in length as anterior border. Palpebral lobe distant from lateral and anterolateral border furrows. Genal spine broad, widening slightly from anterolateral border, at its widest point 30 per cent of librigenal width. Pygidial axis 30-33 per cent width of pygidium, most anterior axial ring higher than those below.

Pygidial doublure with at least 8 distinct terrace ridges.

Remarks. Proetus (s.l.) *astringens* differs from *P. concinnus* mainly in the broad glabella, that tapers forwards strongly, larger L0, which is more convex and elevated, a shorter occipital ring, eye positioned distant from lateral border, and a narrower pygidial axis. It differs in many respects from *P. concinnus* and, most likely, represents a new genus. The broad posterior end of the glabella, narrow occipital lobe, and narrow pygidial axis are also seen in *P.* (s.l.) *latifrons* (M^{c}Coy, 1846) from the ?late Llandovery of Ireland and probably belongs to the same genus as *P.* (s.l.) *astringens.* Both species are known from a few specimens only and no new material was found as part of the present study. Assignment of this species to a new genus awaits further material.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* to *incipiens* biozones).

Occurrence. This species is known from the base of the Middle Elton Formation near Perton (locality 30), and the Upper Elton and Lower Bringewood formations of the Welsh Borderland. As part of the present study no new material was found.

Genus FALCATOPROETUS Lütke, 1990

Type species. By original designation, Lütke 1990 (p. 37), *Proetus* (s.l.) *falcatus* Owens, 1973 from the ?early Ludlow Series of Dudley, West Midlands, England.

Other species. This genus is known only from the type species.

Diagnosis. Modified from Lütke 1990 (p. 37). Occipital lobe long (sag.); palpebral lobes elevated above glabella; glabella parallel-sided to frontal lobe, which tapers gently forwards; no preglabellar field; anterior border long; thoracic segments with minute preannulus; posterior pygidial axial rings poorly defined; 4-5 bicomposite, fused flat-topped ribs, anterior ones partly crossing wide border, pygidial border weakly developed.

Remarks. See *Falcatoproetus falcatus* remarks.

Falcatoproetus falcatus (Owens, 1973)

*1973 *Proetus* (s.l.) *falcatus* sp. nov. Owens, p. 23, pl. 2, figs 8, 13.

. 1978 *Proetus* (s.l.) *falcatus* Owens; Thomas, p. 40, pl. 9, fig. 15.

. 1984 *Proetus* (s.l.) *falcatus* Owens; Thomas *et al*., pp. 53, 56.

. 1988 *Proetus* (s.l.) *falcatus* Owens, 1973; Morris, p. 188 [with synonymy].

. 1990 *Falcatoproetus falcatus* (Owens); Lütke, p. 37, pl. 8, figs 53-54.

. 1994 *Falcatoproetus falcatus* (Owens, 1973); Lieberman, p. 24.

Type material. Holotype, by original designation; NHM 59022 (specimen missing), originally described from the ?early Ludlow Series of Dudley, West Midlands, England.

Other material. 4 complete specimens (OUM C772-775) from the Coalbrookdale Formation (Sheinwoodian) of Malvern Tunnel, Worcestershire and a complete specimen (BU 1819) from the Much Wenlock Limestone Formation (Homerian) of Dudley, West

Midlands, England.

Diagnosis. As for genus.

Description. See Owens (1973, p. 23).

Remarks. Differences between *F. falcatus* and *Proetus concinnus* include the less prominent L0; weak glabellar furrows (rather than deep), a longer anterior border, the palpebral lobes are raised above the glabella, glabella parallel sided up to frontal lobe then gently converges forwards, a weak pygidial border, and narrower pygidial pleural ribs.

Stratigraphical range. Wenlock (Homerian; *riccartonensis* Biozone) to ?Ludlow (?Gorstian; ?*nilssoni* Biozone).

Occurrence. This species is known from the Coalbrookdale Formation (Sheinwoodian) near Malvern Tunnel, Worcestershire; Much Wenlock Limestone Formation (Homerian) and undifferentiated ?early Ludlow rocks of Dudley, West Midlands.

Genus PLESIOWENSUS Lieberman, 1994

Type species. By original designation; Lieberman (1994, p. 37), *Proetus obconicus* Lindström, 1885, originally described from the Eke Formation (Ludfordian), Lau Backar, Gotland, Sweden.

Other species. *P.* (s.l.) *confossus* (Owens, 1973), from the Much Wenlock Limestone Formation (Homerian, *ludensis* Biozone), Dudley, West Midlands; *P. chlupaci* (Šnajdr, 1980), from the Přídolí Formation (Přídolí, *transgrediens* Biozone) of Bohemia; *P. oppidanus* (Thomas, 1978), from the Wenlock Coalbrookdale Formation (Sheinwoodian, *riccartonensis* Biozone) of Walsall, West Midlands; and *P. raymondi* sp. nov. from the Lower Leintwardine Formation of the Ludlow District, Shropshire.

Diagnosis. Modified from Lieberman (1994, p. 35). Genal spine furrow intersects most posterior midpoint of genal spine; posterior edge of L0 curves forwards laterally; glabella with weakly incised furrows; S2 and S3 curving posteriorly; preglabellar field short or absent; terrace ridges on anterior border generally transverse but wavy and separated; pygidial axis narrow (tr.), most anterior 2 or 3 pygidial axial rings elevated above rest; pleural areas scalloped; dorsal pygidial border absent or weakly developed. Glabella granular or smooth, pitting on librigenal field.

Remarks. *Plesiowensus* differs from *Proetus* mainly in having a more elongate glabella tapering forwards strongly, a narrower occipital lobe, a less prominent L0 that does not expand as much laterally, posterior end of eye distant from lateral border furrow, S3 curving posteriorly, the anterior end of the glabella not as strongly directed downwards towards anterior border in lateral view, a narrower pygidial axis, the most anterior 2 or 3 pygidial axial rings raised above those below, and pitting on the cheeks. Species now assigned to *Plesiowensus* were previously referred to *Lacunoporaspis* (see *Proetus* remarks) but were regarded by Lieberman (1994) as separate and he revised *Lacunoporaspis* accordingly. The main differences between *Plesiowensus* and

Lacunoporaspis are: posterior border furrow straight (rather than curving posteriorly), anterior branch of facial sutures diverge from each other (rather than parallel), wavy and separate terrace ridges on the anterior border (rather than closely spaced and linear), anterior most 2 or 3 pygidial axial rings raised above rest (rather than all of even height), pygidial pleurae flat (rather than gently rounded posteriorly) and a lack of a strong pygidial border in *Plesiowensus*.

Plesiowensus obconicus (Lindström, 1885)

Plate 23, figures 1-12

1848 *Proetus latifrons* M^{c}Coy; Salter *in* Phillips and Salter, p. 337, pl. 6, figs 1, 1a-c.

*v**1885 *Proetus obconicus* Lindström, p. 78, pl. 15, figs 22-24.

? 1954 *Proetus* sp.; Richter and Richter, p. 20, pl. 1, fig. 17.

? 1969 *Proetus?* sp.; Alberti, p. 368, pl. 46, fig. 17.

v. 1973 *Proetus* (*Lacunoporaspis*) *obconicus* Lindström; Owens, p. 17, pl. 4, figs 11-19; pl. 5, fig. 1 [with synonymy].

. 1984 *P.* (*Lacunoporaspis*) *obconicus* Lindström; Thomas *et al*., p. 56.

. 1988 *Proetus* (*Lacunoporaspis*) *obconicus* Lindström, 1885; Morris, p. 189 [with synonymy].

. 1994 *Plesiowensus obconicus* (Lindström, 1885); Lieberman, p. 37.

Type material. Lectotype selected by Owens (1973, p.17); RM Ar29035, original of

Lindström (1885, pl. 15, fig. 23), Eke Formation (Ludfordian), Lau Backar, Gotland, Sweden.

Other material. 11 cranidia, 2 librigena, 14 pygidia, a thoracopygidium, and a complete specimen in BU. This species was collected from localities 15, 20, 22, and 24. See Owens (1973, p. 17) for a complete list of specimens at NMW, NHM, BGS, and SM.

Diagnosis. Modified from Owens (1973, p. 18). Long genal spine; prominent L0; glabella elongate, conical, weakly inflated; preglabellar field very short; cheek and lateral parts of preglabellar field pitted; pleural and interpleural furrows not reaching pygidial margin, pygidial border poorly defined; exoskeleton mainly smooth, but with sporadic localized granules.

Description. In addition to Owens (1973, p. 18). L0 oval, representing around 16-20 per cent of occipital width. Preoccipital part of glabella width 82-88 per cent that of length. Anterior border convex, as long sagittally as exsagittally. Length of anterior border 13-15 per cent of cranidial length. At its widest point anterolateral border 30-33 per cent width of librigena. Pygidium 1.7-2 times as wide as long. Anterior end of axis with a width 27-30 per cent width of pygidium, terminates 74-75 percent towards pygidial margin. 7-9 pygidial axial rings, 5-6 pairs of pleural ribs.

Remarks. This species is recorded from the Elton Group here for the first time, which is the oldest record to date.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* Biozone to Ludfordian; *leintwardinensis* Biozone).

Occurrence. P. obconicus occurs in the Lower Elton Formation of Ludlow (locality 15), the Upper Elton Formation near Ledbury (locality 33), and the Lower Leintwardine Formation of Ludlow (locality 20, 22, 24). Owens (1973, p. 17) recorded this species from numerous localities in the Bringewood and Leintwardine groups of the Welsh Borderland and Wales, and the Eke Formation (Ludfordian) of Gotland. This species is most abundant in the upper part of the Lower Leintwardine Formation and the lower part of Upper Leintwardine Formation.

Plesiowensus aff. *obconicus* (Lindström, 1885)

Plate 23, figure 13

Material. A single external mould of a cranidium, with part of occipital ring missing, from the Upper Bringewood Formation (Gorstian, *incipiens* Biozone), locality 13.

Description. Glabella elongate, strongly tapering forwards. Preoccipital area of glabella 71 per cent as wide as long. Glabellar furrows very faint and shallow, reaching axial furrows. S1, arises around 30 per cent way along preoccipital part of glabella. S1 initially oblique, then curves posteriorly, shallowing before reaching occipital furrow. S2 arising around half-way along preoccipital part of glabella, terminating a little over half-way towards sagittal line. S3, oblique, around one-third shorter than S2. Preglabellar field absent, anterior border touching preglabellar furrow. Anterior border convex, as long sagittally as exsagittally. Length of anterior border around 21 per cent length of cranidia. Terrace ridges on anterior border shallow and faint.

Remarks. *Plesiowensus* aff. *obconicus* is similar to the type species with regards to the elongate glabella. The glabella in this species is has an even more elongate than the type species, however, the preglabellar field is absent, and the anterior border is longer.

Plesiowensus raymondi sp. nov.

Plate 24, figures 1-9

Derivation of name. After my father Raymond, for all of his support throughout my PhD.

Type material. Holotype assigned herein; cranidium BU 4809 from locality 24. The paratypes are 2 cranidia (BU 4810, 4812), a pygidium (BU 4813), and a librigena (BU 4816) from locality 24; and a cranidium (BU 4811) and 3 pygidia (BU 4814-15, BU 4930) from locality 22. All are from the Lower Leintwardine Formation.

Diagnosis. L0 weak; preoccipital area of glabella pyriform, almost as wide (tr.) as long (sag.); L1 well rounded, bulging laterally at posterior end; anterior border longer sagittally than exsagittally, longer than occipital ring; pygidial axis termination poorly defined, pleural and interpleural furrows reaching pygidial margin; pygidial border absent.

Description. Occipital ring narrowing slightly laterally. L0 elliptical in outline, gently convex, defined by faint furrows. Glabella elongate, tapering gently forwards, 1.2 times longer than wide. L1 bulging abaxially at base so that width of preoccipital area of glabella is 96-98 per cent of length. Glabellar furrows barely perceptible on most specimens, but reaching axial furrows. S1 arises around 35 per cent way along preoccipital part of glabella, narrowing at both ends. S1 initially oblique then curving posteriorly, terminating as a sharp point around three-quarters way towards occipital furrows. S2 oblique, as long and deep as S1, arising half-way along preoccipital part of glabella, terminating around 22 per cent towards sagittal line. S3, oblique, equal in depth but around half as long as S2, terminating at a position above distal end of S2. Preglabellar furrow equal in length and depth to anterior border furrow. Anterior border convex, with a sagittal length of around 15-17 per cent of cranidial length. Sagittal length of anterior border around 1.17-1.19 times longer than exsagittal length. Faint discontinuous terrace ridges on anterior border.

Librigenal field and anterolateral border gently convex. Posterior border furrow equal in depth and length as anterolateral border furrow. Epiborder furrow distinct. At its widest point anterolateral border 38 per cent that of librigenal width. Eye around 62 per cent length of librigenal field, close to anterolateral border.

Pygidium a little less than twice as wide as long. 9 pygidial axial rings, anterior 3 raised. Axial rings decreasing in elevation posteriorly, ring furrows better defined anteriorly than posteriorly. Anterior end of axis width 28 per cent of pygidial width, terminating 75 per cent towards pygidial margin. 5 pleural ribs, widening gently adaxially. Pleural and interpleural furrows faint, less well defined close to margin.

Remarks. P. raymondi sp. nov. differs from the type species in possessing a longer anterior border which is slightly narrower exsagittally than sagittally, a less well defined L0, the occipital ring narrows slightly laterally, the L1 bulges laterally, S1 does not reach the axial furrow, the glabella not tapering forward as strongly, the preoccipital part of glabella being almost as wide as long, glabellar furrows are not as well defined, a longer preglabellar field, the librigenal field is less convex, the pleural and interpleural furrows reach the pygidial margin, and the lack of a pygidial border. *P. raymondi* sp. nov. is most like *P. oppidanus* (Thomas, 1978) from the Wenlock Coalbrookdale Formation of Walsall; similarities include the weak L0, wide L1, glabellar furrows faint, S1 and S2 not reaching axial furrows, eye extends close to anterolateral border, posterior pygidial axial ring furrows not as well defined as anterior ones, pygidial axial terminus poorly defined. Differences between *P. raymondi* sp. nov. and *P. oppidanus* include the even wider L1, preoccipital part of glabella being almost as wide as long, a longer preglabellar field, a flatter librigenal field, anterior border slightly narrower exsagittally than sagittally, the pleural and interpleural furrows reaching the pygidial margin, a shorter pygidial axis with more axial rings, and a lack of a weak pygidial border in *P. raymondi* sp. nov. The broad base of the preoccipital part of the glabella is reminiscent of the pyriform glabella in *Proetus* (s.l.) *astringens*. The width of the glabella in *P.* (s.l.) *astringens* is larger than the total glabellar length but in *P. raymondi* sp. nov. it is around 20 per cent smaller, however.

Stratigraphical range. Ludlow (Ludfordian; *leintwardinensis* Biozone).

Occurrence. This species occurs in the Lower Leintwardine Formation of the Ludlow District (localities 22 and 24).

Discussion.

Based on his cladistic analysis, Lieberman (1994) noted that *Plesiowensus* formed a paraphyletic group and assigned *P. oppidanus* (Thomas, 1978), *P. chlupaci* (Šnajdr, 1980) and *P. confossus* (Owens, 1973) to *Plesiowensus* with question. Only the type species and *P. confossus* were included in the analysis and no comparison was made with the other *Plesiowensus* species. Lieberman (1994) noted that *P. obconicus* differs from *P. confossus* in possessing apodemes on the lateral fields of the pygidial axis, pygidial axial rings behind third segment flexing anteriorly medially (rather than posteriorly), most anterior end of anterior border rounded (rather than straight), anterior branch of facial suture deflects abaxially sharply at around 45 degrees (20 degrees in *P. confossus*), furrow on genal spine deflects sharply abaxially from lateral border furrow then straightens and runs down the middle of the genal spine parallel to margin (in *P. confossus* straight), and a straight genal spine (rather than curving adaxially), anterior border longer than L0. The last character noted by Lieberman (1994) is in error: in *P. obconicus* for example, L0 is shorter to a little longer than the anterior border. *P. oppidanus, P. chlupaci,* and *P. raymondi* sp. nov. share all of the above characters with *P. obconicus* with exception of the first two. Additional differences between *P. confossus* and the other *Plesiowensus* species include a shorter genal spine, better defined glabellar furrows, a wider and more convex glabella, and a wider pygidial axis. *P. confossus* may represent a new genus but it is assigned here to *Plesiowensus* (s.l.) based on the genal spine furrow intersecting the most posterior midpoint of genal spine, eye distant from lateral border, the elongate glabella tapering strongly forwards, wavy terrace ridges on anterior border, and the anterior most three axial rings raised above those below. *P. oppidanus*, *P. chlupaci,* and *P. raymondi sp. nov.* seem to be closely related to *P. obconicus* and are regarded here as belonging to *Plesiowensus* *sensu stricto*. A further phylogenetic analysis is required that includes all of the *Plesiowensus* species in order to better assess their relationships. The issue of paraphyly in *Plesiowensus* identified by Lieberman (1994) may be resolved by the use of additional characters (such as the length to width ratio of preoccipital glabellar area and width of pygidial axis) at a higher resolution (such as accounting for a weak pygidial border).

Genus WARBURGELLA Reed, 1931

Type species. Original designation; *Asaphus Stokesii* Murchison, 1839, p. 656, Much Wenlock Limestone Formation (Homerian), Dudley, West Midlands, England.

Diagnosis. See Ormiston 1967 (p. 61).

Subgenus WARBURGELLA Reed, 1931

Type species. As for genus.

Diagnosis. From Owens (1973, p. 66). Tropidium or tropidal ridges always present; transverse preglabellar ridge commonly present; preoccipital part of glabellar as wide as long to a little longer than wide; thorax of 8-10 segments.

Warburgella (*Warburgella*) aff. *baltica* Alberti, 1963

Plate 24, figure 14

Material. A single cranidium (BU 4931) from the Lower Elton Formation (Gorstian; *nilssoni* Biozone), at locality 15.

Remarks. The long preglabellar field is consistent with the subgenus *Prantlia* Přibyl, 1946 but the well developed and rounded L0, the relatively wide glabella at L1 (compared to *Prantlia*), the relatively short occipital lobe, the presence of a tropidium running parallel to the anterior border, and the absence of a transverse preglabellar ridge suggests that the specimen belongs to *Warburgella*. It bears resemblance to *Warburgella* (*W.*) *baltica* Alberti, 1963 but differs in possessing shorter L0, an absence of a prominent central tubercle on the occipital lobe, and a much longer preglabellar field. This specimen probably represents a new species. A formal description awaits further material.

Subgenus OWENSELLA Přibyl and Vaněk, 1978

Type species. Proetus (sg.?) *ludlowensis* Alberti, 1967, from the Lower Leintwardine Formation (Ludfordian), Mary Knoll House, near Ludlow, Shropshire, England.

Diagnosis. Tropidium absent; transverse preglabellar ridge weak; preglabellar furrow transverse to very gently rounded; preoccipital part of glabella longer than wide; L0 convex, distinct; 8 thoracic segments.

Warburgella (*Owensella*) *ludlowensis* (Alberti, 1967)

Plate 24, figures 10-13

*1967 *Proetus* (sg.?) *ludlowensis* Alberti p. 483, pl. 1, fig. 2.

v. 1973 *Warburgella* (*Tetinia*) *ludlowensis* (Alberti, 1967); Owens, p. 72, pl. 14, figs 13?, 14,, 16-18, non fig. 15 [=*Warburgella* (?*Warburgella*) sp.] pl. 15, figs 1-2; text-fig. 10 [with synonymy].

. 1984 *Warburgella* (*Tetinia*) *ludlowensis* (Alberti); Thomas *et al.*, p. 56.

. 1988 *Warburgella* (*Owensella*) *ludlowensis* (Alberti, 1967); Morris, p. 237 [with synonymy].

Type material. Holotype by original designation; SMF 23363, original of Alberti 1967, pl. 1, fig. 2; Lower Leintwardine Formation (Ludfordian), Mary Knoll House, near Ludlow, Shropshire, England.

Other material. See Owens (1973, p. 72) for a list of specimens. A cranidium (BU 4932) from the Lower Leintwardine Formation of locality 22.

Diagnosis. As for subgenus.

Description. See Owens (1973, p. 73).

Remarks. This species was designated as the type species of the subgenus *Owensella* by Přibyl and Vaněk, 1978. Later Owens (1973) assigned '*P. ludlowensis*' Alberti, 1967 to *Tetinia* Chlupáč, 1971, type species *T. minuta* (Přibyl and Vaněk, 1962) from the Lower Devonian of Czech Republic, which he then regarded as a subgenus of *Warburgella*. The present author is in agreement with Šnajdr (1980) in that *Tetinia* represents a distinct genus. *Tetinia* differs from *Warburgella* in the less well defined L0 without furrow, a longer preglabella field, no tropidium or preglabellar ridge, deeper S2 and S3, a wider librigena, the pygidial axis is better defined posteriorly, and a convex pygidial border. '*P*. *ludlowensis*' differs from *T. minuta* in the shorter anterior border, well defined S2 and S3, the glabella is wider and does not taper forwards as strongly, L0 are well defined and convex, and a weaker pygidial border (rather than stronger and convex). '*P*. *ludlowensis*' is similar to *Warburgella* but it differs in possessing a transverse or a gently rounded preglabellar furrow, a less convex and more elongate glabella, an absence of a tropidium and tropidal ridges, a shorter eye that is distant from the lateral border furrow, and typically fewer thoracic segments. The differences between '*P*. *ludlowensis*' and *Warburgella* species is regarded here to be of subgeneric importance.

Only one specimen belonging to this species has been collected, as part of the present study.

Stratigraphical range. Ludlow (Gorstian; *incipiens* Biozone to Ludfordian; *leintwardinensis* Biozone).

Occurrence. This species is known from several localities in the Upper Bringewood Formation, and the Lower and Upper Leintwardine formations of the Welsh Borderland and Wales (see Owens 1973, p. 72). In addition it occurs in the Bailey Hill Formation (Ludfordian), higher part of Cwm Jenkin *c*. 5 km west-northwest of Knighton, Powys, Wales.

3.4.13 Family AULACOPLEURIDAE Angelin, 1854

Genus CYPHASPIS Burmeister, 1843

Type species. By subsequent designation of Whidborne 1889; *Phacops ceratophthalmus* Goldfuss, 1843 from the Middle Devonian (Eifelian), of Gees, near Gerolstein, Germany.

Diagnosis. See Adrain and Chatterton (1996, p. 101) for a revised diagnosis.

Remarks. Thomas and Owens (1978) and Thomas (1978) noted that there are several species which differ from the type species in lacking a stalked eye and a deep pit at the base of the genal spine, have a tuberculate pygidium, possessing only 2-3 pygidial axial rings (rather than 4-5), and show a lower convexity. Thomas and Owens (1978) considered these differences to be of generic or subgeneric importance and assigned these species to *Cyphaspis sensu lato* (for example *C. elachopos* Thomas). Adrain and Chatterton (1996) suggested that the Devonian *C. ceratophthalma* (Goldfuss, 1843), from the Middle Devonian (Eifelian) of Germany, represents a derived form of this genus and those species assigned by Thomas and Owens (1978) and Thomas (1978) to *Cyphaspis* s.l. really belong to *Cyphaspis* s.s. For a complete list of *Cyphaspis* species see Adrain and Chatterton (1996, p. 100).

Cyphaspis differs from other aulacopleurids occurring in the British Ludlow mainly in that S1 is parallel to a sagittal line, the frontal lobe strongly overhangs the preglabellar field and anterior border, and the occipital ring does not narrow behind L1.

Cyphaspis elachopos Thomas, 1978

Plate 25, figure 1

*v**1978 *Cyphaspis* (s.l.) *elachopos* Thomas, p. 30, pl. 7, figs 5, 8-13 [with synonymy].

. 1984 *Cyphaspis* (s.l.) *elachopos* Thomas; Thomas *et al.*, pp. 53, 56.

. 1988 *Cyphaspis* (s.l.) *elachopos* Thomas, 1978; Morris, p. 66.

. 1996 *Cyphaspis elachopos* Thomas, 1978; Adrain and Chatterton, p. 100.

Type material. Holotype by original designation; BM It14158, from the Coalbrookdale Formation (Wenlock Series), near Dudley, West Midlands, England.

Diagnosis and description. This species was diagnosed and described in full by Thomas (1978, p. 30).

Remarks. This species can be distinguished from all other British Ludlow Aulacopleuridae mainly in the occipital lobe not narrowing behind L1, a shorter L1, small eyes positioned distant from lateral border furrow, and the preglabellar field is shorter (sag.) than anterior border.

Stratigraphical range. Wenlock (Sheinwoodian; *riccartonensis* Biozone) to Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. This species is known from the Coalbrookdale and Much Wenlock Limestone formations, and rarely in the early Ludlow of Dudley, Malvern, and Walsall.

Cyphaspis sp.

Plate 25, figures 2-4, ?5, 6

Material. Cranidium BGS DEW 3036 is from the Elton Group, from a stream section, 1.69 km west of the church, Coed-y-paen (ST 32299978), Gwent, Wales; 2 cranidia (BU 4817-18) from the Upper Elton Formation at locality 51, a cranidium and partial thorax (BU 4819) from the Lower Leintwardine Formation at locality 19, and a poorly preserved complete specimen (BGS DEX 8256) from the Elton Group in a stream 690 m from the Downs, Much Wenlock, Shropshire, most likely belongings to this species.

Remarks. Specimens belonging to this species are laterally compressed making them elongate and transversely convex. The material is too poorly preserved to make comparisons with *Cyphaspis elachopos*.

Stratigraphic range. Ludlow (Gorstian; *scanicus* Biozone to Ludfordian; *leintwardinensis* Biozone).

Genus MAUROTARION Alberti, 1969

Type species. By original designation; *Harpidella maura* Alberti, 1967, from the Ludlow (Gorstian; *nilssoni* Biozone) of El Ghira, SE of Rabat, northwest Morocco.

Diagnosis. This genus was originally diagnosed by Alberti (1969) and modified by Adrain and Chatterton (1995, p. 318) and later by Curtis and Lane (1997, p. 31). The diagnosis provided here is modified from the latter. Glabella of low convexity; posterior end of occipital ring flat or gently curving downwards; L1 variable in size, but with little lateral extension from general outline of glabella; anterior border furrow follows a shallow inverted ‘V’; anterior border long with posterior two-thirds usually flattened, longest sagittally; palpebral lobe large; librigena with lateral borer typically inflated and broader than posterior border, its field usually narrow.

Other species. See Adrain and Chatterton (1995, p. 318). Species noted here are *M. aitholix* (Thomas, 1978) from the Coalbrookdale Formation (Homerian, *nassa* and *ludensis* biozones), Wenlock Edge, Shropshire, and possibly from the late Wenlock of Penylan Quarry, near Cardiff; and *M. lanei* sp. nov. from the Elton Group and Lower Leintwardine Formation of the Ludlow District and the Hafod Fawr Formation of Builth (Gorstian; *scanicus* Biozone to Ludfordian; *leintwardinensis* Biozone).

Remarks. Maurotarion is close to *Harpidella* but differs mainly in that the posterior end of the occipital ring is transverse or curves gently downwards (strongly curving in *Harpidella*), the occipital ring narrows to a lesser extent behind L1, longer preglabellar field, longer anterior border that is longer sagittally than exsagittally; anterior border furrow oriented like a shallow inverted ‘V’, larger eyes, generally narrower librigenal field, librigenal lateral border wider than posterior border, and a inflated base on the genal spine (see Adrain and Chatterton 1995, p. 318 for discussion). One of the more noticeable differences is the slight expansion of L1 laterally in *Maurotarion,* so that the axial furrows curve gently around L1. In *Harpidella* L1 expands strongly laterally causing the axial furrow to bulge outwards and curve strongly around L1. The more widespread genus

Otarion differs from *Maurotarion* in a more elongate glabella, a shorter preglabellar field, the posterior end of the occipital ring curves strongly downwards, has more thoracic segments and pygidial axial rings, and has tubercles on the pygidium.

Maurotarion lanei sp. nov.

Plate 25, figures 7-11

Derivation of name. After Dr Phil Lane for collecting much of the material used in this study, and for his support during my PhD.

Type material. Holotype, cranidium (BU 4820), from the Upper Elton Formation at locality 16. The paratypes are 5 cranidia; BU 4820-22 from the Upper Elton Formation at locality 16; BU 4823 from the Lower Leintwardine Formation at locality 19; and BU 4824 from the Hafod Fawr Formation (Cwar Glas Member) of locality 44. A complete specimen (BGS DEZ1638) from the Elton Group of Mortimer Forest.

Diagnosis. Genal spine long; occipital ring convex and long, slightly longer than anterior border (sag.); occipital furrow long; L1 around one-fifth width of glabellar; S2 indistinct; granules dense on cranidium, sparse on anterior border and arranged parallel to anterior border furrow. Pygidium with 4 axial rings, most anterior two rings with distinct furrows.

Description. Glabella convex, 0.80-0.86 times as wide as long. Occipital ring narrowing laterally, narrowest point behind L1, 1.6-1.7 times smaller than sagittal length. Axial furrows deeper than occipital furrow. L1 triangular in outline, bulging only slightly laterally, 31-36 per cent length (sag.) of glabella. S1 equal in depth and length to axial furrows. S1 oblique from top of L1, then half way towards base of L1 curves gently posteriorly, straightens towards base of L1 becoming parallel to an exsagittal line before curving strongly around base of L1. S2 indistinct, observed only in well preserved specimens, curves posteriorly from a position three-quarters towards preglabellar furrow and dies out at a position half way between S2 and S1. Preglabellar field 16-20 per cent of cranidial length. Anterior border convex, 10-14 per cent length of cranidium (sag.). Posterior branch of facial suture oblique, crosses posterior border near epiborder furrow. Doublure narrow, flattened, with a series of distinct terrace ridges. Genal spine 1.7 (n=1) times longer than length of librigena, gently curving posteriorly. Large granules cover cranidium with smaller less numerous ones in between these. Granules roughly equal in density on glabella and preglabellar field, but larger in size on glabellar. Anterior border with only a few granules. Large granules only on L1 in contact with each other. Occipital ring 0.17-0.22 times length of glabella. Very large centrally placed granule half length of occipital ring, around 2 times larger than other large granules.

Thoracic axis at its widest point 0.32 times (n=1) width (tr.) of thorax. Articulating furrows deep and narrow, becoming faint posteriorly. Pleural furrows deep and long, shallowing adaxially. Interpleural furrows narrower than pleural furrows, consistent in depth and length laterally.

Pygidium 2.8 times wider than long; axis 0.33 times pygidial width (tr). 4 axial rings, anterior most two with deep ring furrows, posterior rings with very faint furrows. Pleural ribs faint, ?4 pleural ribs. Most anterior interpleural furrows deep, posterior pleural furrows very faint or not discernable. Pleural furrows shallow, well defined on anterior most pleural rib only. Pleural furrows narrowing adaxially, dying out just before axis.

Remarks. This species is closest to *M. aitholix* with respect to the presence of densely packed granules on the glabella and preglabellar field, indistinct S2, long preglabellar field, anterior border slightly longer sagittally than exsagittally, pleural furrows faint not reaching axis. *M. lanei* sp. nov. differs from *M. aitholix* (Thomas, 1978), from the Coalbrookdale Formation of Wenlock Edge (Shropshire), in having an occipital ring that is longer than the anterior border, deeper occipital ring furrows, narrower L1, longer genal spines, granules on the anterior border, the granules are more dense on the glabella than on the preglabellar field, a narrower pygidial axis, more pygidial axial rings, and the axial rings are better defined posteriorly. *M. lanei* is also similar to *M. maurum* but differs mainly in having granules on the frontal lobe, preglabellar field, anterior border, and on the anterior end of the occipital ring; the large granule on the occipital ring is in the centre (rather than near the most posterior end); and the occipital ring is longer than the anterior border.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* Biozone to Ludfordian; *leintwardinensis* Biozone).

Occurrence. This species occurs in the Upper Elton and Lower Leintwardine formations of Ludlow (locality 16 and 19 respectively), and the Hafod Fawr Formation of Builth, Wales (locality 44).

Maurotarion cf. *lanei*

Plate 26, figures 1-2

Material. A cephalon and thorax (BGS GSM 36741) from undifferentiated early Ludlow rocks near Ludlow, Shropshire; and a partial cranidium (BGS GSM HN384) from the Bailey Hill Formation in a quarry 970 metres at 117 degrees southeast from the Winkles (Trig Point), Bishops Castle, Shropshire.

Remarks. This material differs from specimens assigned to *M. lanei* sp. nov. in possessing an elongate glabella that tapers forwards more strongly. No granules are evident in this material, most likely due to preservation. More specimens are required to better assess these differences.

Stratigraphical range. Ludlow (Gorstian; precise age unknown).

3.4.14 Family SCHARYIINAE Osmólska, 1957

Genus SCHARYIA Přibyl, 1946

Type species. By original designation; *Proetus micropygus* Hawle and Corda, 1847, p. 78 Ludlow-Přídolí Series, Prague, Czech Republic.

Scharyia siceripotrix Owens, 1974

*v**1974 *Scharyia siceripotrix* sp. nov., Owens, p. 689, pl. 98, figs 1-9.

. 1984 *Scharyia siceripotrix* Owens; Thomas *et al.*, p. 56.

. 1988 *Scharyia siceripotrix* Owens, 1974; Morris, p. 206.

Type material. Holotype by original designation; NMW 71.6G.488, Lower Elton Formation (Gorstian; *nilssoni* Biozone), near Oldcastle Farm (locality 35), Colwall Green, Hereford and Worcester, England.

Other material. For a complete list of specimens belonging to this species see Owens (1974, p. 689).

Diagnosis and description. See Owens (1974, p. 689).

Remarks. No new material has been found belonging to this species since its original designation. *S. siceripotrix* can be readily distinguished from all other British Ludlow Proetida by the rather long eye and preglabellar field, subtriangular glabella, prominent occipital ring, relatively large pygidium with the distinctive border, and short pygidial axis.

Stratigraphical range. Ludlow (Gorstian; *nilssoni* Biozone).

Occurrence. Other than the type locality this species occurs in the Lower Elton Formation from a road cutting 680 m from Ledbury Station (SO 71553857), Herefordshire and from the Lower Elton Formation of Millichope, near Wenlock Edge, Shropshire.

Order ASAPHIDA Salter, 1864

3.4.16 Family RAPHIOPHORIDAE Angelin, 1854

Genus RAPHIOPHORUS Angelin, 1854

Type species. By subsequent designation of Raymond 1925, p. 30; *Raphiophorus setirostris* Angelin, 1854, p. 81; *Tretaspis* Shale (Ashgill Series), Draggå bro, Dalarna, Sweden.

Diagnosis. See Thomas (1978, p. 53)

Other species. See Thomas (1978, p. 53) and Edgecombe and Sherwin (2001, p. 90) for a list of species. The species discussed here are *R. aloniensis* (Marr and Nicholson, 1888), Upper Skelgill Beds (Aeronian, *convolutus* Biozone) of the Lake District, England; *R. niagarensis* (Van Ingen, 1901), St Clair Limestone (Wenlock) of America**;** *R. jikaensis* (Chapman, 1912), Melbourne Formation (Gorstian, *nilssoni* Biozone), Australia; *R. parvulus* (Forbes, 1848), see occurrence below; *R. roualti* (Barrande, 1852), from the Wenlock-Ludlow of Poland and Wenlock of Bohemia; *R. sandfordi* Edgecombe and Sherwin, 2001, Cotton Formation (Telychian, *turriculatus* Biozone), New South Wales, Australia.

Raphiophorus parvulus (Forbes, 1848)

Plate 4, figures 26-27; Plate 26, figures 3-15

*v**1848 *Ampyx parvulus* Forbes [description] *in* Phillips and Salter, p. 350, pl. 10, figs

1-3.

. 1849 *Ampyx parvulus*; Forbes *in* Salter, p. 4 for pl. 10 [note].

v. 1915 *Ampyx roualti* BARR.; Hede, p. 40, pl. 4, figs 1-2.

. 1969 *Raphiophorus roualti* (BARRANDE 1852); Alberti, p. 463, pl. 42, fig 7.

1975 *Raphiophorus roualti*; Laufeld et al. p. 220.

v. 1978 *Raphiophorus parvulus* (Forbes); Thomas, p. 54, pl. 14, figs 1-4, 6-8, 10-11, 13-15 [with synonymy].

. 1979 *Raphiophorus parvulus* (Forbes); Thomas, p. 450, pl. 1, fig. 21.

. 1984 *Raphiophorus parvulus* (Forbes); Thomas *et al.*, pp. 52, 56.

. 1988 *Raphiophorus parvulus* (Forbes, 1848); Morris, p. 198 [with synonymy].

Type material. Lectotype selected by Thomas (1978, p. 54); BGS GSM 36751-36752 original of Forbes 1848, pl. 10, figs 2, 2a, Ludlow Series (?Gorstian), High Vinnals, southwest of Ludlow, Hereford and Worcester, England.

Other material. In addition to Thomas (1978, p. 55) 2 almost complete specimens, 13 cephala, 1 thorax and part cephalon, 1 thorax and pygidium, housed at BU. This species was collected from localities 1, 4-6, 8, 16-17. A cranidium (LO 2822t) and a pygidium (LO 2823t) from the Colonus Shale (Homerian; *ludensis* Biozone), Smedstorp, Sweden (locality a of Hede, 1915). Numerous specimens belonging to this species can be found in BGS, BU, NMW, SM, TCD.

Diagnosis. After Thomas (1978, p. 55): genal spine without grooves, at least four times as long as thorax and pygidium combined; lateral pit present; posterior border furrow confined to abaxial half of fixed cheek, with shallow posterior fossa near its abaxial end; single basal muscle impression; cephalic anterior spine at least 3.75 times as long as rest of cranidium. Pygidium with 2-3 axial rings, 1-2 pairs of interpleural furrows.

Description. In addition to the features noted by Thomas (1978, p. 55), two muscle impressions at posterior ends of glabella, near axial furrows. Muscle impressions elliptical, around 0.33 times length of genal field. Axial furrows, interrupted by muscle impression, deeper and wider at posterior end. Cranidium around 1.18-1.45 times as long as thorax and pygidium combined. Glabella 2 times longer than genae so that it overhangs greatly. Cheek convex, steepening forwards, the highest point close to axial furrow.

Remarks. R. aloniensis (Marr and Nicholson, 1888) is the only other species of *Raphiophorus* known from the Silurian of Britain. Thomas (1978) noted that *R. aloniensis* differs from *R. parvulus* in the wider posterior end of the glabella, separate S1 and S2, genal spine directed back in a straight line (rather than gently curved), and the first and second thoracic pleural ribs are macropleural.

R. jikaensis (Chapman, 1912) is the closest species to *R. parvulus* with regards to the relatively narrow and convex genae, the length of the cranidium, and the narrow posterior end of the glabellar. Chapman (1912) noted *R. jikaensis* as differing from *R. parvulus* in possessing a wider pygidium and narrower axis, and these taxa were regarded by him as separate subspecies. Sandford (2000) described additional differences including a narrower thoracic axis and a fainter occipital furrow in *R. jikaensis*. Both *R. parvulus* and *R.*

jikaensis have faint occipital furrows, and the width of the thoracic axial rings relative to the thorax overlap (24-28 per cent in *R. parvulus* and 24-26 per cent in *R. jikaensis*), and cannot be used to differentiate them. The length of the muscle impression relative to the genal length (0.33 in *R. parvulus* and 0.50 in *R. jikaensis*), the shorter pygidial axis in *R. jikaensis* (12 per cent of pygidial width compared to 17-19 per cent in *R. parvulus*), and the more strongly curved genal spines in *R. jikaensis* best distinguish this species from *R. parvulus. R. roualti* (Barrande, 1852) is also very similar to *R. parvulus*, differing only in the slightly larger and more forwardly convex genae, the glabella not overhanging the genae as much, and the interpleural furrows curve anteriorly only at the most proximal ends (Thomas 1978, p. 55). Another closely related species, *R. niagarensis* (Van Ingen, 1901) is known form two incomplete cephala only (see Holloway 1980), and is not sufficiently preserved to tell if this represents a distinct species. The length of the cranidium of *R. niagarensis* in relation to the genae is consistent with that of *R. parvulus* and they are possibly conspecific.

The small and convex genae, the long and more forwardly projecting glabella, discontinuous posterior border furrow adaxially, longer first thoracic segment, and abaxially curved pleural furrows distinguish species around *R. parvulus* with those close to *R. sandfordi* Edgecombe and Sherwin, 2001. These differences are probably of subgeneric importance.

Stratigraphical range. Wenlock (Sheinwoodian; *murchisoni* Biozone) to Ludlow (Gorstian; *scanicus* Biozone).

Occurrence. R. parvulus is known from the Coalbrookdale Formation (Wenlock) of

Wenlock Edge, Ludlow, Abberley Hills; the Wenlock (Sheinwoodian; *murchisoni* to *riccartonensis* Biozones) of the Long Mountain area; the Lower Mottled Mudstones (Homerian; *nassa* Biozone), Nantglyn Flags Formation, of north Wales; the Lower, Middle, and Upper Elton formations of the Ludlow district, the Lower Elton Formation of Abberley Hills, and the Middle Elton Formation near Perton (locality 30). This species occurs at the base of the Colonus Shale (Homerian; *ludensis* Biozone), at Smedstorp (locality a of Hede 1915) and Östra Odarslöv, southern Sweden; the Wenlock of Germany; and the early Ludlow of northwest Morocco.

3.5 TRILOBITE ASSOCIATIONS OF ENGLAND AND WALES

3.5.1 *Introduction*

In palaeontology the terms ‘community’, ‘association’, and ‘assemblage’ are often used, and sometimes interchangeably, when describing a particular phylum or organisms which occupy a similar mode of life within a particular lithofacies. In the strictest sense communities should refer to all taxonomic groups coexisting in a particular environment (Kauffman and Scott 1976), and should consider microscopic and megascopic organisms and trophic structure (see Frest *et al.* 1999 for a full discussion). Due to the effects of preservation and lack of taphonomic studies this is not practical in palaeontological studies, however, and the term community should be used with caution. Although this term has been used by many authors they are actually describing a guild, “a group of species that exploit the same class of environmental resources in a similar way” (Simberloff and Dayan 1991, p. 115). The majority of papers seen by the preset author, where faunas and their palaeoenvironment are described, the term guild is more appropriate (for examples see papers in Boucot and Lawson 1999). For consistency the present author follows Kauffman and Scott (1976), and later authors (Frest *et al.* 1999, Turvey and Zhou 2004, Budil *et al*. 2007, Mergl *et al.* 2008, Storey and Thomas 2008) where the term 'association' (assemblage of some authors) is used to describe a subsection of a community which may consider mode of life, geographic extent, and a particular trophic level or fossil group. The term 'assemblage' generally refers to taxa which tend to be found together, without drawing any conclusions about the life-assemblages from which they might have been derived, or their implied environmental significance (Lawson 1975).

Trilobite associations are described here and are used to denote co-occurring taxa related to a particular lithofacies. A complete revision of all fossil associations in the British Ludlow is beyond the scope of this study. It is anticipated that the trilobite associations described here can be combined with others towards a more complete understanding of palaeoecosystems in the British Ludlow. In its widest sense the term 'palaeocommunity' can then be defined based on commonly co-occurring associations related to a particular palaeoenvironment.

Time-averaging is another problem when attempting to reconstruct fossil ecosystems where a particular horizon may contain faunas of different ages, commonly representing over thousands or tens of thousands of years (Kidwell 1998). The terms palaeocommunity and associations are used here to represent longer ranging co-occurring taxa that occupy a particular environment.

Many benthic associations have been documented from the various platform and basinal facies occurring in the Silurian (see Boucot and Lawson 1999 for examples), but few contain a detailed description of the entire fauna. The composition of trilobite faunas have been shown by several authors (for example Thomas and Lane 1999) to be of environmental significance. Although trilobites are referred to in many of the Silurian brachiopod associations described, the majority of these list the most common trilobite species only while details on the remainder of the trilobite fauna are lacking. Since a particular trilobite association can co-occur with different brachiopod associations it is practical to describe the trilobite associations separately.

In the British Ludlow brachiopods frequently dominate shelf sequences in England and Wales. Several brachiopod associations were recognised by Watkins (1979) and were subsequently revised by later authors (see Lawson 1999*a*, *b*). Mikulic and Watkins (1981), Thomas *et al.* (1984), and Thomas and Lane (1999) are the only detailed accounts of the distribution and description of trilobite faunas in the British Silurian. Based on collections amassed, a comprehensive museum survey, and the systematic work of the present study, a more complete account of trilobites occurring in the Ludlow platform facies of England and Wales is presented herein. Several of the trilobite associations described here broadly fit into those described by Thomas and Lane (1999). There are, however, several new trilobite associations described here that differ from those of previous authors.

Although complete specimens do occur, trilobites from the British Ludlow are commonly disarticulated making relative abundance counts difficult. Mikulic and Watkins (1981) based their counts on pygidia which is frequently the most abundant fragment of each taxon. However, there are several taxa such as *Raphiophorus*, *Ananaspis*?, *Exallaspis*, and *Alcymene* where the cephala are much more common than pygidia and they are thus underrepresented in Mikulic and Watkins (1981). In order to provide more accurate counts, the method adopted here follows that in Chapter Two, where the most numerous of cranidia plus cephala, pygidia plus thoracopygidia, left librigena, and right librigena, plus the number of complete specimens are used to provide relative abundance counts. Due to ecdysis many of the trilobite specimens will be moults, and this may lead to over-estimation of relative abundance. Given that there is at least some size-sorting in the samples, the number of moult stages represented is probably quite small as most of the juveniles will have been removed. Mikulic and Watkins (1981) suggested that up to six holaspid moult stages of *Dalmanites* pygidia and five holaspid moult stages of *Proetus* occur in the Middle Elton Group. Owing to the similar number of moult stages seen in trilobite taxa, and the relatively consistent sizes across the Ludlow shelf (Mikulic and Watkins 1981), comparing relative abundances between and within the trilobite faunas should not be biased significantly by moulting.

Trilobite associations are typically based on their most abundant taxa, although this is not always possible as in the *Barriepiscator-Miraspis* Association (Chapter Two) where the nominate genera do not always dominate. The trilobite associations in the Middle Elton Formation, the Hafod Fawr Formation, and the Leintwardine Group are defined quantitatively. The trilobite associations named herein are based on taxa that commonly co-occur in a formation at the same localities, or at the same stratigraphic position in localities that are closely situated. In most cases trilobites occurring in a particular formation or member are seen throughout the sequence. Presence/absence is used here to describe the remainder of the faunas where the sample size is too low to provide relative abundances or where the trilobites are numerically small (for example the Whitcliffe Group).

3.5.2 *Trilobite assemblages in the Ludlow Series: Gorstian Stage*

Hafod Fawr Formation

The Cwar Glas Member (Gorstian, around *scanicus* to *incipiens* biozones) of the Hafod

Fawr Formation (=Grammysia Beds of Squirrell and White 1978) comprises bedded siltstones and fine to medium grained sandstones. Fossils are common in the bands of brown rottenstone and sandstone at localities 43-45. Here the fauna belongs to the trilobite *Homalonotus knightii-Acaste* cf. *subcaudata* Association of Thomas and Lane (1999), where the nominate taxa dominate. Thomas and Lane (1999, p. 454) stated that *H. knightii* comprises around 80 per cent of the fauna. In the present study, based on 64 specimens *Acaste* cf. *subcaudata* comprises around 64.8 per cent of the fauna, with *H. knightii* representing around 32.4 per cent (Table 3.3). *Maurotarion lanei* sp. nov. occurs also, but this is rare.

Taxon	complete	cephala/ cranidia	librigenae	hypostomes	thoracic segments	pygidia
Acaste cf. *subcaudata*	-	22	-	-	1	24
Homalonotus knightii	-	3	-	-	1	12
Maurotarion lanei	-	1	-	-	-	-

Table 3.3. Counts of trilobite taxa from the Hafod Fawr Formation, Cwar Glas Member. The counts are based on 64 specimens representing a minimum of 37 individuals.

This difference may be due to sample sizes or local variations in relative abundances. Squirrel and White (1978, p. 12) also recorded several brachiopods including *Salopina*, *Protochonetes ludloviensis*, and *Microsphaeridiorhynchus nucula* (=‘*C*’. *nucula* in Squirell and White 1978), and the bivalve *Grammysia*. This fauna is the equivalent of the Bivalve-*Microsphaeridiorhynchus nucula* Association named by Lawson (1999). The *Homalonotus knightii-Acaste* Association is thought to represent a BA1 unit (Thomas and Lane 1999), where the bulk of the fauna (70 per cent or more) comprises the nominate taxa. Thomas and Lane (1999, p. 455) commented upon the similarities between the *H. knightii-Acaste* and the older *Acaste subcaudata-Trimerus* Association.

A similar but less restricted shelly fauna occurs throughout the ‘normal facies’ (Gorstian, *nilssoni- scanicus* biozones) of the Hafod Fawr Formation (=Coed Wenallt Beds of Squirrel and White 1978) in association with interbedded sandstones, siltstones and silty mudstones. Towards the top of this unit (*scanicus* Biozone), just below the Cwar Glas Member, *Homalonotus knightii*, *Alcymene* (sl.) aff. *lawsoni*, *Dalmanites tuberculatocaudatus*, and *Diacalymene*? sp., occur with the brachiopods *Protochonetes ludloviensis* and *Microsphaeridiorhynchus nucula.*

Elton Group

The trilobite fauna of the Lower Elton Formation (*nilssoni* Biozone) is a diverse but low abundance assemblage comprising 14 genera. The low sample sizes from this formation, as part of the present study, makes relative abundances unreliable. Work by Lawson (1975, 1999*a*) showed that the most common element of the trilobite fauna is ‘*Dalmanites myops*’, with ‘*Leonaspis* sp.’, a ‘calymenid’, and a ‘proetid’ occurring also (Lawson 1999*a*, p. 368). Based on collections of the present study, *Dalmanites* spp., *Calymene oliveae* and *Proetus* cf. *concinnus* seem to be the most common. *Raphiophorus parvulus*, *Exallaspis coronata*, *Richterarges bucklandii*, *Scharyia siceripotrix, Balizoma variolaris, Cyphaspis elachopos, Acaste inflata*, *Acastocephala*? sp., *Warburgella* (*W.*) aff. *baltica*, *Plesiowensus obconicus*, a cheirurid sp., and a sculletuid sp. are rare, the last four being represented by single specimens only. Small brachiopods are the most abundant fossils, in particular *Glassia obovata.*

Fossils in the Middle Elton Formation (*nilssoni-scanicus* biozones) are common and include graptolites, numerous small brachiopods, trilobites, bivalves, and rare orthocone cephalopods and crinoids. The shelly fauna, in particular trilobites, are more numerous in the olive-grey mudstones at the base of the formation, but towards the top the fauna becomes patchy and there it consists mainly of small brachiopods (White and Lawson 1978). The trilobite fauna in the Middle Elton Formation is more abundant but less diverse compared with that in the Lower Elton Formation. A total of 6 trilobite genera and 10 species have been found, as part of the present study, from the Middle Elton Formation.

Taxon	complete	cephala/ cranidia	librigenae R/L	hypostomes	thoracic segments	pygidia
Dalmanites spp.	1	50	2L, 2R	2	13	67
Raphiophorus parvulus	3	19	-	-	1	1
Exallaspis coronata	1	5	3L, 2R	-	-	3
Ananaspis? *nuda*	-	9	-	-	-	5
Calymene oliveae	1	-	-	-	-	1
Aulacopleuridae indet.	-	1	1R	-	1	-

Table 3.4. Counts of trilobite taxa from the base of the Middle Elton Formation of the Ludlow District. For librigena right (R) and left (L) are listed separately. The counts are based on 194 specimens representing a minimum of 112 individuals.

Dalmanites is the most abundant and based on counts (Table 3.4) in this study from the base of the formation, it represents around 60.7 per cent of the trilobite fauna, and in some sections it was noted by Mikulic and Watkins (1981, p. 112) to represent 17 per cent of the total benthos. *Dalmanites nexilis* comprises most of the dalmanitid material but *D. obtusus, D. tuberculatocaudatus,* and *D.* aff. *nexilis* occur as rarities. *Raphiophorus parvulus* is the second most abundant taxon, representing around 19.6 per cent of the fauna. Other common trilobites occurring in this association with the more common *Dalmanites* and

Raphiophorus are *Ananaspis*? *nuda* (8.0 per cent) and *Exallaspis coronata* (9.8 per cent). *Calymene oliveae*, and an aulacopleurid are rare, being represented by 2 specimens in the case of the former two and a single specimen in the latter. *Alcymene* (s.l.) aff. *lawsoni* occurs in the Middle Elton Formation also (Siveter 1983), but it was not found as part of the present study. Most of the trilobite species in the Middle Elton Formation show a patchy distribution with the exception of *D. nexilis*, which was found at almost all of the localities sampled from this unit, and this is presumably related to its high abundance.

Trilobites show a similar abundance in the olive-grey calcareous siltstones and mudstones of the Upper Elton Formation to the underlying Middle Elton Formation. As before, in the Middle Elton Formation, *Dalmanites nexilis* is the most abundant trilobite, and it occurs with *Exallaspis coronata, Raphiophorus parvulus* and *Maurotarion lanei* in the Ludlow District. At Usk *D. nexilis* occurs with *Acastocephala*? sp., *Calymene oliveae, Cyphaspis* sp., *Dalmanites obtusus,* and *Exallaspis coronata*, and in areas around Ledbury and Malvern it occurs with *Homalonotus* cf. *knightii*, *Plesiowensus obconicus*, and *Proetus* cf. *concinnus*. The geographical and stratigraphic distribution of trilobites in the Elton Group are summarised in Table 3.5.

Lower Elton Formation	Middle Elton Formation	Upper Elton Formation
Ludlow District (Mid-Shelf)		
Acastocephala? sp. *Balizoma variolaris* *Calymene* sp. *Dalmanites nexilis* *Plesiowensus obconicus* *Proetus* cf. *concinnus* *Raphiophorus parvulus* *Richterarges bucklandii* *Warburgella* (*W.*) *baltica* Cheirurinae indet.	*Ananaspis*? *nuda* *Calymene oliveae* *Dalmanites nexilis* *D.* aff. *nexilis* *D. tuberculatocaudatus* *Exallaspis coronata* *Raphiophorus parvulus* Aulacopleuridae indet.	*Dalmanites nexilis* *D.* aff. *nexilis* *Exallaspis coronata* *Maurotarion lanei* *Raphiophorus parvulus*
Wenlock Edge and Upper Millichope (Mid-Shelf)		
Acaste inflata *Exallaspis coronata* *Proetus concinnus* *Scharyia siceripotrix*	*Ananaspis*? *nuda* *Alcymene* (s.l.) aff. *lawsoni* *Dalmanites nexilis* *Exallaspis coronata* *Raphiophorus parvulus*	*Exallaspis coronata* *Proetus* (s.l.) *astringens*
Woolhope and Perton (Mid-Shelf)		
Alcymene (s.l.) aff. *lawsoni* *Dalmanites nexilis* *Proetus* cf. *concinnus* Acastidae indet. Scutelluidae indet.	*Ananaspis*? *nuda* *Dalmanites nexilis* *D.* aff. *nexilis* *D. obtusus* *Exallaspis coronata* *Raphiophorus parvulus* *Proetus* (s.l.) *astringens*	*Calymene* sp. *Dalmanites nexilis*
Ledbury/Malvern (Inner Shelf)		
Dalmanites aff. *nexilis* *D. obtusus* *D. tuberculatocaudatus* *Scharyia siceripotrix*	Possible occurrence of *Ananaspis*? *nuda*	*Dalmanites nexilis* *Homalonotus* cf. *knightii* *Plesiowensus obconicus* *Proetus* cf. *concinnus*
Usk (Inner Shelf)		
Dalmanites sp.	*Dalmanites* sp.	*Acastocephala*? sp. *Calymene oliveae* *Cyphaspis* sp. *Dalmanites nexilis* *D.* aff. *nexilis* *D. obtusus* *Exallaspis coronata*

Table 3.5. A summary of the geographical and stratigraphical distribution of trilobites in the Elton Group.

The trilobite fauna in the Middle Elton Formation co-occur with the *Glassia obovata*

Association of Watkins (1979, also see Lawson 1999*b*, p. 388) and with his ‘transition fauna’ in the Upper Elton Formation. (Mikulic and Watkins 1981, p. 112). The fauna in the Middle Elton Formation is thought to represent a depth of around BA5 (Lawson 1999*a*, *b*). The Lower, Middle, and Upper Elton formations, of the Ludlow District, contain a trilobite fauna that is dominated by *Dalmanites nexilis*, occurring with *Raphiophorus parvulus*, and *Exallaspis coronata*, and often *Calymene* and an aulacopleurid. Geographic variations in the fauna may reflect subtle variations in palaeoenvironment. It is most likely that these geographic differences are a result of variations in sampling, however.

The trilobite fauna in the Middle Elton Formation bears a strong resemblance to the *Dalmanites caudatus*-*Raphiophorus parvulus* Association of Thomas and Lane (1999), but differs in that the most abundant species is *D. nexilis* (rather than *D. caudatus*), the occurrence of genera such as *Exallaspis* and *Ananaspis*?, and the absence of *Tapinocalymene* and *Decoroproetus*. Despite these differences *Dalmanites* is the most common trilobite constituent in association with *Raphiophorus parvulus*, a calymenid, numerous small brachiopods such as *Glassia*, slaviid bivalves (for example *Cardiola*), orthoconic cephalopods, graptolites, and the occurrence of these in offshore mudstones. The two associations described are, therefore, regarded here as belonging to the same association type. Since different *Dalmanites* species are the most abundant element of the fauna it seems appropriate to term this the *Dalmanites*-*Raphiophorus parvulus* Association. In the Coalbrookdale (Homerian) and Middle Elton formations the *Dalmanites*-*Raphiophorus parvulus* Association is represented by a low diversity high abundance fauna occurring in laminated mudstones, indicating a stressed environment with low oxygen levels.

The fauna of the Mottled Mudstones (Nantglyn Flags Formation), Llanrwst District, of

North Wales contains a similar fauna to that of the Middle Elton Formation which includes the occurrence of *Dalmanites, Raphiophorus, Ananaspis*?, and *Glassia* (Chapter Two). *Dalmanites* is not the most abundant trilobite in the Mottled Mudstones, however, and the fauna includes *Struveria, Barriepiscator,* and *Miraspis* indicative of the *Barriepsicator-Miraspis* Association. As discussed in Chapter Two, the Mottled Mudstones probably reflects the shallowest extent of the *Barriepiscator-Miraspis* Association. The similarity between the fauna of the Middle Elton Formation and the Mottled Mudstones most likely shows the *Barriepiscator-Miraspis* Association grading into the shallower *Dalmanites-Raphiophorus* Association.

The occurrence of trilobite taxa typical of shallower-water (such as *Balizoma variolaris, Plesiowensus obconicus, Richterarges bucklandii*, *Proetus* cf. *concinnus* and *Homalonotus* cf. *knightii*) and the lack of orthocone cephalopods and abundant graptolites in the Lower and Upper Elton formations suggest that they were deposited at shallower depths than the Middle Elton Formation. The abundance of *Dalmanites* and the associated *Raphiophorus parvulus*, in the Lower Elton Formation and Upper Elton Formation, suggest that their faunas belong to the *Dalmanites-Raphiophorus parvulus* Association. It is entirely possible that the occurrence of taxa such as *Homalonotus* cf. *knightii*, which is represented by one specimen, may have been washed in from farther up the palaeoslope, however. Watkins (1979) described the brachiopod fauna in the Upper Elton Formation, and regarded it as transitional between that of the Middle Elton Formation and Lower Bringewood Formation. It would appear, therefore, that the trilobite fauna in the Upper Elton Formation (and probably the Lower Elton Formation) represents the shallowest extent of the *Dalmanites-Raphiophorus parvulus* Association.

Bringewood Group

In the Bringewood Group (Gorstian; *incipeins* Biozone) trilobites occur in the bioturbated siltstone and calcitic siltstone facies of the Lower and Upper Bringewood formations. The amount of material collected from the Bringewood Group, as part of the present study, is too small to measure relative abundances.

Lower Bringewood Formation	Upper Bringewood Formation
Leintwardine (Outer Shelf)	
Dalmanites sp.	
Ludlow District (Mid-Shelf)	
Balizoma obtusus rosensteinae *Dalmanites nexilis* *D. obtusus* *Encrinurus stubblefieldi* *Exallaspis coronata* *Maurotarion* sp. *Richterarges bucklandii* *Plesiowensus obconicus* *Proetus* (s.l.) *astringens*	*Balizoma obtusus rosensteinae* *Dalmanites nexilis* *D. obtusus* *Encrinurus stubblefieldi* *Plesiowensus obconicus* *P.* aff. *obconicus*
Wenlock Edge and Upper Millichope (Mid Shelf)	
Balizoma obtusus rosensteinae *Exallaspis coronata* *Proetus* (s.l.) *astringens*	*Balizoma obtusus rosensteinae* *Exallaspis coronata* *Plesiowensus obconicus*
Woodbury (Mid Shelf)	
Alcymene sp. *Balizoma obtusus rosensteinae* *Dalmanites obtusus* *Maurotarion* sp. *Proetus* (s.l.) *astringens*	*Dalmanites obtusus*
Woolhope (Mid-Shelf)	
	Alcymene lawsoni
Ledbury/Malvern (Inner Shelf)	
Balizoma sp. *Dalmanites obtusus*	*Balizoma obtusus rosensteinae*
Usk (Inner Shelf)	
Balizoma obtusus rosensteinae *Dalmanites obtusus* *Plesiowensus obconicus*	

Table 3.6. A summary of the geographical and stratigraphical distribution of trilobites in the Bringewood Group.

The mid shelf of the Lower Bringewood Formation includes the trilobite species *Proetus* (s.l.) *astringens, Balizoma obtusus rosensteinae, Exallaspis coronata, Alcymene lawsoni, Dalmanites nexilis*, *Dalmanites obtusus,* and *Plesiowensus obconicus* (Table 3.6). Based on the counts in Mikulic and Watkins (1981, p. 108) *Dalmanites* and *Proetus* (s.l.) are the most abundant trilobites, representing up to 6 per cent of the total benthic fauna. *Alcymene* sp. and *Balizoma* are common elements of the trilobite fauna too, comprising up to 4 and 3 per cent of the total benthic fauna respectively. *Dalmanites obtusus* is typically the most abundant *Dalmanites* species throughout the Bringewood Group, although at Vinnal Hill near Ludlow *D. nexilis* can be found in profusion. The trilobite assemblage described here bears resemblance to the *Plesiowensus obconicus-Encrinurus-Alcymene* Association of the Leintwardine Group. *Plesiowensus* and *Encrinurus* are uncommon in the Lower Bringewood Group, however, and the relatively high abundance of *Dalmanites*, and the presence of *Exallaspis* is reminiscent of the *Dalmanites-Raphiophorus* Association. The trilobite fauna here most likely represents a distinct association based on the seemingly high relative abundance of *Dalmanites obtusus* and *Proetus* (s.l.) *astringens*. More material is needed to describe this fauna fully and it is informally termed the ‘Bringewood transition fauna’ here. This trilobite fauna occurs with a diverse shelly fauna dominated by brachiopods of the *Mesophilidostrophia lepisma-Shagamella minor-Atrypa reticularis* Association (see Lawson 1999*b*, p. 380 for equivalent associations), where the nominate species comprise half of the total biota. Bryozoa and ostracods are common also and they comprise 6 per cent and 1.5 per cent of the fauna respectively (Lawson 1999*b*). The *Mesophilidostrophia lepisma-Shagamella minor-Atrypa reticularis* Association, of the in the Welsh Borderland main and inner shelf regions, represents a depth of BA3-4 (Lawson

1999*b*). Higher in the Lower Bringewood Formation, such as the inner shelf at Usk, yields a similar trilobite fauna comprising *Dalmanites obtusus*, *Balizoma obtusus rosensteinae*, and *Plesiowensus obconicus*. Here the trilobite fauna is associated with brachiopods of the *Atrypa reticularis*-*Sphaerirhyncia wilsoni*-*Shagamella minor* Association and it represents a depth of BA3 (Lawson 1999*b*).

The trilobite fauna recorded from Upper Bringewood Formation comprises *Dalmanites nexilis*, *Balizoma obtusus rosensteinae*, *Plesiowensus* aff. *obconicus*, *Warburgella* (*Owensella*) *ludlowensis*, *Alcymene lawsoni*, and *Exallaspis coronata*. *Proetus* (s.l.) *latifrons* and *Dalmanites obtusus* are not known from the Upper Bringewood Formation, and it would seem that their last occurrence is in the underlying formation. The Upper Bringewood Formation also marks the first known occurrence of *Warburgella* (*Tetinia*) *ludlowensis* which continues into the Ludfordian. It would appear, therefore, that the trilobite fauna of the Upper Bringewood Formation represents the grading from the fauna of the Lower Bringewood Formation to the *Plesiowensus obconicus*-*Encrinurus*-*Alcymene* Association of the Leintwardine Group. The differences between the fauna of the Upper and Lower Bringewood formations may be due to sampling, however, as there are several taxa that occur in the latter and the Leintwardine Group that do not occur in the former. As part of the present study, specimens from the Upper Bringewood Formation were collected from a single locality on the south side of Wigmore Road, near Ludlow (locality 13). The associated brachiopod fauna from this locality belongs to the *Atrypa reticularis*-Coral Association of Watkins (1979), which was subsequently renamed as the *Atrypa reticularis*-*Strophoprion euglypha* Association by Lawson (1999*a*, *b*), and it represents a depth of BA3. Brachiopods dominate the fauna, with corals being the second most abundant group. Bryozoa, crinoid ossicles, and the gastropod *Poleumita* sp. are common. For convenience the trilobite fauna in the Upper Bringewood Formation will be referred to as the 'upper phase of the Bringewood transition fauna', whereas that in the Lower Bringewood Formation will be referred to as the 'lower phase'.

3.5.3 *Trilobite assemblages in the Ludlow Series: Ludfordian Stage*

Leintwardine Group

Trilobites typically represent around 1 per cent of the biota (Lawson 1999*a*) in the coquinoid siltstones of the Lower Leintwardine Formation (*leintwardinensis* Biozone). Bioturbation occurs throughout and in many of the sections primary bedding has been obliterated, although traces of lamination remain (Watkins 1979). Towards the top of the sequence trilobites are more common and the following species occur: *Plesiowensus obconicus*, *P. raymondi*, *Balizoma obtusus rosensteinae*, *Encrinurus stubblefieldi*, *Alcymene lawsoni*, *A. puellaris*, *Warburgella* (*Owensella*) *ludlowensis*¸ *Cyphaspis* sp., *Maurotarion lanei*, *Dalmanites nexilis*, and *Acastella spinosa*. Based on counts of the present study, *Plesiowensus, Encrinurus*, and *Alcymene* are the most abundant representing 41 per cent for the former, and 21 per cent for the last two, of the trilobite fauna (Table 3.7).

Taxon	complete	cranidia	librigena-R/L	hypostome	thoracic segments	pygidia
Plesiowensus	1	17	2L, 1R	-	-	13
Encrinurus	-	4	1L, 1R	-	2	9
Alcymene	1	8	-	-	-	1
Balizoma	-	1	-	-	-	4
Cyphaspis	1	-	-	-	-	-
Maurotarion	-	1	-	-	-	-
Warburgella (*Owensella*)	-	1	-	-	-	-

Table 3.7. Counts of trilobite taxa from the Lower Leintwardine Formation of the Ludlow

District. Left (L) and right (R) librigena are listed separately. The counts are based on 69 specimens representing a minimum of 43 individuals.

Plesiowensus obconicus is the most abundant trilobite species and it was noted by Owens (1973, p. 17) to reach its peak at the boundary between the Lower and Upper Leintwardine formations. The trilobite fauna described here is thus termed the *Plesiowensus obconicus-Encrinurus-Alcymene* Association. The younger *Calymene-Balizoma* Association of Chlupáč (1987), from the Pozary Formation (Přídolí) of Bohemia, contains a similar fauna dominated by brachiopods, and containing the trilobites *Balizoma, Calymene,* and *Otarion,* although it differs in containing trilobites such as *Prionopeltis* which are characteristic of that fauna. The *Plesiowensus obconicus-Encrinurus-Alcymene* Association occurs with brachiopods belonging to the *Shaleria ornatella* Association of Watkins (1979) where the nominate brachiopod dominates but *Atrypa, Leptaena, Salopina, Protochonetes,* and *Isorthis* occur also. Bivalves are the second most abundant group and represent 7 per cent of the biota (Watkins 1979). Rare groups include gastropods, bryozoans and cephalopods. The fauna represents a depth of BA3 (Lawson 1999*a*) and occurs in the middle and inner shelf areas of the Welsh Borderland. A similar fauna occurs in the Upper Leintwardine Formation of the Ludlow District but differs in the absence of *Maurotarion lanei, Cyphaspis* Sp., and *Plesiowensus raymondi*. Due to a lack of material a relative abundance of this fauna is not possible here but the fauna does not appear to differ significantly from the *Plesiowensus obconicus-Encrinurus-Alcymene* Association. The trilobite fauna of the Lower and Upper Leintwardine formations are therefore regarded here as conspecific.

The inner shelf at Usk appears to contain a different fauna compared with the mid shelf (Table 3.8). *Plesiowensus obconicus* and *Warburgella* (*O.*) *ludlowensis*, which are characteristic of mid shelf regions, are not known from Usk. Until the Lower Leintwardine Formation and Upper Leintwardine Formation have been adequately sampled, it is unclear if they reflect environmental differences between the inner Shelf at Usk and the mid shelf at Ludlow or a sampling artefact.

Lower Leintwardine Formation	Upper Leintwardine Formation
Leintwardine (Outer-Shelf)	
Alcymene lawsoni *Plesiowensus obconicus* *Warburgella* (*O.*) *ludlowensis*	*Plesiowensus obconicus* *Warburgella* (*O.*) *ludlowensis*
Ludlow District (Mid-Shelf)	
Alcymene lawsoni *A. puellaris* *Balizoma obtusus rosensteinae* *Cyphaspis* sp. *Dalmanites* sp. *Encrinurus stubblefieldi* *Plesiowensus obconicus* *P. raymondi* *Maurotarion lanei* *Warburgella* (*O.*) *ludlowensis*	*Alcymene puellaris* *Balizoma obtusus rosensteinae* *Encrinurus stubblefieldi* *Plesiowensus obconicus* *Warburgella* (*O.*) *ludlowensis*
Wenlock Edge (Mid-Shelf)	
Plesiowensus obconicus *Warburgella* (*O.*) *ludlowensis*	*Plesiowensus obconicus* *Warburgella* (*O.*) *ludlowensis*
Woolhope (Mid-Shelf)	
Alcymene puellaris	*Acastella spinosa*
Ledbury/Malvern (Inner Shelf)	
	Acastella spinosa *Plesiowensus obconicus*
Usk (Inner Shelf)	
Acastella spinosa *Acastocephala*? sp. *Alcymene puellaris* *Dalmanites* sp.	*Acastella spinosa* *Acastocephala*? sp. *Alcymene puellaris* *Dalmanites nexilis* *Exallaspis coronata*

Table 3.8. A summary of the geographical and stratigraphical distribution of trilobites in the Leintwardine Group.

Although trilobites occur commonly, between the upper part of the Lower Leintwardine Formation and lower part of the Upper Leintwardine Formation the fauna shows a drop in abundance across most groups with declines recorded in the brachiopods (although they remain the dominant group), gastropods, bryozoans and trilobites. Bivalves increase in abundance, however, to represent 5 per cent of the biota (Watkins, 1979). Although brachiopods generally represent the major component of the faunas in the Bringewood and Leintwardine groups their dominance can alternate stratigraphically with the trilobite fauna.

Whitcliffe Group

The fauna of the coquinoid siltstone facies of the Whitcliffe Group (Ludfordian, *bohemicus* to *O. snajdri*-*O. crispa* biozones) is represented by a low diversity community where brachiopods (80 per cent) and bivalves (10 per cent) dominate, with bryozoa and ostracods occurring also. Trilobites are low in abundance, many being known from a single specimen, and occur only sparsely throughout the group. In no particular order, the trilobites known to occur in the Whitcliffe Group are *Homalonotus knightii, Trimerus* (?*Ramiotis*) *salteri*, *Alcymene lawsoni, Alcymene puellaris, Encrinurus stubblefieldi, Acastella spinosa*, and *Acastella macrocentra*. *Homalonotus knightii* and *Acastella spinosa* are the only trilobites known to occur in both the Lower and Upper Whitcliffe formations (Table 3.9). *Encrinurus stubblefieldi* and *Alcymene puellaris* have only been recorded from the Lower Whitcliffe Formation, while *Acastella macrocentra* has only been found in the Upper Whitcliffe Formation, while the stratigraphical position of *Trimerus* (?*Ramiotis*) *salteri* and *Alcymene lawsoni* in the Whitcliffe Group are unknown.

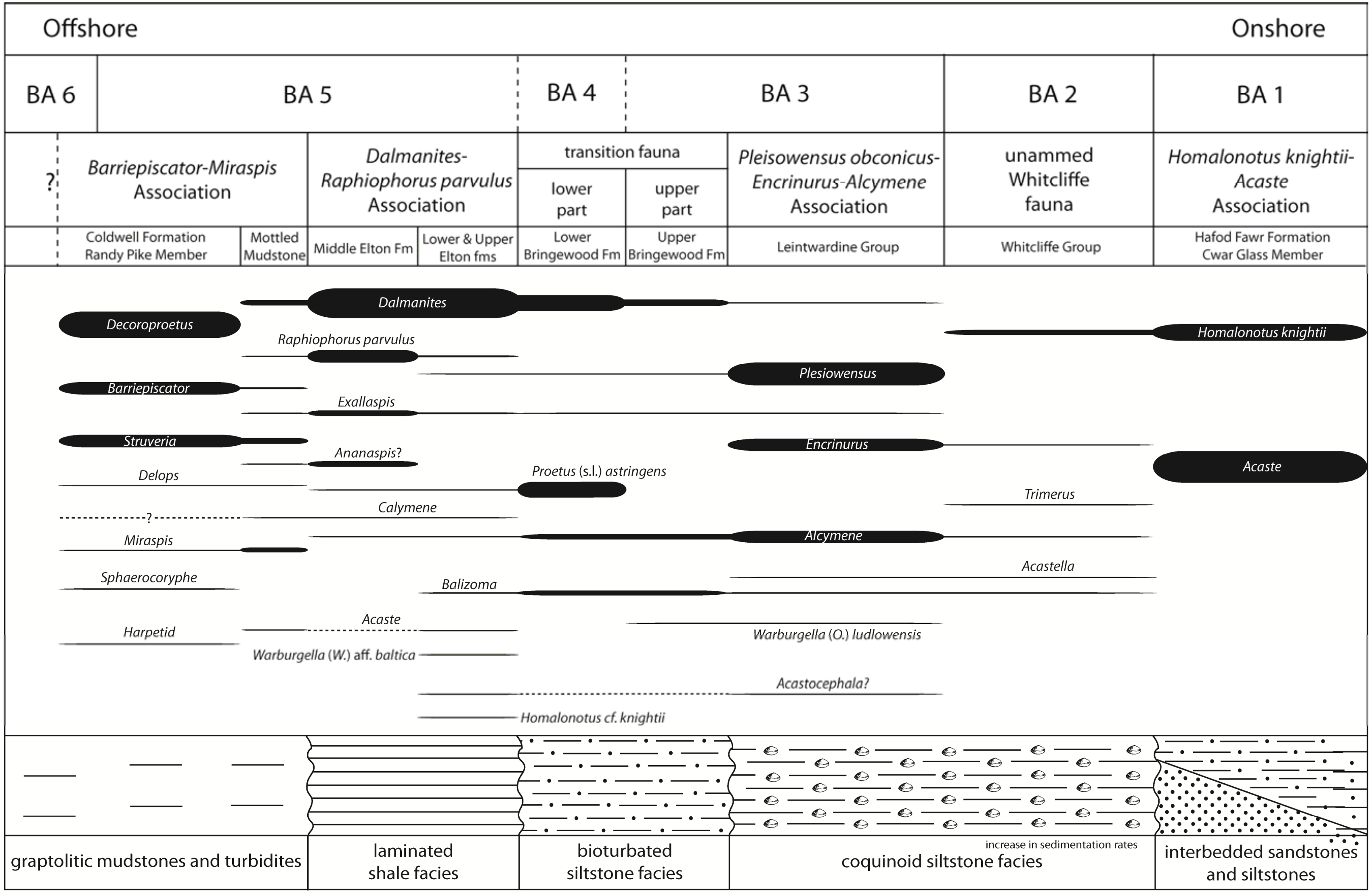
Lower Whitcliffe Formation	Upper Whitcliffe Formation	Whitcliffe Group (?formation)
Ludlow District (Mid-Shelf)		
Balizoma obtusus rosensteinae *Encrinurus stubblefieldi* *Homalonotus knightii*	*Acastella spinosa* *Homalonotus knightii*	*Alcymene lawsoni* *Trimerus* (?*R.*) *salteri*
Shucknall Inlier (Mid-Shelf)		
	Acastella macrocentra	
Ledbury/Malvern (Inner Shelf)		
Alcymene puellaris		

Table 3.9. A summary of the geographical and stratigraphical distribution of trilobites in the Whitcliffe Group.

Due to the lack of material available from the Whitcliffe Group, it is probable that the absence of trilobite species from a particular division of this group is due to sampling, however. Based on Mikulic and Watkins (1981) *H. knightii* is the most abundant trilobite comprising up to 4 per cent of the total benthic fauna. The *Protochonetes ludloviensis* Association of Watkins (1979), renamed as the *Salopina lunata- Protochonetes ludloviensis* Association by Lawson (1999*a*), is known from the Whitcliffe Group. The fauna is thought to represent a depth of BA2 (Lawson 1999*a*, p. 369).

A summary of the trilobite faunas and their depth relationships are illustrated below (Text-Figure 3.9).

Text-Figure 3.9. A summary of the trilobite faunas and their depth relationships described in Chapter Two and Three. Approximate relative abundances are indicated, based on counts of the present study and those of Mikulic and Watkins (1981).


Offshore
Onshore
BA 6
BA 5
BA 4
BA 3
BA 2
BA 1
?
Barriepiscator-Miraspis Association
Dalmanites-Raphiophorus parvulus Association
transition fauna
lower part
upper part
Pleisowensus obconicus-Encrinurus-Alcymene Association
unammed Whitcliffe fauna
Homalonotus knightii-Acaste Association
Coldwell Formation Randy Pike Member
Mottled Mudstone
Middle Elton Fm
Lower & Upper Elton fms
Lower Bringewood Fm
Upper Bringewood Fm
Leintwardine Group
Whitcliffe Group
Hafod Fawr Formation Cwar Glass Member
Dalmanites
Decoroproetus
Raphiophorus parvulus
Homalonotus knightii
Plesiowensus
Barriepiscator
Exallaspis
Struveria
Encrinurus
Ananaspis?
Acaste
Delops
Proetus (s.l.) astringens
Trimerus
Calymene
?
Alcymene
Miraspis
Acastella
Sphaerocoryphe
Balizoma
Acaste
Harpetid
Warburgella (O.) ludlowensis
Warburgella (W.) aff. baltica
Acastocephala?
Homalonotus cf. knightii
graptolitic mudstones and turbidites
laminated shale facies
bioturbated siltstone facies
increase in sedimentation rates
coquinoid siltstone facies
interbedded sandstones and siltstones

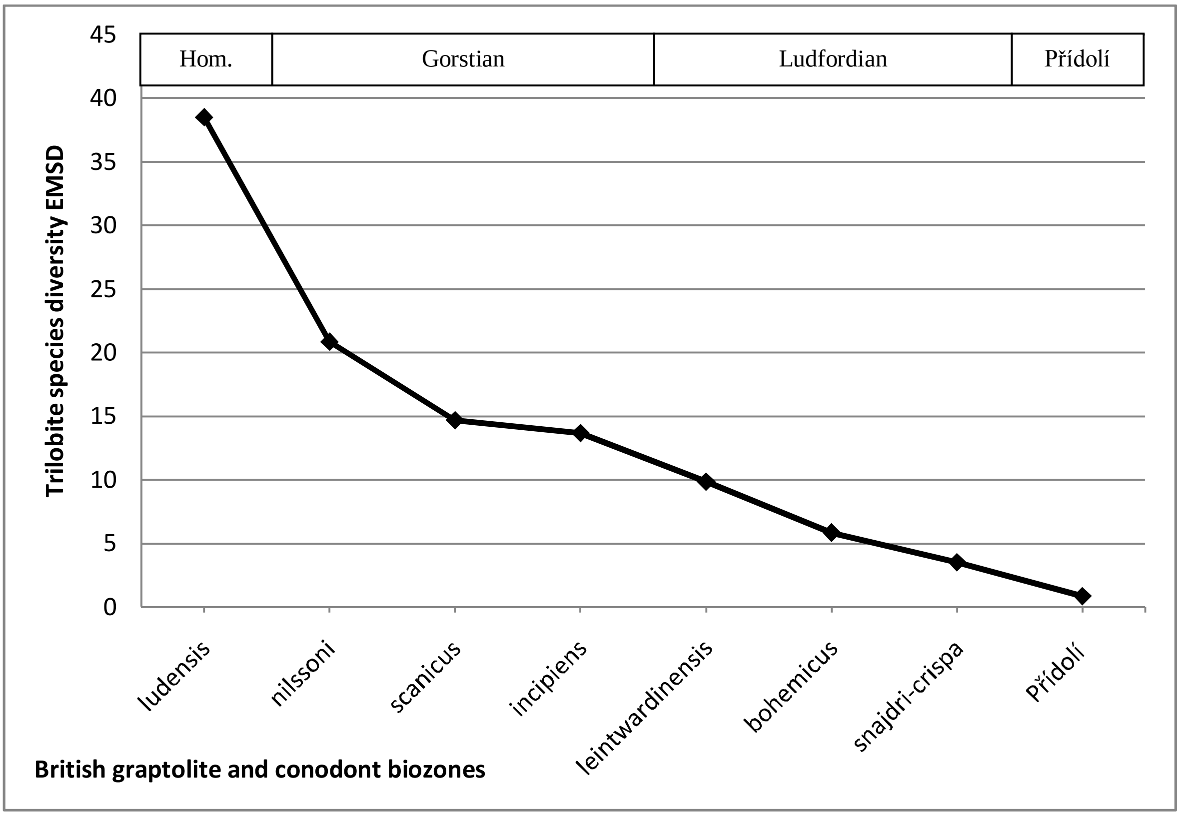
3.5.4 *Trilobites in the Přídolí Series*

Trilobites occur only as rarities in the Přídolí Series and are too few in number and abundance to define trilobite assemblages. *Cryphina*? *gdoumontensis* (as noted by Thomas *et al.* 1984) is the youngest known Silurian trilobite occurring in the *noetlingi* Beds of Buckinghamshire.

3.5.5 *Trilobite diversity and faunal reorganisation*

Based on the present study, a total of 15 families, 36 genera, and 53 species (42 are formally named) of trilobites are known to occur in the late Silurian of Britain. The generic and specific diversity of the Ludlow and Přídolí are lower than that of the Wenlock, and there are only five genera (*Alcymene*, *Warburgella*, *Homalonotus*, *Acastella*, and *Cryphina*?) from the British late Silurian that are not known from the Wenlock.

Trilobite biodiversity decreases significantly in Britain from the Homerian *ludensis* Biozone to the Gorstian *nilssoni* Biozone (Text-Figure 3.10).

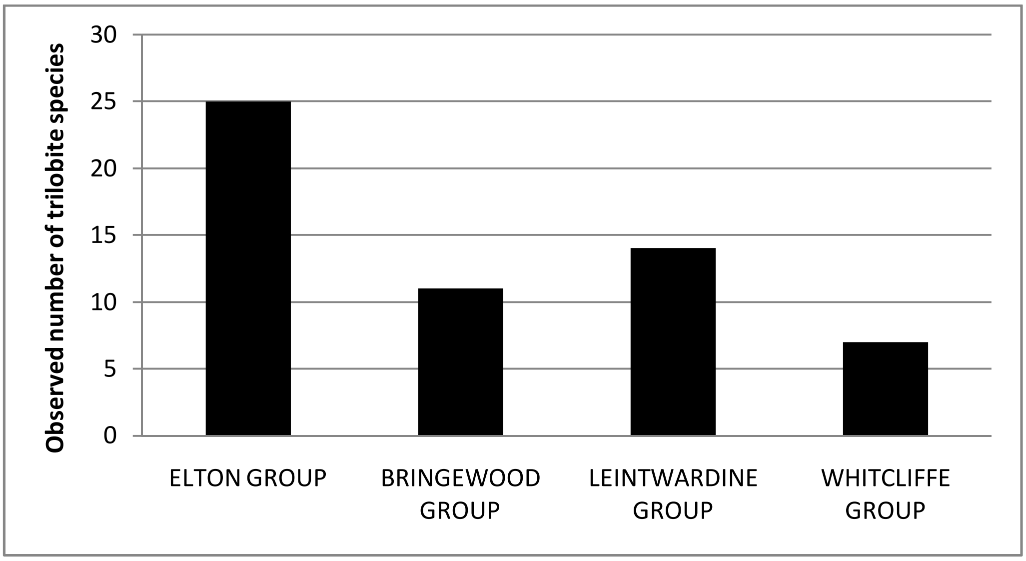


Text-Figure 3.10. Trilobite species diversity in Britain (Y-axis) against the British graptolite biozones (X-axis) for the latest Homerian (*ludensis* Biozone), Gorstian (*nilssoni* to *incipiens* biozones), Ludfordian (*leintwardinensis, bohemicus* Biozone, and *O. snajdri-O. crispa* conodont Biozone), and Přídolí (not subdivided). The biodiversity is calculated as Estimated Mean Standing Diversity, to minimise biases and to better estimate the distribution of taxa in each interval (this method is discussed in detail in Chapter Four).

The decrease in biodiversity is partly due to the termination of Much Wenlock Limestone Formation conditions, and its associated Konzentrat-Lagerstätte, at the close of the Wenlock, but this may also reflect the more restricted fauna of the Ludlow. Trilobite biodiversity in the Gorstian *nilssoni* Biozone is notably higher than the rest of the late Silurian. During this interval British trilobites are more geographically widespread than the rest of the Ludlow, occurring in a range of environments from the high diversity fauna of the Elton Group, several shallow water facies in Wales (for example the Hafod Fawr Formation), and the basinal facies including the Welsh Basin, the Lake District, and Builth.

The occurrence of trilobite faunas in calcitic mudstones (the *Barriepiscator-Miraspis* Association, for example) within distant basins indicates a widespread ventilation of bottom waters, and it is thought to be linked to a eustatic sea level fall at the end of the Wenlock, and continuing local shallowing in the foreland basin setting of the Lake District basin (Storey and Thomas 2008). This is short lived, and by the end of the *nilssoni* Biozone most British trilobite taxa previously in basinal settings are extinct, leading to a drop in biodiversity into the *scanicus* Biozone. By the late Ludfordian (*bohemicus* Biozone to *O. snajdri-O. crispa* conodont Biozone) trilobites in Britain are few in number and seem to be mostly restricted to the mid and outer shelf regions. Although there is a general retraction in the spatial distribution of trilobites in the late Gorstian and Ludfordian (for example *Dalmanites nexilis*) several taxa become more abundant and widespread. *Plesiowensus obconicus*, for example, is rare in the Gorstian and is restricted to the Ludlow district of the mid shelf but in the early Ludfordian it is known from several localities across the mid and outer shelf of the Welsh Borderlands, and the Welsh Basin. Another example is *Acastella spinosa*, which in the late Ludfordian (post-*bohemicus* Biozone) migrates north from Usk and Woolhope and spreads over a larger area over the mid and outer shelf of the Welsh Borderland. Both of these occur during eustatic regressions (Shergold 1967). Cherns (1988) suggested that the appearance of *Alcymene puellaris* and *Encrinurus stubblefieldi* in the Upper Leintwardine Formation (Ludfordian) represents faunal immigrations from Baltica. Although this may be true of *A. puellaris*, *E. stubblefieldi* occurs in the Hafod Fawr Formation (Gorstian) of Wales which is around the same age as its earliest occurrence in Gotland.

The sequence from the Elton to Whitcliffe groups generally reflects a shallowing upwards sequence, and shows environments from the deep to shallow ends of the Ludlow shelf. Mikulic and Watkins (1981, and see Watkins 1979) sampled the benthic fauna from the base of the Middle Elton Formation to the top of the Upper Whitcliffe Formation, and showed that trilobite diversity and abundance decreased throughout the Ludlow, in relation to sedimentological changes. They showed that trilobite diversity and abundance was higher in the bioturbated muds of the Elton Group, but lower in the coquinoid siltstone facies of the Leintwardine and Whitcliffe groups. Watkins (1979) postulated that the increase in sedimentation rate, a decrease in clay content, and an increase in silt content was responsible for the decrease in trilobite numbers, and controlled the composition of the trilobite faunas. The findings of the present study are based on more taxa but the results are similar in that the number of trilobite species decrease from the Elton to the Whitcliffe groups (Text-Figure 3.11).



Text-Figure 3.11. bar chart of the number of trilobite species observed from the Elton, Bringewood, Leintwardine, and Whitcliffe groups.

The number of trilobite species observed in the Bringewood Group is lower than the Leintwardine Group, however, although there are three species that occur rarely in the Leintwardine and Elton groups, and their absence from the Bringewood Group is most likely due to sampling.

Even though the trilobite diversity observed does not consistently decrease across the Ludlow shelf gradient (i.e. from the Bringewood to Leintwardine groups) the trilobite associations are markedly different, with diversity and abundance highest in the relatively deep mudstone facies of the Elton Group. Here the *Dalmanites-Raphiophorus parvulus* Association occurs where *Dalmanites*, *Raphiophorus*, *Ananaspis*?, and *Exallaspis* dominate. The shallower bioturbated siltstone facies of the Bringewood Group shows a much lower trilobite abundance and diversity, although there is an increase in the abundance of *Proetus* where it and *Dalmanites* are the most common trilobite constituents. *Dalmanites* continues to decline whereas proetids increase in relative abundance in the shallower coquinoid siltstone facies of the Leintwardine Group. Here *Plesiowensus obconicus* dominates the trilobite fauna with *Encrinurus* and *Alcymene*. Proetids decline into the Whitcliffe Group leaving a trilobite fauna dominated by *Homalonotus*.

The shifts in the various trilobite associations through the Ludlow do appear to correlate with changes in sedimentology. Trilobites such as *Dalmanites*, *Raphiophorus*, and *Exallaspis*, seem to have preferred quieter conditions in organic rich offshore muds whereas *Homalonotus* is often associated with coarse clastic inshore sediments. The functional morphology of many of the trilobites discussed here is outlined in Thomas and Lane (1984). Trilobites possessing spines are more numerically abundant in the muddy offshore facies of the Elton Group than they are in the shallower siltstone and coquinoid facies. *Dalmanites* possesses genal spines that are long, horizontal, and flattened and a pygidial posterior spine presumably to spread its weight in soft sediment. *Exallaspis* and *Raphiophorus* also possess spines, the latter containing very long genal and cephalic spines (Thomas 1978). The spines in *Raphiophorus* are conical, rather than flattened, and their main purpose may have been for protection rather than to retard sinking, however (Thomas and Lane 1984). The sigmoidal preglabellar field, flattened anterior border, flattened genal spines, and broad doublure in *Decoroproetus* seems to be an adaptation to soft sediments also (Thomas and Lane 1984). *Decoroproetus* is numerically abundant in the *Barriepiscator-Miraspis* Association of the Coldwell Formation (Chapter Two) and the *Dalmanites-Raphiophorus parvulus* Association of the Coalbrookdale Formation (Thomas 1979). In the shallower siltstone facies of the Bringewood Group and the coquinoid siltstone facies of the Leintwardine and Whitcliffe group abundant trilobites are convex, and their genal spines are small or absent. The shallow water *Homalonotus* and *Trimerus* are effaced and have streamline bodies, a convex thorax, and a wide axis; they were probably burrowers (Gill 1949, Sdzuy 1957, Thomas and Lane 1984, Sandford 2005).

Trilobites decrease in diversity and abundance from deeper distal settings of the Ludlow shelf to the shallower proximal environments. Increasing sedimentation rates, an increase in the frequency of storm events, and decreasing levels of organic matter in the substrate seem to have been important factors in controlling trilobite distribution patterns on the Ludlow shelf. The overall drop in trilobite diversity through the Ludlow is most likely related to the widespread deposition of the coquinoid facies related to the shallowing of the sea, and the filling up of the basins. The reduction of the geographic extent of many trilobite species occurs also, although several species appear to expand and increase in their abundance for short intervals. A drop in diversity and abundance in other groups including brachiopods, bivalves, and gastropods also occurs from the deep to shallow ends of the Ludlow shelf (Watkins 1979, p. 252), although this seems to be more pronounced in the trilobites. The *Homalonotus knightii-Acaste* cf. *subcaudata* Association, from the Gorstian Cwar Glas Member of the Hafod Fawr Formation, is the shallowest Ludlow trilobite association known, the trilobites being represented by the nominate species and *Maurotarion* only.

PLATES 5-26

All of the specimens figured here are of internal moulds or latex casts of external moulds, most of which belong to the former. Photographs are of internal moulds except where stated otherwise.

EXPLANATION OF PLATE 5

Figure 1. *Kosovopeltis*? sp. pygidium BGS GSM 36744, dorsal view, from the Ludlow of Ledbury (exact horizon unknown). Scale bar represents 5 mm.

Figure 2. Scutelluidae indet. cephalon BU 4777; dorsal view; Lower Elton Formation, locality 27. Scale bar represents 5mm.

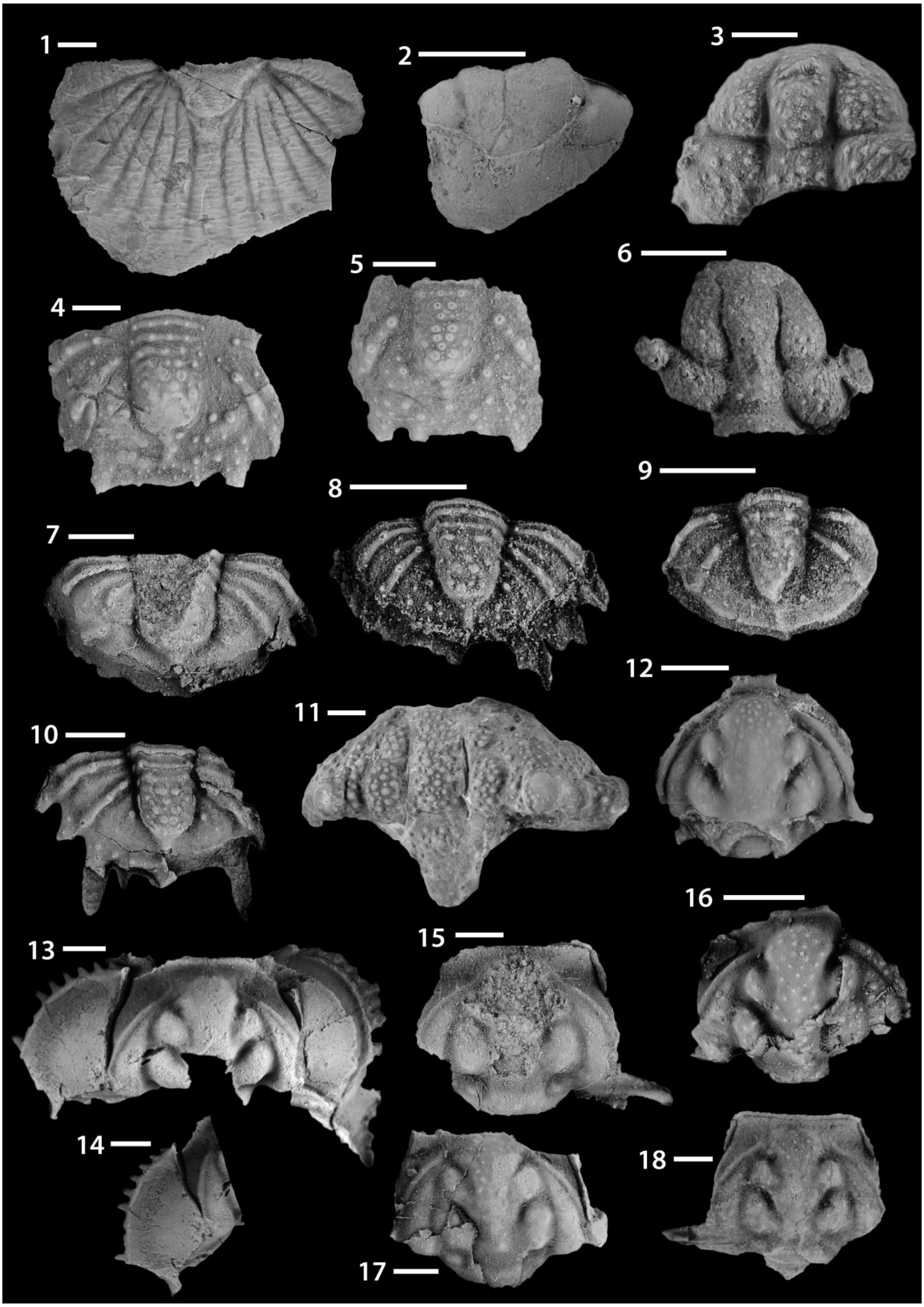
Figures 3-10. *Richterarges bucklandii* (Milne Edwards, 1840). 3-5 are from the Much Wenlock Limestone Formation, Dudley. **3.** cephalon SM A96179. **4.** Syntype, pygidium SM A10268, dorsal view. **5.** Syntype, pygidium SM A10269, dorsal view. **6.** cephalon BGS GSM 4239; dorsal view; from the early Ludlow of Denbighshire (exact horizon unknown), SH 9832 6795. **7-9.** from the Lower Elton Formation. **7.** pygidium NMW 74.30G.208a; dorsal view, from an old quarry near Cwm, near Monkswood, Usk, Gwent, SO 334 0155. **8.** pygidium BU 4778, dorsal view, from locality 15. **9.** pygidium BU 4779, dorsal view, from locality 15. **10.** pygidium LM G9554; dorsal view; from the Lower Leintwardine Formation, Haye Park, Mortimer Forest, Ludlow. Scale bars represent 2 mm.

Figures 11-12. *Acidaspis brightii* Murchison, 1839 from the early Ludlow of the Wych, near Malvern. **11.** cephalon BGS GSM 36733, dorsal view. **12.** cranidium BGS GSM 36732, dorsal view. Scale bars represent 2 mm.

Figures 13-18. *Exallaspis coronata* (Salter, 1853). 13-14. Lectotype cephalon BGS GSM 36738 from the Gorstian of High Vinnalls, near Ludlow. **13.** figure of entire specimen. **14.** close up of right librigena. 15, 18 are from the Upper Elton Formation of locality 17, 16-17 are from the Middle Elton Formation of localities 14 and 3 respectively. **15.** cranidium

BU 4825, dorsal view. **16.** cranidium BU 4826, dorsal view. **17.** cranidium BU 4827, dorsal view. **18.** cranidium BU 4828, dorsal view. Scale bars represent 2 mm.

PLATE 5



EXPLANATION OF PLATE 6

Figures 1-10. *Exallaspis coronata* (Salter, 1853). 1, 3, and 5 are from the ?Irfon Formation; 2, 6, and 8 are from the Upper Elton Formation; 4 and 9 are from the Middle Elton Formation; 10 is from the Upper Leintwardine Formation. **1.** cranidium BU 4829, dorsal view, locality 47C . **2.** cranidium BU 4830, dorsal view, locality 17. **3.** cranidium BU 4831, dorsal view, locality 47G. **4.** cranidium BU 4832, dorsal view, locality 1. **5.** librigena BU 4833, dorsal view, locality 47C. **6.** librigena BU 4834, dorsal view, locality 17. **7.** pygidium BGS GSM 36735, dorsal view, from the Ludlow (exact horizon unknown) of Vinnal Hill. **8.** pygidium BU 4835, dorsal view, locality 17. **9.** a near complete specimen BU 4836, dorsal view, locality 5. **10.** pygidium BU 4837, dorsal view, locality 52. Scale bars represent 2 mm.

Figures 11-16. *Homalonotus knightii* König, 1825. **11.** Holotype thorax and pygidium NHM It 42175, dorsal view, from the Ludlow Series of Powys, Wales. **12.** cephalon BGS GSM 33247, dorsal view, from the late Ludlow of Cwm Craig ddu. **13.** complete specimen BGS GSM 36850, dorsal view, from the late Ludlow of Ludlow Castle. **14.** cephalon of BGS GSM 36850, dorsal view. **15.** hypostome BGS GSM 36852, ventral view, from the late Ludlow of Whitcliffe. **16.** close up of cephalon of complete specimen BGS GSM 33248, dorsal view, from the late Ludlow of Whitcliffe. Scale bars represent 5 mm.

PLATE 6

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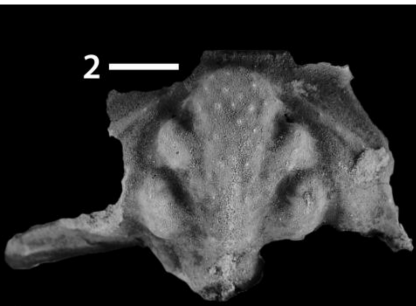

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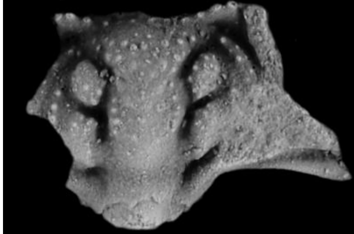

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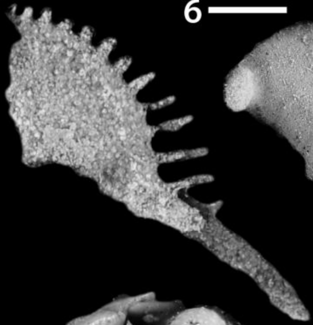

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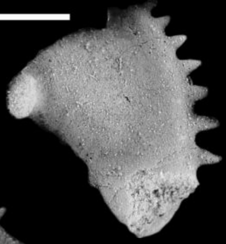

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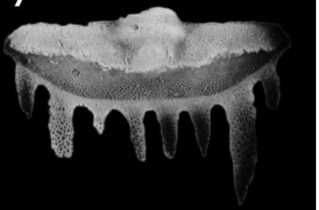

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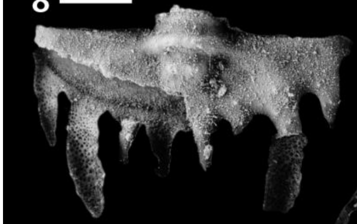

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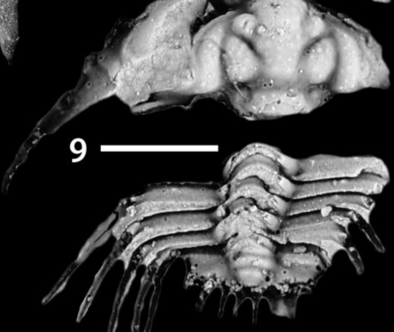

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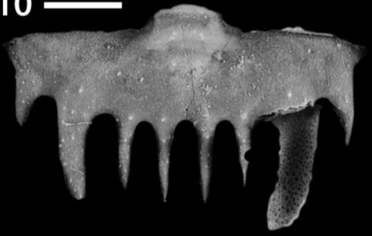

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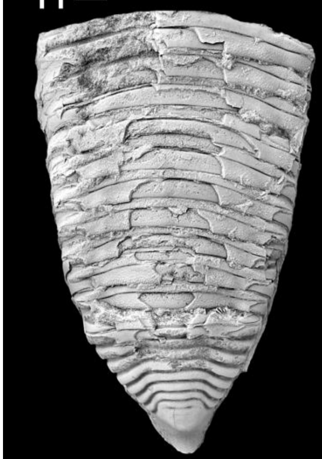

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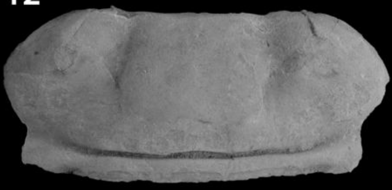

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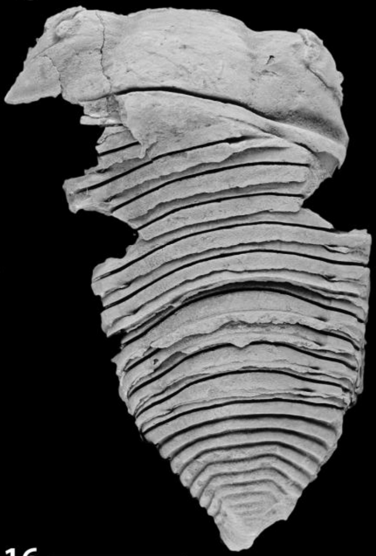

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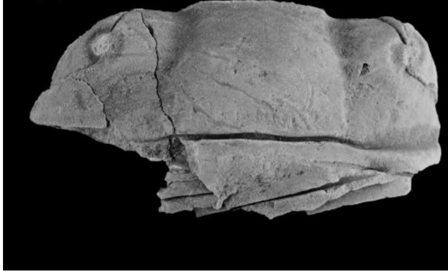

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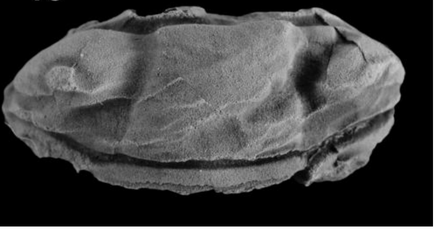


EXPLANATION OF PLATE 7

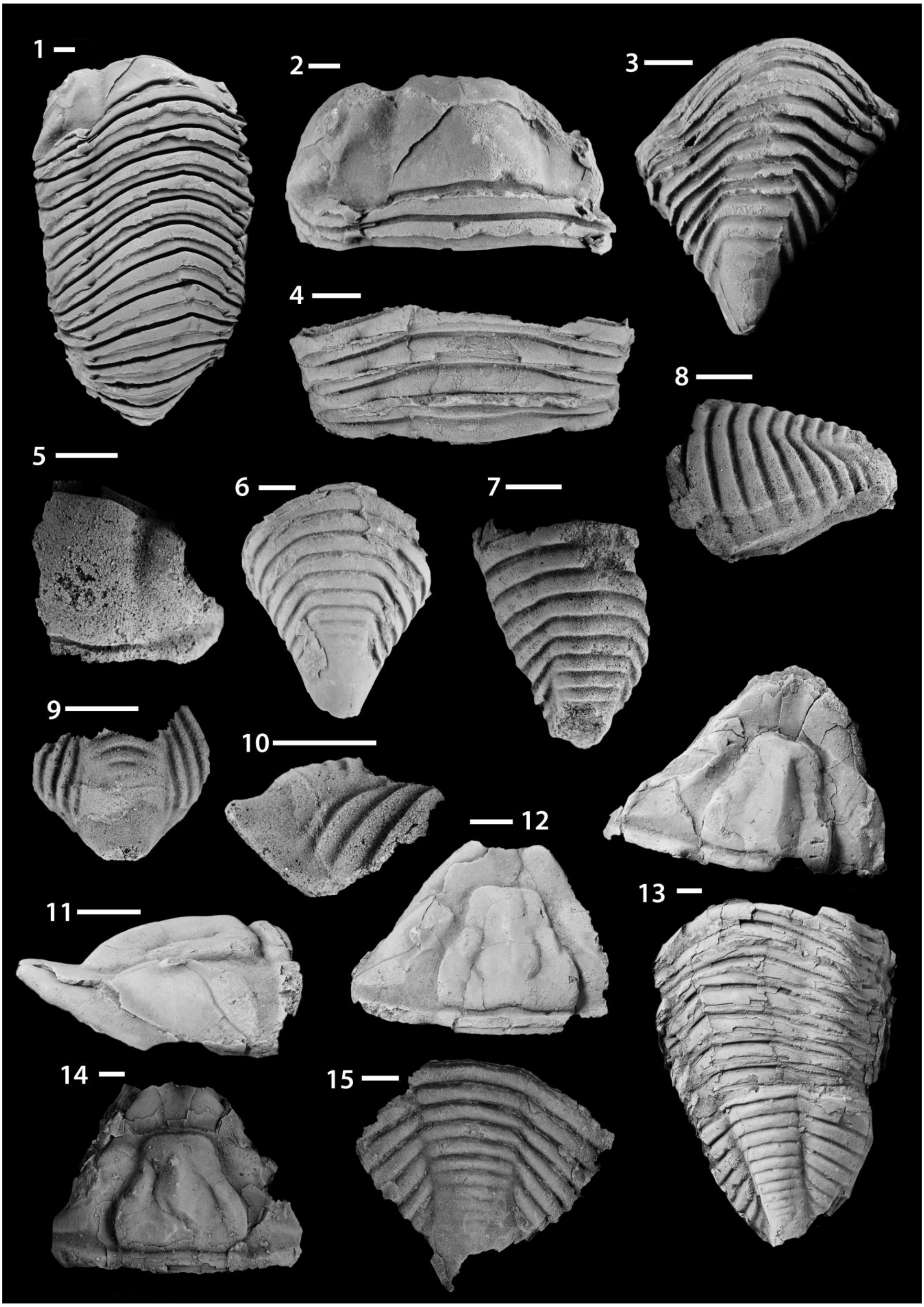
Figures 1-3, 5-10. *Homalonotus knightii* König, 1825. **1-3**. complete specimen BGS GSM 6589, dorsal views, from the late Ludlow of Presteign, Powys, **2.** close up of cephalon, **3.** close up of pygidium. **5.** cephalon BU 4838, dorsal view, locality 45. **6.** pygidium BGS GSM 36849, dorsal view, from the late Ludlow of Ludlow Castle. **7-8.** pygidium BU 4839, dorsal (7.) and lateral (8.) views; Hafod Fawr Formation, Cwar Glass Member, locality 45. **9-10.** pygidium BU 4951, dorsal (9.) and lateral (10.) views; Hafod Fawr Formation, Cwar Glass Member, locality 45.

Figure 4. *Homalonotus* cf. *knightii* König, 1825. part thorax BU 4780, dorsal view, locality 33.

Figures 11-15. *Trimerus* (*Trimerus*) *johannis* (Salter, 1865) from the Coalbrookdale Formation of Usk. Figures 11-13 photographed by Phil Hurst, copyright NHM. **11-12.** Paralectotype cephalon NHM It14523, lateral (11.) and dorsal (12.) views. **13.** Lectotype complete specimen NHM It14521, dorsal view. **14.** cephalon BGS GSM 36147, dorsal view. **15.** pygidium BGS GSM 36150, dorsal view.

All scale bars represent 5 mm.

PLATE 7



EXPLANATION OF PLATE 8

Figures 1-4. *Trimerus* (*Trimerus*) *johannis* (Salter, 1865) from the Coalbrookdale Formation of Usk. 1-2 from the Homerian Coalbrookdale Formation, Usk; photographed by Phil Hurst, copyright NHM. **1.** Paralectotype thorax and pygidium NHM It14525, dorsal view. **2.** Paralectotype thorax and pygidium, NHM It14522, dorsal view. **3.** thorax and pygidium, BGS GSM 36743, dorsal view. **4.** pygidium BGS GSM 1387, dorsal view, from the Ludlow of Rainy Rock, Wooltack Bay, Pembrokeshire.

Figure 5. *Trimerus* (?*Ramiotis*) *salteri* (Morris, 1988). Holotype cephalon BGS GSM 36855, dorsal view, from the Whitcliffe Group, Whitcliffe.

Figures 6-16. *Calymene oliveae* sp. nov. 6 is from the Middle Elton Formation of locality 1, 7-13 and 15 are from the Lower Elton Formation of locality 36, 14 and 16 are from the ?Irfon Formation of locality 47A. **6.** Holotype cephalon BU 4781, dorsal view. **7-8.** cephalon BU 4791, dorsal (6.) and lateral (7.) views. **9.** latex cast of external mould of cephalon BU 4785; dorsal view. **10.** latex cast of external mould of cephalon BU 4783, dorsal view. **11-12.** cephalon BU4792, dorsal (11.) and lateral (12.) views. **13.** latex cast of external mould of cephalon BU 4784, dorsal view. **14.** latex cast of external mould of cephalon BU 4795, dorsal view. **15.** cephalon BU 4789, dorsal view. **16.** Librigena BU 4797, dorsal view.

All scale bars represent 5 mm.

PLATE 8

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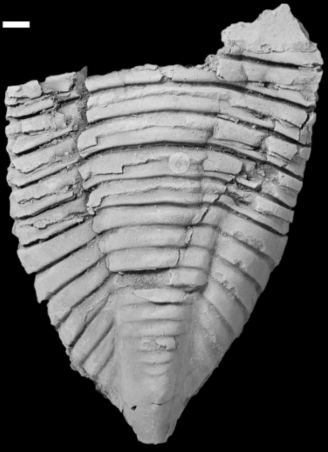

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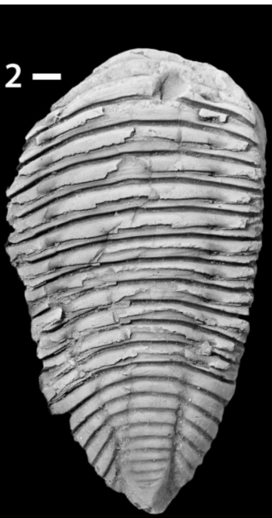

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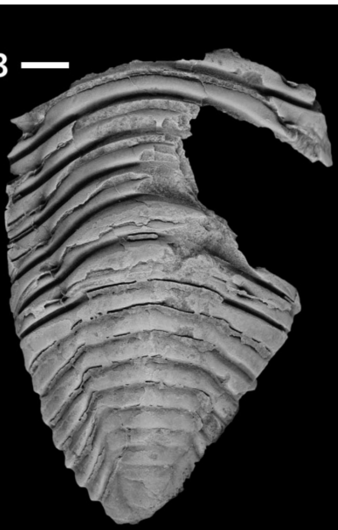

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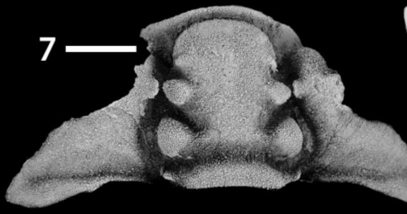

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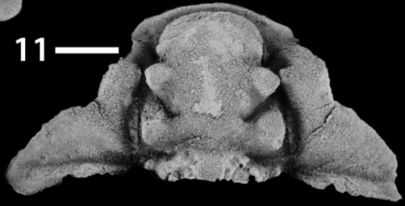

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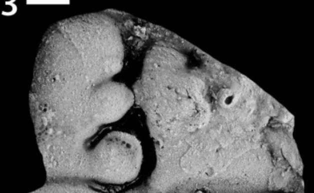

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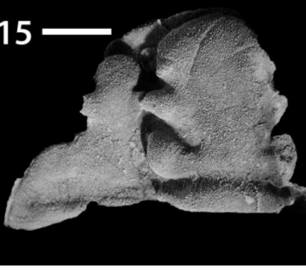

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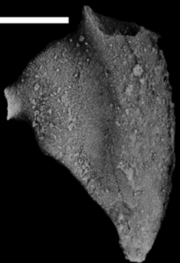


EXPLANATION OF PLATE 9

Figures 1-5. *Calymene oliveae* sp. nov. 1, 2, and 4 are from the ?Irfon Formation, 3 is from the Middle Elton Formation, figure 5 is from the Lower Elton Formation. **1.** cephalon BU 4786, dorsal view; locality 47.C. **2.** pygidium BU 4799, dorsal view, locality 47.C. **3.** pygidium BU 4800, dorsal view, locality 11. **4.** thorax and pygidium BU 4805, dorsal view, locality 47.A. **5.** pygidium BU 4801, dorsal view, locality 36.

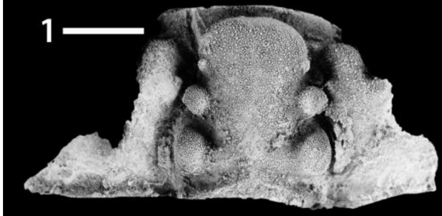
Figures 6-8. *Alcymene neointermedia* (Richter and Richter, 1954). Complete specimen NHM It9145, dorsal (6. and 8.), and lateral (7.) views. Museum label reads 'Wenlock Limestone, Malvern', although it is probably from the early Ludlow of Gotland. Photographs by Phil Crabb, copyright NHM.

Figures 9-15. *Alcymene lawsoni* (Shirley, 1962). 9-10 and 12 are from the higher part of Lower Leintwardine Formation, Mocktree Quarries, *c.* 2 km northeast of Leintwardine [SO 4167 7537]; 11 is from the Lower Leintwardine Formation, from the south side of Tatteridge Hill [SO 4209 7259], near Leintwardine; 13-14 are from the early Ludlow of Leintwardine; 15 is from the Whitcliffe Group, Whitcliffe. **9-10.** latex cast of external mould of cephalon OUM C.29801, dorsal (1.) and lateral (2.) views. **11.** Holotype cephalon NHM It16000, dorsal view. **12.** latex cast of external mould of pygidium OUM C.29814, dorsal view. **13.** cephalon BGS GSM 19685, dorsal view. **14.** pygidium BGS GSM 19683, dorsal view; early Ludlow, Leintwardine. **15.** pygidium BGS GSM 19698, dorsal view.

Figure 16. *Alcymene* cf. *lawsoni* (Shirley, 1962). cephalon BGS RK 3992, dorsal view; early Ludlow, Craig-bach, Denbighshire.

All scale bars represent 5 mm.

PLATE 9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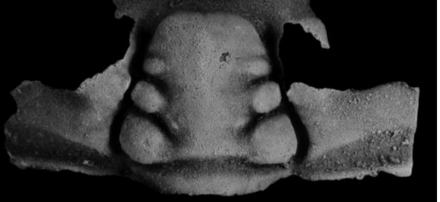
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EXPLANATION OF PLATE 10

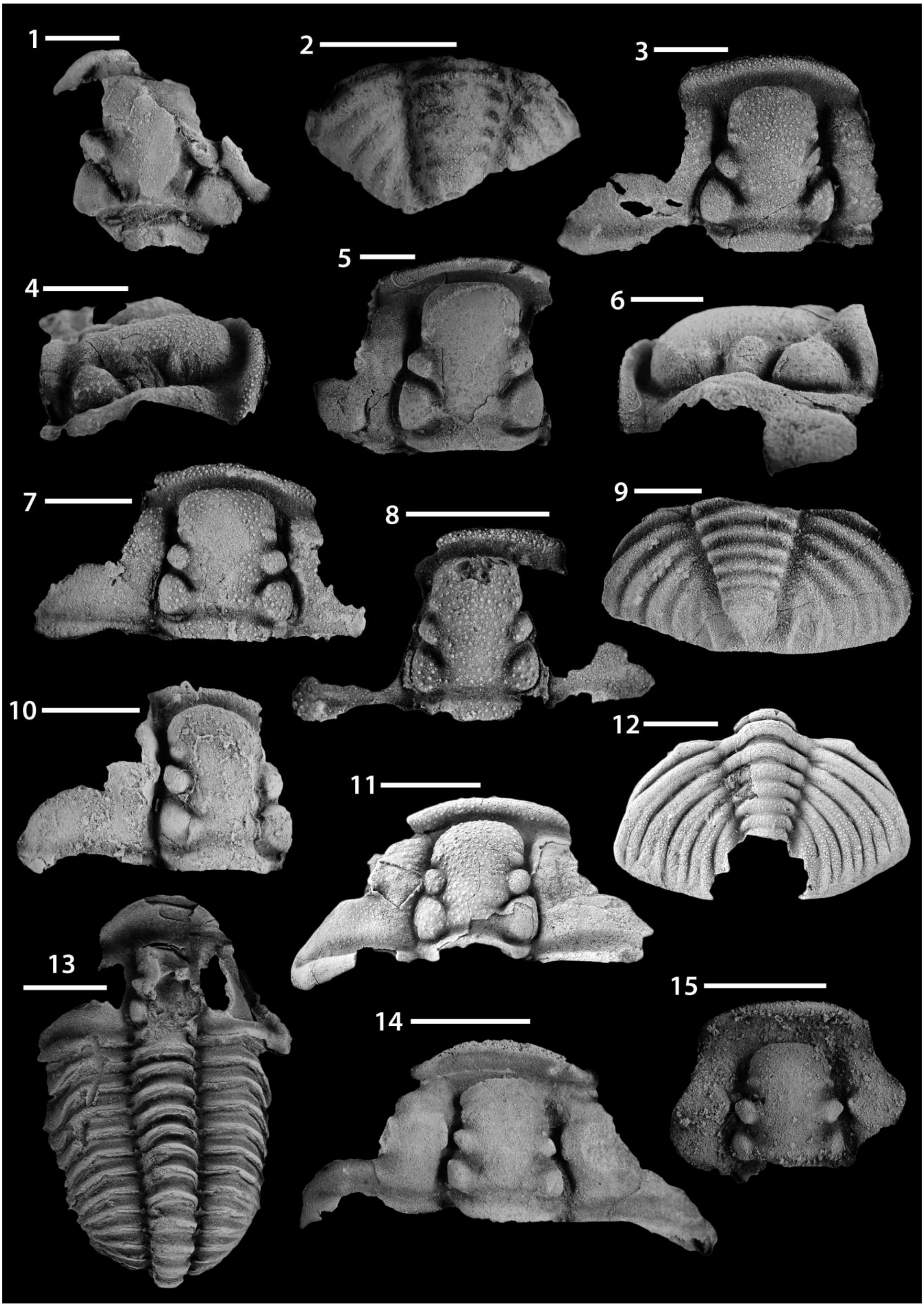
Figures 1-2. *Alcymene* cf. *lawsoni* (Shirley, 1962) from the early Ludlow, Craig-bach, Denbighshire. **1.** cephalon BGS RIK 3992a, dorsal view. **2.** pygidium BGS RIK 3988, dorsal view.

Figures 3-12. *Alcymene* (s.l.) aff. *A. lawsoni*. 3-4 are from the ?Irfon Formation, locality 47.D; 5-9 are from the ?Irfon Formation of locality 47.G; 10 is from the Lower Elton Formation of locality 27; 11-12 are from the Middle Elton Formation of Upper Millichope, Wenlock Edge. **3-4.** cephalon BU 4840, dorsal (3.) and lateral (4.) views. **5-6.** cephalon BU 4841, dorsal (5.) and lateral (6.) views. **7.** cephalon BU 4842, dorsal view. **8.** cephalon BU 4843, dorsal view. **9.** pygidium BU 4844, dorsal view. **10.** cephalon BU 4845, dorsal view. **11.** cephalon NHM It16045, dorsal view; photographed by Phil Crabb, copyright NHM. **12.** pygidium NHM It16046, dorsal view, photographed by Phil Crabb, copyright NHM.

Figures 13-15. *Alcymene puellaris* (Reed, 1920). **13.** Holotype complete specimen SM A3320, dorsal view; the lower Longhope Beds?, small quarry 410 m E of Longhope Church, Gloucestershire. **14.** cephalon BGS DEW 4640, dorsal view; Upper Leintwardine Formation, Old Quarry, 3350 yards east 41 degrees south of Coed-y-Paen Church, ST 35789651. **15.** cephalon BGS DEX 873, dorsal view; Lower Leintwardine Formation, Old Quarry NE of the Haie, Newnham, SO 680107.

All scale bars represent 5 mm.

PLATE 10



EXPLANATION OF PLATE 11

Figures 1-8. *Alcymene puellaris* (Reed, 1920). **1-2** cephalon BU 4846, dorsal (1.) and lateral (2.) views; Lower Leintwardine Formation, locality 22. **3.** cephalon BGS GSM 4025, dorsal view; Upper Leintwardine Formation, Lane Section 1.7 km south 28 degrees east of the Church, Coed-y-Paen, ST 34309698. **4.** cephalon BU 4847, dorsal view; Upper Leintwardine Formation, locality 52. **5.** cephalon BGS DEW 6176, dorsal view; Upper Leintwardine Formation, Old Quarry SW of Coed-y-Paen Church, ST 33409593. **6.** complete specimen BGS GSM 19688, dorsal view, late Ludlow (?Leintwardine Group), USK. **7.** pygidium BU 4848, dorsal view; Upper Leintwardine Formation, locality 52. **8.** pygidium BU 4849, dorsal view; Upper Leintwardine Formation, locality 52.

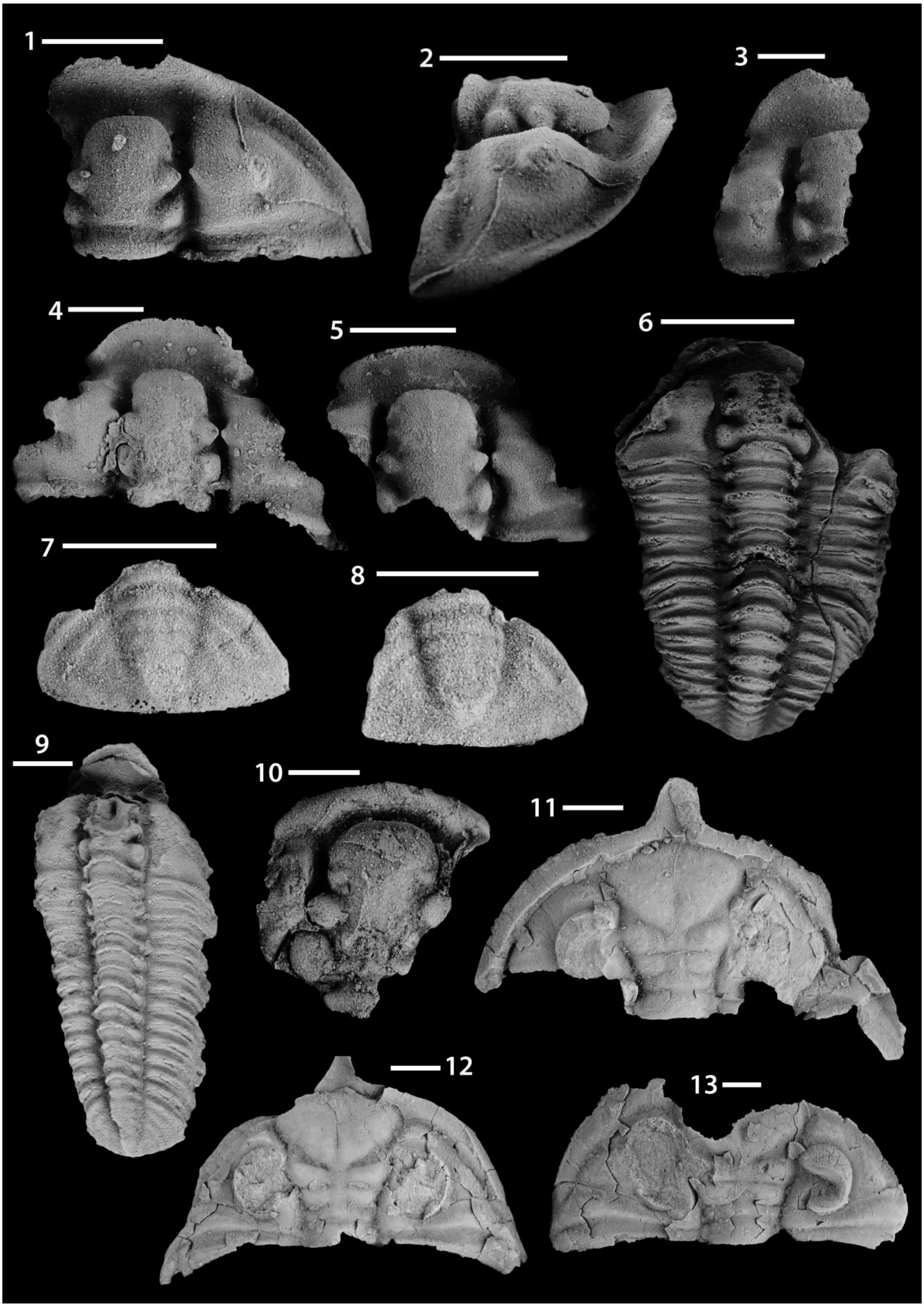
Figure 9. *Alcymene* cf. *puellaris* (Reed, 1920). complete specimen BGS GSM 104357, dorsal view; Bannisdale Formation, Crook of Lune Flag Quarry, 5 km northwest of Sedbergh, Lake District.

Figure 10. *Diacalymene*? sp. cranidium BU 4949, dorsal view; uppermost Coed Wenallt Beds, locality 46A.

Figures 11-13 *Dalmanites caudatus* (Brünnich, 1781) from the Coalbrookdale Formation, Ironbridge power station, Shropshire (topotype material). **11.** Cephalon BU 4943, dorsal view. **12.** Cephalon BU 4944, dorsal view. **13.** Cephalon BU 4945, dorsal view.

All scale bars represent 5 mm.

PLATE 11



EXPLANATION OF PLATE 12

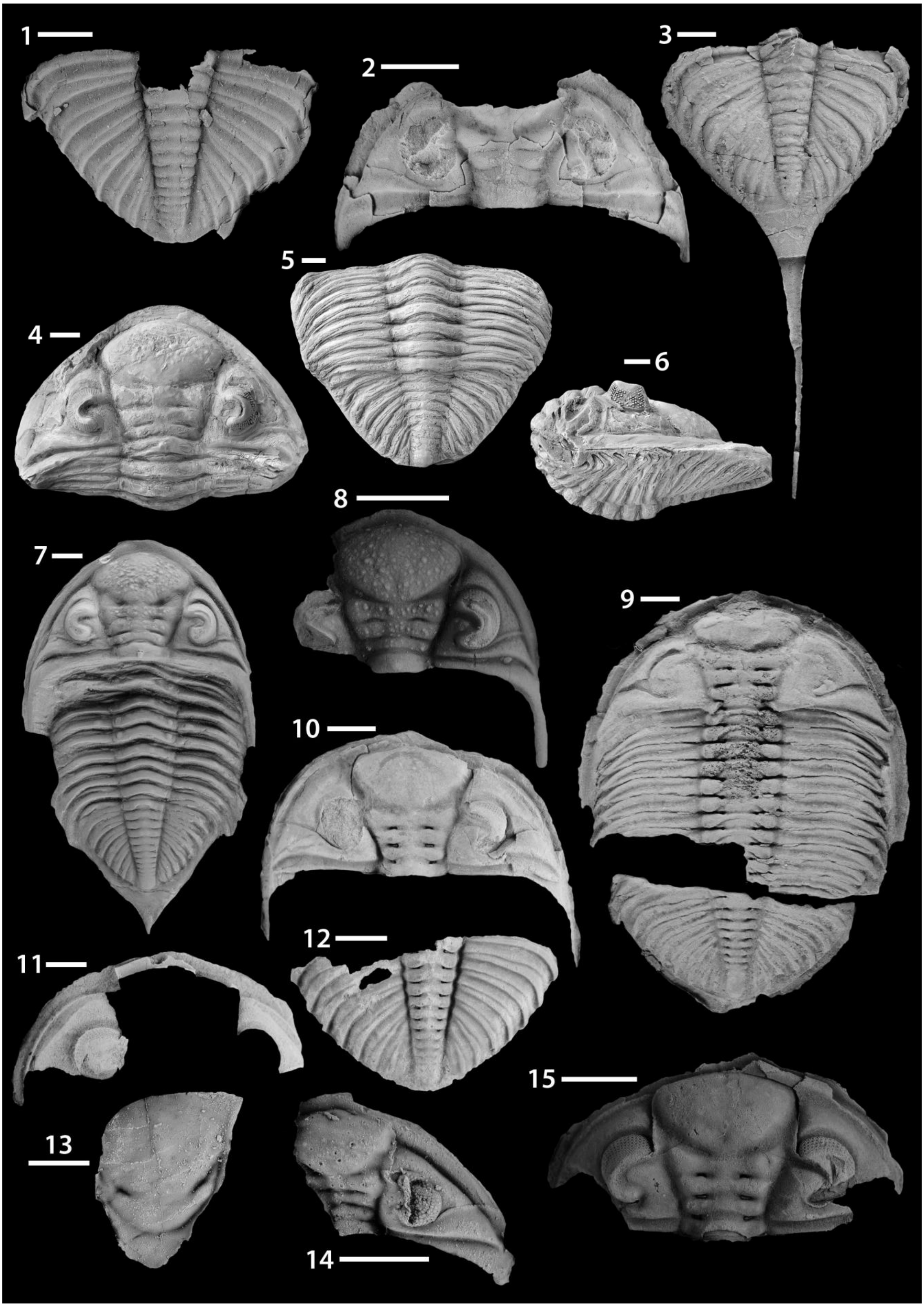
Figures 1-3. *Dalmanites caudatus* (Brünnich, 1781) from the Coalbrookdale Formation, Ironbridge power station, Shropshire (topotype material). **1.** Pygidium BU 4946, dorsal view. **2.** Cephalon BU 4947, dorsal view. **3.** Pygidium BU 4948, dorsal view.

Figures 4-8. *Dalmanites myops* (König, 1825) from the Much Wenlock Limestone Formation of Dudley, West Midlands. **4-6.** holotype enrolled specimen NHM It54865, dorsal (4 and 5) and lateral (6) views; photographed by Phil Crabb, copyright NHM. **7.** complete specimen BIRUG 3131, dorsal view. **8.** cephalon BGS GSM 19348, dorsal view.

Figures 9-15. *Dalmanites nexilis* (Salter, 1864). 10-12 and 15 are from the Bringewood Group of Vinnal Hill, Ludlow. **9.** Lectotype complete specimen BGS GSM 19371, dorsal view; early Ludlow near Ledbury. **10**. Paralectotype cephalon BGS GSM 19368, dorsal view. **11.** Paralectotype partial cephalon BGS GSM 19370, dorsal view. **12.** Paralectotype pygidium BGS GSM 19369, dorsal view. **13.** latex cast of external mould of hypostome BU 4850, ventral view; Upper Leintwardine Formation, locality 52. **14.** Latex cast of external mould of cephalon BU 4851, dorsal view; Upper Elton Formation, locality 51. **15.** cephalon BGS GSM 19395, dorsal view.

All scale bars represent 5 mm.

PLATE 12

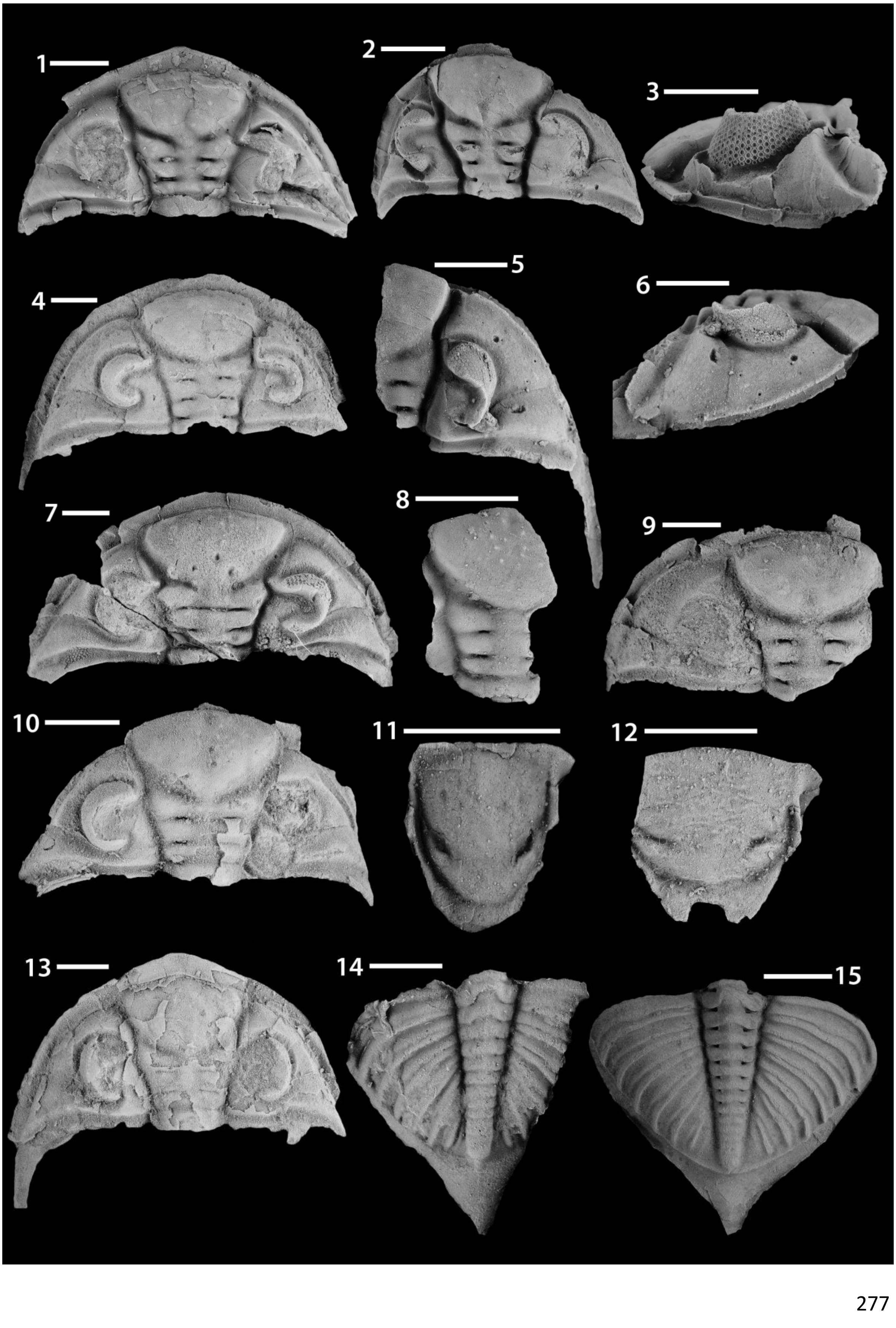


EXPLANATION OF PLATE 13

Figures 1-15. *Dalmanites nexilis* (Salter, 1864). 1-6, 9, 10, and 13 are from the Middle Elton Formation, 7-8, 12, and 14 are from the Upper Elton Formation. **1.** cephalon BU 4852, dorsal view, locality 1. **2-3.** cephalon BU 4853, dorsal (2.) and lateral (3.) views, locality 14. **4.** cephalon BU 4854, dorsal view, locality 30. **5-6.** cephalon BU 4855, dorsal (5.) and lateral (6.) views, locality 4. **7.** cephalon BU 4856, dorsal view, locality 51. **8.** cranidium BU 4857, dorsal view, locality 51. **9.** cephalon BU 4858, dorsal view, locality 4. **10.** cephalon BU 4859, dorsal view, locality 30. **11.** hypostome BU 4860, ventral view; Upper Leintwardine Formation, locality 52. **12.** hypostome BU 4861, ventral view, locality 33. **13.** cephalon BU 4862, dorsal view, locality 30. **14.** latex cast of external mould of pygidium BU 4863, dorsal view, locality 51. **15.** pygidium BGS GSM 19393, dorsal view; Bringewood Group, Vinnal Hill, Ludlow.

All scale bars represent 5 mm.

PLATE 13



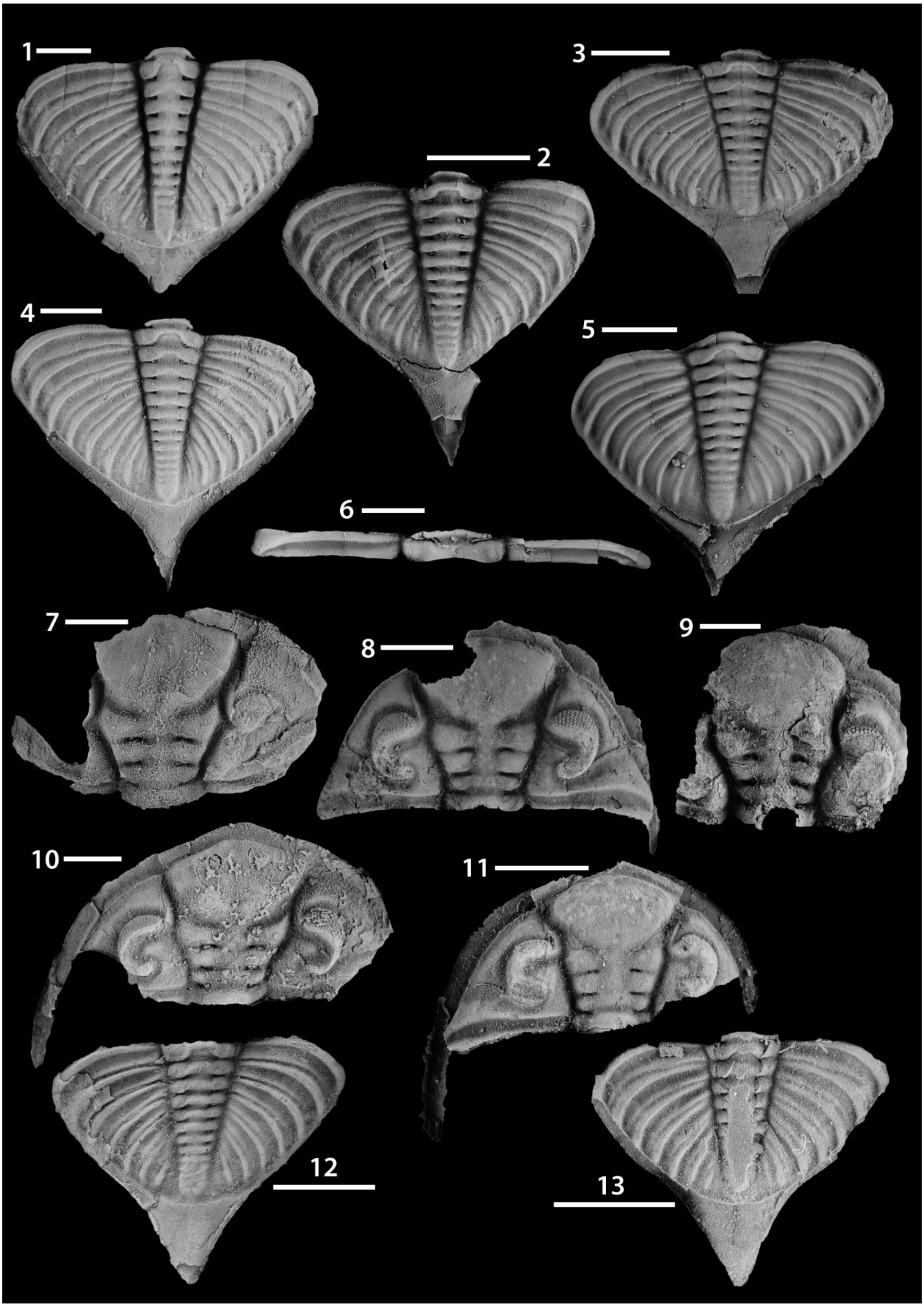
EXPLANATION OF PLATE 14

Figures 1-6. *Dalmanites nexilis* (Salter, 1864). 1-2, 4, and 6 are from the Middle Elton Formation. **1.** pygidium BU 4864, dorsal view, locality 4. **2.** pygidium BU 4865, dorsal view, locality 4. **3.** pygidium BU 4866, dorsal view; Upper Elton Formation, locality 17. **4.** pygidium BU 4867, dorsal view, locality 30. **5.** pygidium BU 4868, dorsal view; Upper Leintwardine Formation, locality 52. **6.** thoracic BU 4869, dorsal view, locality 4.

Figures 7-13. *Dalmanites* aff. *nexilis* (Salter, 1864). **7.** cephalon BU 4870, dorsal view; Middle Elton Formation, locality 3. **8.** cephalon BU 4871, dorsal view; Upper Elton Formation locality 51. **9.** cephalon BU 4872, dorsal view; Lower Elton Formation, locality 32. **10.** cephalon BU 4873, dorsal view; Middle Elton Formation, locality 4. **11.** cephalon OUM C.20988, dorsal view; late Ludlow, Malvern. **12.** pygidium OUM C.20984, dorsal view; late Ludlow, Malvern. **13.** pygidium BU 4874, dorsal view; Upper Elton Formation, locality 18.

All scale bars represent 5 mm.

PLATE 14

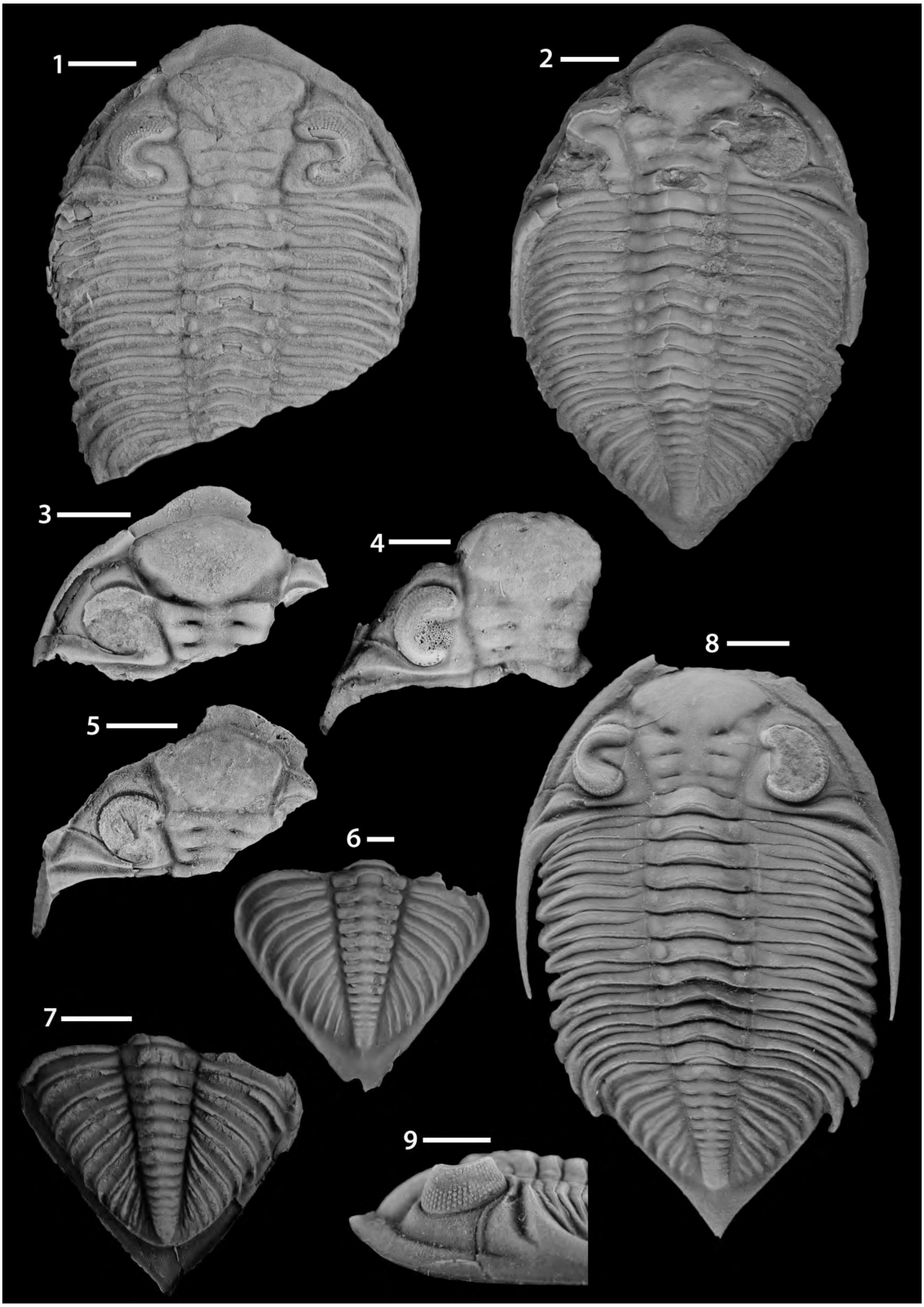


EXPLANATION OF PLATE 15

Figures 1-9. *Dalmanites obtusus* (Lindström, 1885). **1.** near complete specimen BGS GSM 19399, dorsal view; early Ludlow, Leintwardine. **2.** complete specimen BGS GSM 19365, dorsal view, early Ludlow, northeast Leintwardine. **3.** cephalon BU 4875; dorsal view, Upper Elton Formation, locality 51. **4.** Latex cast of external mould of cephalon BU 4876, dorsal view; Lower Bringewood Formation, locality 50. **5.** Latex cast of external mould of cephalon BU 4877, dorsal view; Lower Bringewood Formation, locality 50. **6.** pygidium BGS GSM 19291, dorsal view; Much Wenlock Limestone Formation, Ledbury. **7.** pygidium BGS ZP 3473, dorsal view; early Ludlow, Denbighshire. **8-9.** complete specimen BGS GSM 19400, dorsal (8.) and lateral (9.) views; early Ludlow, near Ledbury.

All scale bars represent 5 mm.

PLATE 15



EXPLANATION OF PLATE 16

Figures 1-4. *Dalmanites tuberculatocaudatus* (Murchison, 1839). **1.** complete specimen OUM C.11, dorsal view; from the Gorstian of Ledbury Tunnel, Malvern. **2.** cephalon BU 4878, dorsal view; Middle Elton Formation, locality 2. **3.** pygidium BU 4879, dorsal view; Middle Elton Formation, locality 14. **4.** pygidium BU 4880, dorsal view; Coed Wenallt Beds (=Hafod Fawr Formation), locality 46.C.

Figures 5-6. *Acaste downingiae* (Murchison, 1839). Lectotype, complete specimen OUM C.7. lateral (5.) and dorsal (6.) views, from the Much Wenlock Limestone Formation of Dudley.

Figures 7-10. *Acaste inflata* (Salter, 1864). **7-8.** Lectotype enrolled specimen C.9, dorsal view; Much Wenlock Limestone Formation, Ledbury Railway Tunnel. Figures 9-10 are from the Lower Elton Formation of Shadwell Quarry, Much Wenlock. **9.** cranidium OUM C.28807, dorsal view. **10.** pygidium OUM C.28808, dorsal view.

All scale bars represent 5 mm.

PLATE 16

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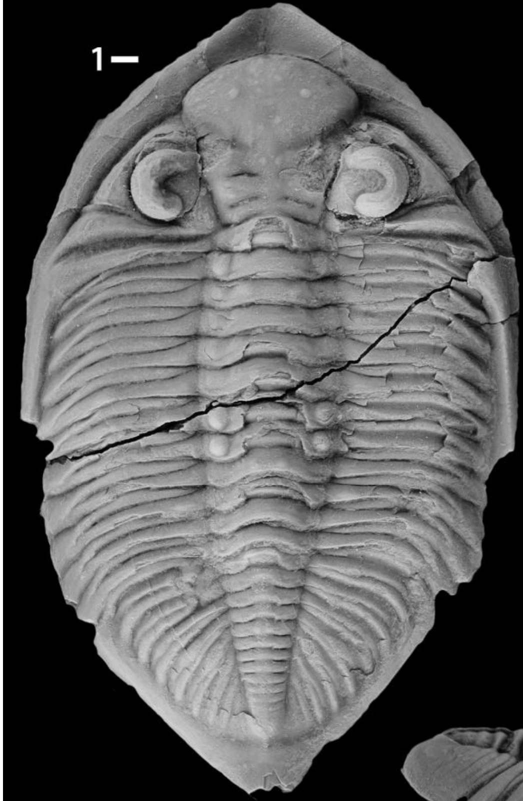

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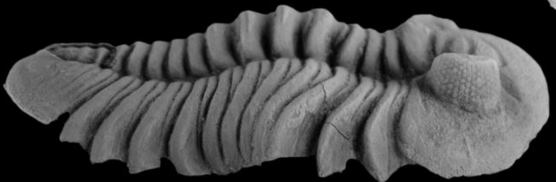

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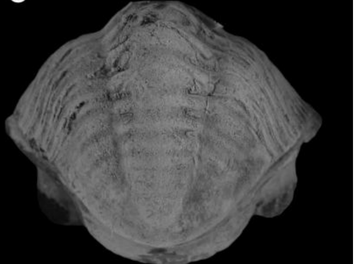

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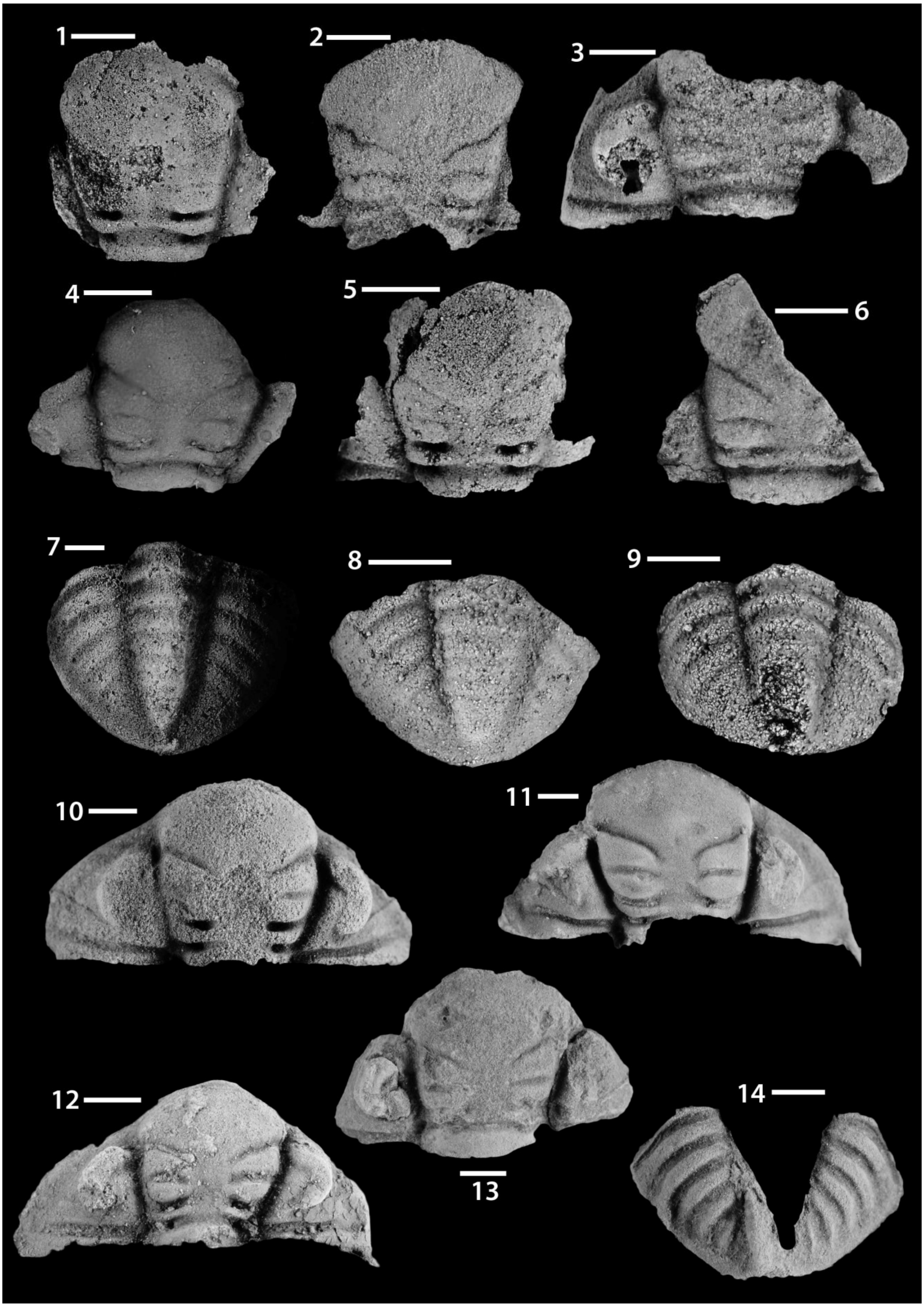
EXPLANATION OF PLATE 17

Figures 1-9. *Acaste* cf. *subcaudata* (Murchison, 1839), from the Hafod Fawr Formation. 1, 3, and 5-9 are from the Cwar Glass Member; 2 and 4 are from the Coed Wenallt Beds (=unnamed member of the Hafod Fawr Formation). **1.** cranidium BU 4881, dorsal view, locality 45. **2.** cranidium BU 4882, dorsal view, locality 46A. **3.** cephalon BU 4883, dorsal view, locality 44. **4.** cephalon BU 4884, dorsal view, locality 46.C. **5.** cephalon BU 4885, dorsal view, locality 45. **6.** cranidium BU 4886, dorsal view, locality 43. **7.** pygidium BGS HC1091, dorsal view, Lan Quarry, Rhondda Cynon Taff, SN 6599 2063. **8.** pygidium BU 4887, dorsal view, locality 45. **9.** pygidium BU 4888, dorsal view, locality 45.

Figures 10-14. *Acastella spinosa* (Salter, 1864). **10.** cephalon BGS GSM 102589, Upper Whitcliffe Formation, Whitcliffe Chase, Ludlow, dorsal view. **11.** cephalon BGS GSM 19412, dorsal view; Upper Whitcliffe Formation, Whitcliffe Chase, Ludlow. **12.** cephalon BGS GSM 102588, dorsal view, Upper Whitcliffe Formation, quarry southwest of Diannawell Cote, 352 metres southwest of Patton Grange, Much Wenlock, Shropshire. **13.** cephalon BGS GSM 19413, dorsal view; Whitcliffe Group, Whitcliffe, Ludlow. **14.** pygidium BGS GSM 19414, dorsal view; Whitcliffe Group, Ludlow.

All scale bars represent 2 mm.

PLATE 17



EXPLANATION OF PLATE 18

Figure 1. *Acastella spinosa* (Salter, 1864). Cephalon NMW 78.52G.128, dorsal view; Lower Leintwardine Formation) from a temporary trench west of Cwm-bwrwch Wood, southwest of Llandegledd Reservoir Dam, Usk, Gwent, ST 322 982- ST 322 985.

Figures 2-3. *Acastella* cf. *spinosa* (Salter, 1864) from the ?Irfon Formation. **2.** cephalon BU 4889, dorsal view, locality 47.B. **3.** pygidium BU 4890, dorsal view, locality 47.G.

Figures 4-5. *Acastella minor* (M^{c}Coy, 1851), from the Kirkby Moor Formation, Benson Knott, Kendal. **4.** Lectotype cephalon SM A37142, dorsal view. **5.** cephalon SM A37195, dorsal view.

Figures 6-7. *Acastella prima* Tomczykowa, 1962 from the Kirkby Moor Formation. **6.** pygidium BGS TMcKH 1032, dorsal view; Gatebeck, north of Kirkby Lonsdale, Westmoreland. **7.** Latex cast of external mould of pygidium BGS TMcKH 1336, dorsal view; Holme Scales, Hutton Bridgend, southeast of Kendal.

Figures 8-9. *Acastocephala*? sp. A, from the Tresglen Formation (Gorstian, *nilssoni* Biozone), Berach Quarry, Golden Grove, Carmarthenshire. **8.** cephalon BGS HC 801, dorsal view. **9.** latex cast of external mould of pygidium BGS DEX 3120, dorsal view.

Figures 10-15. *Acastocephala*? sp. B. **10.** cephalon BGS GSM 19403, dorsal view, Tresglen Formation, Berach Quarry, Golden Grove, Carmarthenshire . **11-12.** cephalon BU 4891, dorsal (11.) and lateral (12.) views; lower part of Hafod Fawr Formation, locality 48. **13.** cast of external mould of cephalon BU 4892, dorsal view; lower part of Hafod Fawr

Formation, locality 48. **14.** cephalon BU 4893, dorsal view; Lower Elton Formation, locality 15. **15.** pygidium BU 4894, dorsal view; Lower Elton Formation, locality 15.

All scale bars represent 2 mm.

PLATE 18

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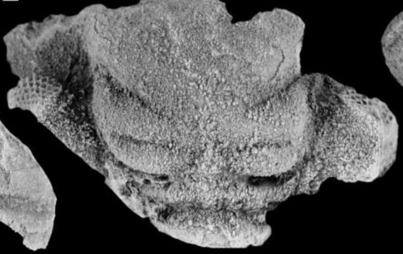

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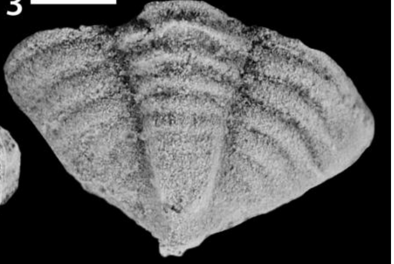

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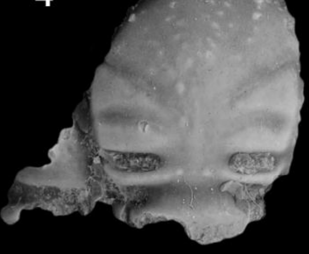

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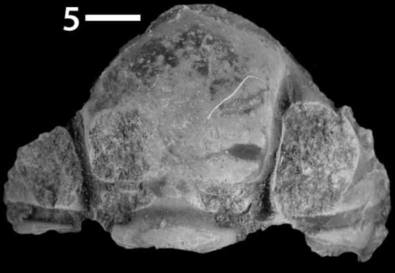

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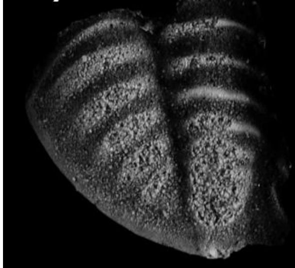

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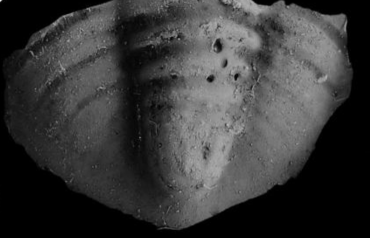

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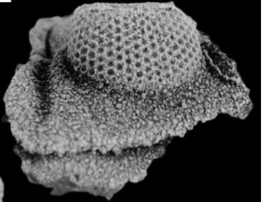

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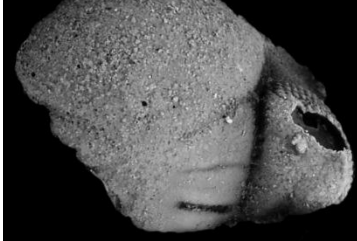

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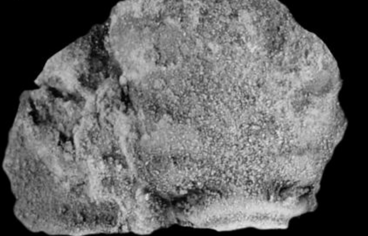

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EXPLANATION OF PLATE 19

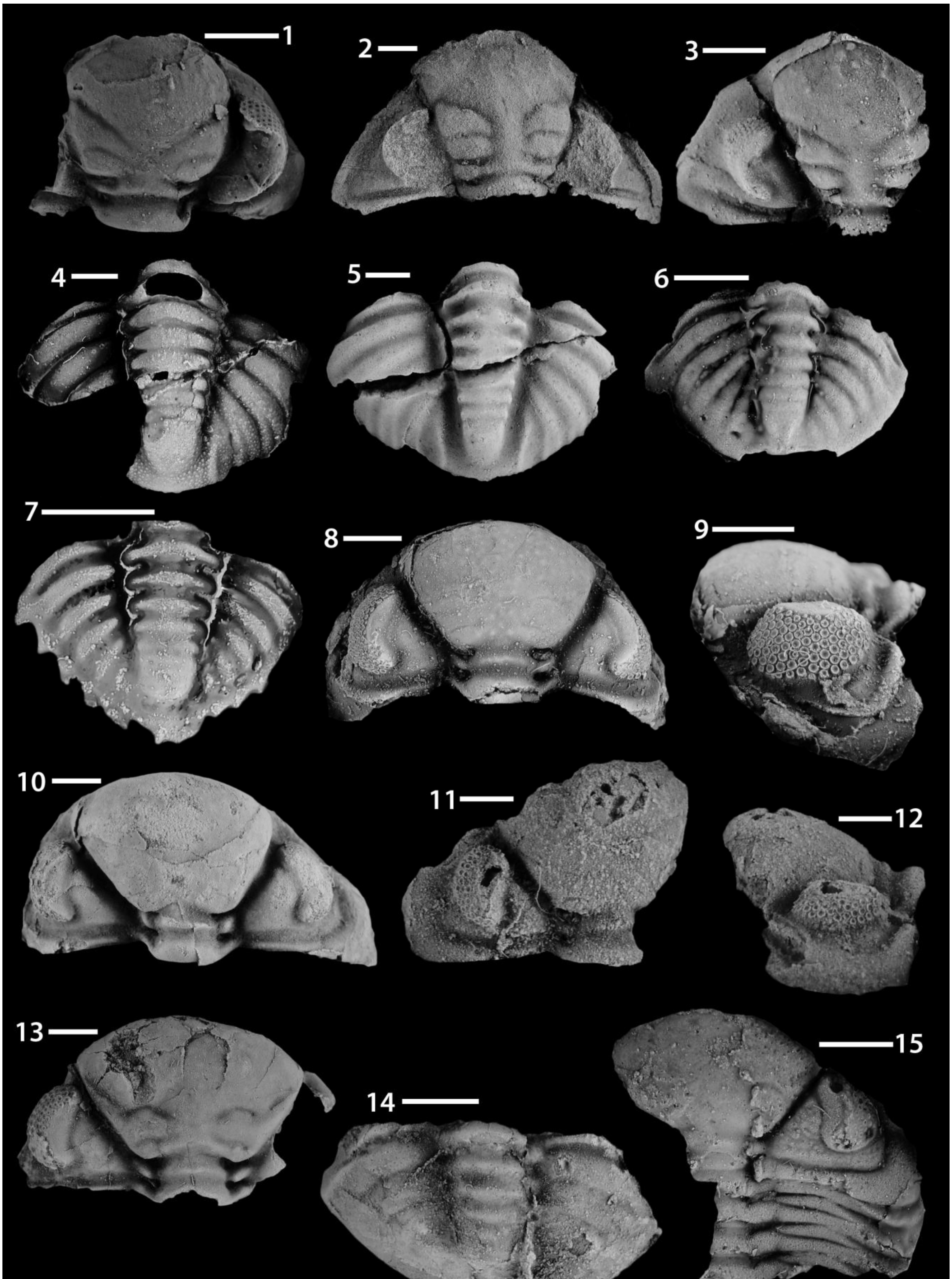
Figures 1-6. *Acastocephala*? sp. C. **1.** cephalon BU 4895, dorsal view; Hafod Fawr Formation, locality 48. **2.** cephalon NMW 78.52G.121, dorsal view; Lower Leintwardine Formation from a temporary trench west of Cwm-bwrwch Wood, southwest of Llandegledd Reservoir Dam, Usk, Gwent, ST 322 982- ST 322 985. **3.** cephalon BU 4896, dorsal view, Upper Leintwardine Formation, locality 52. **4-5.** pygidium BU 4897a-b, dorsal view, internal mould (a, 4.), latex cast of external mould (b, 5.); Upper Elton Formation, locality 51. **6.** pygidium BU 4898, dorsal view, Upper Leintwardine Formation, locality 52.

Figure 7. *Cryphina andegavensis* Oehlert, 1889. latex cast of external mould of pygidium BGS GSM 51866 Přídolí of the Little Missenden Borehole (370 metres), Buckinghamshire, SU 902 982.

Figures 8-15. *Ananaspis*? *nuda* (Salter, 1864). **8-9.** cephalon LM G3064, dorsal (8.) and lateral (9.) view; Elton Group, Upper Millichope, Shropshire. **10.** cephalon BGS 19386, dorsal view, early Ludlow, Vinnal Hill. **11-12.** cephalon BU 4899, dorsal (11.) and lateral (12.) view; ?Irfon Formation, locality 47D. **13.** cephalon BU 4900, dorsal view; Middle Elton Formation, locality 3. **14.** pygidium BU 4901, dorsal view; Middle Elton Formation, locality 3. **15.** latex cast of external mould of cephalon and part thorax BU 4902, dorsal view; ?Irfon Formation, locality 47E.

All scale bars represent 2 mm.

PLATE 19



EXPLANATION OF PLATE 20

Figures 1-2. *Ananaspis*? *nuda* (Salter, 1864). **1.** complete specimen BGS GSM 19405, dorsal view; early Ludlow, Cut Throat Lane, near Ledbury. **2.** pygidium BU 4950, dorsal view; Middle Elton Formation, locality 3.

Figure 3. Cheirurinae indet. A. cephalon with attached segments BU 4807, dorsal view; Elton Group, locality 42.

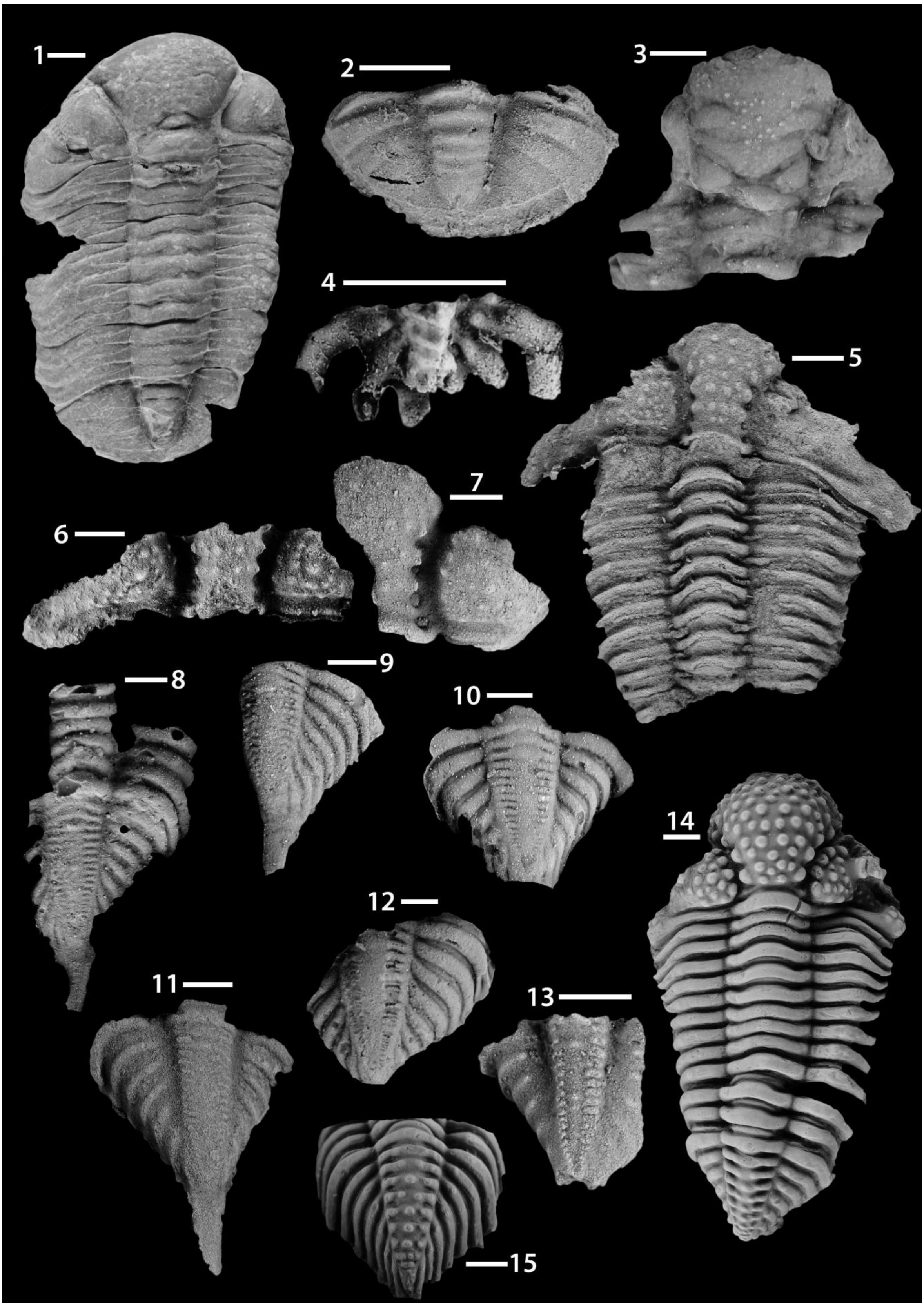
Figure 4. Cheirurinae indet. B. pygidium BU 4808, dorsal view; Lower Elton Formation, locality 15.

Figures 5-13. *Encrinurus stubblefieldi* Tripp, 1962. 6-9, 12 and 13 are from the Lower Leintwardine Formation. **5.** Paratype cephalothorax BGS GSM 36844, dorsal view; 'Upper Ludlow Shales', N.E. of Pillard's Barn, Shropshire. **6.** cephalon BU 4903, dorsal view; locality 22. **7.** cephalon BU 4904, dorsal view; locality 22. **8.** latex cast of external mould of thoracopygidium BU 4905, dorsal view; locality 24. **9.** latex cast of external mould of pygidium BU 4906, dorsal view; locality 24. **10.** latex cast of external mould of pygidium BU 4908, dorsal view; Hafod Fawr Formation, locality 48. **11.** pygidium BGS GSM 34687, dorsal view; Whitcliffe Group, Whitcliffe, Ludlow. **12.** latex cast of external mould of pygidium BU 4907, dorsal view; locality 24. **13.** pygidium BU 4909, dorsal view; locality 25.

Figures 14-15. *Balizoma variolaris* (Brogniart, 1822). Neotype complete specimen BU 55, dorsal view; from the Much Wenlock Limestone Formation, Dudley.

All scale bars represent 2 mm.

PLATE 20



EXPLANATION OF PLATE 21

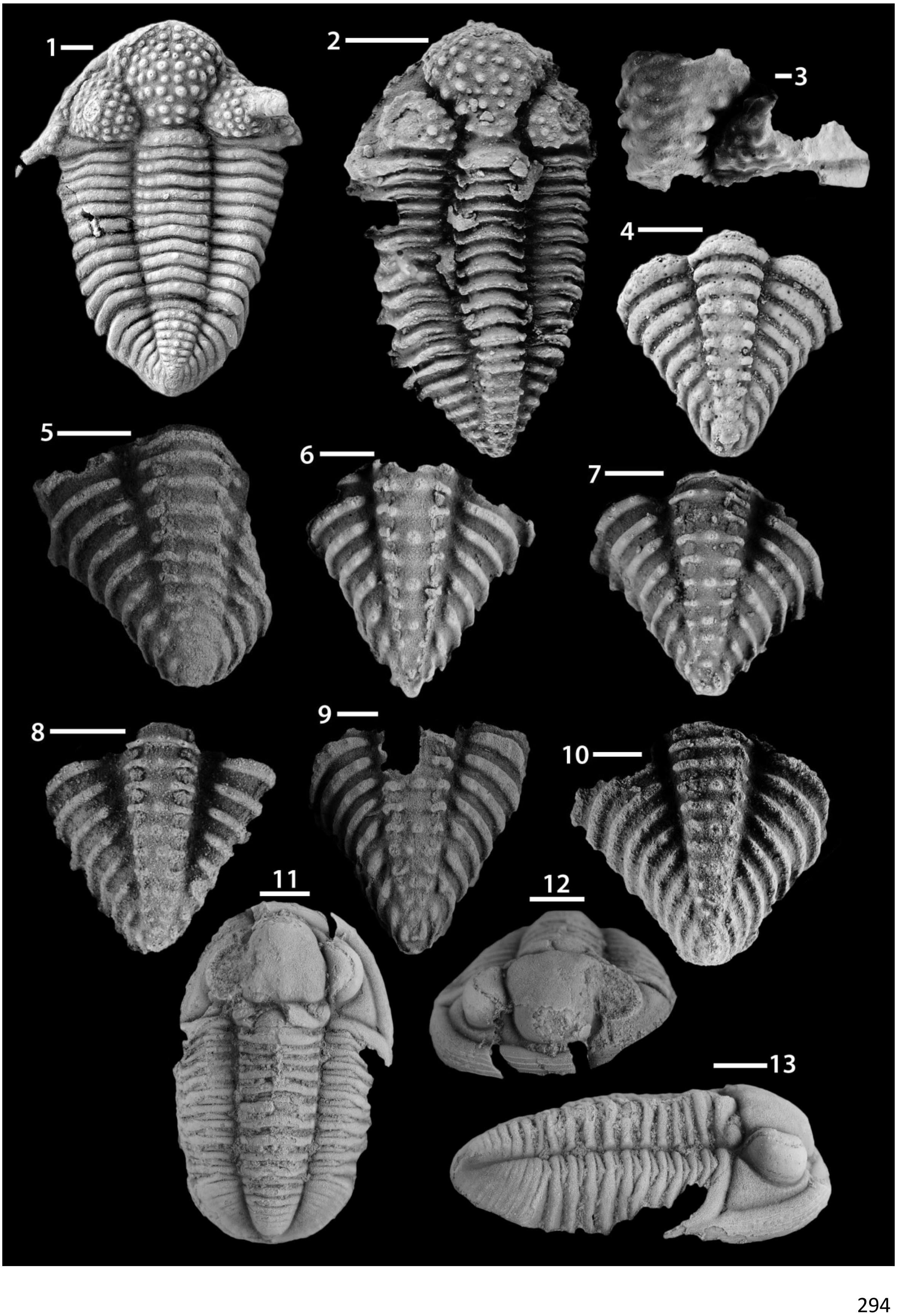
Figure 1. *Balizoma variolaris* (Brogniart, 1822). complete specimen NHM 59035; dorsal view; Lower Elton Formation, Dudley. Photographed by Phil Crabb, copyright NHM.

Figures 2-10. *Balizoma obtusus rosensteinae* (Tripp *et al.*, 1977). 2, 4, 7-8, and 9 are from the Lower Bringewood Formation. **2.** complete specimen BU 4910, dorsal view, locality 50. **3.** cephalon BU 4911, dorsal view; Lower Leintwardine Formation, locality 22. **4.** Holotype pygidium BM It14139, dorsal view, Mortimer Forest, near Ludlow. **5.** pygidium BGS GSM 36848, dorsal view; Lower Whitcliffe Formation, Whitcliffe, Ludlow. **6.** pygidium SM A37.371, dorsal view; from the early Ludlow (?Bringewood Group) of Ledbury. **7.** pygidium BU 4912, dorsal view, locality 50. **8.** pygidium BU 4913, dorsal view, locality 50. **9.** pygidium BGS FG 1533, dorsal view, from an exposure in a field 1140 metres from St Mary's Church Llanfair Kilgeddin, Gwent. **10.** pygidium BU 4914, dorsal view; Lower Leintwardine Formation, locality 22.

Figures 11-13. *Proetus concinnus* (Dalman, 1827). complete specimen NMW 75.25G.398; dorsal (11.), lateral (12.), and anterior (13.) views; Much Wenlock Limestone Formation (*ludensis* Biozone), 274 m west of Wetmoor, Wenlock Edge.

All scale bars represent 2 mm.

PLATE 21



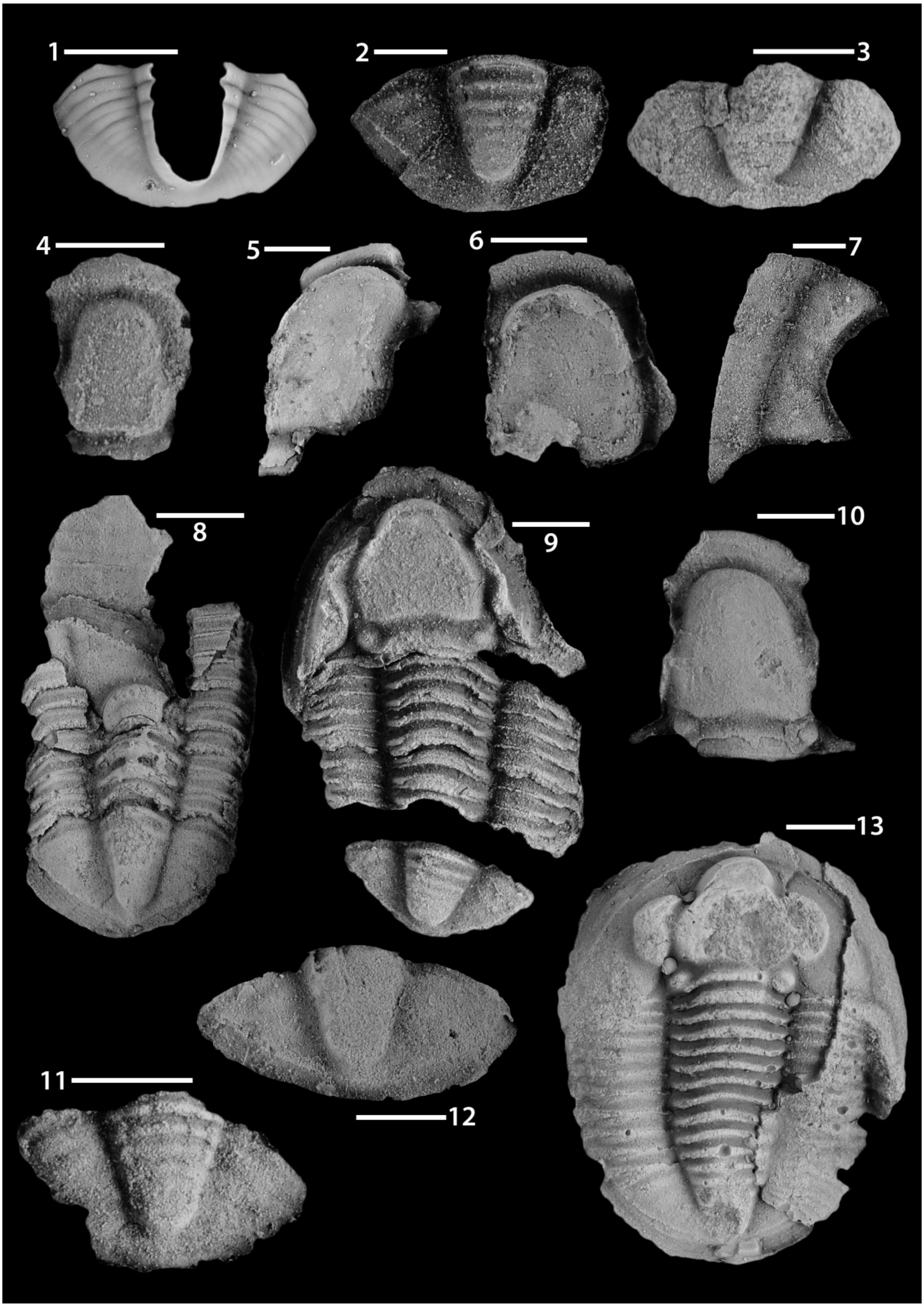
EXPLANATION OF PLATE 22

Figures 1-7. *Proetus* cf. *concinnus* (Dalman, 1827). **1.** pygidium BU 4915, dorsal view; Lower Elton Formation, locality 27. **2.** pygidium BU 4916, dorsal view; Lower Elton Formation, locality 15. **3.** pygidium BU 4917, dorsal view; Lower Elton Formation, locality 27. **4.** cranidium BU 4918, dorsal view; Lower Elton Formation, locality 15. **5.** cranidium BU 4919, dorsal view; Lower Elton Formation, locality 9. **6.** cranidium BU 4920, dorsal view, Upper Elton Formation, locality 33. **7.** librigena BU 4921, dorsal view; Lower Elton Formation, locality 15.

Figures 8-13. *Proetus* (s.l.) *astringens* Owens, 1973. 8-10 are from the Upper Elton Formation, exposure in ditch on south side of Worcester-Hereford road (A4103), near Storridge, Herefordshire, SO 743 480. 12-13 are from Lower Bringewood Formation, Woodbury Quarry, 229-356 metres south-southwest of Woodbury Old farm, 1 mile northeast of Shelsley Beauchamp, Worcester, SO 742 638. **8.** Paratype near complete specimen NMW 71.6G.280, dorsal view. **9.** Holotype near complete specimen NMW 71.6G.494, dorsal view. **10.** Paratype cranidium NMW 71. 6G.279, dorsal view. **11.** Paratype pygidium NMW 71.6G.442, dorsal view; Lower Bringewood Formation, forestry track exposure on southwest side of Mary Knoll Valley, 2 miles southwest of Ludlow Church, SO 486 728. **12.** Paratype pygidium NMW 71.6G.163, dorsal view. **13.** Paratype complete specimen NMW 73.7G.1, dorsal view.

All scale bars represent 2 mm.

PLATE 22



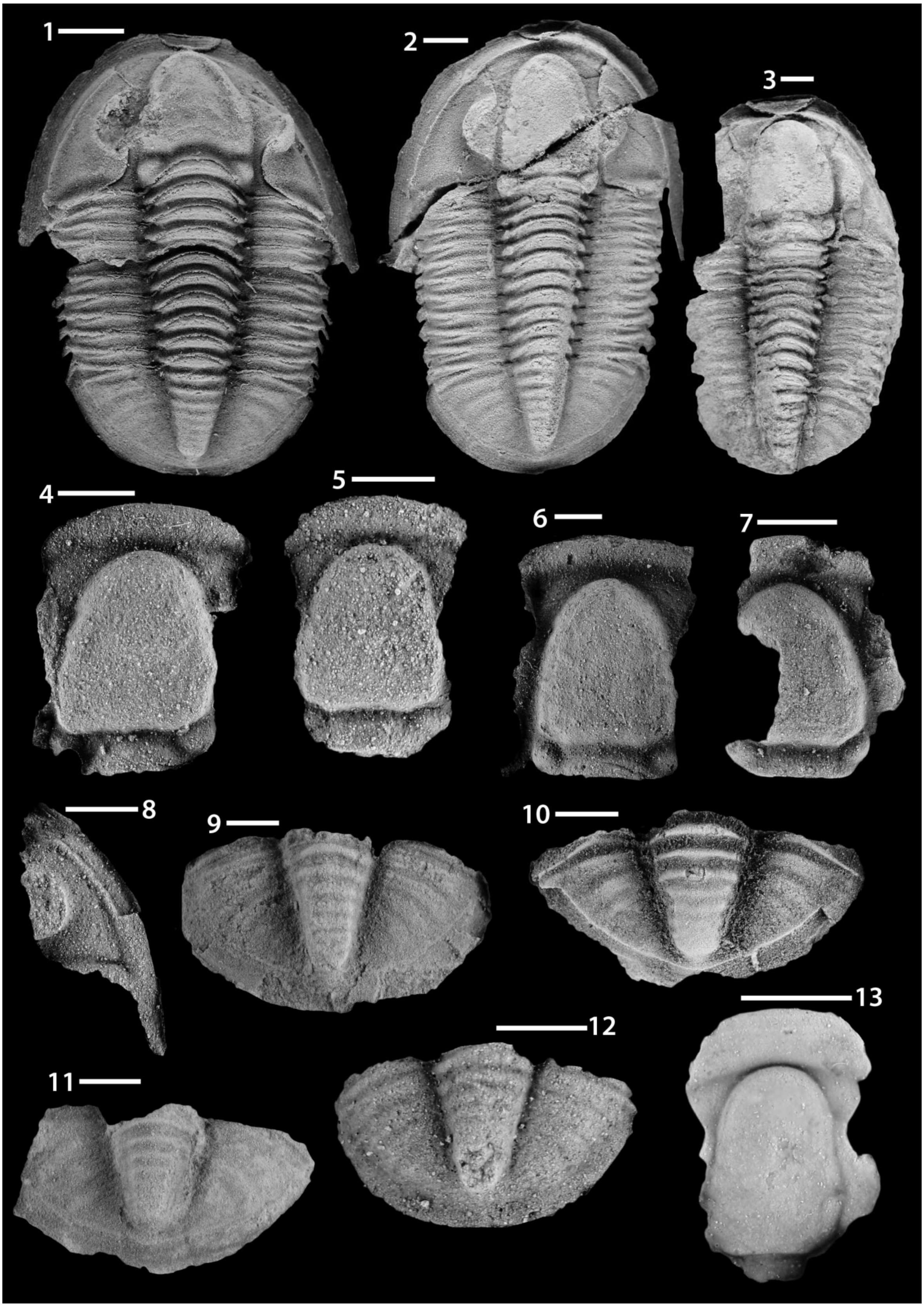
EXPLANATION OF PLATE 23

Figures 1-12. *Plesiowensus obconicus* Lindström, 1885. 4-8 and 12 are from the Lower Leintwardine Formation. **1.** complete specimen NMW 83.31G.318a, dorsal view; Upper Leintwardine Formation, temporary trench west of Llangegfedd Reservoir, Gwent, ST 322 982- 322 985. **2.** complete specimen BGS GSM 36859, dorsal view; late Ludlow, Usk Castle. **3.** complete specimen BGS GSM 36856, dorsal view; Ludlow, Kendal, Westmoreland. **4.** cranidium BU 4922, dorsal view, locality 20. **5.** cranidium BU 4923, dorsal view, locality 22. **6.** cranidium BU 4924, dorsal view, locality 22. **7.** cranidium BU 4925, dorsal view, locality 24. **8.** librigena BU 4926, dorsal view, locality 24. **9.** pygidium BGS GSM 36860, dorsal view; late Ludlow, southwest of Hazle, near Woolhope. **10.** pygidium BU 4927, dorsal view; Lower Elton Formation, locality 15. **11.** pygidium BGS GSM 36861, dorsal view; late Ludlow, southwest Hazle, near Woolhope. **12.** pygidium BU 4928, dorsal view; Lower Leintwardine Formation, locality 24.

Figure 13. *Plesiowensus* aff. *obconicus* Lindström, 1885. latex cast of external mould of cranidium BU 4929, dorsal view; Upper Bringewood Formation, locality 13.

All scale bars represent 2 mm.

PLATE 23



EXPLANATION OF PLATE 24

Figures 1-9. *Plesiowensus raymondi* sp. nov. from the Lower Leintwardine Formation. **1.** Holotype cranidium BU 4809, dorsal view, locality 24. **2.** Cranidium BU 4810, dorsal view, locality 24. **3-4.** cranidium BU 4811, dorsal (3.) and anterior (4.) views, locality 22. **5.** latex cast of external mould of cranidium BU 4812, dorsal view, locality 24. **6.** latex cast of external mould of pygidium BU 4813, dorsal view, locality 24. **7.** pygidium BU 4814, dorsal view, locality 22. **8.** pygidium BU 4930, dorsal view, locality 22. **9.** librigena BU 4816, dorsal view, locality 24.

Figures 10-13. *Warburgella* (*Owensella*) *ludlowensis* (Alberti, 1967). **10.** cranidium BU 4932, dorsal view; Lower Leintwardine Formation, locality 22. **11.** complete specimen NMW 71.21.G1, dorsal view; Lower Leintwardine Formation, old quarry debris on south side of forestry track, southeast of Mary Knoll Valley, 2 miles southwest of Ludlow, SO 489 725. **12.** cranidium NHM It 8819, dorsal view; quarry on Diddlebury-Middle Hope Road, 201 metres northeast of Ferhall Mill, Wenlock Edge, SO 5006 8666; photographed by Phil Crabb, copyright NHM. **13.** cranidium NMW 72.239.1, dorsal view; Bailey Hill Formation (*leintwardinensis* Biozone), higher part of Cwm Jenkin, *c*. 3 miles west-northwest of Knighton, Radnorshire, SO 235 730.

Figure 14. *Warburgella* (*Warburgella*) aff. *baltica* Alberti, 1963. Cranidium BU 4931, dorsal view; Lower Elton Formation, locality 15.

All scale bars represent 2 mm.

PLATE 24

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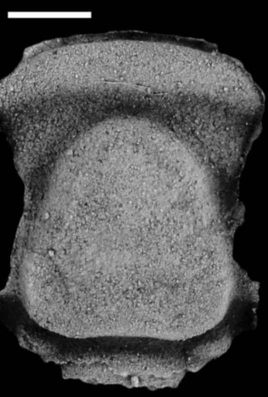

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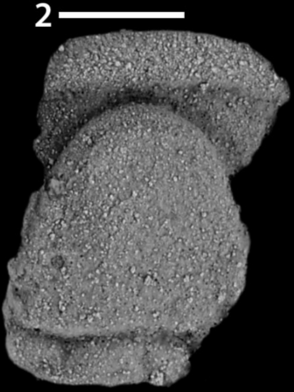

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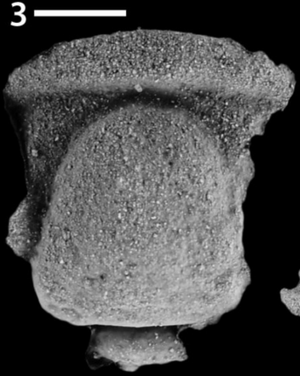

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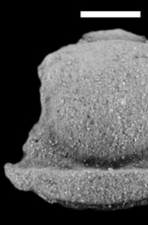

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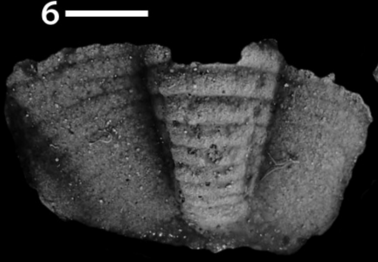

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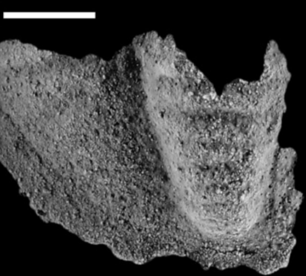

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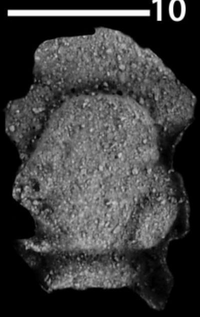

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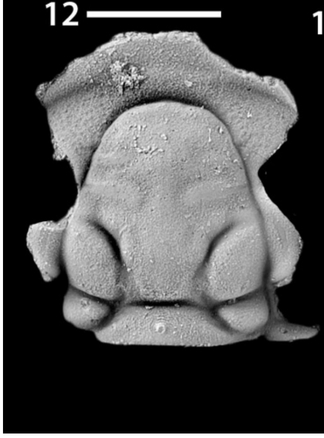

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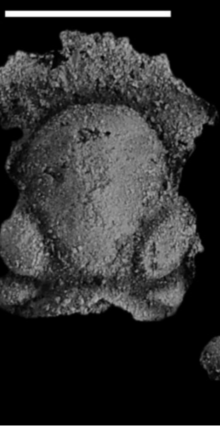

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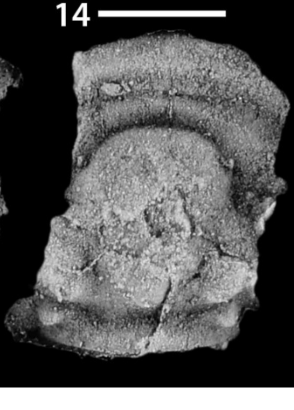


EXPLANATION OF PLATE 25

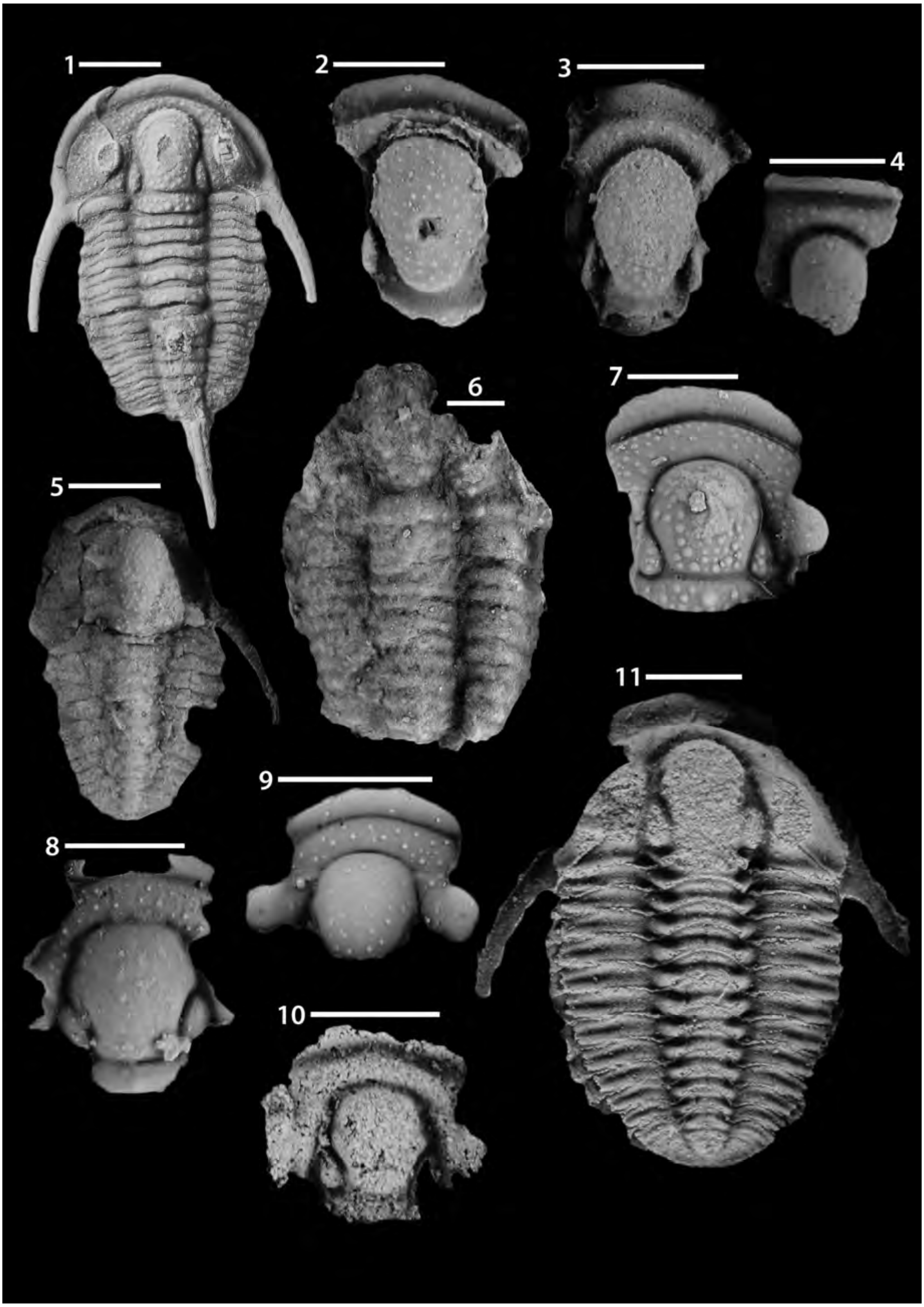
Figure 1. *Cyphaspis elachopos* Thomas, 1978. Holotype near complete specimen NHM It 14158, dorsal view; Coalbrookdale Formation, near Dudley. Photographed by Phil Hurst, copyright NHM.

Figures 2-4, ?5, 6. *Cyphaspis* sp. **2.** cranidium BU 4817, dorsal view, Upper Elton Formation, locality 51. **3.** cranidium BGS DEW 3036, dorsal view, Elton Group, from a stream section, 1.69 km west of the church, Coed-y-paen, ST 32299978, Gwent. **4.** cranidium BU 4818, dorsal view, Upper Elton Formation, locality 51. **5.** complete specimen BGS DEX 8256, dorsal view; Elton Group in a stream 690 m from the Downs, Much Wenlock. **6.** cephalothorax BU 4819, dorsal view; Lower Leintwardine Formation, locality 25.

Figures 7-11. *Maurotarion lanei* sp. nov. **7.** Holotype cranidium BU 4820, dorsal view; Upper Elton Formation, locality 16. **8.** cranidium BU 4822, dorsal view; Upper Elton Formation, locality 16. **9.** cranidium BU 4821, dorsal view; Upper Elton Formation, locality 16. **10.** cranidium BU 4824, dorsal view; Hafod Fawr Formation, Cwar Glass Member, locality 44. **11.** complete specimen BGS DEZ 1638, dorsal view; Elton Group, Mortimer Forest.

All scale bars represent 2 mm.

PLATE 25



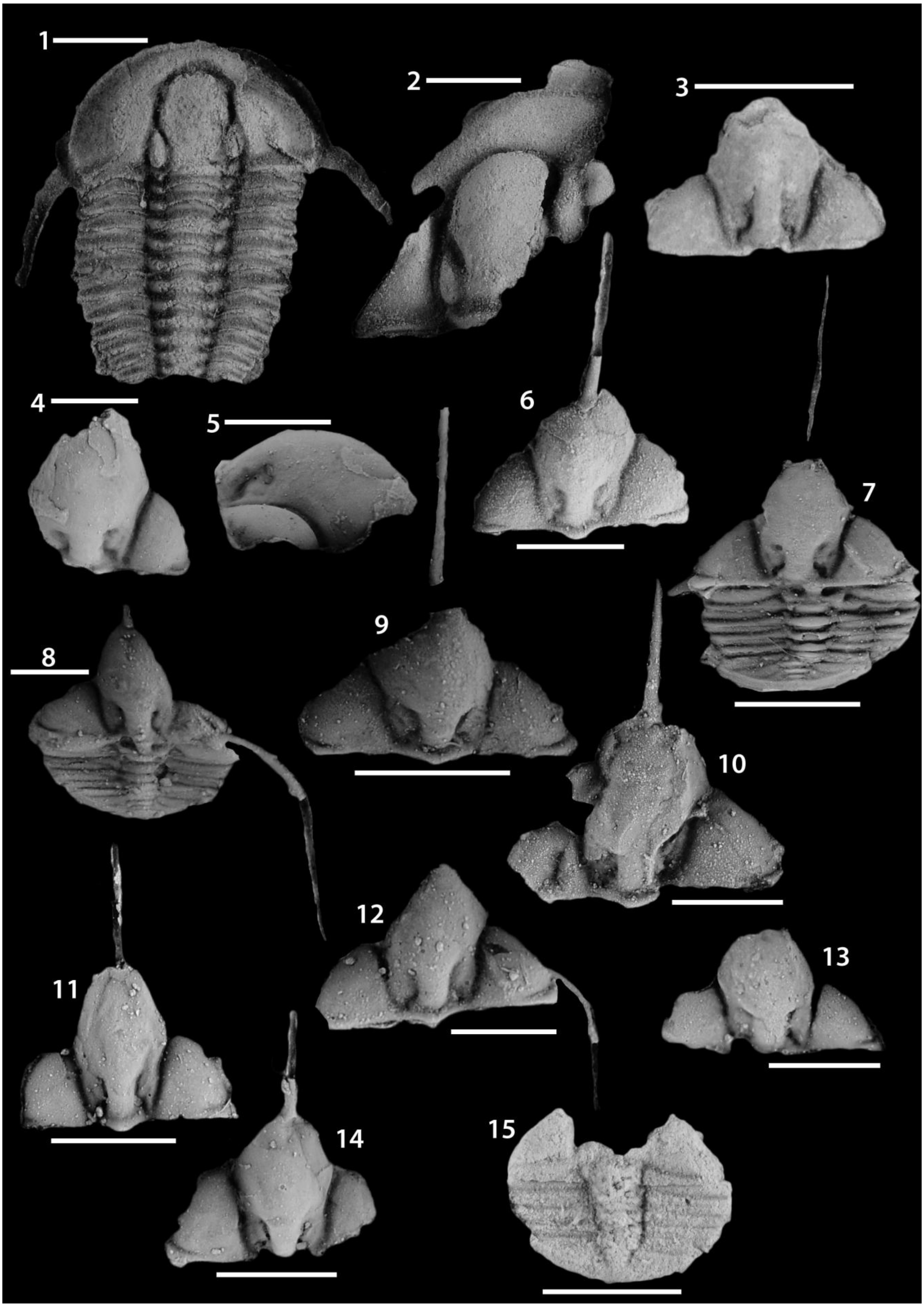
EXPLANATION OF PLATE 26

Figures 1-2. *Maurotarion* cf. *lanei*. **1.** cephalothorax BGS GSM 36741, dorsal view; early Ludlow, Shropshire, exact locality unknown. **2.** cranidium BGS HN 384, dorsal view; Bailey Hill Formation in a quarry 970 metres at 117 degrees southeast from the Winkles (Trig Point), Bishops Castle.

Figures 3-15. *Raphiophorus parvulus* (Forbes, 1848). 6-14 are from the Middle Elton Formation. **3.** Lectotype cephalon BGS GSM 36751, dorsal view; Ludlow (?Gorstian), High Vinnals, southwest of Ludlow. **4-5.** cephalon BU 4933, dorsal (4.), and side (5.) views; Upper Elton Formation, locality 16. **6.** cephalon BU 4934, dorsal view, locality 4. **7.** near complete specimen BU 4935, dorsal view, locality 1. **8.** near complete specimen BU 4936, dorsal view, locality 1. **9.** cephalon BU 4937, dorsal view, locality 1. **10.** cephalon BU 4938, dorsal view, locality 1. **11.** cephalon BU 4939, dorsal view, locality 5. **12.** cephalon BU 4940, dorsal view, locality 1. **13.** cephalon BU 4941, dorsal view, locality 8. **14.** cephalon BU 4942, dorsal view, locality 1. **15.** near complete specimen BGS GSM 36750, dorsal view; Ludlow (?Gorstian), High Vinnals, southwest of Ludlow.

All scale bars represent 2 mm.

PLATE 26



CHAPTER FOUR

SILURIAN TRILOBITE DIVERSITY:
BIOEVENTS AND SEA LEVEL

4.1 INTRODUCTION

4.1.1 *Silurian episodes and events*

THE Silurian is the shortest system in the Phanerozoic, spanning only *c.* 27.7 Ma (Ogg *et al.* 2008), and traditionally it has been regarded as a time of environmental and biological stability. Recent studies, however, have shown that several bioevents occurred during the Silurian, associated with abrupt and pronounced changes in the ocean-atmosphere system and perturbations in the global carbon cycle (Calner 2008). Based on changes in the conodont faunas and associated lithologies of Gotland. Jeppsson (1990) suggested a model that described shifts between two stable climatic states, termed Primo and Secundo episodes. The former is associated with low atmospheric CO_2, humid low latitudes, and cold high latitudes while the latter is characterised by higher atmospheric CO_2, dry low latitudes, and warmer high latitudes. Deep oceanic water in Primo episodes was produced by the sinking of cold dense water in cold high latitudes, resulting in oxygenated deep-waters. In Secundo episodes deep oceanic water formed from the sinking of saline rich water at intermediate latitudes, resulting in a salinity stratified ocean and anoxic bottom waters (see Jeppsson 1990 and Calner 2008 for a full discussion). Several Primo and Secundo episodes have been described in detail for the Llandovery (Aldridge *et al.* 1993), Wenlock (Aldridge *et al.* 1993, Jeppsson *et al.* 1995), and late Silurian (Jeppsson and Aldridge 2000). Bioevents occur between many of the Primo and Secundo episodes predominantly affecting the graptolites and conodonts.

Global diversity studies on Silurian graptolites (Melchin *et al.* 1998 and references therein) have recognised a total of nine short-lived bioevents characterized by elevated extinction rates and drops in diversity. The Sandvika Event, occurring in the late Aeronian (*sedgwickii* Biozone), and the Ireviken Event, in the late Telychian (*lapworthi* Biozone) to early Sheinwoodian (*centrifugus-murchisoni* Biozone), are known to affect trilobites (Chatterton *et al.* 1990, Calner 2008).

4.1.2 *Trilobite diversity*

Silurian trilobites were globally distributed (Adrain *et al.* 2000), commonly constituting a significant percentage of fossil assemblages, and displayed a substantial degree of variation in morphology and mode of life (Thomas and Lane 1984). Trilobites are known to occur in a range of Silurian environments (Thomas 1979, Chlupáč 1987, Thomas and Lane 1999), from relatively deep basinal facies to shallow nearshore facies. Due to ecdysis and their mineralised exoskeleton trilobites have a high preservation potential (Foote and Raup 1996) making them a useful group for diversity studies (Tarver *et al.* 2007). Adrain *et al.* (2000) described trilobite species richness at global and local levels for the Silurian; this was plotted at the Series level, and thus it is not sufficiently detailed to assess the relationships between Silurian climate and trends in trilobite diversity.

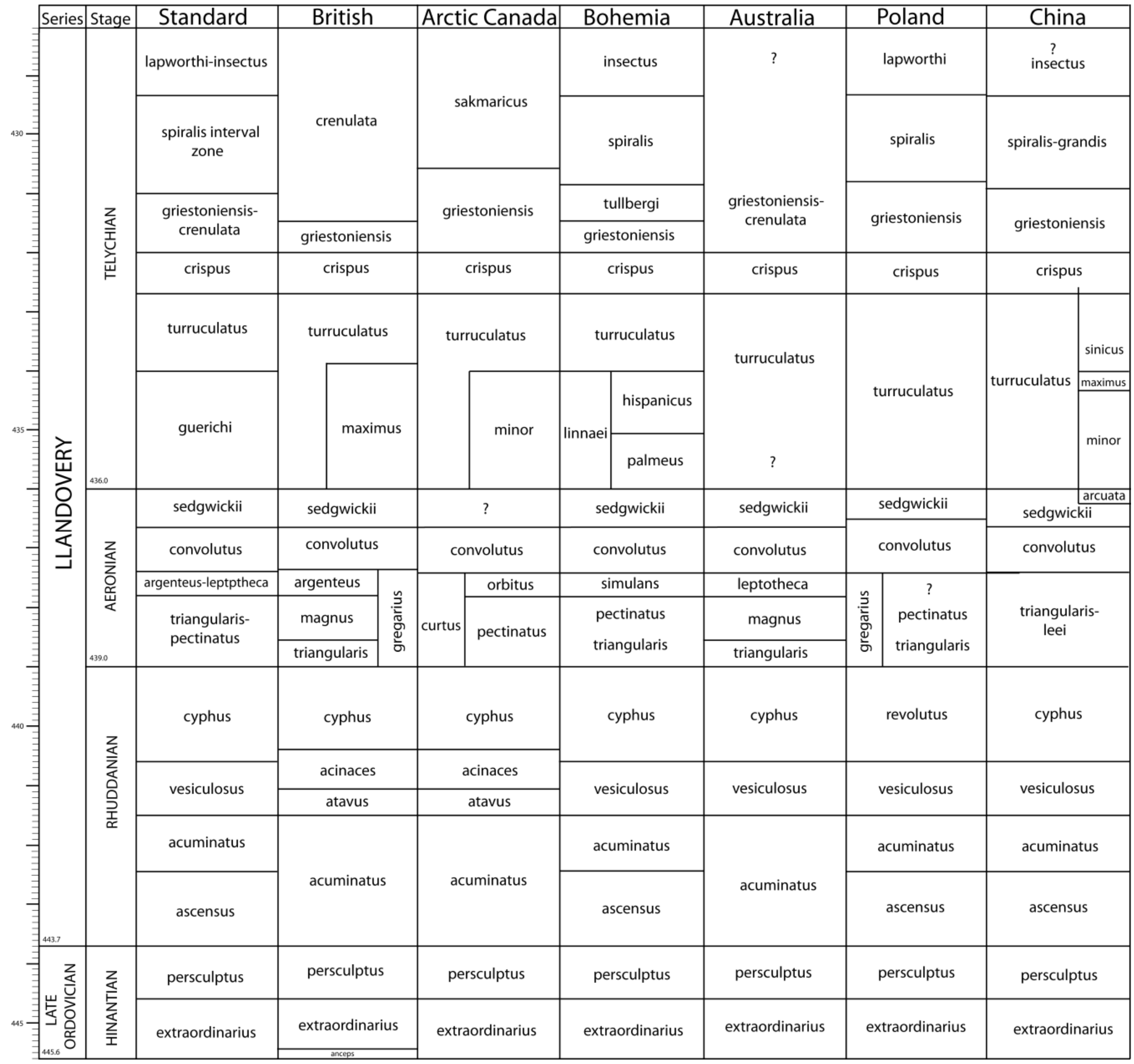
Based on an extensive literature survey, a global trilobite species diversity curve is plotted against the Hirnantian-Silurian standard graptolite biozone scheme for the first time. The dataset of the present study contains over one thousand trilobite species comprising around three hundred genera. Problems associated with diversity studies such as correlation, stratigraphical precision, taxonomic bias, preservation bias, sampling bias, and effects of abundance on diversity are discussed below. The diversity study presented in this chapter is preliminary, and although the effects sampling and abundance are acknowledged in this chapter they are not corrected for directly here. Several trilobite bioevents are documented, many of which have not been recognised previously, and are associated with falls in sea level.

4.2 MATERIAL AND METHODS

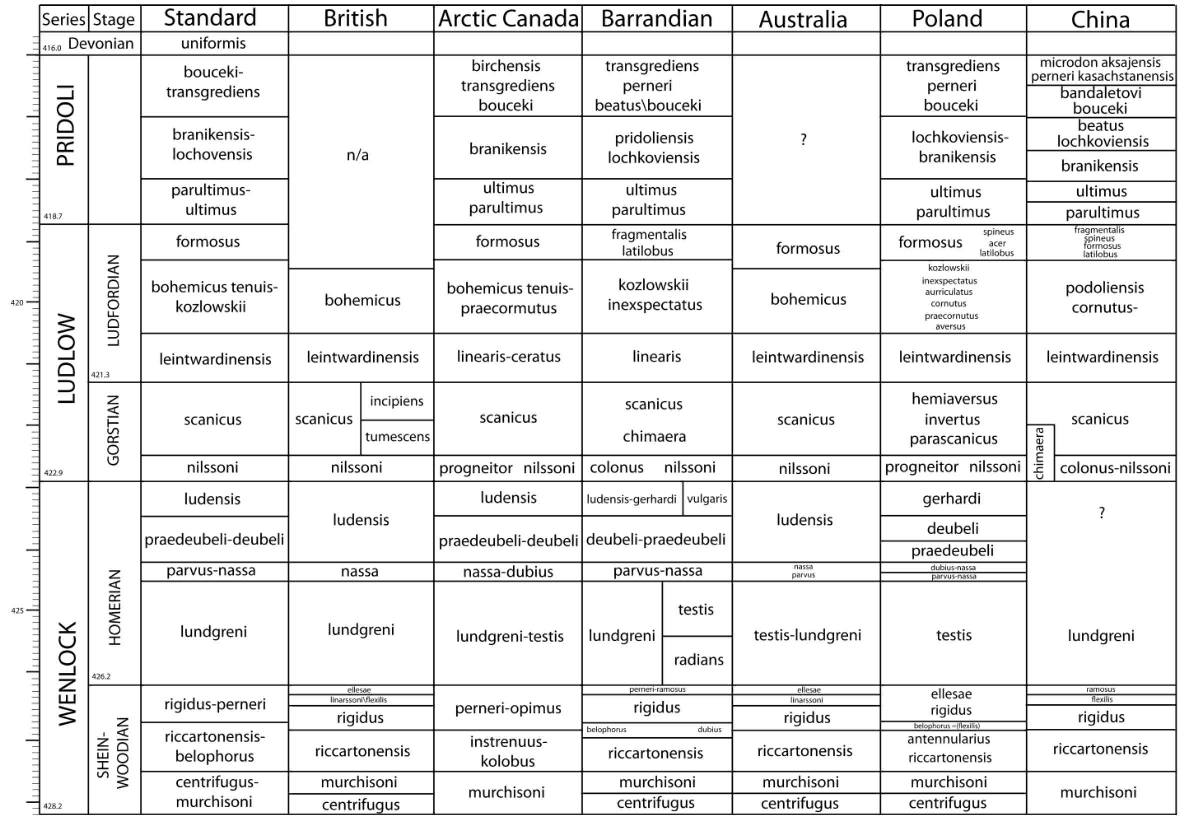
4.2.1 *Correlation*

Appropriate time bins are necessary for any high-resolution diversity study and these ideally should be short and of equal duration (Sepkoski and Koch 1996, Alroy *et al.* 2008, Lio *et al.* 2010, Cermeño 2012). Due to lack of precise dating this is very difficult to achieve for lower Palaeozoic studies (Melchin *et al.* 2004), however. Graptolite biozones are not of the same length, but represent the shortest widely correlatable intervals that can be recognized in the Silurian (Melchin *et al.* 2004), with an average duration of 1 Ma (based on Ogg *et al.* 2008). Fluctuations in sea-level and palaeoclimate can also be considered at this resolution (Johnson 2006, Calner 2008, Ogg *et al.* 2008, and see Johnson 2010 for a review). For these reasons trilobite diversity is plotted against the standard graptolite biozones. To plot such a diversity curve requires trilobite assemblages from around the world to be dated to one or more of the standard graptolite biozones. This is not easily achieved, as local areas may have their own biozones, or biozones with the same name do not represent exactly the same age in different areas (Melchin *et al.* 1998, Loydell

2012). Several correlation schemes exist (Štorch 1994, Melchin *et al.* 1998, Lenz and Kozłowska-Dawidzikuk 2002, Lenz and Kozłowska-Dawidzikuk 2004, Štorch and Massa, 2006) and these are summarised in Text-figures 4.1 and 4.2. The regional biozones are correlated against the global standard graptolite biozones, which were originally defined by Koren *et al.* 1996 and refined by Melchin *et al.* (2004) and Ogg *et al.* (2008).



Text-Figure 4.1. Correlation of graptolite biozones for principle Hirnantian and Llandovery outcrop areas. Based on Štorch (1994), Koren *et al.* (1996), Melchin *et al.* (1998), Lenz and Kozłowska-Dawidzikuk (2002), Štorch and Massa (2006), Ogg *et al.* (2008), and Loydell (2012).



Series	Stage	Standard	British	Arctic Canada	Barrandian	Australia	Poland	China
416.0 Devonian		uniformis						
PRIDOLI		bouceki-transgrediens	n/a	birchensis transgrediens bouceki	transgrediens perneri beatus\bouceki	?	transgrediens perneri bouceki	microdon aksajensis perneri kasachstanensis bandaletovi bouceki
		branikensis-lochovensis		branikensis	pridoliensis lochkoviensis		lochkoviensis-branikensis	beatus lochkoviensis branikensis
418.7		parultimus-ultimus		ultimus parultimus	ultimus parultimus		ultimus parultimus	ultimus parultimus
LUDLOW	LUDFORDIAN	formosus		formosus	fragmentalis latilobus	formosus	formosus spineus acer latilobus	fragmentalis spineus formosus latilobus
420		bohemicus tenuis-kozlowskii	bohemicus	bohemicus tenuis-praecormutus	kozlowskii inexspectatus	bohemicus	kozlowskii inexspectatus aurriculatus cornutus praecornutus aversus	podoliensis cornutus-
	421.3	leintwardinensis	leintwardinensis	linearis-ceratus	linearis	leintwardinensis	leintwardinensis	leintwardinensis
	GORSTIAN	scanicus	scanicus incipiens tumescens	scanicus	scanicus chimaera	scanicus	hemiaversus invertus parascanicus	scanicus
422.9		nilssoni	nilssoni	progneitor nilssoni	colonus nilssoni	nilssoni	progneitor nilssoni	chimaera colonus-nilssoni
WENLOCK	HOMERIAN	ludensis	ludensis	ludensis	ludensis-gerhardi vulgaris	ludensis	gerhardi	?
		praedeubeli-deubeli		praedeubeli-deubeli	deubeli-praedeubeli		deubeli praedeubeli	
		parvus-nassa	nassa	nassa-dubius	parvus-nassa	nassa parvus	dubius-nassa parvus-nassa	
425	426.2	lundgreni	lundgreni	lundgreni-testis	lundgreni testis radians	testis-lundgreni	testis	lundgreni
	SHEIN-WOODIAN	rigidus-perneri	ellesae linarssoni\flexilis rigidus	perneri-opimus	perneri-ramosus rigidus	ellesae linarssoni rigidus	ellesae rigidus	ramosus flexilis rigidus
		riccartonensis-belophorus	riccartonensis	instrenuus-kolobus	belophorus dubius riccartonensis	riccartonensis	belophorus =(flexilis) antennularius riccartonensis	riccartonensis
428.2		centrifugus-murchisoni	murchisoni centrifugus	murchisoni	murchisoni centrifugus	murchisoni centrifugus	murchisoni centrifugus	murchisoni

Text-Figure 4.2. Correlation of graptolite biozones for principle Wenlock, Ludlow, and Přídolí outcrop areas. Based on Štorch (1994), Koren *et al.* (1996), Melchin *et al.* (1998), Lenz and Kozłowska-Dawidzikuk (2002), Lenz and Kozłowska-Dawidzikuk (2004), Ogg *et al.* (2008), and Loydell (2012).

Where graptolites do not occur, conodont biozones of Ogg *et al.* (2008) are used here to assign trilobite taxa to an equivalent graptolite biozone. There are several regional biozones which are equal to more than one standard graptolite biozone, for example, the *perneri-opimus* Biozone of Canada (= upper *riccartonensis-belophorus and perneri-opimus* standard biozones). In such circumstances, the trilobite taxa concerned are plotted in all the equivalent standard graptolite biozones. In the late Silurian of Britain, the last graptolites to occur represent the Ludfordian *bohemicus* Biozone making it difficult to correlate younger British Silurian faunas with those elsewhere. No graptolites are known from the Upper Whitcliffe Formation but conodonts of the Ludfordian *O. snajdri* and *O. crispa* biozones (Märss and Miller 2004) occur, which are equivalent to the *bohemicus tenuis-kozlowskii* and *formosus* graptolite biozones respectively (Sadler *et al.* 2009). For the trilobites occurring in the Upper Whitcliffe Formation, it is not known which conodont biozones they occur in, and they are assumed to span the whole formation. The trilobite fauna occurring in the lower Kirkby Moor Formation is roughly the same age as those in the Upper Whitcliffe Formation (Shaw 1971). In areas such as North Greenland, USA, and South America the ages of formations occurring there have been correlated to British or standard graptolite biozones (for example Berry and Boucot 1970, Berry and Boucot 1972, and Hurst 1980), and are not included in the correlation charts.

4.2.2 *Data collection*

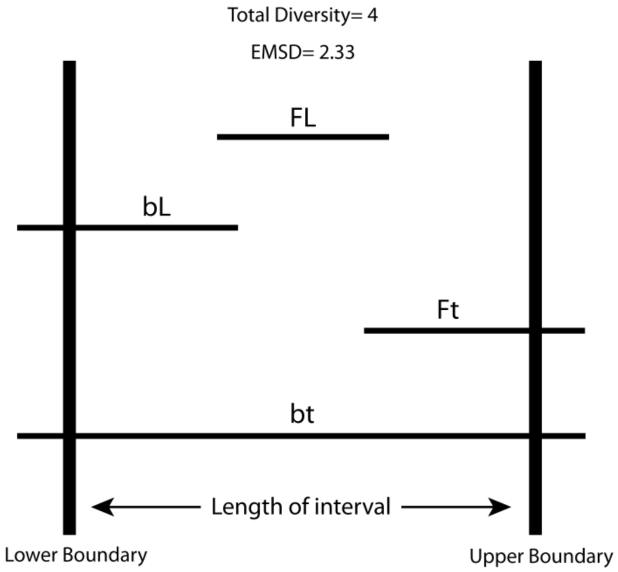
This study is based on a global dataset of Hirnantian and Silurian trilobite occurrences derived from the published literature and the Paleobiology Database. Although the present author found the Paleobiology Database to be a useful starting point, the use of such a database is not sufficient on its own to reconstruct the high resolution diversity curve intended here. The Paleobiology database was surveyed in 2009 and then many of the trilobite taxa were missing, stratigraphic ranges were incomplete, synonyms were lacking, and there were stratigraphic errors. Trilobite stratigraphic ranges are plotted herein mainly by consulting published monographs, systematic papers, faunal lists, geological field guides, and stratigraphic charts. Occurrences in the literature are checked against the most recent stratigraphic studies available to ensure that the ages of each fauna are up to date. The literature survey is supplemented by the authors own work on the British Ludlow, the study of Silurian trilobite collections in the British Geological Survey (Keyworth), Lapworth Museum of Geology (University of Birmingham), National Museum of Wales (Cardiff), Natural History Museum (London), Naturhistoriska riksmuseet (Stockholm), Sedgwick Museum (Cambridge), Oxford University Museum, Ludlow Museum (Shropshire), and discussion with staff in those institutions. The resulting database contains species occurrences (localities and formations/members), synonymy lists, and details of each formation (stratigraphic extent and formation synonyms).

First and last appearance data (= FAD and LAD) of 1082 species have thus been determined. Additionally the presence/absence of each taxon has been recorded for each standard graptolite biozone.

4.2.3 *Measuring biodiversity and bioevents*

Taxic diversity curves commonly represent total diversity (Feist 1991, Sepkoski 1993, 1997, Chlupáč 1994, Melchin *et al.* 1998, Sheehan 2001, Fröbisch 2008) or estimated mean standing diversity, EMSD (Foote 2000*a*, Hammer 2003, Fröbisch 2008, Kaminski *et al.* 2010). EMSD is equivalent to 'Balanced Total Diversity' (BTD) of Nestor (2009). Total diversity is simply the total number of taxa in a given interval. This method is prone to biases, however, such as variations in interval length, turnover, preservation, and sampling effects (for example Harper 1975, Miller 2000, Foote 2000*a*, Alroy *et al.* 2001, Smith 2001, Bambach *et al.* 2004, Smith and McGowan 2008, Mannion *et al.* 2011). Additionally, total diversity assumes that all taxa in an interval span its entire duration. The geological time-scale is an artificial construct, and what needs to be established is the distribution of taxa in time- the average diversity at any given point. Simply dividing the total diversity by the interval length (average number of taxa/Ma) again assumes that diversity throughout the interval is even.

EMSD tries better to estimate the distribution of taxa within an interval by weighting taxa (see Text-Figure 4.3). For consistency, abbreviations (bt, Ft, bL, and FL) used in this chapter follow the usage of Foote (2000*a*).



Text-Figure 4.3. Classes of taxa: range through (bt), upper boundary cross (Ft), lower boundary cross (bL), and singleton (FL). Adapted from Foote (2000*a*, fig. 1).

Taxa crossing both the lower and upper boundaries (bt) must span the entire interval and so are given a weighting of 1.0. Those taxa crossing the upper (Ft) or lower boundaries (bL) only are estimated to occur in at least half of the interval and are given a weighting of 0.5. It has been suggested by Foote (2000*a*) that taxa confined to an interval (singletons, or FL) should be omitted, as they are more likely to be a result of preservation or collection biases. A high number of singletons within an interval could also reflect high turnover resulting in an overestimation of diversity. This works best when intervals are very short. However, longer intervals are more likely to contain singleton taxa that are not a result of biases and, if omitted, would result in much of the data being lost (Uhen and

Peyenson 2007). Omitting singletons also risks underestimating taxonomic rates (Fitzgerald and Carlson 2006, Fröbisch 2008). The present study follows the practice of Hammer (2003) whereby singletons are considered to occur in one third of the interval on average and are given a weighting of 0.33. The range through assumption is used also, where a taxon is assumed to occur in every interval between its FAD and LAD.

EMSD provides a better estimate of fossil diversity (Mihaljević *et al.* 2010) by minimising the effects of interval length and goes some way to correcting for preservation and sampling biases (Foote 2000*a*, Fröbisch 2008, Mihaljević *et al.* 2010). This is because taxa particularly vulnerable to these biases (FL, bL, Ft) are given the smallest weighting, while less affected taxa (bt) have a higher one. EMSD is used here, but total diversity (species richness) and sampled diversity is used in an attempt to identify biases (Peters and Foote 2001, Fröbisch 2008, Mannion *et al.* 2011).

Bioevents may not simply be associated with a drop in diversity but instead high turnover (Jablonski 2005, Fröbisch 2008), high origination and extinction rates, which on their own can represent a significant event (Azanza *et al.* 1999, Kostopoulos *et al.* 2007). High extinction rates followed by high origination rates in the same or following interval may not produce a noticeable drop in diversity, however, and drops in diversity can be due to falling originations rather than rising extinction rates (Bambach *et al.* 2004). To ensure these types of bioevents are not missed origination and extinction rates will be included also (Fröbisch 2008). Taxonomic rates are estimated using the Van Valen Metric (Van Valen 1984) and per-capita rate (Foote 2000*a*). Taxonomic rates, for the Van Valen Metric, are derived for a given interval by calculating the proportion of taxa (to EMSD) originating (number of FAD's) or going extinct (number of LAD's) divided by the interval length (Van Valen 1984). For originations (p) per-capita rates are defined as a function of the ratio between the number of taxa ranging through the interval and the number crossing the upper boundary; for extinctions (*q*) it is defined as a function of the ratio between the number of taxa ranging through the interval and those crossing the lower boundary (Foote 2000*a*). In both cases *p* and *q* are divided by the interval length (see Table 4.1).

Taxa class	Symbol
Singleton	FL
Lower boundary cross only	bL
Upper boundary cross only	Ft
Range through (both boundaries crossed)	bt
Metric	Definition
Total diversity (N_{tot})	$N_{FL} + N_{bL} + N_{Ft} + N_{bt}$
Sampled diversity (N_s)	N_{tot} – absent N_{bt}
Number of originations (N_o)	$N_{FL} + N_{Ft}$
Number of extinctions (N_e)	$N_{FL} + N_{bL}$
Estimated Mean Standing Diversity (EMSD)	$[N_{FL}/3] + [N_{bL}/2] + [N_{Ft}/2] + N_{bt}$
EMSD-St.	EMSD/formations N_{tot}
Van Valen metric origination	$([N_{FL} + N_{Ft}]/\mathrm{EMSD})$/interval length Ma
Van Valen metric extinction	$([N_{FL} + N_{bL}]/\mathrm{EMSD})$/interval length Ma
Estimated per-capita rate originations (*p*)	$-\ln(N_{bt}/[N_{Ft}+N_{bt}])$/interval length Ma
Estimated per-capita rate extinctions (*q*)	$-\ln(N_{bt}/[N_{bL}+N_{bt}])$/interval length Ma

Table 4.1. Table showing the classes of taxa and the different diversity metrics used in this chapter (based on Foote 2000*a*).

Foote (2000*a*, *b*) showed that his per-capita rate is a better estimate of taxonomic rates, compared with the Van Vallen Metric, since the later is influenced by internal length. The Van Vallen Metric includes singleton taxa which, as described above, are more prone to biases. Excluding singletons entirely may underestimate taxonomic rates (Fitzgerald and Carlson 2006), however. The present author follows Fröbisch (2008) where the Van Valen metric and per-capita rates are both included for comparison.

4.2.4 *Stratigraphic precision*

Not all of the taxa and formations in this diversity study can be assigned confidently to a standard graptolite biozone. In this study, taxa are randomly assigned to a biozone in intervals where the precise age is not known, thus limiting the effects of stratigraphic imprecision. For taxa with poorly localized FADs and LADs the range-through assumption is used, after randomly allocating a biozone for each, to fill in any apparent stratigraphic gaps. If species occur in a formation where the precise age is known it could be assumed they span the entire formation. This will work well if the formation in question ranges over only a few biozones, but if the duration of the formation is very long it would greatly extend a species stratigraphic range; this can result in artificially higher diversity in affected intervals (McGowan and Smith 2007). Based on the present dataset a trilobite species, on average, occurs in three standard graptolite biozones. For this exercise, if the formation occurs over more than three biozones the taxon is randomly assigned to three biozones from the formation's stratigraphic range.

Although stratigraphic resolution can bias the stratigraphic range of taxa (Foote and Raup 1996, McGowan and Smith 2007), in this study the total diversity remains unchanged when taxa with poorly localized or unconfident stratigraphical ranges are removed. It seems, therefore, that stratigraphic precision does not impact significantly on Silurian trilobite diversity.

4.2.5 *Taxonomic bias*

Taxa described under open nomenclature (~600 records) were not counted in determining the overall species diversity. Such records reflect tentative or uncertain assignments (e.g. aff., cf., sp., sp. 1 or A), and it is unclear what proportion represent distinct species.

Including such taxa in the diversity study would artificially raise diversity and turnover in intervals where they are more common. Variations in the taxonomic practice between authors and the quality of described material would contribute towards this. Discounting species under open nomenclature can lead to problems in intervals where such taxa are the only record of a particular genus, however. To account for this, a species under open nomenclature is assumed to represent a distinct species in intervals where a genus is known to occur, but no named species has been recognized. This helps to minimise missing data, which would otherwise be higher in parts of the Llandovery. Based on publications and unpublished work on British material, over 4,400 synonyms were collected and assigned to names in current use, to prevent overestimation of trilobite diversity.

Many publications (for example Raup 1976; Foote 1992, 1993; Robeck *et al.* 2000; Westrop and Adrain 2001; Smith 2001; Forey *at al.* 2004) note the problems affecting species level diversity. Species are harder to recognise than genera, and misidentifications can result in spurious range extensions affecting diversity (Crampton *et al.* 2006). This bias is unlikely to alter the overall signal in diversity curves (Sepkoski 1993, Adrain and Westrop 2000, Crampton *et al.* 2006), however.

Despite species related problems, such as species/subspecies concepts (discussed in Chapter Two) and the problem of *nomina dubia*, the taxonomic issues surrounding genera can be worse. There are many examples of Silurian trilobite genera that are less well defined and comparing different but closely related genera can be difficult. Genera such as *Ananaspis*, *Kosovopeltis*, *Proetus*, *Dalmanites*, *Calymene*, and *Leonaspis* have been used in the past as ‘taxonomic dustbins’ where species have been assigned to them that comprise considerable morphological variation (Owen 1973, Ramsköld and Werdelin 1991, Edgecombe *et al.* 2004, Lieberman 1994), and this has resulted in many species (*incertae sedis*) being assigned questionably to those genera. Over the years there has been an increasing tendency to split genera, leading to a two-fold increase between 1983 and 2002 (Jell and Adrain 2002), into finer taxonomic groups that can be harder to distinguish (e.g. *Calymene*, *Proetus*). Cladistic analyses have shown several trilobite genera to be paraphyletic/polyphyletic (Ramsköld and Chatterton 1991, Ramsköld and Werdelin 1991, Lieberman 1994, Congreve and Lieberman 2011), which can alter stratigraphic ranges in generic diversity studies (Villier and Navarro 2004). Many genera are in need of systematic revision, and until more cladistic analyses are undertaken it is unclear what proportion represent monophyletic groups.

Based on counts of the present study the total number of trilobite genera, for the Hirnantian and Silurian, is around 300. Given that the number of trilobite species herein is more than treble number of genera, and that most of the trilobite species names in the literature are valid (Adrain 2008), it seems that the taxonomic issues are more likely to be an issue in a genus level diversity curve. In addition, measuring diversity above the species level is more likely to underestimate downward or upward trends (Raup 1979*a*, Markov 2003), and is potentially more sensitive to the pull of the recent (Raup 1979*b*). For these reasons species diversity is considered here.

4.2.6 *Preservation bias*

Various methods can be used to estimate the effects of preservation and collection biases. Estimates of rock volume, thickness, or outcrop area are examples (Raup 1976, Smith 2001, Crampton *et al.* 2003, Smith and McGowan 2005, Smith and McGowan 2007, McGowan and Smith 2008), but are impractical at the biozone level. Such approaches make no allowance for lithological variation (Peters and Foote 2001). Since the occurrence of Silurian trilobite taxa tends to be facies related (Thomas 1979, Chlupáč 1987, Thomas and Lane 1999), lithological variation in an interval is an important factor. The number of formations containing trilobites is used here as a convenient measure of lithological variation. Formations not containing trilobites, but yielding a rich shelly fauna with which trilobites are commonly associated are included also (Mannion *et al.* 2011), as they have the potential to preserve trilobite taxa. Formations could be weighted the same way as taxa in EMSD as they do not always occur through entire biozones. For example, biostratigraphy and field relations show that the Lower and Middle Elton formations do not span the entire *nilssoni* Biozone. In spite of this formations are unweighted here, as the majority of formations in the present dataset most likely occur through a good deal more than one-third of a biozone based on available stratigraphic schemes (for example, Cocks *et al.* 1992, Aldridge *et al.* 2000, Holland and Bassett 2002, Jeppsson *et al.* 2006). In any case these are small in number (around 10 per cent of the dataset) and are fairly evenly distributed.

Instead of simply comparing EMSD with the number of formations the data needs to be normalized. This is achieved by dividing the trilobite diversity (in this case EMSD) by the number of formations (Fröbisch 2008). The resulting ratio will be large when many taxa are present in few formations and low when there are few taxa and many formations. The dataset for the present study includes 490 formations from the Hirnantian and Silurian.

Links between the number of formations and diversity have been discussed (Peters and Foote 2001, Peters 2005, Peters 2008, Meyers and Peters 2011). In order to assess the degree of bias the total number of species (species richness or N_{tot}) will be compared against the number of formations (Peters and Foote 2001, Fröbisch 2008, Peters 2008, Meyers and Peters 2011) for the Silurian. As species N_{tot} is unweighted it is more likely to show a correlation with formations N_{tot} if any biases exist (Peters and Foote 2001, Fröbisch 2008). The number of sampled species (N_s) will be compared with N_{tot} also. N_s will only include the sampled diversity, i.e. taxa are excluded if they have not been found in an interval even if they are known to occur (such as range through species). The latter should be more prone to biases than species N_{tot} and be better suited to spotting preservation or sampling biases (Peters and Foote 2001). Species N_{tot} and N_s, are plotted against the number of formations on a scatter graph. Statistical correlations are tested against Pearson's correlation coefficient (r).

4.2.7 *Sampling bias*

Another bias to consider is that the more intensively an interval is sampled, the more likely taxa are to be found, resulting in a higher apparent diversity (Raup 1975, 1976, 1979*b*; Signor 1985; Sepkoski 1994; Alroy *et al.* 2001, Peters and Foote 2001). Rather than sampling effort, it is more important to account for sampling completeness. Intervals of higher diversity will need to be sampled less intensively than lower diversity intervals to find more taxa. One approach to compensating for this is to construct a discovery curve through time for a given interval (Tarver *et al*. 2007, Mannion *et al.* 2011). Assuming research effort has not decreased, the interval has been completely or nearly completely sampled when the curve becomes asymptotic. The problem with discovery curves is it is difficult to reach asymptote, because the latest new taxa are less likely to be synonymised (Solow *et al.* 1995, Alroy 2002). An alternative method for measuring synonymy rates was proposed by Alroy (2002), termed the 'flux ratio method', and accounts for the risk of changing synonyms (whether it be validated, invalidated, and revalidated etc) over time. The flux ratio method was refined by Solow and Benton (2010).

Methods of standardising diversity curves, including rarefaction and the use of modelling, are discussed in the literature (Simberloff 1972; Raup 1975; Tipper 1979, Alroy 1996, 2000; Miller and Foote 1996; Alroy *et al.* 2001; Crampton *et al.* 2006; Mannion *et al.* 2011). The number of fossil localities is a direct measure of the number of localities sampled (McGowan and Smith 2008) and it has been used to compare with and sample-standardize diversity curves (Alroy *et al.* 2001; Fara 2002; Crampton *et al.* 2003, 2006; Kiessling 2008). The problem of using the number of fossil localities is that it does not account for failed sample attempts (McGowan and Smith 2008). In addition, there are issues with what constitutes a locality; the localities of Murchison (1839) and Salter (1864) for example, cover larger areas than those defined in Lawson (1973, 1977) for the Ludlow Series of Britain.

A further issue is the degree to which different geographic regions have been sampled, i.e. the extent to which diversity curves are global (McGowan and Smith 2008). With regards to the dataset of the present study Europe, North America, Canada, and Australia are well represented for the Silurian. China and Greenland are less well represented, however, and there is little data from northwest Africa and South America. The Silurian rocks of South America are less well known than other continents and the outcrop area and number of formations is significantly lower than that of Europe (see Berry and Boucot 1972). It would appear, therefore, that there is a regional bias in the dataset towards North America and Europe, with Australia (and to an extent China) representing the only significant data from the southern hemisphere.

Sampling bias is not directly corrected for here, although the number of formations may at least partly account for this (Peters and Foote 2001, Fröbisch 2008, Butler *et al.* 2011, Mannion *et al.* 2011). A relationship between the number of formations and sampling seems reasonable as sequences that have been more finely divided are more likely to have been better sampled. Peters and Foote (2001) showed that the number of formations may be a good indicator of research effort which is often difficult to disentangle from sampling, whereas Mannion *et al.* (2011) used the number of formations as a proxy for outcrop area. Peters and Ausich (2008) combined species occurrences and formations limited by geographic area to create ‘biofacies’ which they used to correct sampling bias for Ordovician and early Silurian crinoids.

4.2.8 *Abundance and diversity*

Different abundance distributions can lead to different estimates of sampled alpha diversity (Koch 1978), which in turn can bias global diversity signatures (Alroy 2000, Alroy *et al.* 2001, Powell and Kowalewski 2002). It is much harder to get a sufficiently large sample to properly estimate diversity for an interval when a few taxa are highly abundant, and others are rare, compared to an interval with a more even abundance distribution (Powell and Kowalewski 2002), for example. In addition, within habitat time-averaging can also alter relative abundance and diversity measures (Tomašových and Kidwell 2010). Changes in abundance may also truncate a taxon’s stratigraphical range as low abundance would be expected during its origination and extinction phases, the *Signor-Lipps effect* (Signor and Lips 1982).

The data do not exist to calculate relative abundances or absolute specimen counts at the biozone level for many of the collections described in the literature, and those that do exist probably represent a biased subsample of original sampling in the field (Koch 1978, Davis and Pyenson 2007). It is beyond the scope of this study to survey all of the museum collections for Silurian trilobites, to rarefy the different samples (Davis and Pyenson

2007); the collections include a substantial amount of unpublished material from Britain and Gotland alone.

4.3 RESULTS

For convenience, Hirnantian-Silurian standard graptolite biozones are represented by a code in the text-figures and tables (see Table 4.2) throughout the results section.

STANDARD GRAPTOLITE BIOZONE	STAGE	Code
Normalograptus? *extraordinarius*	Hirnantian (Late Ordovician)	H1
Normalograptus? *persculptus*	Hirnantian (Late Ordovician)	H2
Akidograptus ascensus	Rhuddanian	S1
Parakidograptus acuminatus	Rhuddanian	S2
Orthograptus vesiculosus	Rhuddanian	S3
Coronograptus cyphus	Rhuddanian	S4
Demirastrites triangulatus – pectinatus	Aeronian	S5
Monograptus argenteus – leptotheca	Aeronian	S6
Lituigraptus convolutus	Aeronian	S7
Stimulograptus sedgwickii	Aeronian	S8
Spirograptus guerichi	Telychian	S9
Spirograptus turriculatus	Telychian	S10
Monograptus crispus	Telychian	S11
Monograptus griestoniensis – crenulata	Telychian	S12
Oktavites spiralis Interval Zone	Telychian	S13
Cyrtograptus lapworthi – insectus	Telychian	S14
Cyrtograptus centrifugus – murchisoni	Sheinwoodian	S15
Monograptus riccartonensis – belophorus – antennularis	Sheinwoodian	S16
Cyrtograptus rigidus – perneri	Sheinwoodian	S17
Cyrtograptus lundgreni	Homerian	S18

Pristiograptus parvus – Gothograptus nassa	Homerian	S19
Colonograptus praedeubeli – deubeli	Homerian	S20
Colonograptus ludensis	Homerian	S21
Neodiversograptus nilssoni	Gorstian	S22
Lobograptus scanicus	Gorstian	S23
Saetograptus leintwardinensis	Ludfordian	S24
Neocucullograptus kozlowskii, Polonograptus podoliensis	Ludfordian	S25
Monograptus formosus	Ludfordian	S26
Monograptus parultimus – ultimus	Přídolí	S27
Monograptus branikensis – lochkovensis	Přídolí	S28
Monograptus bouceki – transgrediens – perneri	Přídolí	S29

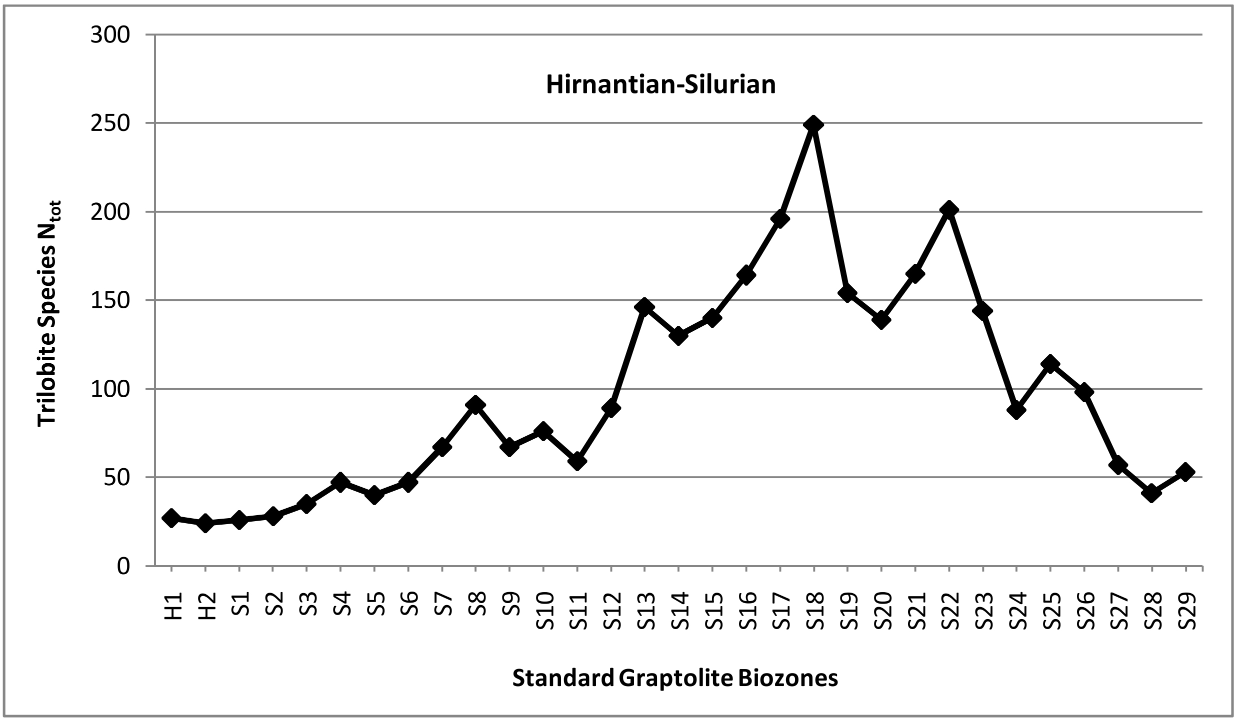
Table 4.2: The codes used for the Hirnantian-Silurian standard graptolite biozones in the text-figures and graphs of this section are represented in this table. These are numbered oldest to youngest. The prefix H and S are used for biozones in the Hirnantian Stage (late Ordovician) and the Silurian System respectively.

4.3.1 *Diversity* N_{tot}

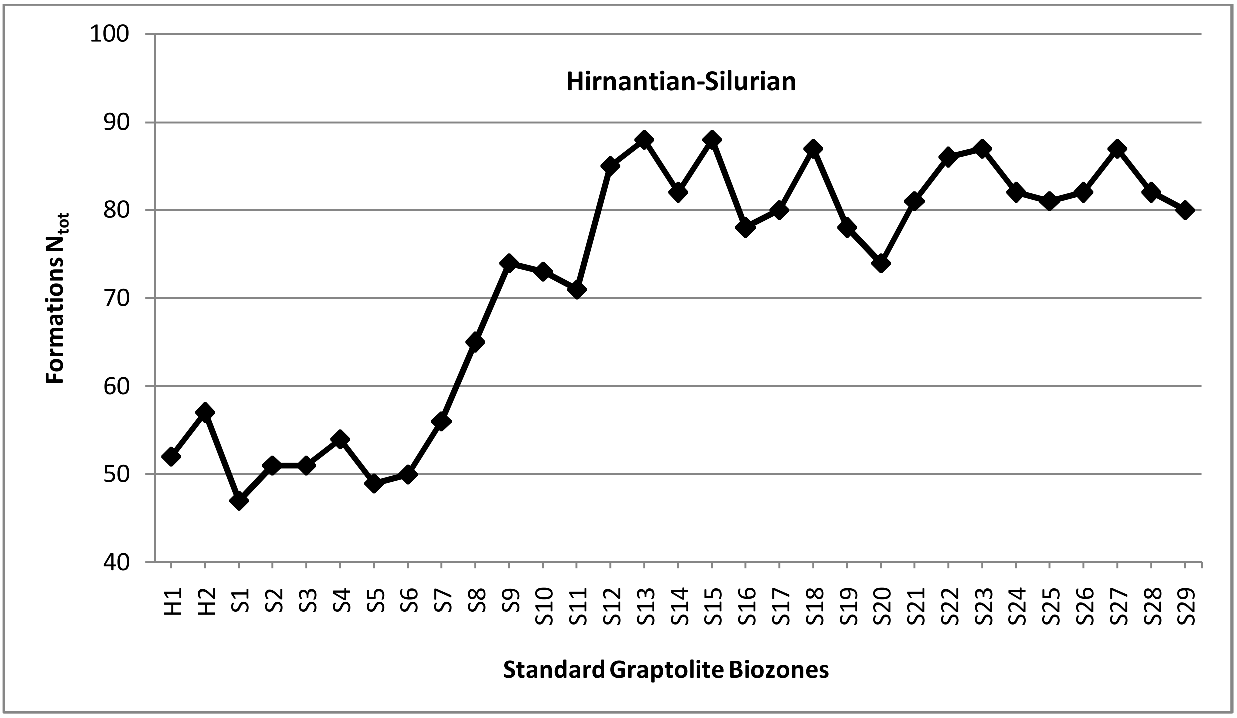
Raw data indicates an increase in trilobite species diversity from the late Hirnantian to the Wenlock (Text-Figure 4.4). A peak in diversity occurs at the base of the Homerian (*lundgreni* Biozone, S18), and diversity is also high in the early Gorstian (*nilssoni* Biozone, S22). Several drops in diversity are noted throughout the Silurian: these occur between the latest Aeronian (*sedgwickii* Biozone, S8) and the basal Telychian (*guerichi* biozones, S9), during the early Telychian (*turriculatus* to *crispus* biozones, S10-S11), the late Telychian (*spiralis* to *lapworthi* biozones, S13-S14), the Homerian (*lundgreni* to *praedeubeli-deubeli* biozones, S18-20), the early Gorstian (*nilssoni* Biozone, S22) to early Ludfordian (*leintwardinensis* Biozone, S24), and the Ludfordian (*kozlowskii* Biozone, S25) to Přídolí (*branikensis-lochkovensis* Biozone, S28). The *lundgreni* to *praedeubeli-deubeli* biozones and *nilssoni* to *leintwardinensis* biozones show the largest reduction in trilobite species, with losses of 110 in the former and 113 in the latter. The number of trilobite species in the Silurian appears to fluctuate markedly. These variations may be real biological signals or the result of a bias, such as the temporal variation in the sedimentary rock record.

The total number (N_{tot}) of formations plotted against trilobite species N_{tot} (Text-Figure 4.6) show a moderate positive correlation (Pearson's $r=0.69$) for the Hirnantian-Silurian, which appears to be significant ($p<0.05$). There is quite a lot of scatter, however, and the correlation is much stronger for the Hirnantian-Llandovery (see Text-Figure 4.7) compared with the Wenlock-Přídolí (Text-Figure 4.8). Formations N_{tot} are lower in the Llandovery (compared with the rest of the Silurian) and increase to the Wenlock with increasing species diversity (Text-Figure 4.5). During the Wenlock, formations N_{tot} mostly do not correlate with species N_{tot} although an increase in species N_{tot} from the Sheinwoodian *rigidus-perneri* Biozone (S17) to Homerian *lundgreni* Biozone (S18), and a decrease from the *lundgreni* Biozone to the *praedeubeli-deubeli* Biozone (S20) occur during times of increasing and decreasing formations N_{tot} respectively. The Ludlow and Přídolí apparently show no correlation and numbers of species and formations seem to fluctuate independently. The correlation between formations and species N_{tot} is not proof of causality but it seems reasonable that the number of preserved/sampled environments would impact upon the total diversity (Peters and Foote 2001, Fröbisch 2008, Butler *et al.* 2011, Mannion *et al.* 2011).

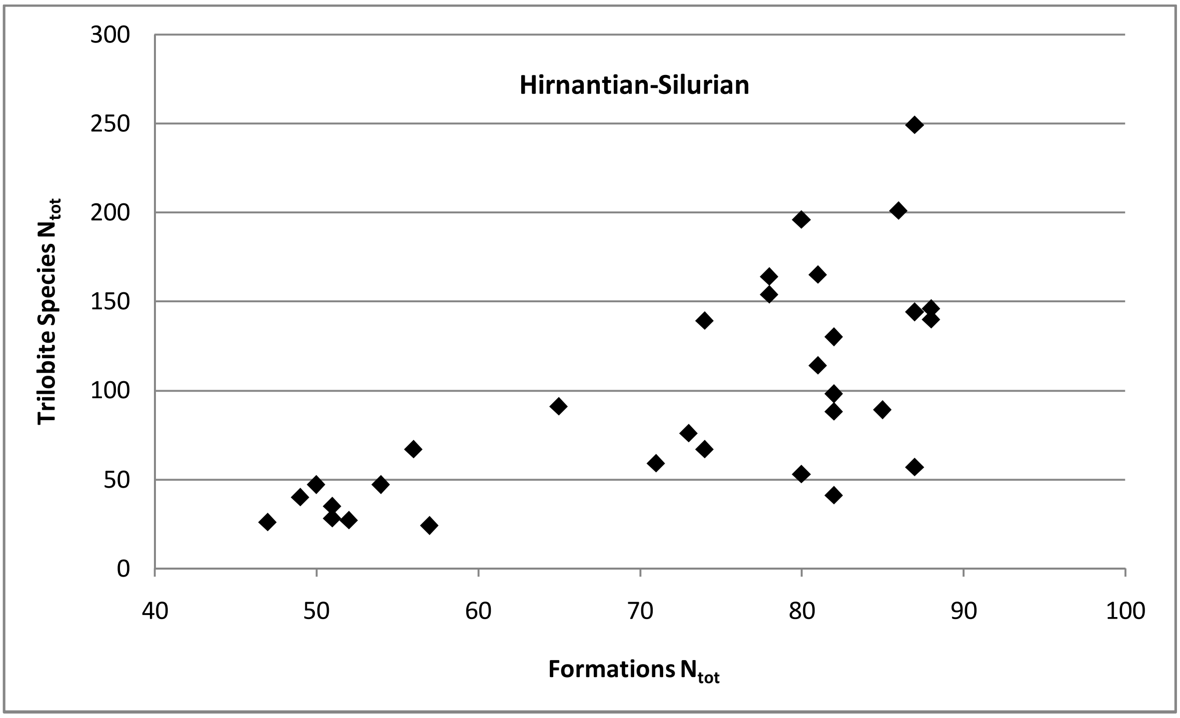
The sampled diversity (N_s) should be a better indicator of biases (compared with species N_{tot}) as the taxa that have not been found in an interval, even though they occur in younger and older rock, are excluded. Species N_s here shows the same overall diversity trend (Text-Figure 4.9) as species N_{tot} and a moderate positive correlation with formations N_{tot} (Text-Figure 4.10), however. This indicates that the use of older and younger occurrences to ‘fill in gaps’ in a species stratigraphical range is not sufficient on its own to minimize the effects of biases.



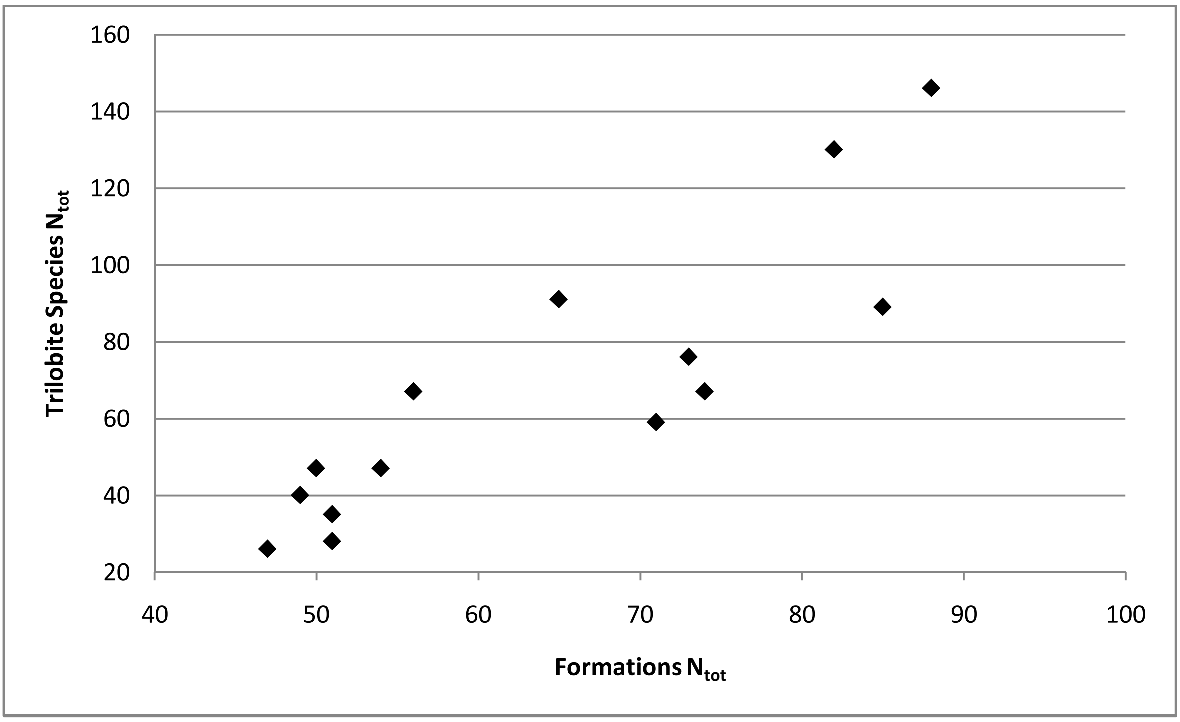
Text-Figure 4.4. Graph of trilobite species N_{tot} plotted against standard graptolite biozones.



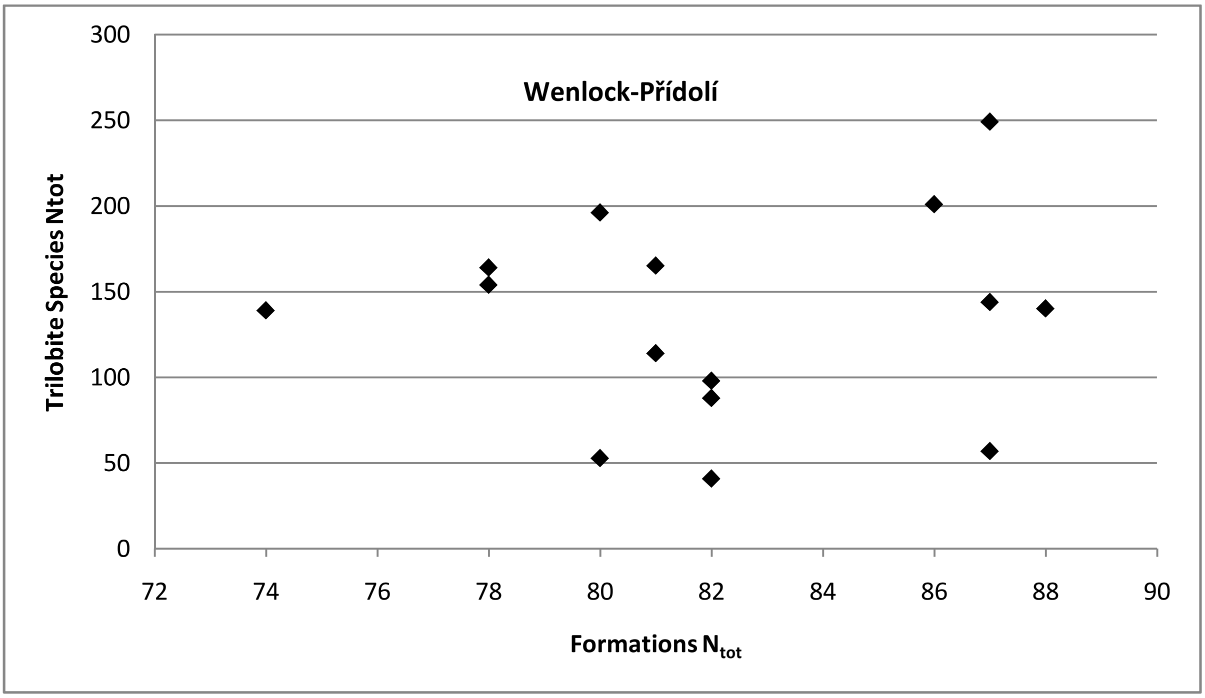
Text-Figure 4.5. Graph of formations N_{tot} plotted against standard graptolite biozones.



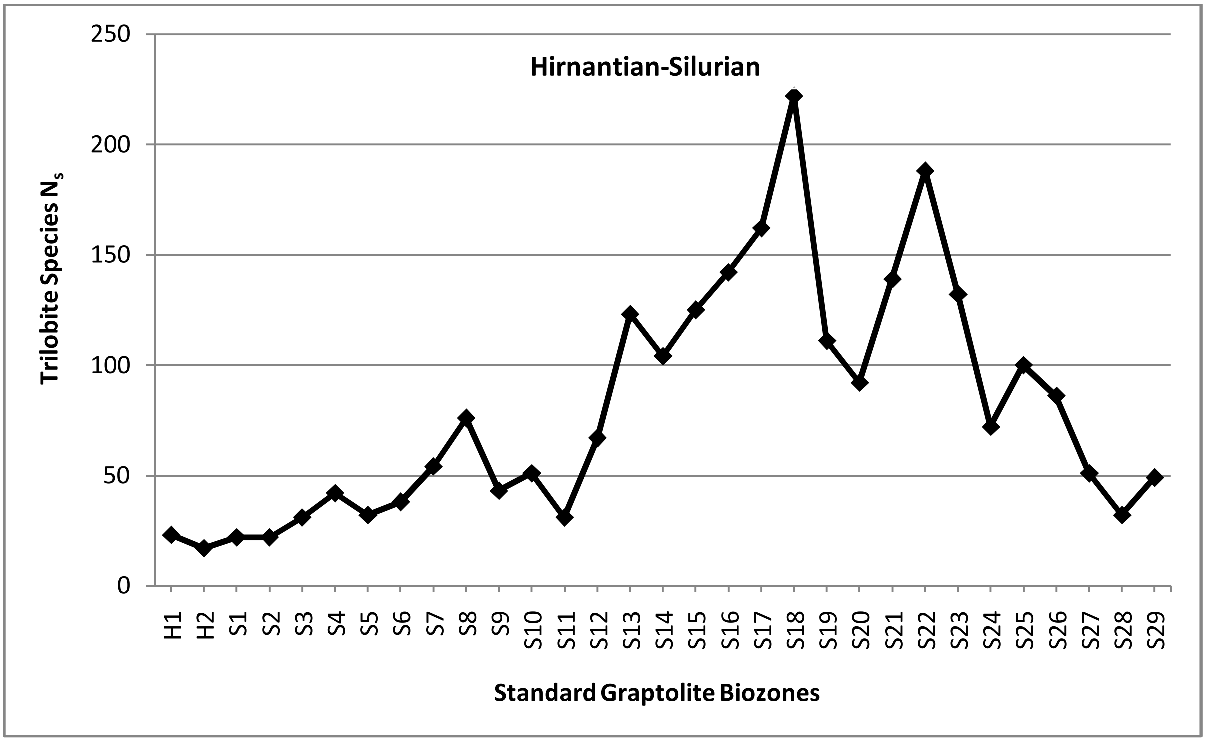
Text-Figure 4.6. Scatter graph of trilobite species N_{tot} plotted against formations N_{tot} for the Hirnantian-Silurian. Pearson's correlation coefficient $r=0.69$, $p<0.05$.



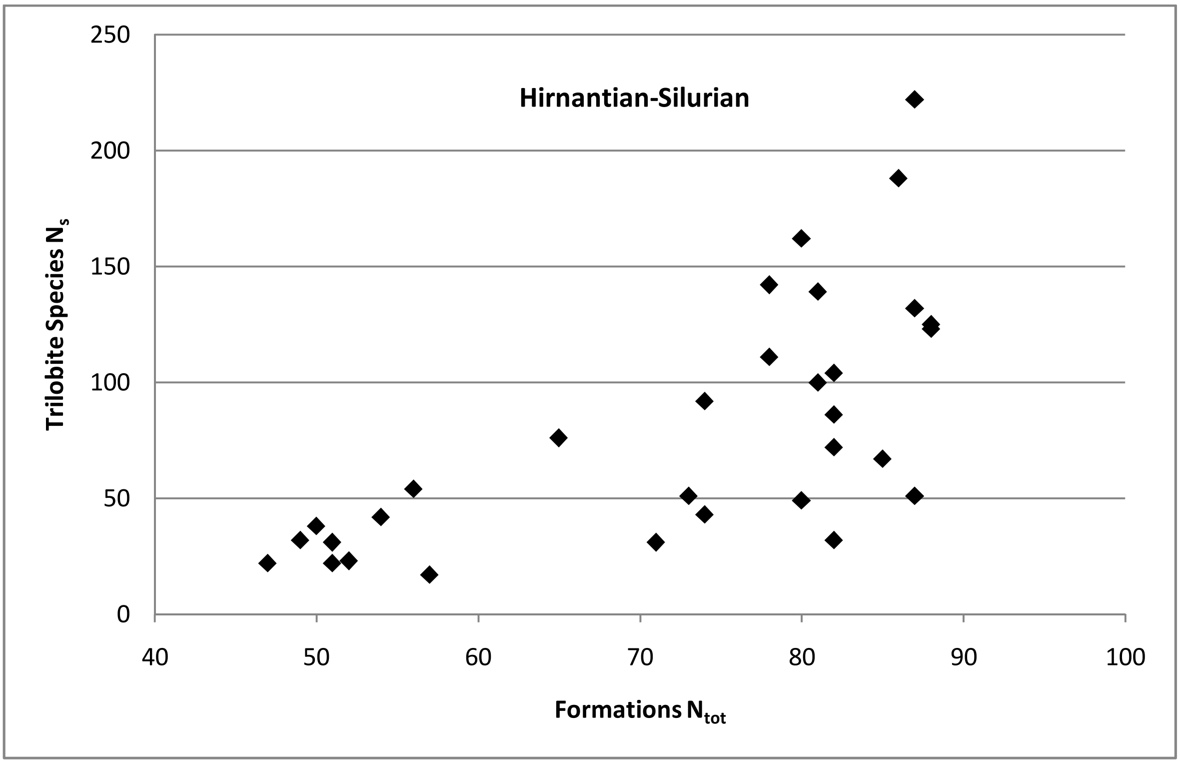
Text-Figure 4.7. Scatter graph of trilobite species N_{tot} plotted against formations N_{tot} for the Hirnantian-Llandovery. Pearson's correlation coefficient $r=0.87$, $p<0.05$.



Text-Figure 4.8. Scatter graph of trilobite species N_{tot} plotted against formations N_{tot} for the Wenlock-Přídolí. Pearson's correlation coefficient r=0.09, p=0.73.



Text-Figure 4.9. Graph of trilobite species N_s against standard graptolite biozones.



Text-Figure 4.10. Scatter graph of trilobite species N_s plotted against formations N_{tot}, for the Hirnantian-Silurian. Pearson's correlation coefficient r=0.69, p<0.05.

4.3.2 *Estimated Mean Standing Diversity*

Estimated Mean Standing Diversity (EMSD) was calculated for each interval based on the number of singleton, lower and upper boundary cross, and range through taxa (see Table 4.3).

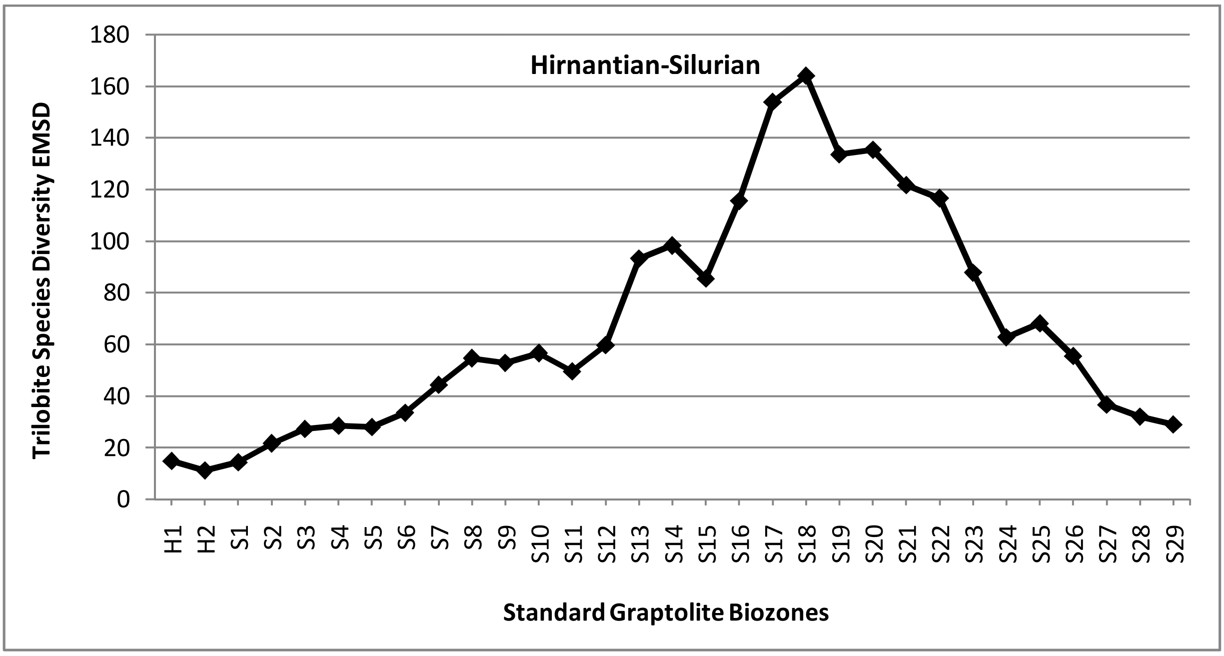
Taxa	H1	H2	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14
FL	10	14	4	2	2	9	3	3	10	23	4	5	6	17	34	16
bL	8	6	0	6	0	20	1	15	4	27	1	23	6	11	9	31
Ft	3	1	18	4	13	5	19	8	28	15	22	9	5	25	51	11
bt	6	3	4	16	20	13	17	21	25	26	40	39	42	36	52	72

Taxa	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29
FL	6	11	9	53	5	3	17	41	16	16	26	30	17	6	18
bL	50	13	25	65	16	0	52	50	73	12	29	36	10	5	19
Ft	51	69	47	34	18	3	12	64	18	17	28	9	8	5	5
bt	33	71	115	97	115	133	84	46	37	43	31	23	22	25	11

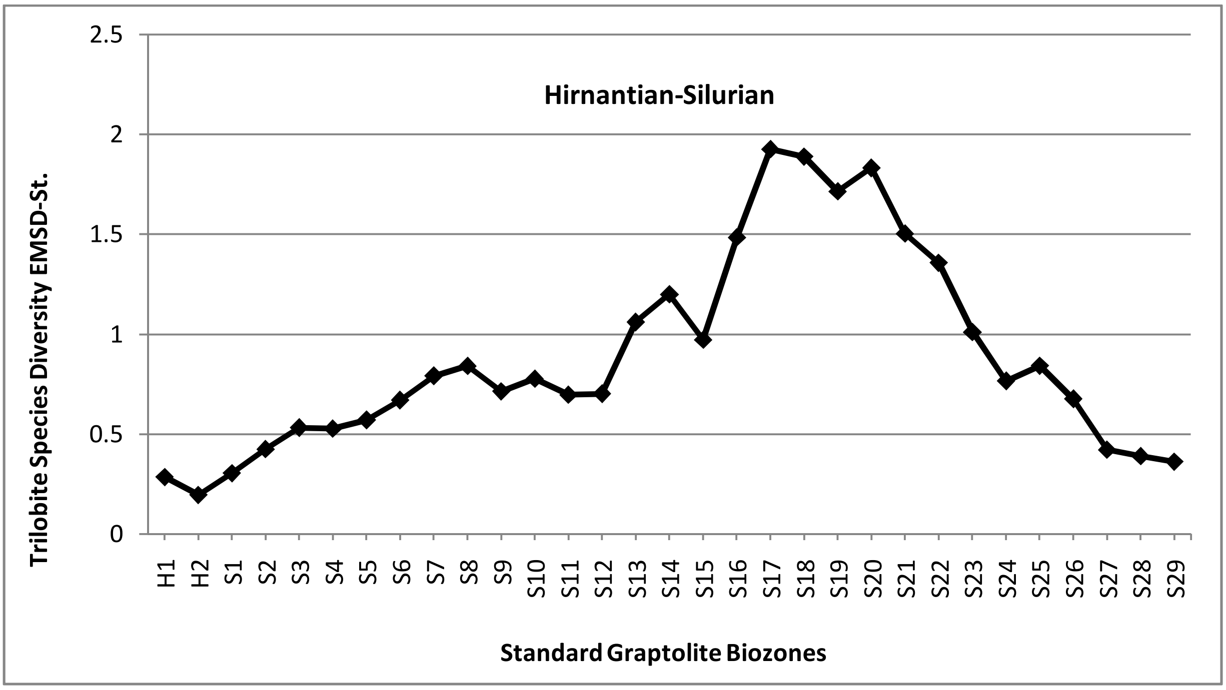
Table 4.3. Table to show total numbers of trilobite singleton (FL), lower boundary cross (bL), upper boundary cross (Ft), and range through (bt) species, based on determined FAD's and LAD's from the literature, for each interval. EMSD, extinction rates, and origination rates were calculated from these values (see method).

Hirnantian-Silurian trilobite species EMSD (Text-Figure 4.11) is similar to species N_{tot} in that diversity levels increase from the Hirnantian to the Wenlock, and then decrease through the Ludlow to the end of the Silurian. Several biozones have relatively lower species EMSD values compared with species N_{tot} due to their higher numbers of singletons than boundary crosses (see Table 4.3). The most notable is the *nilssoni* Biozone (S22), which shows a drop in EMSD from the *ludensis* Biozone (S21), due to the high numbers of singletons and relatively low numbers of range through species (due to high turnover) compared with the Homerian (S18-21).

Trilobite species EMSD standardised against the number of formations (EMSD-St.) is more likely closer to true diversity as it accounts for both the distribution of taxa in an interval and fluctuations in formations N_{tot}. EMSD-St. (Text-Figure 4.12) shows a very similar result to EMSD but differs mainly in that the late Sheinwoodian *rigidus-perneri* Biozone (S17) represents the peak in Silurian trilobite diversity. This is due to the much lower numbers of singletons, more range through species, and fewer formations N_{tot} of the latter compared to the Homerian *lundgreni* Biozone.



Text-Figure 4.11. Graph of trilobite species Estimated Mean Standing Diversity (EMSD) plotted against standard graptolite biozones.



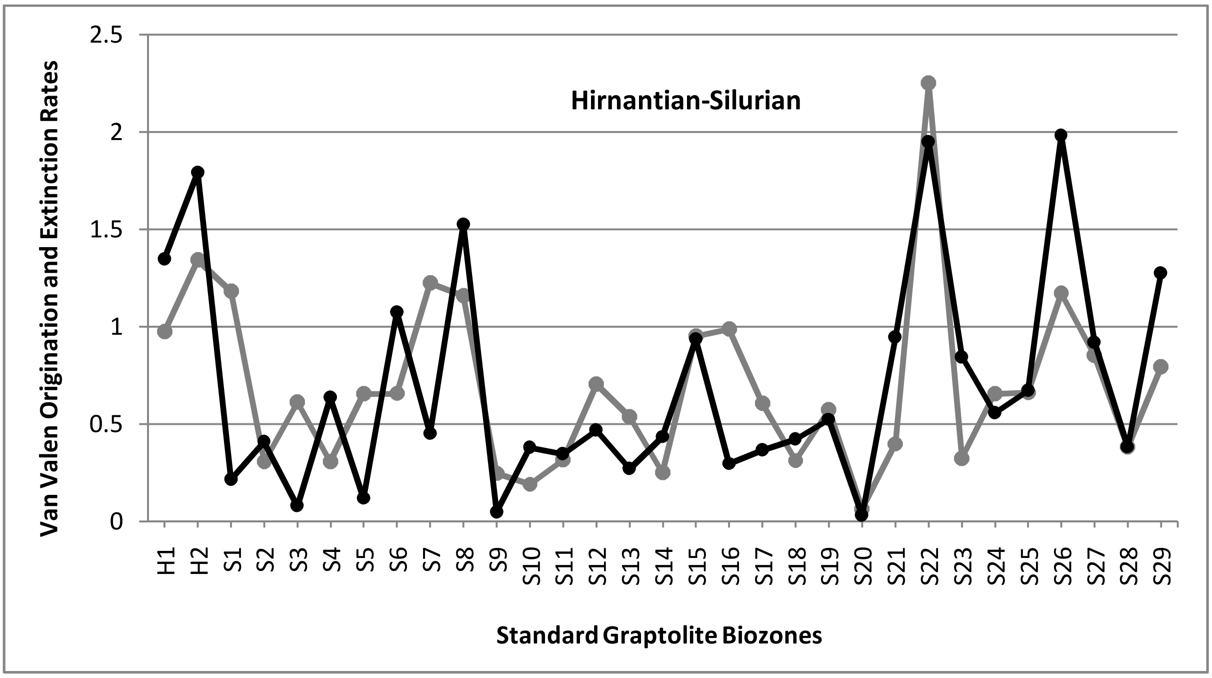
Text-Figure 4.12. Graph of trilobite species Estimated Mean Standing Diversity standardised against the number of formations (EMSD-St.) plotted against standard graptolite biozones.

The Llandovery is lower in both formations N_{tot} and species EMSD-St., although the difference in EMSD-St. between the latter and the Wenlock is smaller than that seen in species N_{tot}. A sampling standardised diversity study of crinoids by Peters and Ausich (2008) shows a similar pattern to EMSD-St here where diversity increases from the Hirnantian through the Llandovery, with a slight drop from the Aeronian to the Telychian. The increase in trilobite diversity seen in the present study, during the Llandovery, is consistent with a recovery from the late Ordovician mass extinctions (see Krug and Patzkowsky 2004), and biases are probably exaggerating rather than masking a biological signal (compare sampled diversity in Text-Figure 4.9 with standardized diversity in Text-Figure 4.12). Unless otherwise stated trilobite diversity for the remainder of this chapter refers to species diversity EMSD-St (Text-Figure 4.12).

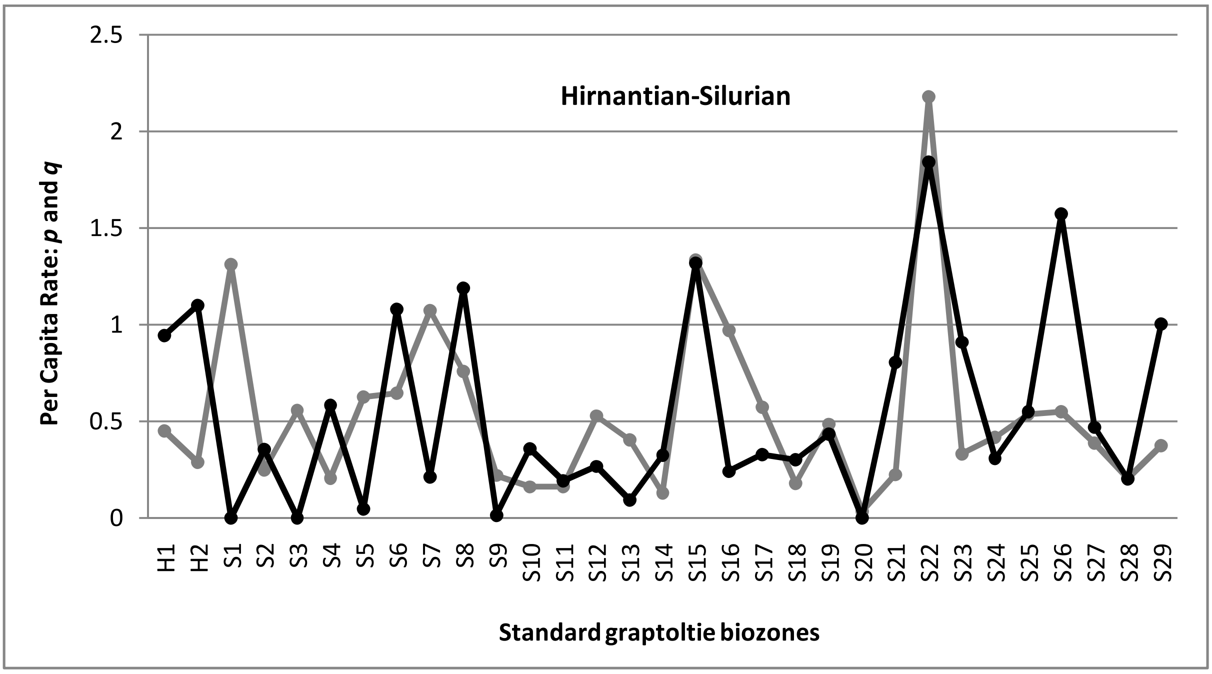
4.3.3 *Origination and extinction rates*

Origination and extinction rates are plotted using the Van Valen Metric (Text-Figure 4.13) and Per Capita Rate (Text-Figure 4.14). Although the Per Capita Rate is less prone to bias than the Van Valen Metric (Foote 2000*a*), both metrics produce almost identical results here. One of the more noticeable differences is the lower Van Valen rates in the *centrifugus* Biozone (S15), which is the result of the relatively low number of singleton species in that interval (Table 4.3). The increase in trilobite diversity (Text-Figure 4.12) through the Llandovery seems to be a result of generally high origination rates (compared to extinctions). Small fluctuations such as the small drop in diversity between the Aeronian *sedgwickii* Biozone (S8) and the Telychian *guerichi* Biozone (S9) are a result of elevated extinction rates. Although extinction rates are higher than origination rates for the Rhuddanian *cyphus* (S4) and the Aeronian *argenteus-leptotheca* (S6) biozones, diversity increases in the following intervals due to an increase in origination rates. Trilobite diversity increases towards the late Sheinwoodian to a maximum (S17) as a result of low extinction rates, rather than high origination rates. The Ludlow is a time of decreasing diversity due to elevated extinction rates.

The Gorstian *nilssoni* Biozone (S22) is represented by the highest origination rates for the whole Silurian, and based on the Per Capita Rate the highest extinction rates also. Although the origination rates in the *nilssoni* Biozone are higher than the extinction rates in the *ludensis* Biozone (S21) the diversity drops between the latter and the former. This is due to the much lower numbers of range through species and higher number of singletons in the *nilssoni* Biozone compared with the Wenlock. The *nilssoni* Biozone is short also (~0.4 Ma) resulting in even higher taxonomic rates. The high turnover in the *nilssoni* Biozone is responsible for an apparent increase in diversity from the *ludensis* Biozone when considering species N_{tot}. Very high extinction rates in the Ludfordian *formosus* Biozone (S26) results in a continuing decline in trilobite diversity into the Přídolí.



Text-Figure 4.13. Van Valen Metric origination (grey) and extinction (black) rates plotted against standard graptolite biozones.



Text-Figure 4.14. Per Capita Rate *p* (grey) and *q* (black) plotted against standard graptolite biozones.

4.3.4 *Trilobite families*

The total species EMSD and the number of species as a percentage of EMSD, for the most common Silurian trilobite families, for each interval are presented respectively in Table 4.4 and 4.5. In the Rhuddanian (S1-S4) and the Aeronian (S5-S8) the odontopleurids are the most diverse family, representing 16-27 per cent of species EMSD. The high turnover in the late Aeronian *sedgwickii* Biozone (S8) results in a decrease in species EMSD in the odontopleurids, aulcopleurids, phacopids, lichids, and proetids. The other families seem to increase in EMSD during this time, and by the early Telychian *guerichi* Biozone (S9) the encrinurids are the most diverse family (17 per cent), followed by the odontopleurids (12.5 per cent). The odontopleurids continue to decline towards the basal Sheinwoodian *centrifugus* Biozone (S15).

Extinction rates are higher than origination rates at the end Telychian (S14) leading to a reduction in diversity in the encrinurids, cheirurids, harpetids, phacopids, and the proetids. High turnover rates during the *centrifugus* Biozone result in the greatest decrease in species EMSD in the encrinurids. At the same time the calymenids, cheirurids, harpetids, homalonotids, phacopids, proetids, and scuetuluids decrease in species EMSD too, but these drops are relatively small. Encrinurids continue to decline through the Wenlock while the odontopleurids increase. By the Sheinwoodian the odontopleurids are the most diverse family again (12.6 per cent), and its species EMSD increases steadily to the Homerian *ludensis* Biozone (S21). High extinction rates in the Gorstian *nilssoni* Biozone (S22) result in a fall in species EMSD, most notably in the odontopleurids. The scuetuluids reach their highest species EMSD in the Gorstian, and in the *scanicus* Biozone (S22) they are the most diverse family (17.8 percent).

Family (EMSD)	H1	H2	S1	S2	S3	S4	S5	S6	S7	S8	S9
Acastidae	0.3	0.3	0.3	0.3	0.3	0.3	0.5	0.5	0.3	0.3	0.3
Aulacopleuridae	0.3	0.3	1.5	3.0	3.0	2.0	2.0	2.5	2.5	1.8	0.8
Calymenidae	0.3	0.3	0.3	0.5	1.0	1.0	1.5	2.0	3.3	4.8	5.8
Cheiruridae	0.3	0.3	0.3	0.5	1.5	1.0	0.5	1.3	1.3	2.2	3.0
Dalmanitidae	2.5	1.0	1.6	1.0	1.0	0.8	0.3	0.5	2.5	4.5	5.5
Encrinuridae	1.5	1.0	2.0	2.5	4.0	5.0	5.33	5.0	5.7	7.5	9.5
Harpetidae	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.5	1.3	1.3	1.5
Homalonotidae	0.8	1.5	2.0	2.0	2.3	1.0	0.3	0.3	0.3	0.3	0.3
Lichidae	0.8	1.0	0.5	0.8	1.0	1.8	1.5	2.0	3.0	3.8	3.0
Odontopleuridae	3.3	2.0	3.8	6.0	7.0	6.0	7.0	8.3	9.0	9.2	6.8
Phacopidae	0.3	0.3	0.8	1.8	2.0	2.5	1.5	3.0	4.8	5.0	3.0
Proetidae	2.5	2.7	0.5	1.0	2.5	4.5	4.0	4.0	6.2	7.7	6.5
Raphiophoridae	0.5	0.5	0.5	0.5	0.3	0.3	0.3	0.3	0.3	0.3	0.3
Scutelluidae	0.3	0.3	1.0	1.0	0.5	1.5	2.5	2.8	2.5	4.0	4.3

Family (EMSD)	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20
Acastidae	0.3	0.3	0.5	1.5	2.0	2.0	3.0	4.0	5.3	6.0	6.0
Aulacopleuridae	0.83	0.5	1.5	3.2	1.5	2.0	6.3	9.0	8.3	4.5	5.0
Calymenidae	6.5	7.0	7.5	10.0	11.5	10.0	12.7	14.5	13.5	10.0	9.0
Cheiruridae	3.5	2.5	4.3	12.0	12.2	9.5	11.0	17.8	20.3	13.0	13.5
Dalmanitidae	5.5	4.5	5.7	6.5	6.0	8.3	12.8	15.3	12.8	10.0	11.5
Encrinuridae	11.5	11.2	11.8	19.8	23.5	15.0	12.5	15.5	16.7	12.8	12.8
Harpetidae	2.0	2.3	2.5	3.3	2.3	1.0	1.0	1.0	0.5	0.3	0.3
Homalonotidae	0.3	0.3	0.5	2.0	3.0	3.2	2.8	3.0	3.5	4.0	4.0
Lichidae	2.8	3.0	3.3	2.0	2.5	4.7	11.7	16.7	14.5	13.5	13.0
Odontopleuridae	7.7	6.0	7.0	9.8	7.5	6.8	12.5	19.5	25.0	20.3	21.0
Phacopidae	2.5	1.5	2.0	4.7	5.3	4.0	4.5	7.5	8.7	8.2	8.0
Proetidae	8.0	7.8	8.8	9.8	11.0	9.0	11.3	14.0	18.2	17.0	17.0
Raphiophoridae	0.3	0.3	0.3	0.3	0.3	1.0	2.0	2.0	2.0	2.0	2.0
Scutelluidae	3.5	1.8	2.3	4.2	3.3	4.5	7.5	10.7	10.8	9.0	9.3

Family (EMSD)	S21	S22	S23	S24	S25	S26	S27	S28	S29
Acastidae	4.8	2.8	1.8	3.0	5.3	6.7	7.3	8.7	6.7
Aulacopleuridae	5.5	5.2	2.8	1.5	2.7	3.0	1.3	1.0	1.0
Calymenidae	8.0	7.3	6.5	7.8	6.7	4.3	4.3	2.3	3.5
Cheiruridae	12.8	13.3	9.5	4.8	4.8	4.0	1.5	0.5	0.3
Dalmanitidae	11.0	8.8	5.5	3.5	2.5	2.0	2.0	1.5	1.0
Encrinuridae	12.0	15.0	12.5	11.7	10.7	5.3	2.7	2.3	1.0
Harpetidae	0.3	0.3	0.3	0.3	0.8	0.8	0.3	0.3	0.3
Homalonotidae	3.5	3.2	2.0	2.5	3.5	3.7	2.0	2.0	1.5
Lichidae	10.7	6.5	3.8	0.5	0.5	0.8	0.3	0.5	1.2
Odontopleuridae	18.2	13.3	6.5	5.5	6.2	4.7	3.5	1.5	1.0
Phacopidae	7.8	7.5	4.5	3.0	4.3	4.6	2.8	2.5	2.0
Proetidae	15.8	14.3	12.5	10.5	11.3	9.5	6.5	6.5	7.5
Raphiophoridae	2.0	2.3	1.5	1.0	1.0	0.5	0.3	0.3	0.3
Scutelluidae	6.3	14.7	15.7	4.5	6.0	3.7	0.3	0.3	0.5

Table 4.4. Table showing species Estimated Mean Standing Diversity for the most common Silurian trilobite families. Values representing 10 per cent or greater are highlighted.

Family (%EMSD)	H1	H2	S1	S2	S3	S4	S5	S6	S7	S8	S9
Acastidae	2.0	2.5	2.1	1.5	1.2	1.1	1.7	1.4	0.7	0.6	0.6
Aulacopleuridae	2.0	2.5	9.6	13.2	10.5	6.6	6.8	7.2	5.5	3.3	1.5
Calymenidae	2.1	2.6	2.1	2.2	3.6	3.4	5.1	5.7	7.4	8.6	10.7
Cheiruridae	2.1	2.6	2.2	2.2	5.3	3.4	1.7	3.8	2.9	3.9	5.5
Dalmanitidae	16.0	7.9	7.6	4.5	3.6	2.8	1.1	1.4	5.5	8.0	10.1
Encrinuridae	9.6	7.9	13.0	11.2	14.2	16.8	18.2	14.4	12.5	13.4	17.4
Harpetidae	2.1	2.6	2.2	1.5	1.2	1.1	1.1	1.4	2.9	2.4	2.8
Homalonotidae	5.3	11.8	13.0	9.0	8.3	3.4	1.1	1.0	0.7	0.6	0.6
Lichidae	5.3	7.9	3.3	3.7	3.6	6.1	5.1	5.7	6.6	6.8	5.5
Odontopleuridae	21.3	15.8	25.0	26.9	24.9	20.1	23.9	23.9	19.9	16.4	12.5
Phacopidae	2.0	2.6	5.4	8.2	7.1	8.4	5.1	8.6	10.7	8.9	5.5
Proetidae	16.0	21.1	3.3	4.5	8.9	15.1	13.6	11.5	13.6	13.7	11.9
Raphiophoridae	3.2	3.9	3.3	2.2	1.2	1.1	1.1	1.0	0.7	0.6	0.6
Scutelluidae	2.0	2.6	6.5	4.5	1.8	5.0	8.5	8.1	5.5	7.1	8.0

Family (%EMSD)	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20
Acastidae	0.6	0.7	0.8	1.6	2.0	2.3	2.6	2.6	3.2	4.5	4.4
Aulacopleuridae	1.4	1.0	2.5	3.4	1.5	2.3	5.4	5.8	5.1	3.3	3.7
Calymenidae	11.2	13.7	12.4	10.6	11.6	11.6	10.9	9.4	8.2	7.4	6.6
Cheiruridae	6.0	4.9	7.1	12.7	12.2	11.0	9.5	11.5	12.4	9.7	9.9
Dalmanitidae	9.5	8.8	9.3	6.9	6.0	9.7	11.0	9.9	7.8	7.4	8.4
Encrinuridae	19.8	21.8	19.5	21.0	23.7	17.4	10.7	10.0	10.2	9.6	9.4
Harpetidae	3.4	4.6	4.1	3.5	2.3	1.2	0.9	0.6	0.3	0.2	0.2
Homalonotidae	0.6	0.7	0.8	2.1	3.0	3.7	2.4	1.9	2.1	3.0	2.9
Lichidae	4.9	5.9	5.5	2.1	2.5	5.4	10.0	10.8	8.8	10.0	9.5
Odontopleuridae	13.2	11.7	11.5	10.4	7.6	7.9	10.7	12.6	15.2	15.1	15.4
Phacopidae	4.3	2.9	3.3	4.9	5.4	4.6	3.9	4.8	5.3	6.1	5.9
Proetidae	13.8	15.3	14.6	10.4	11.1	10.4	9.7	9.1	11.1	12.7	12.5
Raphiophoridae	0.6	0.7	0.5	0.4	0.3	1.2	1.7	1.3	1.2	1.5	1.5
Scutelluidae	6.0	3.6	3.8	4.4	3.4	5.2	6.4	6.9	6.6	6.7	6.9

Family (%EMSD)	S21	S22	S23	S24	S25	S26	S27	S28	S29
Acastidae	4.0	2.4	2.1	4.7	7.8	11.1	19.3	24.7	20.5
Aulacopleuridae	4.5	4.4	3.2	2.4	3.9	5.4	3.5	3.0	3.3
Calymenidae	6.5	6.2	7.4	12.3	9.0	7.8	11.4	7.1	11.7
Cheiruridae	10.5	11.3	10.8	7.6	7.1	7.2	3.9	1.5	1.1
Dalmanitidae	9.0	7.5	6.2	5.5	3.7	3.6	5.3	4.5	3.3
Encrinuridae	9.8	12.7	14.2	18.4	15.6	9.6	7.0	7.1	3.3
Harpetidae	0.3	0.3	0.4	0.5	1.2	1.5	0.9	1.0	1.1
Homalonotidae	2.9	2.7	2.3	3.9	5.1	6.6	5.3	6.1	5.1
Lichidae	8.7	5.5	4.3	0.8	0.7	1.5	0.9	1.5	3.9
Odontopleuridae	14.9	11.3	7.4	8.7	9.0	8.4	9.2	4.5	3.3
Phacopidae	6.4	6.4	5.1	4.7	6.4	8.4	7.5	7.6	6.7
Proetidae	12.9	12.2	14.2	16.5	16.6	17.1	17.4	19.8	25.6
Raphiophoridae	1.6	2.0	1.7	1.6	1.5	0.9	0.9	1.0	1.1
Scutelluidae	5.2	12.5	17.8	7.1	8.8	6.6	0.9	1.0	1.7

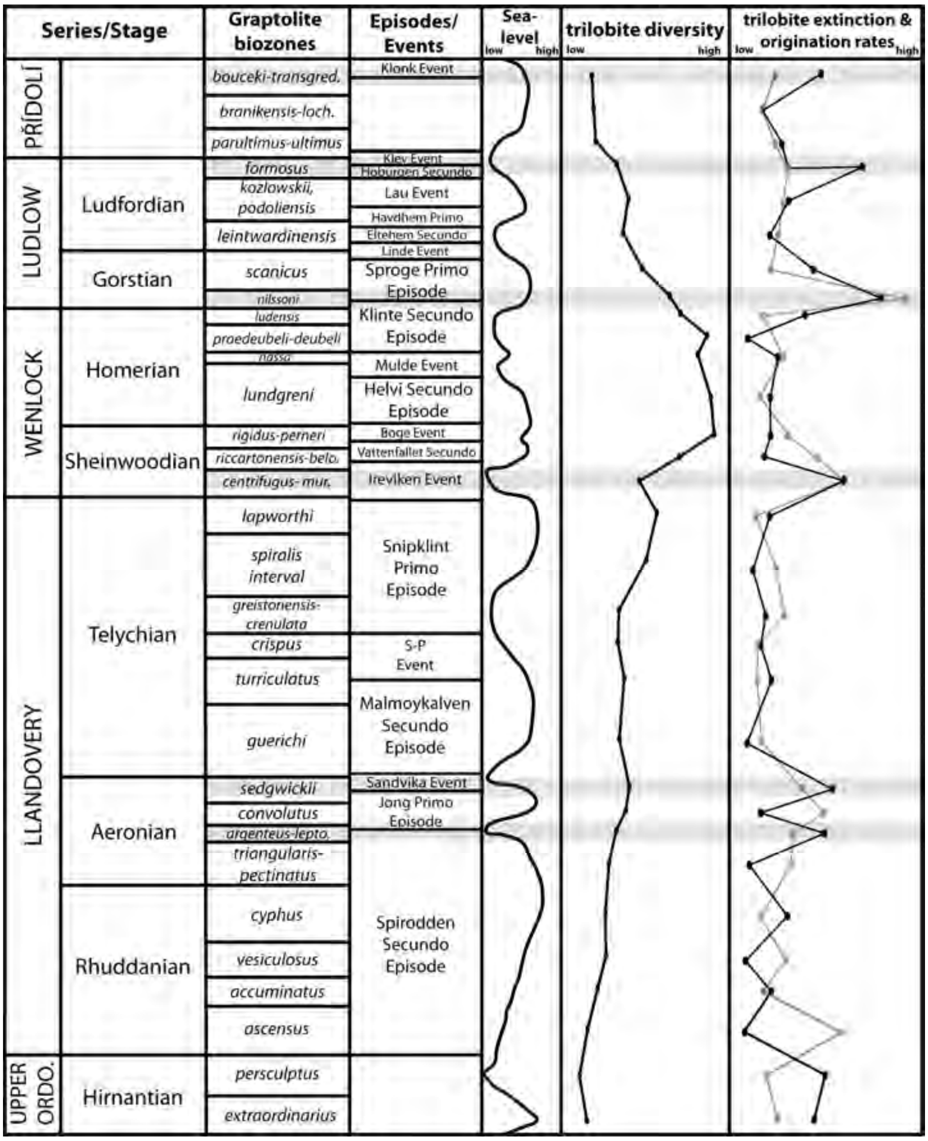
Table 4.5. Table showing the number of species for the most common Silurian trilobite families as a percentage of Estimated Mean Standing Diversity. Values of 10 per cent or greater are highlighted.

The encrinurids and proetids are the most diverse in the early and mid Ludfordian (S24-S25), but extinctions in the *formosus* Biozone (S26) result in the encrinurids falling to levels of the late Wenlock. Throughout the remainder of the Ludlow and Přídolí most groups are generally in decline. Proetids and acastids increase in number, however, and are the most diverse families in the late Ludfordian and Přídolí. The raphiophorids, which show a low diversity for the Hirnantian and Silurian, are extinct by the close of the Přídolí.

Based on the results here it would seem that high rates of turnover in the *sedgwickii, centrifugus, nilssoni,* and *formosus* biozones were associated with the most diverse family being replaced by another in the following intervals. During intervals of lower species EMSD (Hirnantian, Llandovery, late Ludlow, and Přídolí) up to three families dominate with at least one contributing around 20 per cent towards species EMSD. In intervals of higher diversity (much of the Wenlock) the diversity between families are more evenly distributed.

4.3.5 *Trilobite diversity and bioevents*

Silurian faunal events, associated with turnover and extinctions, are well established in the literature (Jeppsson 1990, 1998, Aldridge *et al.* 1993; Jeppsson *et al.* 1995; Barnes *et al.* 1996; Melchin *et al.* 1998; Jeppsson and Aldridge 2000; Lehnert *et al.* 2007; Calner 2008). A total of nine events characterised by elevated extinctions are known for graptolites and conodonts during the Silurian while trilobite extinctions have been previously recognised during the Sandvika (Chatterton *et al.* 1990) and Ireviken events (Calner 2008). Six Silurian trilobite bioevents are recognised here, which are associated with elevated extinction rates (Text-Figure 4.15).



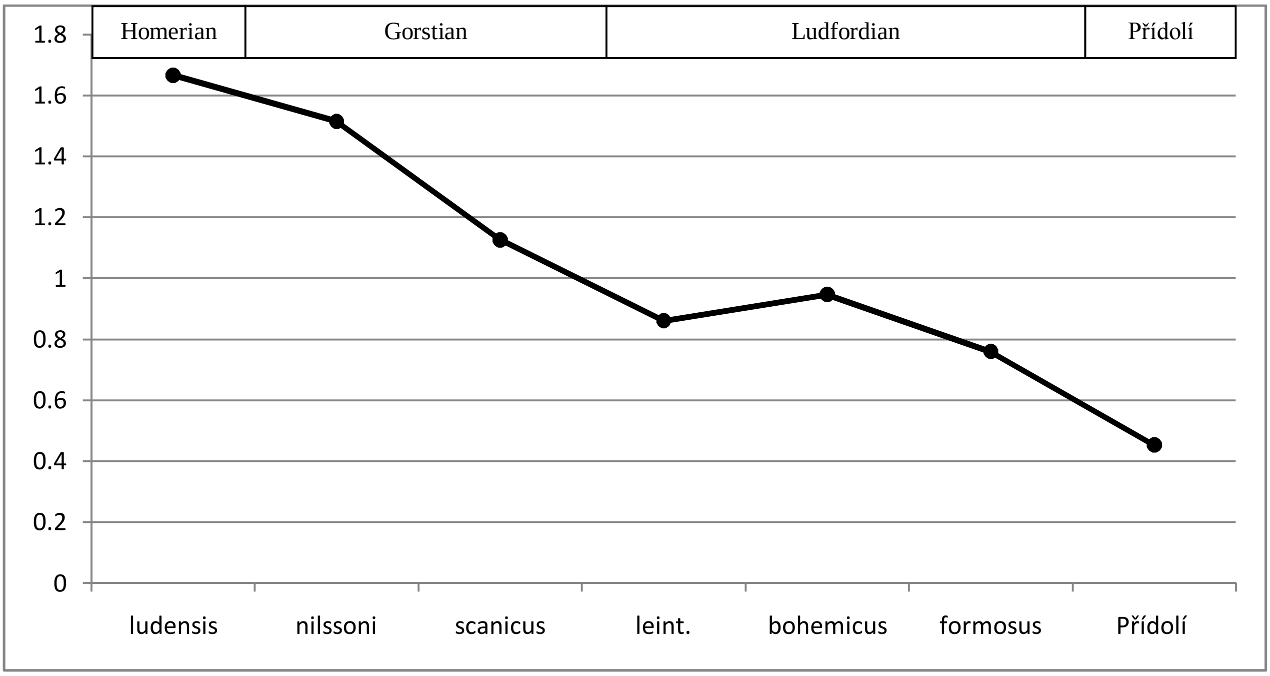
Text-Figure 4.15. Hirnantian-Silurian trilobite diversity (EMSD-St.) and evolutionary rates (extinctions are black, originations are grey) of this chapter correlated with sea level, episodes and graptolite events (based on Ogg *et al.* 2008). Trilobite events characterised by high extinction rates\turnover are indicated by grey horizontal bars. For a review on Silurian sea level see Johnson (2010).

In order of intensity these occur during the early Gorstian (*nilssoni* Biozone), the late Ludfordian (*formosus* Biozone), the early Sheinwoodian (*centrifugus-murchisoni* Biozone), the late Aeronian (*sedgwickii* Biozone) the mid Aeronian (*argenteus-leptotheca*

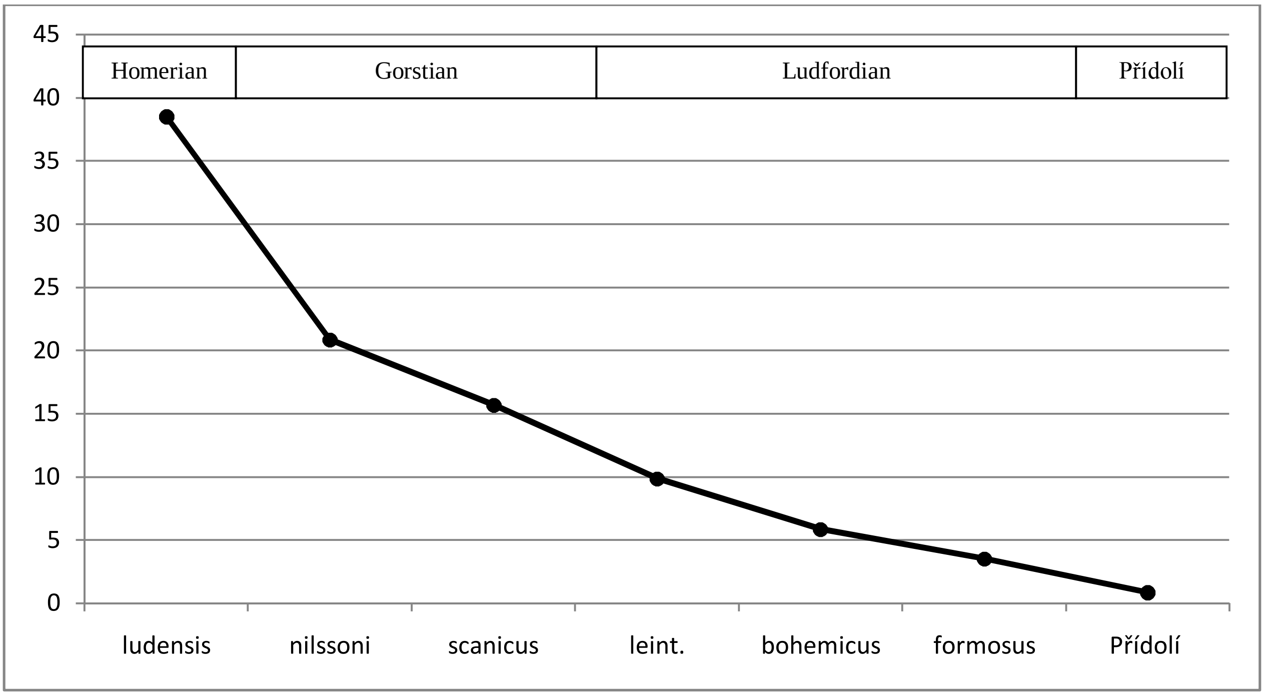
Biozone), and the late Přídolí (*bouchki-transgrediens* Biozone). All are associated with high turnover except the *formosus* and the *bouchki- transgrediens* biozones where the origination rates are much lower than the extinction rates. Trilobite diversity seems unaffected overall during most of the events, however, due to high origination rates in the interval concerned or following interval. The trilobite events are defined herein as intervals of elevated extinctions which are often associated with high turnover. Based on the above trilobite events are recognised during the Sandvika (*sedgwickii* Biozone), Ireviken (*centrifugus-murchisoni* Biozone), Klev (*formosus* Biozone) and Klonk (*bouceki-transgrediens* Biozone) events, and occur between Primo and Secundo episodes. The trilobite events occurring in the early Gorstian and mid Aeronian, do not occur during known graptolite or conodont extinction events, although the former occurs between the Klinte Secundo Episode and the Sproge Primo Episode.

There seems to be a weak correlation between Silurian trilobite evolutionary rates (EMSD-St.) and eustacy. All but the *nilssoni* trilobite bioevents, and the Klonk event occur during sharp sea level falls. Diversity generally increases through the Llandovery to the Wenlock, possibly due to more stable climatic conditions with longer Primo and Secundo episodes (the Spirodden Secundo Episode is the longest in the Silurian), longer phases of marine transgressions, and larger gaps between extinction events. The longer periods of highstands may be responsible for the recovery phases seen in the Llandovery where extinction rates often fall below that of origination rates. The relatively high diversity in the late Sheinwoodian and early Homerian occurs during a highstand. During the late Wenlock to Přídolí sea level fluctuates more rapidly and the primo and secundo episodes are much shorter. This is probably why extinction rates are generally higher than origination rates during this time. There is a decrease in range through species also resulting in a downward trend in diversity.

The decline in trilobite global species diversity (Text-Figure 4.16) from the latest Wenlock through the late Silurian is also seen in Britain (Text-Figure 4.17). In Britain the drop in diversity is more pronounced between the Homerian *ludensis* Biozone and the Gorstian (*nilssoni* Biozone), however. This large drop in diversity is probably due to the local affect of the Much Wenlock Limestone Formation Lagerstätte and the more restricted fauna in the British Ludlow. British trilobite species diversity declines throughout the remainder of the Ludlow into the Přídolí. In the British late Ludlow deep marine environments were replaced by shallow marine conditions, and largely terrestrial conditions during the Přídolí (Aldridge *et al.* 2000), as a result of the collision of Avalonia and Laurentia (discussed in Chapter One). This decrease in marine environments in Britain is most likely responsible for the decline in trilobites to only a few species by the Přídolí. The collision of Avalonia and Laurentia is a relatively local event and is unlikely to have the same impact on global diversity as it does on Britain. There is a global reduction in preserved basinal environments through the late Ludlow and Přídolí, however, due to eustatic changes (Chlupáč *et al.* 1998). A regression in the late Přídolí resulted in the widespread transition from marine to terrestrial environments (Chlupáč *et al.* 1998). It is possible therefore, that the global decline in diversity during the late Ludlow and Přídolí is at least in part a result of a preservation bias.



Text-Figure 4.16. Global EMSD-St. for the late Wenlock (*ludensis* Biozone) to the Přídolí. Based on Text-Figure 4.12.



Text-Figure 4.17. British EMSD for the late Wenlock (*ludensis* Biozone) to the Přídolí. Based on Text-Figure 3.10. The British biozones have been converted to the graptolite global standard.

The global diversity cure (EMSD-St.) shown in Text-Figure 4.16 should be influenced less by biases, but it still shows an overall drop in diversity through the late Silurian to the lowest diversity in the Přídolí. The drop in diversity through the late Silurian is also seen in chitinozoans of the east Baltic (Nestor 2009) and in graptolite global diversity (Melchin *et al.* 2008). The degree to which these represent a biological signal requires further investigation.

5.1 CONCLUSIONS

The main conclusions of this chapter are summarized below.

1. The total number of trilobite species (N_{tot}) shows a moderate but statistically significant correlation with the number of formations of the Hirnantian Stage and Llandovery Series, indicating a potential preservation bias.
2. The number of sampled species (N_s) shows the same trend as species N_{tot} implying that the bias is not due to 'missing' range through taxa, but possibly due to 'missing' lower or upper boundary crosses (or elevated singletons in intervals with better preservation).
3. Estimated Mean Standing Diversity (EMSD) better estimates the distribution of taxa in an interval by weighting the different classes of taxa, and by doing so is less prone to biases. EMSD and EMSD standardized against the number of formations (EMSD-St.) show a smoother curve than species N_{tot} and N_s. The general picture of the former two is the same as the latter two, where diversity increases to the Wenlock and decreases through the late Silurian. This indicates that the biases are most likely responsible for smaller scale perturbations rather than the overall trend.

4. Six trilobite bioevents are recognised in the Silurian, associated with elevated extinction rates. In the Llandovery and Wenlock these are generally associated with elevated origination rates and thus there is no large drop in diversity. In the late Silurian, however, extinction rates are mostly above origination rates and there is a declining diversity through the Ludlow and Přídolí.
5. The bioevents are mostly associated with sharp sea level falls, although the largest (*nilssoni* Biozone) is associated with a sea level rise. Elevated extinction rates in the late Hirnantian also occur during a time of falling sea level.
6. High turnover in many of the biozones results in replacement, which most often changes the dominant family. In times of lower diversity several families dominate (Llandovery and late Silurian), but in intervals of higher diversity (much of the Wenlock) the species diversity between families is more evenly distributed.
7. The general increase in diversity through the Llandovery is associated with longer primo and secundo episodes, and longer intervals of highstand. The declining diversity in the late Homerian and late Silurian is associated with frequent shifts in climate and sea level.
8. The Sheinwoodian (*rigidus-perneri*) and Homerian (*lundgreni* Biozone) represent the peak in Silurian trilobite diversity.
9. A comparison of the global diversity standardised against the number of formations (EMSD-St.) compared with the EMSD of the British late Silurian indicates that the drop in trilobite diversity may be related to a loss in preserved marine environments.

CHAPTER FIVE

CONCLUSIONS

THE main conclusions of this thesis are outlined herein. For convenience this chapter is ordered thematically based on the trilobite systematics, associations, and global diversity.

5.1 SYSTEMATICS

The trilobites from the late Silurian of England and Wales are described. A total of 15 families, 36 genera, and 53 species are recognised here. These include a new genus and seventeen new species, fourteen of which remain under open nomenclature. Previously identified species such as *Homalonotus knightii* (König), *Dalmanites nexilis* (Salter), *D. tuberculatocaudatus* (Murchison), *Alcymene puellaris* (Siveter), *Trimerus johannis* (Salter), and *T. salteri* (Morris) have not been described in detail before, while the types of *H. knightii*, *D. nexilis*, ‘*D. mobergi*’ Hede, and ‘*D. simrica*’ Hede are figured photographically here for the first time. Several of the trilobite genera occurring in the British late Silurian are revised also. *Acaste downingiae* (Murchison) and *Dalmanites myops* (König), which were previously thought to occur in the British Ludlow, seem to be restricted to the Wenlock. In the case of the latter it has often been mistaken for *D. obtusus* (Lindström) or *D. nexilis*. The trilobites ‘*Delops nobilis marri*’ Rickards and ‘*Struveria howgillensis*’ Rickards from the Coldwell Formation are regarded as conspecific respectively with ‘*Dalmanites mobergi*’ Hede and ‘*D. simricus*’ Hede from the Swedish Colonus Shale. Based on its type species, *D. obtusicaudatus* (Salter), *Delops* is regarded as a senior synonym of *Lygdozoon*. A new genus, *Barriepiscator,* is erected to incorporate taxa formerly assigned to *Delops*: *D. nobilis marr*i, *D. nobilis* (Thomas), and *D. dermaloc* Šnajdr.

A cladistic analysis (Chapter Two) of Silurian dalmanitids shows *Struveria* to group with members of the Synphoriinae and it is reassigned to that subfamily. *Delops* forms a sister group with specimens now assigned to *Barriepiscator*, while *Daytonia* represents the base of a clade that includes *Dalmanites* and *Ommokris*. These findings are consistent with Holloway (1981). *Delops obtusicaudatus* forms the base of a clade containing species formally assigned to *Lygdozoon*.

5.2 ASSOCIATIONS

The most abundant and diverse Silurian trilobite faunas occur in shelf facies, whereas basinal settings are characterized by graptolite and cephalopod bearing-mudstones. There are several examples of trilobites occurring in basinal settings, however. The fauna of the Coldwell Formation (Chapter Two) is one, which occurs in the Lake District Basin. *Decoroproetus scrobiculatus* Owens is the most abundant species in the Coldwell Formation, followed by *Barriepiscator mobergi* and *Struveria simrica*. The brachiopods *Leangella segmentum* (Lindström) and *Protozyga*? sp. are identified for the first time. The sediments associated with the Coldwell Formation are graptolitic turbidites deposited below storm wave base. The Coldwell Formation, characterized by bioturbated calcitic mudstones and localized fossiliferous silty limestones, represents periods of sea floor ventilation, associated with a temporary shallowing (Kneller *et al.* 1994). The trilobite fauna in the Coldwell Formation belongs to the *Barriepiscator-Miraspis* Association (=*Delops-Miraspis* Assemblage of Thomas and Lane 1999). A similar fauna occurs in the

Mottled Mudstones of North Wales and the Swedish Colonus Shale, but they differ from the Coldwell Formation in containing a rich brachiopod fauna and some trilobites typical of the *Dalmanites-Raphiophorus* Association. The Colonus Shale and the Mottled Mudstones most likely represent the shallowest depths of the *Barriepiscator-Miraspis* Association, occupying a depth between that of the Coldwell Formation and the Elton Group. The Coldwell Formation likely represents a depth at the deep end of BA5 and possibly into BA6.

Trilobites from the Elton to Whitcliffe groups (Chapter Three) represent a shallowing up sequence overall. They are characterized by four different palaeoenvironments, each containing a distinctive trilobite fauna. The *Dalmanites-Raphiophorus* Association occurs in the calcareous siltstones and mudstones of the Elton Group, which represents the deepest parts of the Ludlow shelf (BA5). The overlying Bringewood Group (BA3-4) contains a transitional trilobite and brachiopod fauna between the Elton and Leintwardine groups. Trilobite faunas from the shallower coquinoid siltstone facies of the Leintwardine (BA3) and Whitcliffe (BA2) groups are described. The *Plesiowensus obconicus-Encrinurus-Alcymene* Association is defined from the Leintwardine Group, and an unnamed trilobite fauna containing *Homalonotus knightii* occurs in the Whitcliffe Group. The *Homalonotus knightii-Acaste* cf. *subcaudata* Association, from the Hafod Fawr Formation (BA1), represents the shallowest trilobite fauna described from the British Ludlow.

There is a fall in trilobite abundance and diversity from the deep to shallow ends of the Ludlow shelf. Sedimentation rates and clay/silt content appears to have controlled trilobite distribution on the shelf. Trilobite diversity decreases through the British late

Silurian along with a general retraction in the trilobites spatial distribution. This is associated with the shallowing of the Silurian sea and the filling up of the basins.

5.3 GLOBAL DIVERSITY

Silurian trilobite diversity N_{tot} shows a moderate but significant correlation with the number of formations in the Hirnantian-Llandovery, indicating a potential preservation bias for that series. The general increasing diversity trend through the Llandovery is most likely genuine, however, as this is also seen in EMSD (Estimated Mean Standing Diversity) and EMSD standardised against the number of formations. Small scale variations in the Llandovery such as the marked increase in diversity in the late Aeronian (*sedgwickii* Biozone) are probably a result of preservation. Both the total diversity and EMSD show a peak in the early Homerian (*lundgreni* Biozone). When standardised against the number of formations EMSD peaks in the late Sheinwoodian (*rigidus-perneri* Biozone), however. This is due to the much lower numbers of singletons, more range through species, and fewer formations of the latter compared to the Homerian *lundgreni* Biozone.

Several bioevents are recognised for graptolites and conodonts throughout the Silurian which are associated with elevated extinction rates and drops in diversity, or increased turnover. Based on the results in Chapter Four the Sandvika, Ireviken, Klev, and Klonk events appear to affect trilobites. Elevated extinctions also occur in the early Gorstian (*nilssoni* Biozone) and mid Aeronian (*argenteus-leptotheca* Biozone), but these seem restricted to the benthos. The early Gorstian bioevent represents the highest trilobite extinction and origination rates for the whole Silurian, which seems restricted to the benthos. The diversity at the end of the Přídolí returns to levels seen in the basal

Llandovery. The drop in diversity in the late Silurian and Přídolí may partly be due to a loss of preserved deep marine environments and falling sea level.

Many of the trilobite bioevents occur during sea level falls and between Primo and Secundo episodes. The more stable climatic conditions and longer periods of rising sea level may have been responsible for the general increase in trilobite diversity through the Llandovery. The peak in trilobite diversity in the late Sheinwoodian occurs during a highstand. The fall in trilobite diversity from the late Homerian to the end of the Silurian occurs during a time of more rapid sea level change, and shorter Primo and Secundo episodes. During this time the stratigraphical ranges of trilobite species are generally shorter than other parts of the Silurian.

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APPENDIX

DIVERSITY DATA FOR CHAPTER 4

Table A.1. For convenience, the standard graptolite Biozones used in chapter 4 are represented each by a number here. These numbers are referred to thought the Appendix. There are 31 graptolite biozones in total from the Hirnantian (H) through the Silurian (S). The graptolite biozones referred to here are in Ogg *et al*. (2008).

STANDARD GRAPTOLITE BIOZONE	STAGE	NUMBER
Normalograptus? *extraordinarius*	Hirnantian (Late Ordovician)	H1
Normalograptus? *persculptus*	Hirnantian (Late Ordovician)	H2
Akidograptus ascensus	Rhuddanian	S1
Parakidograptus acuminatus	Rhuddanian	S2
Orthograptus vesiculosus	Rhuddanian	S3

Coronograptus cyphus	Rhuddanian	S4
Demirastrites triangulatus – pectinatus	Aeronian	S5
Monograptus argenteus – leptptheca	Aeronian	S6
Lituigraptus convolutus	Aeronian	S7
Stimulograptus sedgwickii	Aeronian	S8
Spirograptus guerichi	Telychian	S9
Spirograptus turriculatus	Telychian	S10
Monograptus crispus	Telychian	S11
Monograptus griestoniensis – crenulata	Telychian	S12
Oktavites spiralis Interval Zone	Telychian	S13
Cyrtograptus lapworthi – insectus	Telychian	S14
Cyrtograptus centrifugus – murchisoni	Sheinwoodian	S15
Monograptus riccartonensis – belophorus – antennularis	Sheinwoodian	S16
Cyrtograptus rigidus – perneri	Sheinwoodian	S17
Cyrtograptus lundgreni	Homerian	S18

Pristiograptus parvus – *Gothograptus nassa*	Homerian	S19
Colonograptus praedeubeli – deubeli	Homerian	S20
Colonograptus ludensis	Homerian	S21
Neodiversograptus nilssoni	Gorstian	S22
Lobograptus scanicus	Gorstian	S23
Saetograptus leintwardinensis	Ludfordian	S24
Neocucullograptus kozlowskii, *Polonograptus podoliensis*	Ludfordian	S25
Monograptus formosus	Ludfordian	S26
Monograptus parultimus – ultimus	Přídolí	S27
Monograptus branikensis – lochkovensis	Přídolí	S28
Monograptus bouceki – *transgrediens – perneri*	Přídolí	S29

Table A.2. Table of FAD’s and LAD’S for Hirnantian and Silurian trilobite species. Species under open nomenclature are included in intervals where a genus occurs but no formally named species have been recognised. Biozones in square brackets are where the precise age is unknown and a biozone age is determined based on the method in chapter 4.

		FAD				**LAD**			
Species	**Family**	**System**	**Series**	**Stage**	**Biozone**	**System**	**Series**	**Stage**	**Biozone**
***Acanthopyge cf. hirsuta* of Lane & Wu, 2002**	Lichidae	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S12
Acanthopyge hirsuta	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Acanthopyge orientalis	Lichidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Acanthopyge parapleura	Lichidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
***Acanthopyge sp.* of Thomas, 1971**	Lichidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Acanthopyge? rohri	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Acaste dayiana	Acastidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Acaste downingiae	Acastidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Acaste inflata	Acastidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Acaste podolica	Acastidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Acaste praeacastopyge	Acastidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
***Acaste sp.*of Curtis & Lane 1998**	Acastidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Acaste subcaudata	Acastidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S23
Acaste zerinae	Acastidae	Silurian	Přídolí	n/a	[S28]	Silurian	Přídolí	n/a	[S28]
Acastella amatrix	Acastidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26

Acastella breviceps	Acastidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Acastella elsana	Acastidae	Silurian	Přídolí	n/a	S29	Devonian	Early	Lochkovian	
Acastella macrocentra	Acastidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Acastella madidipes	Acastidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Acastella minor	Acastidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Přídolí	n/a	?S27
Acastella podolica	Acastidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Acastella prima	Acastidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S28
Acastella spinosa	Acastidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Přídolí	n/a	S29
Acastella virgo	Acastidae	Silurian	Přídolí	n/a	S29	Devonian	Early	Lochkovian	
Acastocephala dudleyensis	Acastidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Acastocephala macrops	Acastidae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Homerian	S21
Acastoides constrictus	Acastidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Acastopyge shergoldi	Acastidae	Silurian	Přídolí	n/a	S28	Silurian	Přídolí	n/a	S28
Acernaspis alacer	Phacopidae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Acernaspis angustifrons	Phacopidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S8
Acernaspis dispersa	Phacopidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Acernaspis estonica	Phacopidae	Silurian	Llandovery	Rhuddanian	[S1]	Silurian	Llandovery	Rhuddanian	[S1]
Acernaspis georgei	Phacopidae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S15
Acernaspis glabra	Phacopidae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Aeronian	S8
Acernaspis konoverensis	Phacopidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Acernaspis norvegiensis	Phacopidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S6
Acernaspis orestes	Phacopidae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S10
Acernaspis quadrilineata	Phacopidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Acernaspis salmoensis	Phacopidae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Acernaspis semicircularis	Phacopidae	Silurian	Llandovery	Rhuddanian	[S2]	Silurian	Llandovery	Rhuddanian	[S2]

Acernaspis sp. **of Koren & Sobolevskaya, 2008**	Phacopidae	Ordovician	Late	Hirnantian	H2	Ordovician	Late	Hirnantian	H2
Acernaspis sufferta	Phacopidae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Acernaspis superciliexcelsis	Phacopidae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S11
Acernaspis woodburnensis	Phacopidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Acernaspis xynon	Phacopidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
Acernaspis? sp. **of Sandford & Holloway, 2006**	Phacopidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Aceroproetus acer	Proetidae	Silurian	Wenlock	?Homerian	[S18]	Silurian	Wenlock	?Homerian	[S18]
Acidaspis (Dalaspis) drzymlai	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Acidaspis (Globulaspis) prominens	Odontopleuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S6
Acidaspis brightii	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Acidaspis grayi	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Acidaspis jessi	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Acidaspis lesperancei	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Acidaspis sp. **of Curtis & Lane, 1998**	Odontopleuridae	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S10
Acidaspis sp. **of Jin et al., 1993**	Odontopleuridae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Acidaspis sp. **of Sepkoski, 1998**	Odontopleuridae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	[H2]
Aegrotocatellus jaggeri	Encrinuridae	Silurian	Ludlow	Ludfordian	[S24]	Silurian	Ludlow	Ludfordian	[S24]
Alcymene alveus	Calymenidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Alcymene lawsoni	Calymenidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S26
Alcymene lindstroemi	Calymenidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Alcymene neointermedia	Calymenidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Alcymene puellaris	Calymenidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Anacaenaspis callipareos	Odontopleuridae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Aeronian	S6
Anacaenaspis cf. pectinata **of**	Odontopleuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S12

Curtis & Lane, 1998									
Anacaenaspis dealgach	Odontopleuridae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Anacaenaspis gigantea	Odontopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Anacaenaspis gotlandensis	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Anacaenaspis pectinata	Odontopleuridae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S16
Anacaenaspis phasganis	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21
Anacaenaspis sp. **of Holloway & Sandford, 1993**	Odontopleuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Ananaspis fecunda	Phacopidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Ananaspis fecundus	Phacopidae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Ludfordian	S26
Ananaspis? amelangorum	Phacopidae	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S19
Ananaspis? decora	Phacopidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Ananaspis? frontosa	Phacopidae	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S19
Ananaspis? kenleyi	Phacopidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Ananaspis? macdonaldi	Phacopidae	Silurian	Llandovery	Telychian	[S14]	Silurian	Wenlock	Sheinwoodian	[S15]
Ananaspis? nuda	Phacopidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Ananaspis? stokesii	Phacopidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Ananaspis? typhlagogus	Phacopidae	Silurian	Llandovery	Telychian	[S13]	Silurian	Wenlock	Homerian	S18
Ananaspis? woiwurrungi	Phacopidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Andinacaste chojnacotensis	Calmoniidae	Silurian	Přídolí	n/a	[S28]	Silurian	Přídolí	n/a	[S28]
Andinacaste espejensis	Calmoniidae	Silurian	Přídolí	n/a	[S28]	Devonian	Early	Lochkovian	
Andinacaste ramiroi	Calmoniidae	Silurian	Přídolí	n/a	[S29]	Silurian	Přídolí	n/a	[S29]
Andinacaste? perroana	Calmoniidae	Silurian	Llandovery	Telychian	[S12]	Silurian	Llandovery	Telychian	[S12]
Apocalymene coppinsensis	Calymenidae	Silurian	Wenlock	Homerian	[S21]	Silurian	Wenlock	Homerian	[S21]
Apocalymene nabrici	Calymenidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Apolichas perconvexus	Lichidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23

Apolichas truncatus	Lichidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Arcticalymene australis	Calymenidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Arcticalymene cooki	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Arcticalymene jonesi	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Arcticalymene matlocki	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Arcticalymene polgari	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Arcticalymene rotteni	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
***Arcticalymene* sp. [of Adrain & Edgecombe, 1997]**	Calymenidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Arcticalymene viciousi	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Arctinurus anticostiensis	Lichidae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S10
Arctinurus boltoni	Lichidae	Silurian	Wenlock	Sheinwoodian	[S16]	Silurian	Wenlock	Sheinwoodian	[S16]
Arctinurus nereus	Lichidae	Silurian	Wenlock	Sheinwoodian	[S17]	Silurian	Wenlock	Sheinwoodian	[S17]
Arctinurus ornatus	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
***Arctinurus* sp. of Watkins, 1993**	Lichidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
***Arthrorhachis* sp. of Temple, 1965**	Metagnostidae	Ordovician	Late	Hirnantian	[H1]	Ordovician	Late	Hirnantian	[H1]
***Ascetopeltis* sp. 2 of Owens, 1973b**	Proetidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Astroproetus acutus	Proetidae	Silurian	Llandovery	Telychian	[S11]	Silurian	Llandovery	Telychian	[S11]
Astroproetus bellus	Proetidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
Astroproetus constrictus	Proetidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Astroproetus curtisi	Proetidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Astroproetus interjectus	Proetidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S6
Astroproetus pseudolatifrons	Proetidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Astroproetus scoticus	Proetidae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S4
***Astroproetus* sp. of Curtis & Lane, 1997**	Proetidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Telychian	S12

***Astroproetus* sp. of Sepkoski 1998**	Proetidae	Ordovician	Late	Katian		Silurian	Late	Hirnantian	[H2]
***Aulacopleura* aff. *konicki* of Ivanova et al., 2009**	Aulacopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Aulacopleura andersoni	Aulacopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Aulacopleura haueri	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Aulacopleura konincki	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S22
Aulacopleura krizi	Aulacopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Aulacopleura pogsoni	Aulacopleuridae	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S10
Aulacopleura roquemaillerensis	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	[S16]	Silurian	Wenlock	Sheinwoodian	[S16]
Aulacopleura socialis	Aulacopleuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S9
Aulacopleura soror	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
***Aulacopleura* sp. [of Snajdr, 1980]**	Aulacopleuridae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
***Aulacopleura* sp. [of Thomas & Lane, 1999]**	Aulacopleuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S7
Aulacopleura wulongensis	Aulacopleuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S6
Aulacopleura? ranfordi	Aulacopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Australoacaste oconnori	Calmoniidae	Silurian	Přídolí	n/a	[S28]	Silurian	Přídolí	n/a	[S28]
Australoacaste palpalensis	Calmoniidae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	[S23]
Australoscutellum longispinifex	Styginidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
***Australoscutellum* sp. [of Chatterton & Campbell]**	Styginidae	Silurian	Wenlock	Homerian	[S21]	Silurian	Wenlock	Homerian	[S21]
Avalanchurus garfunkeli	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Avalanchurus lennoni	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Avalanchurus simoni	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
***Avalanchurus* sp. 2 of Adrain & Edgecombe, 1997**	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
***Avalanchurus* sp. B of Adrain & Edgecombe, 1997**	Encrinuridae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21

Avascutellum edwardsi	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S26
Awaria struvei	Calymenidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Aytounella scotica	Indet.	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Balizoma concomitans	Encrinuridae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Balizoma dakon	Encrinuridae	Silurian	Ludlow	?Gorstian	[S22]	Silurian	Ludlow	?Gorstian	[S22]
Balizoma dimitrovi	Encrinuridae	Silurian	Wenlock	?Homerian	[S20]	Silurian	Wenlock	?Homerian	[S20]
Balizoma hyperborea	Encrinuridae	Silurian	Ludlow	?Ludfordian	[S25]	Silurian	Ludlow	?Ludfordian	[S25]
Balizoma indianensis	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Ludfordian	[L26]
Balizoma inexpectata	Encrinuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Balizoma mareki	Encrinuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Balizoma obtusus	Encrinuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S25
Balizoma ramskoldi	Encrinuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Balizoma transiens	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Balizoma variolaris	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Balizoma? testosteron	Encrinuridae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Barriepiscator dermolac	Dalmanitidae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Barriepiscator mobergi	Dalmanitidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Barriepiscator nobillis	Dalmanitidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Batocara bowningi	Encrinuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Batocara duntroonensis	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Batocara fritillum	Encrinuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S13
Belenopyge parapleura	Lichidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Belenopyge sp. **(of Teller & Boucot, 1999)**	Lichidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Berylacaste berylae	Acastidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Bessazoon buttingtonense	Dalmanitidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12

***Bessazoon* sp. (from Curtis & Lane, 1998)**	Styginidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Telychian	S10
***Bessazoon* sp. (from Sandford & Holloway, 2006)**	Styginidae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S15
Bessazoon tenuimucronatum	Dalmanitidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S12
Bessazoon tigerensis	Dalmanitidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Billevittia adraini	Encrinuridae	Silurian	Llandovery	Telychian	[S11]	Silurian	Llandovery	Telychian	[S11]
***Boemoharpes* sp. [of Santel, 2001]**	Harpetidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Bohemoharpes (B.) ovatum	Harpetidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Bohemoharpes (Bohemoharpes) ovatus	Harpetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Bohemoharpes (Unguloharpes) ungula	Harpetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Bohemoharpes naumanni	Harpetidae	Silurian	Llandovery	Aeronian	S7	Silurian	Wenlock	Homerian	S18
***Bohemoharpes sp.* [of Chlupac, 1987]**	Harpetidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Bohemoharpes vittatus	Harpetidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Borealarges calei	Lichidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Borealarges mikulicorum	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Borealarges morrisoni	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Borealarges reedi	Lichidae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Borealarges tuckerae	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Borkopleura gorella	Odontopleuridae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Brianurus jeffersoni	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Brongniartella benderi	Homalonotidae	Silurian	Llandovery	Rhuddanian	[S3]	Silurian	Llandovery	Rhuddanian	[S3]
Brongniartella pamiricus	Homalonotidae	Silurian	Wenlock	Sheinwoodian	[S15]	Silurian	Wenlock	Sheinwoodian	[S15]
Brongniartella platynota	Homalonotidae	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H1
Brongniartella robusta	Homalonotidae	Ordovician	Late	Hirnantian	[H2]	Silurian	Llandovery	Aeronian	S5

Bumastus agmakros	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Bumastus armatus	Styginidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Sheinwoodian	S17
Bumastus barriensis	Styginidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Bumastus bellmanni	Styginidae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	[S16]
Bumastus bouchardi	Styginidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Bumastus commodus	Styginidae	Ordovician	Late	Hirnantian	H2	Ordovician	Late	Hirnantian	H2
Bumastus cuniculus	Styginidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S23
Bumastus glomerosus	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Bumastus hornyi	Styginidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Bumastus ioxus	Styginidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Sheinwoodian	S17
Bumastus kattoi	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Bumastus sakoi	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Bumastus subquadratus	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Bumastus sulcatus	Styginidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Bumastus vulsus	Styginidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S11
Bumastus? phrix	Styginidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Bumastus? xestos	Styginidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Burmastella asper	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Burmastella bipunctatus	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Burmastella spiculus	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Burmeisteria kseibi	Homalonotidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Calymene aspera	Calymenidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Calymene beyeri	Calymenidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S27
Calymene bisexuata	Calymenidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Calymene blumenbachii	Calymenidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21

Calymene boettneri	Calymenidae	Silurian	Llandovery	Telychian	[S10]	Silurian	Wenlock	Sheinwoodian	[S17]
Calymene breviceps	Calymenidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Calymene chica	Calymenidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Calymene conspicua	Calymenidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Calymene cresapensis	Calymenidae	Silurian	Llandovery	Aeronian	S7	Silurian	Wenlock	Sheinwoodian	S15
Calymene dnestroviana	Calymenidae	Silurian	Přídolí	n/a	[S27]	Silurian	Přídolí	n/a	[S27]
Calymene endemopsis	Calymenidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Calymene excavata	Calymenidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Calymene ferrifera	Calymenidae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	[S23]
Calymene fuliginata	Calymenidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Calymene iladon	Calymenidae	Silurian	Llandovery	Telychian	[S9]	Silurian	Llandovery	Telychian	[S9]
Calymene kaugatumensis	Calymenidae	Silurian	Přídolí	n/a	S28	Silurian	Přídolí	n/a	S28
Calymene latigenata	Calymenidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Calymene latvica	Calymenidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Calymene mimaspera	Calymenidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Calymene minigranulosa	Calymenidae	Silurian	Ludlow	Gorstian	S22	Silurian	Přídolí	n/a	S27
Calymene minimarginata	Calymenidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Calymene nabrici	Calymenidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Calymene neotuberculata	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Calymene oliveae	Calymenidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Calymene orthomarginata	Calymenidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Calymene perforata	Calymenidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Calymene polgari	Calymenidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Calymene replicata	Calymenidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S14
Calymene schmidti	Calymenidae	Silurian	Přídolí	n/a	[S29]	Silurian	Přídolí	n/a	[S29

Calymene soervensis	Calymenidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Calymene spectabilis	Calymenidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Calymene tuberculata	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Přídolí	n/a	S27
Calymene tuberculosa	Calymenidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Calymene vallecitoensis	Calymenidae	Silurian	Wenlock	Homerian	[S19]	Devonian	Early	Lochkovian	
Calymene? frontosa	Calymenidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Calymene? hadyardensis	Calymenidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Calymenella rostrata	Calymenidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S10
***Calymenella* sp. [of Sanchez 1990]**	Calymenidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
***Calymenella* sp. 1 [of Holloway and Sandfod, 2006]**	Calymenidae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S15
Carlopsia glaudii	Proetidae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Ceratocephala avalanchensis	Odontopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Telychian	S13
Ceratocephala barrandii	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Ceratocephala bowningensis	Odontopleuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Ceratocephala crawfordi	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Ceratocephala goniata	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Ceratocephala plummeri	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Ceratocephala rhabdophora	Odontopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S27
Ceratocephala tungstenensis	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Ceratocephala verneuili	Odontopleuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S26
Ceratocephalina charlesworthi	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Ceratocephalina reperta	Odontopleuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S6
Ceratocephalina sevastopuloi	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Ceratonurus gibbosus	Odontopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Cerauromeros hydei	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S23

Cheirurus strux	Cheiruridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Cheirurus centralis	Cheiruridae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Homerian	S21
Cheirurus hitoeganensis	Cheiruridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Cheirurus insignis	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Cheirurus niagarensis	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S23
Cheirurus obtusatus	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S22
Cheirurus phollikodes	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Cheirurus prolixus	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Cheirurus propinquus	Cheiruridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Cheirurus sternbergi	Cheiruridae	Silurian	Wenlock	Homerian	[S18]	Silurian	Přídolí	n/a	S28
Chimaerastella chimaera	Acastidae	Silurian	Ludlow	Gorstian	[S23]	Silurian	Ludlow	Gorstian	[S23]
Chiozoon cowiei	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Chiozoon umisk	Cheiruridae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Chuanqianoproetus constrictus	Proetidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Ciliscutellum ciliensis	Styginidae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Coniproetus (Bohemiproetus) magnicerviculus	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Coniproetus (C.) affinis	Proetidae	Silurian	Přídolí	na	S29	Devonian	Early	Lochkovian	
Coniproetus (Ryckholtia) ryckholti	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Coniproetus balticus	Proetidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Coniproetus tenuiceps	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Coniproetus? subconicus	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Contracheirurus **sp. [of Chatterton & Perry, 1984]**	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Contracheirurus zuvegesi	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Cornuproetus kyphora	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18

Cornuproetus peraticus	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
***Cornuproetus* sp. [from Havlicek & Storch, 1999]**	Proetidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Cornuproetus walliseri	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S24
***Coronocephalus aff. urbis* (of Holloway, 1994)**	Encrinuridae	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S13
Coronocephalus elegans	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Coronocephalus gaoluoensis	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Coronocephalus kitakamiensis	Encrinuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Coronocephalus kobayashii	Encrinuridae	Silurian	Wenlock	Homerian	[S19]	Silurian	Wenlock	Homerian	[S19]
Coronocephalus qiangjiangensis	Encrinuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Coronocephalus rex	Encrinuridae	Silurian	Llandovery	Telychian	S9	Silurian	Wenlock	Sheinwoodian	S15
Coronocephalus rongxiensis	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Coronocephalus spinicaudatus	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Coronocephalus tenuisulcatus	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Crassiproetus? curtisi	Proetidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Cromus beaumonti	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Cromus bohemicus	Encrinuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Cromus canorus	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Cromus intercostatus	Encrinuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Cromus krolmusi	Encrinuridae	Silurian	Ludlow	Ludfordian	[S24]	Silurian	Ludlow	Ludfordian	[S24]
Cromus leirion	Encrinuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S29
Cromus melbournensis	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Cromus orizaba	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Cromus ploeckensis	Encrinuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Cromus princeps	Encrinuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10

Cromus rialpensis	Encrinuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Cromus simpliciculus	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
***Cromus* sp. [of Banks, 1988]**	Encrinuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Cromus spryi	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Cromus storchi	Encrinuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S25
Cromus tamchii	Encrinuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Cromus wagura	Encrinuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Crotalocephalus articulatus	Cheiruridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Crotalocephalus elongatus	Cheiruridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Crotalocephalus hawlei	Cheiruridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Crotalocephalus orientalis	Cheiruridae	Silurian	Ludlow	Gorstian	[S22]	Silurian	Ludlow	Gorstian	[S22]
Crotalocephalus transiens	Cheiruridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S27
Cryphina? gdoumontensis	Acastidae	Silurian	Přídolí	n/a	[S27]	Devonian	Early	Lochkovian	
Cryptolithus portageensis	Trinucleidae	Ordovician	Late	Hirnantian	[H1]	Ordovician	Late	Hirnantian	[H1]
Cuchulain lugi	Indet.	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Curiella tuberculifrons	Encrinuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Curriella clancyi	Encrinuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Curriella newlandensis	Encrinuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S6
Cybantyx anaglyptos	Styginidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Cybeloides (Paracybeloides) girvanensis	Encrinuridae	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H1
Cyphaspis buchbergeri	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Cyphaspis elachopos	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Cyphaspis munii	Aulacopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Cyphoproetus binodosus	Proetidae	Silurian	Llandovery	Telychian	S9	Silurian	Wenlock	Sheinwoodian	S15
Cyphoproetus comitilis	Proetidae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13

Cyphoproetus depressus	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21
Cyphoproetus externus	Proetidae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Aeronian	S8
Cyphoproetus insterianus	Proetidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Cyphoproetus latiaxis	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Cyphoproetus latifrontalis	Proetidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Cyphoproetus pugionis	Proetidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Cyphoproetus putzkeri	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Cyphoproetus semidepressus	Proetidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
***Cyphoproetus* sp. 1 Kegel, 1927**	Proetidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Cyphoproetus strabismus	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Cyphoproetus? alyo	Proetidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
Dalarnepeltis campanulatus	Tropidocoryphidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Dalmanites athamas	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Dalmanites bassleri	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Dalmanites bituberculatus	Dalmanitidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Dalmanites caudatus	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Dalmanites corrugatus	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Dalmanites howelli	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Dalmanites imbricatulus	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Dalmanites jupiterensis	Dalmanitidae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S10
Dalmanites limulurus	Dalmanitidae	Silurian	Llandovery	Telychian	S10	Silurian	Wenlock	Sheinwoodian	S17
Dalmanites longicaudatus	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S19
Dalmanites myops	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Dalmanites nexilis	Dalmanitidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Dalmanites obex	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18

Dalmanites obtusus	Dalmanitidae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Ludfordian	S24
Dalmanites platycaudatus	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Sheinwoodian	S17
Dalmanites ptyktorhion	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Dalmanites punctim	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Dalmanites sudamericanus	Dalmanitidae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	[S23]
Dalmanites transglabelaris	Dalmanitidae	Silurian	Ludlow	Gorstian	[S22]	Silurian	Přídolí	n/a	[S28]
Dalmanites tuberculatocaudatus	Dalmanitidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Dalmanites wandongensis	Dalmanitidae	Silurian	Wenlock	Homerian	S20	Silurian	Ludlow	Gorstian	S22
Dalmanites yparaguayensis	Dalmanitidae	Silurian	Llandovery	Rhuddanian	[S4]	Silurian	Llandovery	Rhuddanian	[S4]
Dalmanites? fezzanensis	Dalmanitidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S5
Dalmanites? puticlifrons	Dalmanitidae	Silurian	Llandovery	Homerian	[S18]	Silurian	Ludlow	Gorstian	[S23]
Dalmanitina (Songxites) wuningensis	Dalmanitidae	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Dalmanitina malayensis	Dalmanitidae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Dalmanitina nanchengensis	Dalmanitidae	Silurian	Llandovery	Rhuddanian	[S1]	Silurian	Llandovery	Rhuddanian	[S1]
Dalmanitoides drevermanni	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S17	Devonian	Early	Lochkovian	
Daytonia mekon	Dalmanitidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Telychian	S11
***Daytonia* sp. (of Temple, 1975)**	Dalmanitidae	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Rhuddanian	S4
Daytonia werthneri	Dalmanitidae	Silurian	Llandovery	Aeronian	S8	Silurian	Wenlock	Homerian	S18
Decoroproetus anaglyptus	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Decoroproetus asellus	Proetidae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	[H2]
Decoroproetus bodae	Proetidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Decoroproetus coderus	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S19
Decoroproetus corycoeus	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Decoroproetus decoratus	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Přídolí	n/a	[S29]
Decoroproetus decorus	Proetidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Ludfordian	S26

Decoroproetus evexus	Proetidae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	[H1]
Decoroproetus farragatus	Proetidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Aeronian	S6
Decoroproetus hircinus	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Decoroproetus mirificus	Proetidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Decoroproetus miser	Proetidae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Decoroproetus nudiformis	Proetidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Decoroproetus parabolinus	Proetidae	Silurian	Wenlock	Homerian	?S18	Silurian	Wenlock	Homerian	?S18
Decoroproetus reussi	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Decoroproetus scrobiculatus (+D. yassensis)	Proetidae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Ludfordian	S26
***Decoroproetus* sp. 1 [of Owens, 1973]**	Proetidae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S4
***Decoroproetus* sp. 2 [of Owens, 1973]**	Proetidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S12
Decoroproetus uniformis	Proetidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Decoroproetus wigwig	Proetidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S19
Decoroscutellum (D.) binotatum	Styginidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Decoroscutellum (D.) haasi	Styginidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Decoroscutellum (D.) haidingeri	Styginidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Deiphon americanus	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S23
Deiphon barrandei	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Deiphon braybrooki	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Deiphon dikella	Cheiruridae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S4
Deiphon fleur	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Deiphon forbesi	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Deiphon grovesi	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Deiphon longifrons	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18

Deiphon salmoni	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
***Deiphon* sp. 1 [of Curits & Lane, 1998]**	Cheiruridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
***Deiphon* sp. 2 [of Curtis & Lane, 1998]**	Cheiruridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S11
Dekalymene crassa	Calymenidae	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Aeronian	S6
Delops (s.l.) weaveri	Dalmanitidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Delops anoplos	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Delops arkansanus	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Delops collatus	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Delops obtusicaudatus	Dalmanitidae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Denckmannites primaevus	Phacopidae	Silurian	Llandovery	Rhuddanian	[S2]	Silurian	Llandovery	Aeronian	[S5]
Denckmannites rutherfordi	Phacopidae	Silurian	Ludlow	Ludfordian	[S25]	Silurian	Přídolí	n/a	S27
***Denckmannites* sp. [of Ayrton et al., 1969]**	Phacopidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Denckmannites volborthi	Phacopidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Diacalymene allportiana	Calymenidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Diacalymene altirostris	Calymenidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Diacalymene diademata	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Diacalymene gabrielsi	Calymenidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Diacalymene horbingeri	Calymenidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Diacalymene schucherti	Calymenidae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S10
Diacalymene subandina	Calymenidae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	S22
Diacanthaspis (Acanthalomina) arctica	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Diacanthaspis (Acanthalomina) minuta	Odontopleuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Diacanthaspis (Acanthalomina)	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S23

minutissima									
Diacanthaspis (Acanthalomina) thorsteinssoni	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Diacanthaspis (Diacanthaspis) hollandi	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Diacanthaspis sladensis	Odontopleuridae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H1
Diacanthaspis suni	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	[S15]	Silurian	Wenlock	Sheinwoodian	[S15]
Dicranogmus pustulatus	Lichidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Dicranogmus skinneri	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Dicranogmus **sp. (of Koren & Sobolevskaya, 2008)**	Lichidae	Ordovician	Late	Hirnantian	H2	Ordovician	Late	Hirnantian	H2
Dicranopeltis decipiens	Lichidae	Silurian	Wenlock	?Sheinwoodian	[S15]	Silurian	Wenlock	?Sheinwoodian	[S15]
Dicranopeltis imperfecta	Lichidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Dicranopeltis pustulosus	Lichidae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Dicranopeltis reporyjensis	Lichidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Dicranopeltis salteri	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Dicranopeltis sauroter	Lichidae	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S13
Dicranopeltis scabra	Lichidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S22
Dicranopeltis **sp. [of Sepkoski, 1998]**	Lichidae	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H1
Dicranopeltis tricornis	Lichidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Dicranopeltis tricornis	Lichidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Dicranopeltis woodwardi	Lichidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Dicranurus nesiotes	Odontopleuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Dicranurus **sp. (of Sandford & Holloway, 2006)**	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Dicranurus **sp. [of Thomas, 1981]**	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	[S15]	Silurian	Wenlock	Sheinwoodian	[S17]
Dicranurus? barbarus	Odontopleuridae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21

Didrepanon delormensis	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Didrepanon falcatum	Cheiruridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Didrepanon squarrosum	Cheiruridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Didrepanon? bimucronatum	Cheiruridae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Dindymene? sp. [of Kobayashi & Hamada, 1986]	Encrinuridae	Silurian	Ludlow	Gorstian	[S22]	Silurian	Ludlow	Gorstian	[S22]
Dipleura praecox	Homalonotidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Distyrax cooperi	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Distyrax peeli	Encrinuridae	Silurian	Llandovery	Telychian	[S12]	Silurian	Llandovery	Telychian	[S12]
Distyrax sp. nov. [of Gass et al., 1992]	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Dnestrovites podolicus	Encrinuridae	Silurian	Ludlow	?Ludfordian	[S26]	Silurian	Ludlow	?Ludfordian	[S26]
Dudleyaspis (Dudleyaspis) uncifera	Odontopleuridae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S15
Dudleyaspis desolator	Odontopleuridae	Silurian	Ludlow	Gorstian	?S22	Silurian	Ludlow	Gorstian	?S23
Dudleyaspis portlockii	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S22
Dudleyaspis quinquespinosa	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Dudleyaspis rutteri	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Edgecombeaspis jahansi	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Edgecombeaspis johansonae	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Sheinwoodian	S17
Edgecombeaspis soehni	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Ekwanoscutellum ekwanensis	Styginidae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Elimaproetus delicatus	Proetidae	Silurian	Llandovery	Rhuddanian	[S3]	Silurian	Llandovery	Telychian	S13
Elimaproetus diabolicus	Proetidae	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S14
Elimaproetus haverfordensis	Proetidae	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S14
Encrinuroides meijiangensis	Encrinuridae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Aeronian	S8
Encrinuroides meitanensis	Encrinuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S14

Encrinuroides zhangjiatunensis	Encrinuridae	Silurian	Ludlow	?Gorstian	[S22]	Silurian	Ludlow	?Gorstian	[S22]
Encrinuroides zhenxiongensis	Encrinuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Encrinurus (Perryus) severnensis	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Encrinurus (Trippia) mullochensis	Encrinuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S11
Encrinurus anticostiensis	Encrinuridae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S10
Encrinurus arenaceus	Encrinuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Encrinurus balticus	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Encrinurus confusevarus	Encrinuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Encrinurus deomenos	Encrinuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S11
Encrinurus egani	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S23
Encrinurus elegantulus	Encrinuridae	Silurian	Llandovery	Telychian	[S11]	Silurian	Llandovery	Telychian	[S11]
Encrinurus intersitus	Encrinuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Encrinurus knockgairdnerensis	Encrinuridae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Encrinurus nereus	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S23
Encrinurus nodai	Encrinuridae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Encrinurus onniensis	Encrinuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S12
Encrinurus ornatus	Encrinuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Wenlock	Sheinwoodian	S15
Encrinurus punctatus	Encrinuridae	Silurian	Llandovery	Telychian	S12	Silurian	Ludlow	Ludfordian	S25
Encrinurus reflexus	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S23
Encrinurus schisticola	Encrinuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Encrinurus shelvensis	Encrinuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S12
Encrinurus similis	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Encrinurus sinicus	Encrinuridae	Silurian	Přídolí	n/a	[S28]	Silurian	Přídolí	n/a	[S28]
Encrinurus speyeri	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Encrinurus squarrosis	Encrinuridae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Aeronian	S6

Encrinurus stateratus	Encrinuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Encrinurus stubblefieldi	Encrinuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S25
Encrinurus subtrigonalis	Encrinuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Encrinurus subvariolaris	Encrinuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	[S29]
Encrinurus thailandicus	Encrinuridae	Silurian	Wenlock	Homerian	[S20]	Silurian	Ludlow	Gorstian	[S23]
Encrinurus tuberculatus	Encrinuridae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Homerian	S21
Encrinurus? stokesii	Encrinuridae	Ordovician	Late	Katian		Silurian	Wenlock	Homerian	S19
***Eokosovopeltis* sp. [of Banks, 1988]**	Styginidae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Eoleonaspis erinaceus	Odontopleuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Eoleonaspis olini	Odontopleuridae	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Eoleonaspis shanensis	Odontopleuridae	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H1
Eoleonaspis yunnanensis	Odontopleuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S8
Eophacops alter	Phacopidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Eophacops bulliceps	Phacopidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Ludfordian	S25
Eophacops fontana	Phacopidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Eophacops handwerki	Phacopidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Eophacops helmuti	Phacopidae	Silurian	Přídolí	n/a	[S27]	Silurian	Přídolí	n/a	[S27]
Eophacops musheni	Phacopidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Eophacops serotinus	Phacopidae	Silurian	Přídolí	n/a	S28	Silurian	Přídolí	n/a	S29
***Eophacops* sp. [of Bogolepova & Kriz, 1995]**	Phacopidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
Eophacops sprogensis	Phacopidae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Eophacops trapeziceps	Phacopidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Eremiproetus (Remacutanger) senex	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S27
Eremiproetus agellus	Proetidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]

***Ewcaste* cf. *quaesita* [of Ramskold & Edgecombe, 1993]**	Phacopidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Ewcaste opatowiensis	Acastidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S29
Ewcaste quaesita	Acastidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Ewcaste samsonowiczi	Acastidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S29
Exallaspis acarescola	Odontopleuridae	Silurian	Llandovery	Aeronian	[S6]	Silurian	Llandovery	Aeronian	[S6]
Exallaspis bufo	Odontopleuridae	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21
Exallaspis coronata	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S24
Exallaspis deflexa	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Exallaspis lothania	Odontopleuridae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Exallaspis mutica	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Exallaspis quadrimucronata	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Exallaspis varbolensis	Odontopleuridae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Aeronian	S6
Exallaspis whittardi	Odontopleuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S10
Excetra iotops	Styginidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Failleana arenacea	Styginidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S14
Failleana maccallumi	Styginidae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S4
Failleana tegartensis	Styginidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Falcatoproetus falcatus	Proetidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Feistia energetica	Calmoniidae	Silurian	Přídolí	n/a	[S28]	Silurian	Přídolí	n/a	[S28]
Flexicalymene scotica	Calymenidae	Ordovician	Late	Hirnantian	[H1]	Ordovician	Late	Hirnantian	[H1]
Flexicalymene senaria	Calymenidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S10
Flexicalymene? vaccarii	Calymenidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S16
Fragiscutum diabolus	Encrinuridae	Silurian	Llandovery	Telychian	~S11	Silurian	Llandovery	Telychian	~S12
Fragiscutum glebale	Encrinuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Frammia artica	Encrinuridae	Silurian	Ludlow	Ludfordian	[S24]	Silurian	Ludlow	Ludfordian	[S24]

Frammia bachae	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Frammia dissimilis	Encrinuridae	Silurian	Ludlow	Ludfordian	[S25]	Silurian	Ludlow	Ludfordian	[S25]
Gaotania bimusa	Odontopleuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S13
Gaotania ovata	Odontopleuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Gerastos subcarinatus	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Gerastos sugiharensis	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Glyptambon verrucosus	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Goldillaenus calvus	Styginidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Goldillaenus nilsoni	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S26
Goldillaenus shiuoharai	Styginidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Gomiites granulatus	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Gotania pulchella	Odontopleuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Gravicalymene hornyi	Calymenidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Gravicalymene vaccina	Calymenidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S13
Hadromeros scotti	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Homerian	S18
Hadromeros williamsi	Cheiruridae	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Rhuddanian	S4
Harpidella (Harpidella) thomasi	Aulacopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Harpidella butorus	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Harpidella elegantula	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Harpidella greggi	Aulacopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Harpidella helenae	Aulacopleuridae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Aeronian	S8
Harpidella instita	Aulacopleuridae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S23
Harpidella megalops	Aulacopleuridae	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S14
Harpidella plana	Aulacopleuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Harpidella pygmaea	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S19

Harpidella rhaptomyosa	Aulacopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Harpidella sentosum	Aulacopleuridae	Silurian	Wenlock	Homerian	?S21	Silurian	Ludlow	Gorstian	?S23
Harpidella spinulocervix	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Harpidella tikkaneni	Aulacopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Harringtonacaste harringtoni	Acastidae	Silurian	Llandovery	Telychian	S13	Devonian	Early	Lochkovian	
Headstroemia eldredgei	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Hedstroemia delicatus	Proetidae	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21
Hedstroemia pachydermatus	Proetidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Hedstroemia sourdoughi	Proetidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Helokybe spio	Proetidae	Silurian	Ludlow	Ludfordian	[S26]	Silurian	Ludlow	Ludfordian	[S26]
Hemiarges extremus	Lichidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Hemiarges hendersoni	Lichidae	Silurian	Llandovery	Telychian	[S10]	Silurian	Llandovery	Telychian	[S10]
Hemiarges heteroclytus	Lichidae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Hemiarges maia	Lichidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Hemiarges serus	Lichidae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S4
Hibbertia amibouei	Harpetidae	Silurian	Llandovery	?Aeronian	[S7]	Silurian	Llandovery	?Aeronian	[S7]
Homalonotus knightii	Homalonotidae	Silurian	Ludlow	Gorstian	S23	Silurian	Přídolí	n/a	S29
Homalonotus rhinotropis	Homalonotidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Hypaproetus guizhouensis	Proetidae	Silurian	Llandovery	Aeronian	[S8]	Silurian	Llandovery	Aeronian	[S8]
Hyrokybe copelandi	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Hyrokybe douglasi	Cheiruridae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Hyrokybe hadnagyi	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Hyrokybe julli	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Hyrokybe meliceris	Cheiruridae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Hyrokybe pharanx	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13

Hyrokybe punctata	Cheiruridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Illaenoides triloba	Styginidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Illaenoides? abnormis	Styginidae	Silurian	Ludlow	Gorstian	[S22]	Silurian	Ludlow	Gorstian	[S22]
Illaenoides? abnormis	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Illaenoides? magnisulcatus	Styginidae	Silurian	Ludlow	Gorstian	[S22]	Silurian	Ludlow	Gorstian	[S22]
Illaenoides? magnisulcatus	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Illaenoscutellum platiceps	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Interproetus albon	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Interproetus consobrinus	Proetidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Interproetus galvani	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Interproetus intermedius	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Interproetus kosovicus	Proetidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Interproetus numvertus	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Interproetus pentaxus	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Interproetus persam	Proetidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Interproetus pralux	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Interproetus soncobrinus	Proetidae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Interproetus susy	Proetidae	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21
Interproetus truncus	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Interproetus venustus	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Interproetus vertummus	Proetidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Interproetus xenon	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Isbergia planifrons	Rorringtoniidae	Ordovician	Late	Hirnantian	[H1]	Ordovician	Late	Hirnantian	[H1]
Isoprusia kofelae	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Ivanopleura dufremoyi	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18

Ivanopleura pokornyi	Odontopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Wenlock	Homerian	S18
Ivops wallanensis	Phacopidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Japonoscutellum geniculatum	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Japonoscutellum japonicum	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Japonoscutellum tumidum	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Johntempleia meifodensis	Encrinuridae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S4
Johntempleia pamae	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Johntempleia prisca	Encrinuridae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Aeronian	S6
Johntempleia shelvensis	Encrinuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S9
Jujuyops nonoctubrensis	Calmoniidae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	[S23]
Kailia capra	Encrinuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Kailia intersulcata	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Kailia quadrisulcata	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Kettneraspis belli	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Kettneraspis beni	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Kettneraspis boltoni	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Kettneraspis caldwelli	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Sheinwoodian	S17
Kettneraspis crenata	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Devonian	Early	Lochkovian	
Kettneraspis dormitzeri	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Kettneraspis geinitziana	Odontopleuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Kettneraspis hollowayi	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Kettneraspis jaanussoni	Odontopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Kettneraspis juengeri	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Kettneraspis lenzi	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Kettneraspis leridae	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22

Kettneraspis lindoei	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Kettneraspis longstaffei	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Kettneraspis orphana	Odontopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Kettneraspis parkini	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Kettneraspis propinqa	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Kettneraspis propinqa	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Kettneraspis reetae	Odontopleuridae	Silurian	Llandovery	Telychian	[S9]	Silurian	Llandovery	Telychian	[S9]
Kettneraspis risbeyi	Odontopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Kettneraspis salopiensis	Odontopleuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Kettneraspis wrightae	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Sheinwoodian	S17
Kosovopeltis acamas	Styginidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Kosovopeltis allaarri	Styginidae	Silurian	Wenlock	?Homerian	[S20]	Silurian	Wenlock	?Homerian	[S20]
Kosovopeltis andersoni	Styginidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Kosovopeltis angusticostatus	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Kosovopeltis borealis	Styginidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Kosovopeltis cunctata	Styginidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Aeronian	S6
Kosovopeltis ennadifi	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Kosovopeltis guangyuanensis	Styginidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Kosovopeltis hidensis	Styginidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Kosovopeltis hornyi	Styginidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Kosovopeltis inopinata	Styginidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S23
Kosovopeltis maroccanica	Styginidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Kosovopeltis partschi	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Kosovopeltis svobodai	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Kosovopeltis tchernychevae	Styginidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12

Kosovopeltis wissmannae	Styginidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Kosovopeltis yichangensis	Styginidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S10
Kosovopeltis? signata	Styginidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Kosovoproetus migrenin	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Ktenoura avavaka	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Ktenoura bicuspidata	Cheiruridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Ktenoura oronapi	Cheiruridae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Ktenoura patula	Cheiruridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S14
Ktenoura postrema	Cheiruridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Ktenoura retrospinosa	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Lacunoporaspis postromanowskyi	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Laethoprusia salax	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Latiproetus biloba	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Latiproetus browningensis	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Latiproetus latilimbatus	Proetidae	Silurian	Llandovery	Aeronian	S8	Silurian	Wenlock	Sheinwoodian	S15
Latiproetus mucronatus	Proetidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Latiproetus obesus	Proetidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Latiproetus tenuis	Proetidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Latiproetus? argaleus	Proetidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Leioscutellum tenuicaudatus	Styginidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Leonaspis bidentata	Odontopleuridae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Leonaspis ezellina	Odontopleuridae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Leonaspis granulosa	Odontopleuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Leonaspis grouensis	Odontopleuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Leonaspis leonhardi	Odontopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	[S28]

Leonaspis nuratensis	Odontopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Lepdioproetus (Dipharangus) xeo	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Lichas argentina	Lichidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S17
Lichas laciniatus	Lichidae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H1
Ligiscus arcanus	Styginidae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Linguocalymene brevis	Calymenidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Linguocalymene flexuosa	Calymenidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Linguocalymene linguata	Calymenidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Liocalymene clintonensis	Calymenidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Liocalymene clintoni	Calymenidae	Silurian	Llandovery	Telychian	S10	Silurian	Wenlock	Sheinwoodian	S15
Liocalymene niagarensis	Calymenidae	Silurian	Llandovery	Telychian	S10	Silurian	Wenlock	Sheinwoodian	S17
Liolalax olibros	Styginidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Litotix armatus	Styginidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21
Llandovacaste birminghamensis	Acastidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S6
Lochkovella grimburgi	Phacopidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Ludfordian	S25
Lodenicia bykos	Tropidocoryphidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Lodenicia dentatula	Tropidocoryphidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Lodenicia herinkiana	Tropidocoryphidae	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21
Luojiashania divergens	Proetidae	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S12
Luojiashania wuchangensis	Proetidae	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S12
Mackenziurus deedeei	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Mackenziurus joeyi	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Mackenziurus lauriae	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S23
Mackenziurus reimeri	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Malimanaspis packardi	Aulacopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25

Maurotarion aitholix	Aulacopleuridae	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21
Maurotarion christi	Aulacopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Maurotarion euryceps	Aulacopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Maurotarion lanei	Aulacopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S24
Maurotarion maurum	Aulacopleuridae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Maurotarion messieri	Aulacopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Maurotarion mystax	Aulacopleuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Maurotarion novellum	Aulacopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Meitanillaenus binodosus	Styginidae	Silurian	Llandovery	Rhuddanian	[S4]	Silurian	Llandovery	Aeronian	S8
Meroperix aquilonaris	Styginidae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Meroperix ataphrus	Styginidae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Metacalymene baylei	Calymenidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Metaleiolichas tuberculatus	Lichidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Microscutellum primigenium	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Mimocryphaeus altecostatus	Acastidae	Silurian	Ludlow	Gorstian	[S22]	Silurian	Ludlow	Gorstian	[S22]
Miraspis mira	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Miraspis parallela	Odontopleuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S12
Miraspis rarissima	Odontopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Miraspis symara	Odontopleuridae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Mucronaspis brevispina	Dalmanitidae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H1
Mucronaspis itacurubensis	Dalmanitidae	Silurian	Llandovery	?Rhuddanian	[S1]	Silurian	Llandovery	?Rhuddanian	[S1]
Mucronaspis mucronata	Dalmanitidae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H1
Mucronaspis olini	Dalmanitidae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2
Neolichas constrictus	Lichidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S12
Neolichas norvegicus	Lichidae	Silurian	Llandovery	Rhuddanian	[S2]	Silurian	Llandovery	Rhuddanian	[S2]

Neolichas silvestris	Lichidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
Nitidocare nitidum	Proetidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Niuchangella meitanensis	Scharyiidae	Silurian	Llandovery	Rhuddanian	[S3]	Silurian	Llandovery	Rhuddanian	[S3]
Nucleurus abyssalis	Encrinuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Nucleurus diabolus	Encrinuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Nucleurus selistensis	Encrinuridae	Silurian	Llandovery	?Aeronian	[S5]	Silurian	Llandovery	?Aeronian	[S5]
Odontopleura (Sinespinaspis) consimilata	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Odontopleura (Sinespinaspis) markhami	Odontopleuridae	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S10
Odontopleura (Sinespinaspis?) semiglabra	Odontopleuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S10
Odontopleura arctica	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Odontopleura bombini	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Odontopleura brevigena	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Odontopleura greenwoodi	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Odontopleura mccallai	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Odontopleura nehedensis	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Odontopleura omega	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Ludfordian	S24
Odontopleura ovata	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S23
Odontopleura prevosti	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Odontopleura salma	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Oidalaproetus convexus	Proetidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Onycopyge liversidgei	Cheiruridae	Silurian	Wenlock	Homerian	?S20	Silurian	Ludlow	Gorstian	S22
Opoa adamsi	Styginidae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Opoa? trinodosa	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Orphanaspis orphanus	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21

Orygmatos yanyeani	Phacopidae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Otarion angustum	Aulacopleuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Otarion beukeboomi	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Otarion brauni	Aulacopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Otarion burmeisteri	Aulacopleuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Otarion clarimonda	Aulacopleuridae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Otarion diffractum	Aulacopleuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S26
Otarion granulata	Aulacopleuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S27
Otarion hollandi	Aulacopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Otarion huddyi	Aulacopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Otarion novaki	Aulacopleuridae	Silurian	Přídolí	n/a	S27	Devonian	Early	Lochkovian	
Otarion obnoxia	Aulacopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Otarion ofelia	Aulacopleuridae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Otarion verrucosum	Aulacopleuridae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Pacificurus borenorensis	Encrinuridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Pacificurus chilorhodus	Encrinuridae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Pacificurus fimbriatus	Encrinuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Pacificurus mamelon	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Pacificurus mitchelli	Encrinuridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Pacificurus rothwellae	Encrinuridae	Silurian	Ludlow	?Gorstian	[S22]	Silurian	Ludlow	?Ludfordian	[S26]
Pacificurus tosensis	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Pacificurus yokokurensis	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Pacificurus? stenorachis	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Paciphacops argentinus	Phacopidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	[S15]
Paleodechenella novozemelica	Proetidae	Silurian	Ludlow	?Gorstian	[S23]	Silurian	Ludlow	?Gorstian	[S23]

Paleodechenella turkestanica	Proetidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S29
Paleodechenella waigatchensis	Proetidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Paleodechenella zaaminica	Proetidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S28
Papillicalymene papillata	Calymenidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S24
Paracybantyx asulcatus	Styginidae	Silurian	Ludlow	?Gorstian	[S22]	Silurian	Ludlow	?Gorstian	[S22]
Parakailia lata	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Paraleiolichas globulus	Lichidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Parayoungia eleyae	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Parayoungia megacranidia	Cheiruridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Parayoungia subglobula	Cheiruridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Parayoungia tuberculata	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Parvigena parvigena	Tropidocoryphidae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	[H1]
Perirehaedulus capra	Encrinuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Perryus bartletti	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Perryus severnensis	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	[S16]
Phacopidella bulliceps	Phacopidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Phacopidella glockeri	Phacopidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Phacopina itacurubensis	Calmoniidae	Silurian	Llandovery	Telychian	[S14]	Silurian	Wenlock	Sheinwoodian	[S17]
Phacopina perroana	Calmoniidae	Silurian	Llandovery	Telychian	[S13]	Silurian	Wenlock	Sheinwoodian	[S15]
Phacops argentinus	Phacopidae	Silurian	Wenlock	Sheinwoodian	S17	Devonian	Early	Lochkovian	
Phacops fecundus	Phacopidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S29
Phacops khatangensis	Phacopidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
Phacops metacernaspis	Phacopidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Phacops trisulcata	Phacopidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Phacops trisulcatus	Phacopidae	Silurian	Llandovery	Aeronian	S8	Silurian	Wenlock	Sheinwoodian	S15

Planiscutellum kitharos	Styginidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Planiscutellum planum	Styginidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Planiscutellum planus	Styginidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Planiscutellum quasiplanum	Styginidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Planiscutellum simulans	Styginidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Platycoryphe dyaulax	Homalonotidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Platycoryphe sinensis	Homalonotidae	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Rhuddanian	[S4]
Platylichas (Rontrippia) grayii	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Gorstian	S22
Platylichas margaritifer	Lichidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Platylichas scoticus	Lichidae	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Aeronian	S6
Plesiowensus chlupaci	Proetidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Plesiowensus confossus	Proetidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Plesiowensus obconicus	Proetidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Plesiowensus oppidanus	Proetidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Plesiowensus raymondi	Proetidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Podowrinella straitonensis	Pterygometopidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Pompeckia wegelini	Cheiruridae	Ordovician	Late	Hirnantian	[H1]	Ordovician	Late	Hirnantian	[H1]
Prantlia (Tetinia) minuta	Proetidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Prantlia grindrodi	Proetidae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Homerian	S21
Prantlia kurzmenensis	Proetidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Prantlia longula	Proetidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S25
Preodontochile camprodonensis	Dalmanitidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Preodontochile springfieldensis	Dalmanitidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Primaspis mackenziensis	Odontopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Primaspis mendica	Odontopleuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22

Primaspis reversa	Odontopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S1
Primaspis suni	Odontopleuridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S14
Prionopeltis akkajensis	Tropidocoryphidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Prionopeltis archiaci	Tropidocoryphidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Prionopeltis dracula	Tropidocoryphidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Prionopeltis incisa	Tropidocoryphidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Prionopeltis klonk	Tropidocoryphidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Prionopeltis miclen	Tropidocoryphidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S25
Prionopeltis praecedens	Tropidocoryphidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S25
Prionopeltis prokopi	Tropidocoryphidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Prionopeltis rara	Tropidocoryphidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Prionopeltis septimus	Tropidocoryphidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Prionopeltis stiatus	Tropidocoryphidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Prionopeltis striata	Tropidocoryphidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Prionopeltis striatus	Tropidocoryphidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Prionopeltis unica	Tropidocoryphidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Prodontochile igoi	Dalmanitidae	Silurian	Llandovery	Aeronian	S7	Silurian	Wenlock	Sheinwoodian	[S16]
Proetus (s.l.) astringens	Proetidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Proetus (s.l.) latifrons	Proetidae	Silurian	Llandovery	Telychian	[S12]	Silurian	Llandovery	Telychian	[S12]
Proetus ainae	Proetidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Proetus concinnus	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S22
Proetus conspersus	Proetidae	Silurian	Ludlow	Gorstian	S23	Silurian	Přídolí	n/a	S29
Proetus delicatus	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Proetus fergali	Proetidae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Proetus kopaninensis	Proetidae	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22

Proetus morinensis	Proetidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S25
Proetus nieszkowskii	Proetidae	Silurian	Přídolí		S29	Silurian	Přídolí	n/a	S29
Proetus signatus	Proetidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S27
Proetus subovalis	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Proetus verrucosus	Proetidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Proetus volkovcyanus	Proetidae	Silurian	Přídolí	n/a	S28	Silurian	Přídolí	n/a	S29
Proromma acanthodes	Cheiruridae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Aeronian	S6
Proromma bregmops	Cheiruridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Proromma powysensis	Cheiruridae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Prostrix amnicola	Encrinuridae	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S13
Protocerauroides lanei	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Pseudocheirurus beyrichi	Cheiruridae	Silurian	Wenlock	Homerian	[S18]	Silurian	Ludlow	Gorstian	[S23]
Pseudocheirurus gomienesis	Cheiruridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Pseudogerastos ryckholti	Proetidae	Silurian	Wenlock	Homerian	?S18	Devonian	Early	Emsian	
Pseudogerastos vaningeni	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Pseudoproetus regalis	Proetidae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S7
Pseudotupolichas chicagoensis	Lichidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Pseudotupolichas ornatus	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S19
Ptilillaenus lojopingensis	Illaenidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S10
Pulcherproetus pulcher	Proetidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Rabuloproetus borekensis	Proetidae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Radiaspis boucoti	Odontopleuridae	Silurian	Wenlock	?Homerian	?S21	Silurian	Ludlow	Gorstian	S23
Radiaspis formosa	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Radiaspis nauseola	Odontopleuridae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Radiaspis norfordi	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16

Radiaspis pecten	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Radiolichas davedaviesi	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Radiolichas raydaviesi	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Radiurus avalanchensis	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Radiurus phlogoideus	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Radnoria elongata	Brachymetopidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Radnoria humillima	Brachymetopidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Radnoria syrphetodes	Brachymetopidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S19
Radnoria triquetra	Brachymetopidae	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S19
Raphiophorus aloniensis	Raphiophoridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Raphiophorus balboi	Raphiophoridae	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S5
Raphiophorus jikaensis	Raphiophoridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Raphiophorus niagarensis	Raphiophoridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Raphiophorus parvulus	Raphiophoridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S23
Raphiophorus rouaulti	Raphiophoridae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Ludfordian	S26
Raphiophorus sandfordi	Raphiophoridae	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S10
Ratinkaspis bifurcatus	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Rhaxeros pollinctrix	Styginidae	Silurian	Llandovery	Telychian	[S11]	Silurian	Llandovery	Telychian	[S11]
Richterarges ambiguus	Lichidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Richterarges bucklandii	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Ludlow	Ludfordian	S24
Richterarges convexus	Lichidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Richterarges ptyonurus	Lichidae	Silurian	Přídolí	n/a	?S28	Silurian	Přídolí	n/a	?S29
Richterarges rolferi	Lichidae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Rongxiella globosa	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Sangzhiscutellum flabelliforme	Styginidae	Silurian	Llandovery	Aeronian	[S6]	Silurian	Llandovery	Aeronian	[S6]

Scharyia corona	Scharyiidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Scharyia micropyga	Scharyiidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Scharyia nympha	Scharyiidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Scharyia scharyi	Scharyiidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Scharyia siceripotrix	Scharyiidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Scharyia wenlockiana	Scharyiidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Scotiella logani	Acastidae	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Scotoharpes domina	Harpetidae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Scotoharpes judex	Harpetidae	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Aeronian	S7
Scotoharpes loma	Harpetidae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Scotoharpes raaschi	Harpetidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Scotoharpes sinensis	Harpetidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Scotoharpes telleri	Harpetidae	Silurian	Wenlock	Homerian	[S20]	Silurian	Wenlock	Homerian	[S20]
Scotoharpes volsellatus	Harpetidae	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S11
Scotoharpes willsi	Harpetidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Sculptoproetus heureka	Styginidae	Silurian	Přídolí	n/a	?S29	Devonian	Early	Lochkovian	
Scutellum borealis	Styginidae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S9
Scutellum niagarensis	Styginidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Scutellum polyactin	Styginidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Selenopeltis caloxyl	Odontopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Selenopeltoides caloxyl	Odontopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Selenopeltoides hawlei	Odontopleuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Sinoluia tibetensis	Raphiophoridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Sinoproetus bindouensis	Proetidae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Songkaia smithi	Aulacopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13

Songkania hanjiadianensis	Aulacopleuridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Songkania socialis	Aulacopleuridae	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Spathacalymene nasuta	Calymenidae	Silurian	Llandovery	Telychian	[S10]	Silurian	Wenlock	Homerian	S18
Sphaerexochus centeo	Cheiruridae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Sphaerexochus dimorphus	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	S22
Sphaerexochus glaber	Cheiruridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Sphaerexochus hiratai	Cheiruridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Sphaerexochus johnstoni	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Sphaerexochus laciniatus	Cheiruridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Sphaerexochus mirus	Cheiruridae	Silurian	Llandovery	Telychian	S12	Silurian	Ludlow	Ludfordian	S25
Sphaerexochus paramirus	Cheiruridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Sphaerexochus planirachis	Cheiruridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Sphaerexochus romingeri	Cheiruridae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Sphaerexochus scabridus	Cheiruridae	Silurian	Wenlock	Sheinwoodian	[S17]	Silurian	Wenlock	Sheinwoodian	[S17]
Sphaerexochus seto	Cheiruridae	Silurian	Llandovery	Telychian	[S9]	Silurian	Wenlock	Sheinwoodian	[S15]
Sphaerexochus sugiyamai	Cheiruridae	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Staurocephalus azuela	Encrinuridae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Staurocephalus lagena	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Staurocephalus murchisoni	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S22
Staurocephalus oarion	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Staurocephalus struszi	Encrinuridae	Silurian	Wenlock	Homerian	[S18]	Silurian	Wenlock	Homerian	[S18]
Staurocephalus susanae	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21
Staurocephalus trichochin	Encrinuridae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Stelckaspis gingiva	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Stelckaspis longispina	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13

Stelckaspis sinedentata	Odontopleuridae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Stelckaspis tuberculosa	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Stelckaspis warreni	Odontopleuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Stenoblepharum norvegicum	Tropidocoryphidae	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	[H1]
Stenoblepharum pentagonoides	Tropidocoryphidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Stenoblepharum striatum	Tropidocoryphidae	Ordovician	Late	Hirnantian	[H1]	Ordovician	Late	Hirnantian	[H1]
Stenoblepharum warburgae	Tropidocoryphidae	Ordovician	Late	Hirnantian	[H2]	Ordovician	Late	Hirnantian	[H2]
Stenopareia aemula	Illaenidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S14
Stenopareia catathema	Illaenidae	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S11
Stenopareia illtyd	Illaenidae	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Stenopareia julli	Illaenidae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Stenopareia linnarssoni	Illaenidae	Ordovician	Late	Hirnantian	[H1]	Ordovician	Late	Hirnantian	[H1]
Stenopareia pulchella	Illaenidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Stenopareia shelvensis	Illaenidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Telychian	S10
Stenopareia somnifer	Illaenidae	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
Sthenarocalymene celebra	Calymenidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Sthenarocalymene kilmorensis	Calymenidae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Sthenarocalymene scutula	Calymenidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Stoermeraspis franconica	Styginidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Stoermeraspis franconicus	Styginidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Stoermeraspis? otarion	Styginidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Struszia dimitrovi	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Struszia epsteini	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Struszia harrisoni	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Struszia martini	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17

Struszia mccartneyi	Encrinuridae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Struszia obtusus	Encrinuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Struszia onoae	Encrinuridae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Struszia petebesti	Encrinuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Struveria orba	Dalmanitidae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Struveria simrica	Dalmanitidae	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Struveria? plinthourgos	Dalmanitidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Taemaspis krausi	Odontopleuridae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Taemaspis llandoveryana	Odontopleuridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Taemaspis rutteri	Odontopleuridae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Tapinocalymene nodulosa	Calymenidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S19
Tapinocalymene volsoriforma	Calymenidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Tetina (T.) minuta	Proetidae	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Thebanaspis channahonensis	Proetidae	Silurian	Llandovery	Aeronian	[S7]	Silurian	Llandovery	Aeronian	[S7]
Thebanaspis? determinata	Proetidae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Thomastus aops	Styginidae	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Thomastus jutsoni	Styginidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Thomastus thomastus	Styginidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Tosacephalus fungiformis	Styginidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Trimerolichas marginatus	Lichidae	Silurian	Llandovery	Aeronian	[S8]	Silurian	Wenlock	Sheinwoodian	S16
Trimerus (?Ramiotis) salteri	Homalonotidae	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Trimerus (Ramiotis) rickardsi	Homalonotidae	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S15
Trimerus (Ramiotis) tomczykowae	Homalonotidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Trimerus (Trimerus) flexuosus	Homalonotidae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	[S23]
Trimerus (Trimerus) grandis	Homalonotidae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	S22

Trimerus (Trimerus) johannis	Homalonotidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	?S22
Trimerus (Trimerus) vomer	Homalonotidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Trimerus cylindricus	Homalonotidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Trimerus delphinocephalus	Homalonotidae	Silurian	Wenlock	Sheinwoodian	[S16]	Silurian	Wenlock	Sheinwoodian	[S16]
Trimerus harrisoni	Homalonotidae	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Trimerus kayseri	Homalonotidae	Silurian	Ludlow	Gorstian	S22	Devonian	Early	Lochkovian	
Trimerus permutus	Homalonotidae	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Trochurus flabellatus	Lichidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21
Trochurus nasuta	Lichidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Sheinwoodian	S17
Trochurus palmata	Lichidae	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Trochurus sarfi	Lichidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Trochurus speciosus	Lichidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Tropidocoryphe? praecurrens	Tropidocoryphidae	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Uriarra kausi	Odontopleuridae	Silurian	Wenlock	Homerian	[S19]	Silurian	Wenlock	Homerian	[S19]
Uripes scutalis	Lichidae	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S21
Wallacia chattertoni	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Wallacia elegantula	Encrinuridae	Silurian	Llandovery	Telychian	~S12	Silurian	Llandovery	Telychian	~S13
Wallacia expansa	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Wallacia hagshawensis	Encrinuridae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Wallacia hypoleprus	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Wallacia jaanussoni	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Wallacia laevis	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Wallacia masterleei	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Wallacia pagei	Encrinuridae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Wallacia triangula	Encrinuridae	Silurian	Llandovery	Telychian	[S14]	Silurian	Llandovery	Telychian	[S14]

Warburgella (Owensella) ludlowensis	Proetidae	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Warburgella (W) capetos	Proetidae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Warburgella (W) scutterdinensis	Proetidae	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Warburgella (W) stokesii	Proetidae	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	?S22
Warburgella capetos	Proetidae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Warburgella rugulosa	Proetidae	Silurian	Ludlow	Ludfordian	S26	Devonian	Early	Lochkovian	
Warburgella tcherkesovae	Proetidae	Silurian	Přídolí	n/a	S28	Devonian	Early	Lochkovian	
Whittingtonia whittingtoni	Odontopleuridae	Ordovician	Late	pre Hirnantian		Silurian	Llandovery	Aeronian	S8
Winiskia perryi	Proetidae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Wuchuanella quadrata	Illaenidae	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Wuoaspis changningensis	Encrinuridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Xenocybe ebyconex	Proetidae	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Xiushuiproetus poyangensis	Proetidae	Silurian	Llandovery	Telychian	?S13	Silurian	Llandovery	Telychian	?S14
Xiushuiproetus shuangheensis	Proetidae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Xiushuiproetus transverses	Proetidae	Silurian	Llandovery	Telychian	?S13	Silurian	Llandovery	Telychian	?S14
Yichangaspis yichangensis	Proetidae	Silurian	Llandovery	Rhuddanian	[S4]	Silurian	Llandovery	Rhuddanian	[S4]
Youngia boucoti	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Youngia brennardi	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Youngia douglasii	Cheiruridae	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Youngia folinsbeei	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Youngia johnsoni	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Youngia kathyae	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Youngia moroides	Cheiruridae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Youngia steineri	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Youngia trispinosa	Cheiruridae	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8

Youngia walli	Cheiruridae	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Zaplaops zaplensis	Phacopidae	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	?S23
Zhejiangoproetus fuyangensis	Proetidae	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Telychian	S10

Table A.3. Table showing the ages of Hirnantian and Silurian formations.

	FAD				**LAD**			
Formation	**System**	**Series**	**Stage**	**Biozone**	**System**	**Series**	**Stage**	**Biozone**
Aberedw	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Acacus	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S14
Acidaspis Limestone	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Akkans Limestone	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Akkaya	Silurian	Ludlow	Ludfordian	S24	Silurian	Přídolí	n/a	S29
Akron	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Alcolea	Silurian	Přídolí	n/a	S29	Devonian	Early	Lochkovian	
Aleqatsiaq Fjord	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Rhuddanian	S4
Alticola Limestone	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S28
Amystery Limestone	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Anderson Creek	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Anji	Ordovician	Late	Hirnantian	H2	Silurian	Llandovery	Rhuddanian	S3
Arcow	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22

Arina	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H1
Attawapiskat	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Austerberg Limestone	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S19
Back Bay	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S11
Badenas	Silurian	Llandovery	Telychian	S13	Silurian	Ludlow	Gorstian	S23
Bagovista	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Baily Hill	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S24
Bainbridge Limestone	Silurian	Ludlow	Gorstian	S22	Silurian	Přídolí	n/a	S29
Baital	Silurian	Ludlow	Gorstian	?S22	Silurian	Přídolí	n/a	?S29
Ballynane	Silurian	Wenlock	Homerian	S20	Silurian	Ludlow	Gorstian	S22
Bannisdale	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S26
Barlow Inlet	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Bateaobao	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S23
Bayinburuk	Silurian	Ludlow	Gorstian	?S22	Silurian	Přídolí	n/a	?S29
Beciscie	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Becscie	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Rhuddanian	S4
Beechhill Cove	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Aeronian	S8
Bertie	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Black Bog Shale	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S25
Blair Shale	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Blaisdon Beds Upper	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Blanding	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Bloomsburg	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S26
Boda Limestone	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2
Bog Quartzite	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S8

Brandon Bridge	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Brassfield Limestone	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Aeronian	S8
Brathay	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Bringewood Lower	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Bringewood Upper	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Bronydd	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Rhuddanian	S4
Browgill	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Brownsport	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Bruflat	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S15
Budnany	Silurian	Přídolí	n/a	S29	Devonian	Early	Lochkovian	
Buildwas	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Builth Mudstones	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S22
Bullung Siltstone	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Ludlow	Ludfordian	?S26
Burgsvik	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Buttington Mudstone	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S12
Bylands Siltstone	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Cabano	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Aeronian	S8
Cae'r mynach	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S27
Camelford	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Camregan Grits, Lower	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Camregan Grits, Upper	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S9
Canberra	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Canon de Caballeros	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Ludfordian	S26
Cape Phillips	Ordovician	Late	Hirnantian	H2	Silurian	Přídolí	n/a	S29
Cape Schuchert	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S10

Cardiola	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Cariy Sandstone	Silurian	Llandovery	Telychian	S9	Silurian	Wenlock	Sheinwoodian	S17
Catavi	Silurian	Ludlow	Gorstian	?S22	Devonian	Early	Emsian	
Cedar Lake Dolomite	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Cerig	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S14
Cerro del Fuerte	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S17
Chaltash	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S29
Chenxiacun	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S14
Chicotte	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Chintin	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Chrysler	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Chwefri	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Aeronian	S7
Clarita	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S20
Clogher Head	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S19
Coalbrookdale	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S19
Cobleskill Limestone	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Cock Rig	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Coldwell	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Colonus Shale	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Ludfordian	S24
Conularia Sandstone	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S7
Coralliferous	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S15
Cordell	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Costerfield Siltstone	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Cotton	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Telychian	S10
Cowleigh Park	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8

Cowombat	Silurian	Ludlow	Gorstian	?S22	Silurian	Ludlow	Ludfordian	?S26
Cowridge Siltstone	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Croaghmar	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Ludfordian	S24
Crummack	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S7
Crychan	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Rhuddanian	S4
Cwm Clyd Sandstone	Ordovician	Late	Hirnantian	?H2	Ordovician	Late	Hirnantian	?H2
Cwm Graig ddu	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Cyrtograptus Shale	Silurian	Llandovery	Telychian	S11	Silurian	Wenlock	Homerian	S19
Dalmanitina bed	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Damery	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Dawes	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Dawukaxia	Silurian	Llandovery	Rhuddanian	?S1	Silurian	Llandovery	Rhuddanian	?S4
Dayanmen	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Decatur Limestone	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Decker	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Deep Creek Siltstone	Ordovician	Late	Hirnantian	H2	Silurian	Llandovery	Aeronian	S8
Deerhope	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S14
Delorme	Silurian	Wenlock	Homerian	S18	Devonian	Early	Emsian	
Dianbei	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Telychian	S11
Dolfawr Mudstones	Silurian	Llandovery	Telychian	S14	Silurian	Wenlock	Sheinwoodian	S15
Dolyhir & Nash Scar Lst	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Douro	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Downton Castle Sandstone	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S28
Drom Point	Silurian	Wenlock	Homerian	S21	Silurian	Wenlock	Homerian	S21
Drumyork Flags	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S13

Dubysa	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Dzwinogorod	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S28
Edgewood Limestone	Silurian	Llandovery	Rhuddanian	?S1	Silurian	Llandovery	Telychian	?S14
Edmunds	Silurian	Ludlow	Gorstian	?S22	Silurian	Ludlow	Ludfordian	?S26
Eke	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
El Carmen	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
El Castro	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Ellis Bay	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Elmside	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Elton Lower	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Elton Middle	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Elton Upper	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Eramosa Dolomite	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Erdaogou	Silurian	Přídolí	n/a	S27	Devonian	Early	Lochkovian	
Eskelhem	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Etelhem	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Fentou	Silurian	Llandovery	Telychian	S9	Silurian	Wenlock	Sheinwoodian	S17
Ferriters Cove	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Fibua	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Flaxley Beds Lower	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Flaxley Beds Upper	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Fleringe	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Fluminimaggiore	Silurian	Wenlock	Sheinwoodian	S17	Devonian	Early	Lochkovian	
Franopol	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Frojel	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18

Furmanovka	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S17
Gahard	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Gasport Dolomite	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Gasworks Mudstone	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S4
Gasworks Sandstone	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S8
Gazelle	Silurian	Llandovery	?Telychian	S9	Devonian	Early	Lochkovian	
Gionyama	Silurian	Llandovery	Rhuddanian	?S1	Silurian	Přídolí	n/a	?S29
Goat Island Dolomite	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Guanyinqiao	Ordovician	Late	Hirnantian	?H1	Silurian	Llandovery	Aeronian	?S5
Guelph	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Ludlow	Ludfordian	?S26
Guelph Dolomite	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Gulanhe	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Hafod Fwar	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Hailes Knob Quartzite	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Ludlow	Ludfordian	?S26
Halla (Mulde)	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21
Hamra	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
Hanchiatien	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Hangvar	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Hardwood Mountain	Silurian	Wenlock	Homerian	S21	Silurian	Přídolí	n/a	S27
Haverford Mudstone	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Rhuddanian	S4
Heceta Limestone	Silurian	Ludlow	Gorstian	?S22	Silurian	Ludlow	Ludfordian	?S26
Henryhouse	Silurian	Ludlow	Gorstian	S22	Devonian	Early		
Henshaw	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Herkimer	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S17
High Mains	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2

Hogklint	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Hopkinton	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Telychian	S11
Huanghuagou	Silurian	Llandovery	Rhuddanian	?S1	Silurian	Llandovery	Telychian	?S14
Hughley Shales	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S12
Huixingshao	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Humvale	Silurian	Ludlow	?Gorstian	?S22	Devonian	Early	Pragian	
Irfon	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Irondequoit Limestone	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Isfara	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S29
Jaagarahu	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S19
Jaani	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S17
Jenhochiao Lower	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Telychian	S14
Jenhochiao Upper	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Jerrestad Mudstone	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2
Joslin Hill	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Wenlock	Homerian	?S21
Jupiter	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S13
Jura	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Juuru	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Kabanka	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Kankakee Limestone	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S8
Kantinovo	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Kaochaitien Lower	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Kaochaitien Upper	Silurian	Llandovery	Telychian	S11	Silurian	Wenlock	Sheinwoodian	S15
Kaochlaplen	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Karaespinsk	Silurian	Llandovery	?Rhuddanian	?S1	Devonian	Early		

Katrinelund	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Kaugatuma	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	?S28
Kekexiongkuduke	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S26
Kentville	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Keyser Limestone	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Kildare Limestone	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2
Killbride	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S12
Kirkby Moor	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S29
Kirkland	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Klenova	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Ludlow	Ludfordian	?S26
Klinta	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Klinteberg	Silurian	Wenlock	Homerian	S20	Silurian	Ludlow	Gorstian	S22
Knockgardner	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Kok	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Ludfordian	S24
Konovka	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Kopanina	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S26
Kosov Bed	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Ktaoua	Ordovician	Late	?		Ordovician	Late	Hirnantian	H2
Kuanti	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S27
Kuanyinchiao	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Kuldiga	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Kuressaare	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Kustin	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
La Chilca	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S3
La Vieille	Silurian	Llandovery	Telychian	S9	Silurian	Wenlock	Sheinwoodian	S17

Lady Burn Conglomerate	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Rhuddanian	S2
Laketown Dolomite	Ordovician	Late	Hirnantian	H1	Silurian	Wenlock	Sheinwoodian	S17
Langara	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2
Langoyene	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Lanna	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Lapes	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
LaPorte City	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Lauchlan	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Laurel Limestone	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Ledbury	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	?S28
Leijiatun	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Leintwardine Lower	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Leintwardine Upper	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S24
Lerberg Marlstone	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Levide	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Lilla Karlso Limestone	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Lilley Dolostone	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Lilley-Peebles transition	Silurian	Wenlock	Homerian	S21	Silurian	Ludlow	Gorstian	S22
Lipeon	Silurian	Llandovery	Telychian	S9	Silurian	Přídolí	n/a	S29
Litohlavy	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S12
Llallagua	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Telychian	S11
Llangammarch	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21
Llessui	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S29
Lojoping	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S10
Longhope Beds Upper	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26

Longmaxi	Ordovician	Late	Hirnantian	H2	Silurian	Llandovery	Rhuddanian	S4
Los Espejos	Silurian	Wenlock	Sheinwoodian	S15	Devonian	Early	Lochkovian	
Louisville	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Loujiashan	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Lungmaxi	Ordovician	Late	Hirnantian	H2	Silurian	Llandovery	Rhuddanian	S4
Majiaochong	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S11
Manchap	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Wenlock	Homerian	?S21
Marjanovka	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Maxwellston Mudstones	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S9
May Hill Sandstone	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Telychian	S10
Mayville	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S8
Melbourne	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Miaokao	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S29
Mifflintown	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S23
Mill Cove	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S19
Millin Mudstone	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Milliners Arm	Silurian	Llandovery	Rhuddanian	?S1	Silurian	Llandovery	Aeronian	?S6
Mills Argillite	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Minija	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S27
Mirny Creek unit Q	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2
Mirny Creek unit R	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S1
Mirrabooka	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Mituva	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Molong Limestone	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Ludlow	Ludfordian	?S26
Mont Wissick	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Ludlow	Ludfordian	?S26

Mosalem	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Aeronian	S6
Motol	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Homerian	S21
Mottled Mudstones Lower	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S19
Mottled Mudstones Upper	Silurian	Wenlock	Homerian	S20	Silurian	Wenlock	Homerian	S21
Moydart	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Much Wenlock Limestone	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Mulloch Hill	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Rhuddanian	S4
Nancheng	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Aeronian	S5
Nar	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
Nevezis	Silurian	Ludlow	Gorstian	?S22	Silurian	Přídolí	n/a	?S29
Newlands	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S6
Niagaran Limestone	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Wenlock	Homerian	?S21
Ningqiang	Silurian	Llandovery	Telychian	?S12	Silurian	Wenlock	Homerian	?S21
Noulette	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Oak Ortchard	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Wenlock	Homerian	?S21
Odins Fjord	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Offley Isalnd	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S13
Ohesaare	Silurian	Přídolí	n/a	~S29	Silurian	Přídolí	n/a	S29
Osgood	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Homerian	S18
Oued Ali	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Oued Ali Clay	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Oved Sandstone	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S28
Overton	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Paadla	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S25
Pailungchiang	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21

Panghsa-Pye	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Peebles Dolostone	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S26
Pembroke	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Pencleuch Shale	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S7
Penfield	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S23
Pengjiayuan	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Penkill	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Pentamerus Beds	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S14
Pentamerus Bjerg	Silurian	Llandovery	Rhuddanian	S4	Silurian	Wenlock	Sheinwoodian	S15
Pentamerus gotlandicus Limestone	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Perham	Silurian	Ludlow	Gorstian	?S22	Silurian	Ludlow	Ludfordian	?S26
Petes	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Petropavlovsk	Silurian	Přídolí	n/a	S27	Devonian	Early		
Pike Arm	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S11
Plas Uchaf	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Plougastel	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Pointe aux Chenes	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Poley Cow	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S13
Pozary (Přídolí)	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S29
Pragowiec	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21
Protovirgularia Grits	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S11
Pupiao, Upper	Ordovician	Late	?Katian		Ordovician	Late	Hirnantian	H2
Pyle Mountain Argillite	Ordovician	Late	?Katian		Ordovician	Late	Hirnantian	H2
Qiaergaye	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Sheinwoodian	S17
Qiaergayes	Silurian	Llandovery	Telychian	?S9	Silurian	Wenlock	Homerian	?S21

Quidong Limestone	Silurian	Wenlock	Homerian	S20	Silurian	Ludlow	Gorstian	S22
Quinton	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Racine	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S23
Raikkula	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S7
Raisin River	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Rashkov	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S28
Read Bay	Silurian	Ludlow	Ludfordian	S24	Silurian	Přídolí	n/a	S29
Red Mountain	Silurian	Llandovery	Rhuddanian	S1	Silurian	Přídolí	n/a	S29
Ree Burn	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Reservoir	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S13
Reynales	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Rhydings	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Richea Siltstone	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Riga	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S19
Rinconada	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Wenlock	Homerian	?S21
Rio San Marco	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Road River	Silurian	Llandovery	Telychian	S9	Silurian	Přídolí	n/a	S29
Roberts Mountain	Silurian	Llandovery	Telychian	S9	Devonian	Early	Lochkovian	
Rochester Shale	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S17
Rockway	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Rongxi	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S12
Rootsikula	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21
Rose Hill	Silurian	Llandovery	Aeronian	S7	Silurian	Wenlock	Sheinwoodian	S15
Rosebank Shale	Silurian	Ludlow	Ludfordian	S25	Silurian	Přídolí	n/a	S29
Rumba	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8

Rusilov	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Rykhta Suite	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Rytteraker	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Aeronian	S8
Saelabonn	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Aeronian	S8
Salamonie Dolomite	Silurian	Wenlock	Sheinwoodian	?S17	Silurian	Wenlock	Homerian	?S18
Salar de Rincon	Silurian	Llandovery	Rhuddanian	?S1	Silurian	Llandovery	Telychian	?S14
Saldus	Ordovician	Late	Hirnantian	H2	Silurian	Llandovery	Rhuddanian	S1
Samuelsen Hoj	Silurian	Llandovery	Telychian	S13	Silurian	Llandovery	Telychian	S13
Sangui Sandstone	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Sargent Bay	Silurian	Ludlow	Ludfordian	S24	Silurian	Přídolí	n/a	S29
Sarnia Zwola	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Saugh Hill Grits	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S5
Sauquoit	Silurian	Llandovery	Telychian	S10	Silurian	Llandovery	Telychian	S11
Scotch Grove	Silurian	Llandovery	Telychian	S12	Silurian	Wenlock	Homerian	S21
Scratch	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Setul Limestone	Ordovician	Middle	?		Silurian	Přídolí	n/a	S29
Shaerbuer	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Wenlock	Homerian	?S21
Shemaha	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Shiniulan	Silurian	Llandovery	Aeronian	S7	Silurian	Llandovery	Telychian	S12
Shiwuzi	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Shiyang	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S4
Shoul Limestone	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Siaohopa	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S11
Sierra Grande	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Siesartis	Silurian	Wenlock	Homerian	S19	Silurian	Wenlock	Homerian	S21

Silverdale	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S23
Sjorvoll	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S17
Skelgill	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Telychian	S11
Slite	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Smyrna Mills	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S22
Sodus	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S10
Solvik	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Aeronian	S8
Songkan	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Sos'va Suite	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Spangande Limestone	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S17
Springfield Sandstone	Silurian	Llandovery	Aeronian	S6	Silurian	Llandovery	Telychian	S14
Sredninskaya	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S12
St Clair Limestone	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
St Martin's Cemetery Beds	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H1
Starcke Limestone	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S21
Steinsfjorden	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Stonehouse	Silurian	Přídolí	n/a	S27	Silurian	Early	Lochkovian	
Sugar Run Dolomite	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Ludlow	Gorstian	S23
Sundre	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Sutherland River	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S26
Syracuse	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Tabuk	Ordovician	Middle	?		Devonian			
Takche	Silurian	Wenlock	Sheinwoodian	?S15	Silurian	Wenlock	Homerian	?S21
Takuan	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S14
Tambolar	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Přídolí	n/a	S29

Tamsalu	Silurian	Llandovery	Rhuddanian	S2	Silurian	Llandovery	Rhuddanian	S4
Tanezzuft	Ordovician	Late	Hirnantian	H2	Silurian	Llandovery	Aeronian	S8
Tegart	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Temeside Shales	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Teremtsy Suite	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Telychian	S14
Ternava	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S18
Thornloe	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Tirabad	Silurian	Wenlock	Sheinwoodian	S17	Silurian	Wenlock	Homerian	S21
Tirnaskea	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Tofta	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Sheinwoodian	S16
Tomashov	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Tommarp	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Tonalee	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Tortworth	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Tralorg	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
Trapiche	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Trefawr	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Aeronian	S7
Trewern Brook Mudstone	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S19
Trubchin	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Tsagan-Bulakian	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Ludlow	Gorstian	S23
Tsviklevtsy	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S24
Tuscarora	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Aeronian	S8
Tycwtta Mudstones	Ordovician	Late	Hirnantian	H1	Silurian	Llandovery	Aeronian	S5
Ty-draw Slates	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Ulunda Mudstone	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2

unnamed [A]	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4
unnamed [B]	Silurian	Ludlow	Ludfordian	S24	Silurian	Ludlow	Ludfordian	S25
unnamed [C]	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Gorstian	S23
unnamed [Tamdrost Shale]	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
upper Llandovery Beds	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Ust'irgisla Beds	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Varbola	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Vargas Pena Shale	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Telychian	S14
Varnitsa	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S28
Velise	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Venusbank	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S8
Verkhneargskaya	Silurian	Přídolí	n/a	S27	Silurian	Přídolí	n/a	S29
Veron Shale	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S26
Vik	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Visby Lower	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Visby Upper	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S15
Wabash	Silurian	Ludlow	Gorstian	S22	Silurian	Přídolí	n/a	S29
Waldron Shale	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S18
Walker Volcanics	Silurian	Wenlock	Homerian	S18	Silurian	Wenlock	Homerian	S21
Wangapeka	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Wanyaoshu	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Wapentake	Silurian	Wenlock	Sheinwoodian	S16	Silurian	Wenlock	Homerian	S18
Waukesha Dolomite	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Homerian	S18
Wenallt	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2
WenChang	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2

Wengxiang Lower	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S14
Wengxiang Upper	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Wenquangou	Silurian	Llandovery	Rhuddanian	S3	Silurian	Wenlock	Sheinwoodian	S17
West Khatanzeya	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Ludfordian	S26
West Point	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Přídolí	n/a	S29
Westfield Sandstone	Ordovician	Late	Katian		Silurian	Llandovery	Rhuddanian	S2
Wether Law Linn	Silurian	Llandovery	Telychian	S14	Silurian	Llandovery	Telychian	S14
Whitcliffe Lower	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S25
Whitcliffe Upper	Silurian	Ludlow	Ludfordian	S25	Silurian	Ludlow	Ludfordian	S26
White Head	Ordovician	Late	Katian		Silurian	Llandovery	Telychian	S14
Whiteoak Sandstone	Silurian	Llandovery	Aeronian	S5	Silurian	Llandovery	Aeronian	S8
Whittaker	Ordovician	Late	Katian		Silurian	Wenlock	Homerian	S21
Wilhelmi	Silurian	Llandovery	Aeronian	?S5	Silurian	Llandovery	Aeronian	?S8
Williamson Shale	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Williamsport Sandstone	Silurian	Ludlow	Gorstian	S22	Silurian	Přídolí	n/a	S29
Willoughby Limestone	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Ludfordian	S26
Willow Glen	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Přídolí	n/a	S29
Willowvale Shale	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S14
Wills Creek Limestone	Silurian	Ludlow	Gorstian	S23	Silurian	Přídolí	n/a	S29
Wilsonia Shales	Silurian	Ludlow	Gorstian	S23	Silurian	Ludlow	Gorstian	S23
Winnica	Silurian	Ludlow	Ludfordian	S26	Silurian	Přídolí	n/a	S27
Woduhe	Silurian	Wenlock	Homerian	S18	Silurian	Ludlow	Ludfordian	S26
Wolcott Limestone	Silurian	Llandovery	Telychian	S9	Silurian	Llandovery	Telychian	S10
Wood Burn	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Aeronian	S8
Woodland	Silurian	Llandovery	Rhuddanian	S4	Silurian	Llandovery	Rhuddanian	S4

Woolhope Limestone	Silurian	Wenlock	Sheinwoodian	S15	Silurian	Wenlock	Sheinwoodian	S16
Wormwood	Silurian	Llandovery	Aeronian	S8	Silurian	Llandovery	Telychian	S10
Wray Castle	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Wufeng	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H1
Wulipo Beds	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Rhuddanian	S2
Wutubulake	Silurian	Přídolí	n/a	S29	Silurian	Přídolí	n/a	S29
Wych Beds	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
Xiajiaqiao	Silurian	Llandovery	Telychian	S13	Silurian	Wenlock	Sheinwoodian	S15
Xiangshuyuan	Silurian	Llandovery	Rhuddanian	S3	Silurian	Llandovery	Telychian	S9
Xibiehe	Silurian	Ludlow	Ludfordian	S24	Silurian	Přídolí	n/a	S29
Xiushan	Silurian	Llandovery	Telychian	S11	Silurian	Llandovery	Telychian	S13
Yan Yean	Silurian	Wenlock	Homerian	S19	Silurian	Ludlow	Gorstian	S22
Yankou	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Yarralumla	Silurian	Ludlow	Gorstian	S22	Silurian	Ludlow	Gorstian	S22
Yass	Silurian	Wenlock	Homerian	S20	Silurian	Ludlow	Gorstian	S22
Yokokurayama	Silurian	Llandovery	Rhuddanian	S1	Silurian	Přídolí	n/a	S29
Yr Allt	Ordovician	Late	Katian		Ordovician	Late	Hirnantian	H2
Yulungssu	Silurian	Ludlow	Ludfordian	S26	Silurian	Ludlow	Ludfordian	S26
Zaamin	Silurian	Ludlow	Ludfordian	S25	Devonian	Early		
Zapla	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Zelkovice	Silurian	Llandovery	Rhuddanian	S1	Silurian	Llandovery	Telychian	S9
Zel'van	Silurian	Llandovery	Telychian	S12	Silurian	Llandovery	Telychian	S12
ZhangChunWu	Ordovician	Late	Hirnantian	H1	Ordovician	Late	Hirnantian	H2
Zhangjiatun	Silurian	Ludlow	Gorstian	?S22	Silurian	Ludlow	Ludfordian	?S26
Zvenigorod	Silurian	Llandovery	Telychian	S9	Silurian	Přídolí	n/a	S29