



## Biostratigraphy of British Silurian nautiloid cephalopods

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**KEY WORDS** - Nautiloid cephalopods, Silurian, Britain, biostratigraphy.

**ABSTRACT** - Distribution of nautiloid cephalopods in the Silurian of England, Wales, and Scotland is reviewed stratigraphically and geographically. Genera are considered first and then species. Seven orders are present: Endocerida (one genus), Actinocerida (three), Orthocerida (17), Ascocerida (one), Oncocerida (at least ten), Discocerida (three), and Tarphycerida (seven). Wenlock and Ludlow faunas are more abundant than those of the Llandovery. Records from the Pridoli are very rare.

**RIASSUNTO** - [Biostratigrafia a cefalopodi nautiloidi nel Siluriano della Gran Bretagna] - La distribuzione dei cefalopodi nautiloidi nel Siluriano dell'Inghilterra, Galles e Scozia viene qui rivista in termini stratigrafici e geografici. L'analisi è stata fatta a livello generico e poi specifico. Sette ordini sono documentati: Endocerida (un genere), Actinocerida (tre), Orthocerida (17), Ascocerida (uno), Oncocerida (almeno dieci), Discocerida (tre) e Tarphycerida (sette). Le faune del Wenlock e del Ludlow sono più abbondanti di quelle del Llandovery. Le testimonianze dei nautiloidi del Pridoli sono invece rare.

### INTRODUCTION

This paper records the results of long examination of British Silurian nautiloid cephalopods, including those from the large collections of the Natural History Museum in London, the British Geological Survey at Keyworth, and the Shropshire County Museum at Ludlow, as well as material from many other museum and university collections. I have had access also to specimens obtained from fieldwork by myself and others and to the available literature.

A most detailed Silurian biostratigraphy is available through the abundant well known and frequently well preserved graptolite faunas and, especially in recent years, from micropalaeontology. Studies of British Silurian shelly faunas have been dominated by those on brachiopods and trilobites. The cephalopods have therefore been relatively neglected. In addition they are often not well preserved, being broken or as more or less flattened moulds. This, in contrast to such faunas as those of Bohemia or the Chinese Yangtze Platform, may preclude investigation of important internal structures. Instead, much reliance must be placed on external morphology including ornamentation.

The data are presented as a table of genera (with their authors) plotted against the seven stages recognised internationally as the Aeronian, Rhuddanian, and Telychian within the Llandovery Series; the Sheinwoodian and Homerian within the Wenlock Series; and the Gorstian and Ludfordian within the Ludlow Series. A full account of Silurian global standard stratigraphy and distribution of Silurian faunas was provided by Holland & Bassett (1989). The genera are grouped in orders, largely as those given in the *Treatise on Invertebrate Paleontology* (Moore, 1964), though, as proposed by Holland (2010), the Order Barrandeoceratida is subsumed in the Tarphyceratida.

The Pridoli Series is not included in the table of genera as in Britain it is represented largely in the continental Old Red Sandstone facies. There are limited occurrences of shallow water marine or quasi marine deposits from

the oldest part of the series, which have yielded very few examples of a relict cephalopod fauna confined to the Order Orthocerida. It includes *Cyrtocycloceras*, *Kionoceras*, *Leurocycloceras*, *Orthocycloceras*, and *Polygrammoceras* (Holland, 2000a).

### DISTRIBUTION OF GENERA

The Silurian Period is a relatively short one compared with other Palaeozoic periods (Gradstein et al., 2012). The overall impression of generic distribution provided here is variously affected by facies distribution, limitations of exposure, and collection failure. Facies patterns can be appreciated from the Geological Society of London's Palaeogeographical Atlas (Cope et al., 1992) and from an earlier assessment of Ludlow facies by Holland & Lawson (1963). Hewett & Watkins (1980) gave an account of Ludlow cephalopod ecology across a tract from shelf to basin in the Welsh Borderland, but their collection points were seriously limited. There is a considerable contrast between the poorly preserved, often fragmentary orthoconic moulds to be found in the graptolitic basin facies and the richer better preserved cephalopod faunas of the various carbonate and silty mudstone facies of the Silurian shelf. Nevertheless some general conclusions are justifiable (Tab. 1).

1. Cephalopods are poorly represented in earlier Llandovery strata but there is usually continuity of deposition from Ordovician to Silurian and many Silurian genera were already present in the Ordovician (single species of only two genera are known from the Rhuddanian; by Aeronian times six or seven genera are known).

2. Much increased variety and numbers in the Telychian (17 genera and at least 18 species) echo the widespread marine transgression of late Llandovery times.

3. The Sheinwoodian (24 genera, 34 species), Homerian (25 genera, 33 species), and Gorstian (26

genera, 47 species) stages yield the richest cephalopod faunas and their similarity recalls the old grouping of Wenlock and Ludlow as Salopian.

4. The Gorstian with its characteristic silty mudstone facies yields some of the most numerous assemblages.

5. Finally, the Ludfordian Stage is characterised by common Orthocerida, though a break down to the specific level will show that certain relict forms become dominant as the shallowing marine facies develops towards the Pridoli. These include *Cyrtocycloceras ibex* (Sowerby in Murchison, 1839), *Kionoceras virgatum* (Sowerby in Murchison, 1839), *Leurocycloceras whitcliffense* Holland, 1965, *Orthocycloceras ibex* (Sowerby in Murchison, 1839), *Polygrammoceras bullatum* (Sowerby in Murchison, 1839), and *Temperoceras ludense* (Sowerby in Murchison, 1839).

#### DISTRIBUTION OF SPECIES

There follow records of British Silurian nautiloid cephalopod species. They are taken in the same sequence as the genera listed in Table 1.

##### Order ENDOCERIDA Teichert, 1933

###### Genus *Tretoceras* Salter, 1858 (one species)

Evans and Holland (1995) described the single specimen of *Tretoceras bisiphonatum* (Sowerby in Murchison, 1839) from the Wormwood Formation (Aeronian-Telychian) of Llandovery.

##### Order ACTINOCERIDA Teichert, 1933

Holland (1998) described five species of Actinocerida, largely from relatively shallow water carbonates or sandy clastics. They are rare and often not well preserved. *Ormoceras baccatum* (Woodward, 1868) is confined to the basal Wenlock Woolhope Limestone, but the other four species *Armenoceras cygneum* (Holland, 1998), *Armenoceras nummularium* (Sowerby in Murchison, 1839), *Armenoceras subconicum* (d'Orbigny, 1850), and *Eldroceras blakei* (Foord, 1888), range from upper Llandovery to Ludlow. Almost all are from England and Wales.

##### Order ORTHOCERIDA Kuhn, 1940

This great 'generalised' order of orthoconic, and to a much lesser extent cyrtoconic, forms dominates British Silurian cephalopod faunas. Seventeen genera and 29 species are recorded.

###### Genus *Cyrtocycloceras* Foerste, 1936 (two species)

*Cyrtocycloceras extricatum* Blake (1882) is rare in Gorstian rocks of shelf facies. *Cyrtocycloceras ibex*

(Sowerby in Murchison, 1839) is one of the commonest Silurian species (Holland, 2007). It is very well represented in both shelf and basin facies from Homerian to Ludfordian. It is especially common in the Ludfordian of the Ludlow district. Detail of its cyrtoconic form and difference from *Orthocycloceras ibex* are given in Holland (2007).

###### Genus *Dawsonoceras* Hyatt, 1884 (four species)

*Dawsonoceras annulatum* (J. Sowerby, 1818) with its very characteristic festooning on the exterior of the shell ranges from Telychian to Ludfordian across facies, but is especially common in Sheinwoodian to Gorstian rocks (Holland, 2002a), including the Much Wenlock Limestone. *Dawsonoceras crassum* and *D. subtile* both from the Homerian to Gorstian, were distinguished as varieties by Foord (1888) on details of the festooning. His variety *perundosum* was not illustrated and is not recognisable. *Dawsonoceras fimbriatum* (Sowerby in Murchison, 1839) is confined largely to the shelf facies of Sheinwoodian to Gorstian age.

###### Genus *Gaspocyrtoceras* Foerste, 1936 (one species)

*Gaspocyrtoceras clarksoni* (Holland, 2000b) is recorded only from the Telychian of the Pentland Hills (Holland, 2000b).

###### Genus *Geisonoceras* Hyatt, 1884 (one species)

*Geisonoceras maclareni* (Murchison, 1859) is a characteristic Scottish Llandovery and Wenlock fossil present in the Girvan area, the Southern Uplands, and the Pentlands (Holland, 2000b). It occurs also in the Sheinwoodian and Gorstian of the Welsh Borderland.

###### Genus *Geisonocerina* Foerste, 1935 (three species)

*Geisonocerina elongatocinctum* (Portlock, 1843) occurs in the Telychian of the Pentlands and is well represented in the Wenlock and Ludlow of both shelf and basin facies in the Welsh Borderland, Wales, and Northern England. Both Foerste (1935) and Sweet in Moore (1964) suspected an artificiality in the separation of this genus, but Holland (2002a) referred to its characteristic ornamentation. *Geisonocerina mocktreensis* (Sowerby in Murchison, 1839) is recorded from the Homerian of North Wales and the Welsh Borderland but also is well represented in the Gorstian and Ludfordian of the shelf facies in the Welsh Borderland. *Geisonocerina? recticinctum* (Blake, 1882) is found in the Homerian and Gorstian of North Wales, the Gorstian of Ludlow, and more commonly in the Ludfordian of the Welsh Borderland.

ORDERS	Nautiloid cephalopod genera	Rhuddanian	Aeronian	Telychian	Sheinwoodian	Homerian	Gorstian	Ludfordian
E	<i>Tretoceras</i> Salter, 1858			+				
Act.	<i>Armenoceras</i> Foerste, 1924		+	+	+	+	+	+
	<i>Eldroceras</i> Foerste, 1924			+	+	+	+	
	<i>Ormoceras</i> Stokes, 1840				+			
Orthocerida	<i>Cyrtocycloceras</i> Foerste, 1936					+	+	+
	<i>Dawsonoceras</i> Hyatt, 1884			+	+	+	+	+
	<i>Gaspocyrtoceras</i> Foerste, 1936			+				
	<i>Geisonoceras</i> Hyatt, 1884		+	+	+	+	+	
	<i>Geisonocerina</i> Foerste, 1935			+	+	+	+	+
	<i>Gorbyceras</i> Shimizu & Obata, 1935		+	+	+			
	<i>Harrisoceras</i> Flower, 1939						+	
	<i>Hemicosmorthoceras</i> Ristedt, 1968				+	+	+	+
	<i>Imbricatoceras</i> Holland, 1992	+	+	+	+	+	+	+
	<i>Kionoceras</i> Hyatt, 1884			+	+	+	+	+
	<i>Leurocycloceras</i> Foerste, 1928a			+			+	+
	<i>Metaspyroceras</i> Foerste, 1932			+		+		+
	<i>Michelinoceras</i> Foerste, 1932				+	+		
	<i>Orthocycloceras</i> Barskov, 1972		+		+	+	+	+
	<i>Parakionoceras</i> Foerste, 1928				+		+	
<i>Polygrammoceras</i> Foerste, 1928			+		+	+	+	
<i>Temperoceras</i> Barskov, 1960				+	+	+	+	
A	<i>Ascoceras</i> Barrande, 1867						+	+
Oncocerida	<i>Amphicyrtoceras</i> Foerste, 1924						+	
	<i>Bassetoceras</i> Holland, 2007					+		
	<i>Cyrtorizoceras</i> Hyatt, 1900				+	+		
	<i>Jeppssonoceras</i> Stridsberg, 1985					+	+	
	<i>Octameroceras</i> Hyatt, 1900			+				
	<i>Oonoceras</i> Hyatt, 1884				+	+		
	<i>Oxygonioceras</i> Foerste, 1925				+			
	<i>Tetrameroceras</i> Hyatt, 1884						+	
	<i>Trimeroceras</i> Hyatt, 1884						+	+
	" <i>Gomphoceras</i> "			+	+	+	+	+
Disc.	<i>Ovocerina</i> Flower, 1948					+		
	<i>Phragmoceras</i> Broderip in Sowerby in Murchison, 1839			+	+	+	+	+
	<i>Protophragmoceras</i> Hyatt, 1900			+	+			
Tarphyocerida	<i>Catyrephoceras</i> Foerste, 1926					+	+	
	<i>Lechritrochoceras</i> Foerste, 1926	+		+	+	+	+	
	<i>Ophioceras</i> Barrande, 1865				+	+	+	
	<i>Peismoceras</i> Hyatt, 1894				+	+		
	<i>Systrochoceras</i> Hyatt, 1894				+		+	
	<i>Trocholites</i> Conrad, 1838		+					
	<i>Uranoceras</i> Hyatt, 1884					+	+	

Tab. 1 - Distribution of Orders and Genera of British Silurian nautiloid cephalopods in the Rhuddanian, Aeronian, and Telychian stages of the Llandovery Series; the Sheinwoodian and Homerian stages of the Wenlock Series; and the Gorstian and Ludfordian stages of the Ludlow Series. Distribution of *Tretoceras* Salter, 1858 and *Trocholites* Conrad, 1838 is shown as transitional between stages. E: Order Endocerida, Act.: Actinocerida, A: Ascocerida, Disc.: Discosorida.

Genus *Gorbyoceras* Shimizu & Obata, 1935  
(one species)

*Gorbyoceras vellatum* (Blake, 1882) is present in the Aeronian of the Girvan area and several specimens are known from this level at Haverfordwest. It occurs also in the Wenlock of the Lower Hill Farm borehole (Holland, 2002a) through the type Wenlock. Holland (2000b) noted a slightly different form in the Telychian of the Pentlands.

Genus *Harrisoceras* Flower, 1939  
(one species)

*Harrisoceras distans* (Sowerby in Murchison, 1839) is rare in the Gorstian of Aymestry, Ledbury, and Woolhope. Holland (2000c) noted its close relationship to *Temperoceras* referred to below.

Genus *Hemicosmorthoceras* Ristedt, 1968  
(one species)

*Hemicosmorthoceras dimidiatum* (Sowerby in Murchison, 1839), often recognisable even in fragments, is present in the Sheinwoodian of Burrington and the Homerian of Denbigh, but becomes widespread in both basin and shelf facies in the Gorstian of Wales and the Welsh Borderland. In the Ludfordian there are records from the basin facies of Clun Forest and the Knighton district.

Genus *Imbricatoceras* Holland, 1992  
(one species)

*Imbricatoceras subundulatum* (Portlock, 1843) has a remarkable range from Rhuddanian to Ludfordian and a wide distribution (Holland, 1992). Its characteristic ornamentation allows recognition even of small fragments. Llandovery representatives are known from South Wales and the Pentlands (Holland, 2000b). It is common in the Sheinwoodian of North Wales and the Welsh Borderland, and the Gorstian and Ludfordian of the Welsh Borderland (Holland, 2002a) and Northern England. Numerous specimens have been recovered from the Gorstian of the Ludlow district. Holland (2002a) suggested that extrapolation from some of the type Wenlock of the Lower Hill Farm borehole would imply an original accumulation of some 80 shells per square metre on the muddy sea floor.

Genus *Kionoceras* Hyatt, 1884  
(four species)

*Kionoceras bacchus* (Barrande, 1868) and *K. filosum* (Sowerby in Murchison, 1839) are largely confined to the Sheinwoodian and Gorstian of the shelf facies in the Welsh Borderland, where they are relatively common (Holland, 2002b). *Kionoceras primaevum* (Forbes, 1845) has a curious taxonomic history (Holland, 2004). It occurs as rather 'ghostly' impressions in Wenlock to

Ludlow Welsh slates of basin facies. *Kionoceras virgatum* (Sowerby in Murchison, 1839) appears in the Scottish Telychian of the Hagshaw Hills and the Pentlands and becomes more common in the Wenlock shelf facies of the Welsh Borderland (Holland, 2000b, 2002a). It is very numerous in the Gorstian, still largely of shelf facies and remains common in the Ludfordian. In this species the characteristic longitudinal fluting of the genus is accompanied by very fine longitudinal and transverse striae.

Genus *Leurocycloceras* Foerste, 1928a  
(two species)

*Leurocycloceras etheridgii* (Blake, 1882) is recorded only from the Scottish Telychian of the Pentlands and the Southern Uplands (Holland, 2000b). The characteristic preservation of *Leurocycloceras whitcliffense* Holland, 1965 as separated moulds of individual camerae was described in detail by Holland (1965). It occurs in the Gorstian from Clun Forest to Ludlow but is very common in the Ludfordian of Wales and the Welsh Borderland (Holland, 2000a).

Genus *Metaspyroceras* Foerste, 1932  
(two species)

*Metaspyroceras* sp. is present in the Telychian of the Pentlands (Holland, 2000b). *Metaspyroceras grayi* (Blake, 1882) is known from the Homerian of the shelf facies at Dudley. *M. undulatocinctum* (Blake, 1882) occurs in the Wenlock basin facies of North Wales and the Ludfordian at Ledbury.

Genus *Michelinoceras* Foerste, 1932  
(one species)

*Michelinoceras argus* (Barrande, 1868) is common through the Sheinwoodian and Homerian of the Lower Hill Farm borehole, where its exceedingly fine riblets may be exquisitely preserved (Holland, 2002a). It is recorded also elsewhere in the Wenlock of the Welsh Borderland and North Wales.

Genus *Orthocycloceras* Barskov, 1972  
(four species)

*Orthocycloceras duponti* (Barrande, 1868) at Builth is confined to the Sheinwoodian, but occurs in the Homerian and Gorstian of many localities in the Welsh Borderland. *Orthocycloceras nicholianum* (Blake, 1882) ranges from Sheinwoodian to Ludfordian in the Welsh Borderland, but is not common. *Orthocycloceras tenuiannulatum* (M'Coy, 1855) is common in the Gorstian of North Wales, Central Wales, and the Welsh Borderland. There are isolated records in the Sheinwoodian at Builth and the Ludfordian at Presteigne. *Orthocycloceras ibex* (Sowerby in Murchison, 1839) is present in the Aeronian of the Southern Uplands, occurs through the Wenlock of

Northern England and the Welsh Borderland (Holland, 2002a), but, above all, is a very common and characteristic fossil of both basin and shelf facies of the Gorstian and Ludfordian throughout England and Wales. Its distinction from *Cyrtocycloceras ibex* has been mentioned already (Holland, 2007).

Genus *Parakionoceras* Foerste, 1928a  
(one species)

*Parakionoceras originale* (Barrande, 1868) is a Sheinwoodian and Gorstian form from the Welsh Borderland and South Wales. It occurs in the Sheinwoodian of the Lower Hill Farm borehole (Holland, 2002a) where its longitudinal grooves can be clearly distinguished from the flutes of *Kionoceras*.

Genus *Polygrammoceras* Foerste, 1928b  
(one species)

*Polygrammoceras bullatum* (Sowerby in Murchison, 1839) is known from the Telychian at Cardiff and a related form occurs in the Pentlands (Holland, 2000b). It is found in the Gorstian of the Welsh Borderland and the Homerian of North Wales (Holland, 2002a). It is a very common and easily recognisable indicator of the Ludfordian in many localities in Wales and the Welsh Borderland. Holland (2002b) discussed its taxonomy and illustrated its internal structure.

Genus *Temperoceras* Barskov, 1960  
(one species)

*Temperoceras ludense* (Sowerby in Murchison, 1839) occurs in the Wenlock of the Welsh Borderland but is characteristically a Ludlow fossil, found very commonly in the Gorstian and Ludfordian. In his description of the external and internal morphology of this species, Holland (2000c) examined over 160 specimens. Some examples are very large. Blake (1882) referred to specimens in Ludlow Museum more than 2 feet (60 cm) in length. From his intimate knowledge of the collections at Ludlow, Norton (1978) mentioned several examples which, if complete, would have exceeded one metre in length.

Order ASCOCERIDA Kuhn, 1949

Genus *Ascoceras* Barrande, 1867  
(two species)

Holland (1999) gave a review of the unusual morphology and ontogeny of the ascoceratid shell. Two species only are known from the British Silurian, both very rare. *Ascoceras barrandei* Salter, 1858 is present in the Ludfordian of Ludlow and *A. vermiforme* Blake, 1882 in the Gorstian of Ledbury and the Ludfordian of Ludlow.

Order ONCOCERIDA Flower in Flower & Kummel, 1950

Nine genera and ten species are recorded. Occurrences of “*Gomphoceras*” forms are also noted.

Genus *Amphicyrtoceras* Foerste, 1924  
(two species)

*Amphicyrtoceras compressum* (Sowerby in Murchison, 1839) and *Amphicyrtoceras rickardsi* Holland, 2007 are known only from the Gorstian of the Welsh Borderland (Holland, 2007).

Genus *Bassettoceras* Holland, 2007  
(one species)

*Bassettoceras isca* (Blake, 1882) is represented in these records by only two specimens from the Homerian of Usk (Holland, 2007).

Genus *Cyrtorizoceras* Hyatt, 1900  
(one species)

*Cyrtorizoceras yochelsoni* Holland, 2007 again is recorded only from the Wenlock, in this case from both Sheinwoodian and Homerian stages at Usk (Holland, 2007).

Genus *Jeppssonoceras* Stridsberg, 1985  
(one species)

Genera and species of oncocerid cephalopods from Gotland were described, defined, and discussed by Stridsberg in his monograph of 1985. Diagnoses of the genera depend upon the configuration of the apertural margin. British material is seldom well enough preserved to show such detail. *Jeppssonoceras pyriforme* (Sowerby in Murchison, 1839) is recognised from the Gorstian of the Welsh Borderland (Holland, 2007).

Genus *Octameroceras* Hyatt, 1900  
(one species)

*Octameroceras scotorum* (Lamont, 1978) is recorded only from the Telychian of the Pentlands (Holland, 2000b).

Genus *Oonoceras* (Hyatt, 1884)  
(one species)

*Oonoceras contrarius* (Barrande, 1866) is found in the Wenlock of Cardiff and Usk. *O. plebium* (Barrande, 1868) is recorded only from a single specimen from the Homerian of Dudley (Holland, (2007).

Genus *Oxygonioceras* Foerste, 1925  
(one species)

*Oxygonioceras oxynotum* (Barrande, 1865) is present in the Sheinwoodian of Dudley (Holland, 2010).

Genus *Tetrameroceras* (Hyatt, 1884)  
(one species)

*Tetrameroceras obovata* (Blake, 1882) is a Gorstian species from Shropshire, including the Ludlow district.

Genus *Trimeroceras* Hyatt, 1884  
(one species)

*Trimeroceras ellipticum* (M'Coy, 1855) occurs in the Gorstian of Leintwardine and the Ludfordian of Ludlow and Ledbury. Many British examples can be referred to only as '*Gomphoceras*' sp. They occur from the Telychian onwards. Apart from a Telychian record from the Pentlands, they are found throughout the Welsh Borderland, commonly in the Wenlock and very commonly in the Gorstian.

Order DISCOCERIDA Flower in Flower & Kummel, 1950

Three genera and at least seven species are recorded.

Genus *Ovocerina* Flower, 1948  
(one species)

*Ovocerina corona* (Blake, 1882) is a distinctive, though rare, form from the Homeric of Ledbury and Dudley.

Genus *Phragmoceras* Broderip  
in Sowerby in Murchison, 1839  
(at least four species)

Holland & Stridsberg (2004) revised and described species of *Phragmoceras* from Gotland and Britain. Nearly 200 specimens of the genus are known from British museum and university collections, though only about half of these can be assigned to a species. *Phragmoceras arcuatum* Sowerby in Murchison, 1839 is common in the Homeric (Much Wenlock Limestone) and Gorstian of the Welsh Borderland, especially from Ledbury and Dudley. *Phragmoceras ventricosum* Sowerby in Murchison, 1839, the other common species, appears to be confined to the Gorstian of the Welsh Borderland. *Phragmoceras exaggeratus* Holland & Stridsberg, 2004, a rare species characterised by a relatively long body chamber, was described from that rich source of Silurian cephalopods, the Gorstian of Ledbury. *Phragmoceras imbricatum* Barrande, 1865 is represented in the British Silurian by a single specimen from the Gorstian of Ludlow. The importance of a single record in palaeogeographical assessment has been shown, for example, by Histon (2012) through her find of *Phragmoceras* sp. in the Silurian of the Carnic Alps. Taking account of *Phragmoceras*, not identifiable at the specific level, its range increases from rare Telychian occurrences at May Hill and in the Pentlands, through the Wenlock of the Welsh Borderland, where it is common in the Homeric of Dudley and Ledbury, through its very common representation in the Gorstian of the Welsh Borderland, and on to the Ludfordian of Dudley and Aymestry.

Genus *Protophragmoceas* Hyatt, 1900  
(two species)

*Protophragmoceras erskinei* Lamont, 1978 was described from the Telychian of the Pentlands (Holland, 2000b) but occurs also in the Sheinwoodian of Ledbury. *Protophragmoceras murchisoni* (Barrande, 1866) is known only from the Sheinwoodian-Homeric of the Lower Hill farm borehole (Holland, 2002a).

Order TARPHYCERATIDA Flower in Flower & Kummel, 1950

Coiled nautiloid cephalopods from the British Silurian were described and their taxonomy revised by Holland (2010). With the exception of *Oxygonioceras*, referred to above, all are from the Order Tarphyceratida. Seven genera and 12 species are recorded.

Genus *Catyrephoceras* Foerste, 1926  
(two species)

*Catyrephoceras giganteus* (Sowerby in Murchison, 1839) is very common in the Gorstian of the Welsh Borderland and South Wales. Ledbury and Mocktree are rich localities for the species. It is the most common of the coiled forms. *Catyrephoceras gyrans* (Blake, 1882) is recorded only from the Homeric of Eastnor and Usk.

Genus *Lechitrochoceras* Foerste, 1926  
(three species)

*Lechitrochoceras cornuarietis* (Sowerby in Murchison, 1839) occurs in the Rhuddanian and Telychian of the Llandovery district and the Sheinwoodian at Presteign. *Lechitrochoceras regulare* (Blake, 1882) is known only from the Homeric Much Wenlock Limestone at Dudley, where it is quite common. *Lechitrochoceras striatum* (Blake, 1882) is represented by a few specimens from the Sheinwoodian of Usk and the Gorstian of Ledbury.

Genus *Ophioceras* Barrande, 1865  
(two species)

*Ophioceras articulatum* (Sowerby in Murchison, 1839) is a rare elegant smaller shell with a characteristic divergent body chamber. It is recorded from the two Wenlock stages and the Gorstian of the Welsh borderland. The other rare species *O. geometricum* (Blake, 1882) from the Homeric of Walsall and the Gorstian of Ledbury, Ludlow, and Dudley, differs in its ornamentation.

Genus *Peismoceras* Hyatt, 1894  
(one species)

*Peismoceras asperum* (Barrande, 1865) occurs rarely in the Sheinwoodian of Burrington near Ludlow and in the Homeric Much Wenlock Limestone of Eastnor and Ledbury.

Genus *Systrochoceras* Hyatt, 1894  
(two species)

*Systrochoceras arietinum* (Barrande, 1865) is present in the Wenlock of Cardiff and North Wales and the Gorstian of Cardiff and Ledbury. Several specimens are recorded from the latter. *Systrochoceras rapax* (Barrande, 1865) occurs in the Sheinwoodian at Dudley and the Gorstian at Ledbury.

Genus *Trocholites* Conrad, 1838  
(one species)

*Trocholites planorbiformis* Conrad, 1842, a very small form characterised by its depressed whorls, is represented by one specimen from the Rhuddanian-Aeronian of Llandovery.

Genus *Uranoceras* Hyatt, 1884  
(one species)

*Uranoceras holtianus* (Blake, 1882), with its very rapidly expanding, smooth, flat sided whorls occurs in the Homerian at Dudley and is very common in the Gorstian of Ledbury.

## CONCLUSIONS

Herein a summary of data on the distribution of nautiloid cephalopods in the Silurian of England, Wales, and Scotland is presented. The faunal distribution has been reviewed stratigraphically and geographically and complete bibliographical coverage in relation to occurrences is given. The study highlights the presence of seven orders and 42 genera as follows: Endocerida (one genus), Actinocerida (three), Orthocerida (17), Ascocerida (one), Oncocerida (at least ten), Discocerida (three), and Tarphycerida (seven). A total of 66 species are documented. Wenlock and Ludlow faunas are more abundant than those of the Llandovery (Tab. 1). Records from the Pridoli are very rare.

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