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One of Many Problems: Taxonomy of the Common Silurian Nautiloid Cephalopod *"Orthoceras" bullatum* J. DE C. SOWERBY

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1 Plate

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Eines von vielen Problemen: Taxonomie des häufigen silurischen nautiloiden Cephalopoden *"Orthoceras" bullatum* J. DE C. SOWERBY

Zusammenfassung

Der häufigste britische nautiloide Cephalopode aus dem Silur *Orthoceras bullatum* J. DE C. SOWERBY 1839 wird unter dem Gattungsnamen *Polygrammoceras*, für den eine neue Diagnose erstellt wird, ausführlich neu beschrieben. Die Bearbeitung dieser Spezies bietet ein gutes Beispiel für die Diskussion taxonomischer Probleme bei silurischen Cephalopodenfaunen und ihre mögliche Lösung.

Abstract

The commonest British Silurian nautiloid cephalopod *Orthoceras bullatum* J. DE C. SOWERBY is fully redescribed under the generic name *Polygrammoceras*, for which a new diagnosis is given. Consideration of this species provides a good example for discussion of taxonomic problems in Silurian cephalopod faunas and their possible solution.

1. Introduction

The Orthocerida (Michelinoceratida of FLOWER in FLOWER & KUMMEL, 1950) is, to quote FLOWER (1962),

" ... the great order of 'generalized' orthocones."

Its members are usually orthoconic, never coiled; typically contain cameral deposits; and primitively have tubular siphuncles. Their septal necks are typically short and often orthochoanitic; their connecting rings are thin. They may have annulosiphonate deposits. As such the order contains very many of the species once assigned to the genus *Orthoceras*. BARRANDE's beautifully illustrated volumes (BARRANDE, 1865–1877) are replete with such forms.

In addition to his broader concern with septal necks, HYATT (1844, 1900) recognised that there are important differences in the ornament of these shells and established new genera accordingly. FOERSTE in the late 1920s and the 1930s described very many North American Ordovician and Silurian cephalopod species.

It fell to TEICHERT (1933, 1935) and FLOWER (1939) to recognise the meaningful morphology of cameral and siphonal deposits, which would thus become significant in taxonomy. FLOWER (1962) provided a good review of the then present and future use of internal structures in family and generic taxonomy within the Order Michelinoceratida

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(now Orthocerida). He referred to his realisation from FOERSTE's careful descriptive work that the use of ornament alone could result in problems of homoeomorphy. However, he did give a qualification:

"It remains true that, in general, form of siphuncle segments is less subject to rapid evolutionary change than are surface patterns, but we have a few lineages in which general surface patterns remain constant, though internal features change."

In modern Palaeozoic nautiloid cephalopod taxonomy total morphology, both internal and external, must, so far as is possible, be taken into account. There has been much work, for instance, on material from China, North America, and the former Soviet Union. For the abundant material from Central Europe BARRANDE's illustrations are so numerous and so clear that it is often possible to assess all necessary features. GNOLI (1997) has provided a most helpful assessment of the present taxonomic status of many of BARRANDE's species. The difficulties arise with other old European collections, where careful revision is now necessary. SERPAGLI, GNOLI, and HISTON (e.g. SERPAGLI & GNOLI, 1977; GNOLI, 1987; GNOLI & HISTON, 1998) are pointing the way with their studies of Silurian peri-Gondwana material from Sardinia, the Carnic Alps, etc. EVANS (1994) has described the meagre and often ill-preserved Silurian material from Ireland.

My own concern is with revision of Silurian cephalopods from England, Scotland, and Wales, of which several thousand specimens have been made available for study. BLAKE's monograph of 1882 is comprehensive in its description of species, many of them common and in some cases of biostratigraphical potential. The problem is to assign these forms to meaningful genera and hopefully later to understand their phylogeny.

Specimens in all British facies are often found with their body chambers missing and, almost always, with their apical ends broken off. In the graptolite shale facies they are often flattened and ill preserved, though, as FLOWER (1962, p. 23) so rightly noted of their documentation,

" ... without the knowledge provided by such descriptions our concept of the faunas would have been even more incomplete."

Preservation in other facies is frequently in more or less calcareous clastics, where an infilling of sediment unfortunately all too often obliterates most, if not all of the internal structures.

It is only by examining all available collections that one has the chance to find the rare specimen that shows critical internal structure or can be sectioned to show this. In what follows, consideration of the species *Orthoceras bullatum* J. DE C. SOWERBY 1839 provides a case history of the problems involved in taxonomic revision and of the possibility of their solution.

2. *"Orthoceras" bullatum* J. DE C. SOWERBY 1839

I have examined already over 370 specimens of *"Orthoceras" bullatum* from the Wenlock, Ludlow, and Přídolí series of the British Silurian. A few Wenlock specimens are known; those from the Přídolí are extremely rare; most are from the Ludlow Series, and specially from the upper of its two stages, the Ludfordian. Nearly all are from Wales and the Welsh Borderland. It is, in terms of my records, certainly the most common British Silurian cephalopod species. Unfortunately, it is often poorly preserved, though this does not inhibit its recognition. Its fragmentary, more or less compressed moulds (Pl. 1, Fig. 2) have characteristic ornament and characteristic proportions.

The illustration of the type specimen in MURCHISON's Silurian System of 1839 (Pl. 5, Fig. 29) does reveal the siphuncle where part of the phragmocone has been broken away. Its segments are shown as somewhat expanded, being constricted at the septal openings. Curiously, BLAKE's (1882, Pl. 12, Fig. 4) slightly stylised illustration excludes the portion of the specimen which would show the siphuncle.

MCLEARN (1924) in his memoir on the Silurian rocks of Arisaig, Nova Scotia, illustrated for the first time and repeated the original description of *Orthoceras pictoense* DAWSON 1880 and reassigned the taxon as *Orthoceras bullatum* var *pictoense* (DAWSON). It was to this variety that FLOWER (1943) applied the generic name *Polygrammoceras*. His paper on cephalopods from the Silurian of Arisaig includes a section on forms previously described. He wrote as follows:

"This common form of the Moydart is regarded as a variety of the Wenlock O. bullatum SOWERBY. The fine longitudinal lines are considered characteristic of Polygrammoceras FOERSTE, a genus that ranges from Lower Ordovician to Lower Devonian." (FLOWER, 1943, p. 249).

HISTON (1998) took the generic range to Lower Carboniferous. According to BOUCOT et al. (1974) the Moydart Formation is dated as Ludlow.

Thus, ornament is being regarded as diagnostic. This reference led HEWITT & WATKINS (1980), in consideration of cephalopod ecology in the Ludlow Series of the Welsh Borderland, to list the original species as ?*Polygrammoceras bullatum* (J. DE C. SOWERBY, 1839). They referred to FLOWER's attribution as tentative.

Of all the specimens of *Polygrammoceras bullatum* that I have examined, only a single example (Pl. 1, Fig.4) from the Ludlow Series of Ledbury, Herefordshire, which had already been sectioned longitudinally and polished, shows not only the characteristic external morphology but internally reveals annulosiphonate deposits developed towards the apicad end. Fortunately, this was the second specimen figured by BLAKE (1882, Pl. 12, Fig. 5) and is reasonably to be regarded as a paratype.

3. Systematic Palaeontology

Repository abbreviations: BGS = British Geological Survey, Keyworth; OUM = Oxford University Museum; SHRCM = Shropshire County Museum, Ludlow.

Order: Orthocerida KUHN, 1940
Family: Orthoceratida M'COY, 1844
Subfamily: Kionoceratina HYATT, 1900

Remarks: SWEET (1964) gave diagnosis of the subfamily as follows:

"Conchs with more or less well-developed longitudinal surficial ornament of lirae, ribs, ridges, or combinations of these, with or without subordinate transverse ornament of similar nature, or with faint transverse annulations."

The containing family Orthoceratidae was stated to be

" ... typically free of endosiphuncular deposits."

Also, the siphuncle was described as empty in the Silurian type species of the genotype *Kionoceras*

" ... and in most Ordovician species, but with annulosiphonate deposits in some questionably congeneric Silurian and later species."

Rousseau FLOWER's paper of 1962 provided discussion of the problems resulting from the lack of preservation of internal structures. He noted particularly that apicad parts of shells are frequently missing and yet retardation of siphonal and cameral deposits may have resulted in their having been confined there. Reviewing the whole Order Michelinoceratida (Orthocerida in the present paper), he considered it doubtful that any of its members were in fact completely free from cameral or siphonal deposits.

It was probably the importance of the significance of internal structures in the functional morphology of orthoconic nautiloid cephalopods that led to their being regarded in some quarters as significant in taxonomy far beyond the ornament of the shell. I am inclined to believe that a more balanced approach is necessary, in which the latter is not disregarded but is used along with the rare cases in which internal structures are seen. For the present, I follow SWEET (1964) in regarding *Polygrammoceras* as falling within the Subfamily Kionoceratinae, with some knowledge of its internal characteristics providing a useful pointer to the way ahead. Family status may eventually prove to be more appropriate.

Genus: *Polygrammoceras* FOERSTE, 1928

Type species: *Polygrammoceras twenhofeli* FOERSTE, 1928. By original designation. Ellis Bay Formation, Ordovician, Anticosti, Canada.

Emended diagnosis: FOERSTE (1928) proposed the name *Polygrammoceras* for the group of orthocones

" ... in which the surface of the shell is vertically striated, ribbed, or barred, but not fluted."

Between these ornaments are narrow grooves or shallow, relatively flat spaces. Thus a distinction was being made between this genus and *Kionoceras*, with its fluted surface and less dense longitudinal ornament. To all this SWEET (1964) added straight transverse sutures (a doubtful attribute); circular cross-section; and siphuncle between centre and venter. To these should be added: camerae relatively short; septa relatively shallow; septal necks cyrtochoanitic, leading to expanded connecting rings; annulosiphonate deposits likely to be present towards apex.

Remarks: FLOWER (1962) was concerned that the type species *Polygrammoceras twenhofeli* might not be satisfactorily representative of its group, being "somewhat anomalous" in its proportions and "therefore suspect". This is unconvincing. FOERSTE's (1928) other assigned species fit the generic diagnosis. They are given a longer range of occurrence within the Ellis Bay Formation, thus extending into the Llandovery.

Polygrammoceras bullatum (J. DE C. SOWERBY, 1839)

(Pl. 1, Figs. 1–4)

1839 *Orthoceras bullatum* SOWERBY in MURCHISON, Pl. 5, Fig. 29.
1839 *Orthoceras striatum* SOWERBY in MURCHISON, p. 612, description of plate.
1855 *Orthoceras bullatum* (SOW.); M'COY, p. 313.
1881 *Orthoceras Pictoense* DAWSON, p. 343.
1882 *Orthoceras bullatum* SOWERBY; BLAKE, p. 129, Pl. 12, Figs. 4,5.
1888 *Orthoceras bullatum* SOWERBY; FOORD, p. 40.
1924 *Orthoceras bullatum* var. *pictoense* (DAWSON); MCLEARN, p. 155; Pl. 23, Figs. 1,4,5; Pl. 24, Fig. 9; Pl. 20, Fig. 19.
1943 *Polygrammoceras bullatum* (SOWERBY); FLOWER, p. 249.
1963 *Michelinoceras [Orthoceras] bullatum* (J. DE C. SOWERBY); HOLLAND, LAWSON & WALMSLEY, p. 155.
1980 ?*Polygrammoceras bullatum* (J. DE C. SOWERBY); HEWITT & WATKINS, p. 113.
1989 *Orthoceras bullatum* J. DE C. SOWERBY; SMITH, p. 35.

Holotype: BGS Geol. Soc. Coll. 6715 (Pl. 1, Figs. 1, 3); "Upper Ludlow" i.e. Ludfordian Stage, Ludlow Series; Ludlow, Shropshire.

Paratype: OUM C94 (Pl. 1, Fig. 4), "Aymestry Limestone" i.e. Lower Bringewood Formation, Gorstian Stage, Ludlow Series, Ledbury, Herefordshire.

Other material: SHRCM G05408 (Pl. 1, Fig. 2), Lower Whitcliffe Formation, Ludfordian Stage, Ludlow Series, Mill Street Weir, Ludlow, Shropshire. The Ludlow Museum is especially rich in specimens of this species.

Diagnosis: Orthocone with rate of increase about 10 or 11 degrees, though this may decrease in the body chamber. Ornament of fine riblets with flattish spaces between, about 3 to 5 per mm, projecting also on the inside of the shell. Cameral depth about 10 to 20 percent of diameter. Sutures somewhat oblique. Septal necks cyrtochoanitic. Siphuncle somewhat eccentrically placed, its segments expanded to spindle shaped or subglobular.

Description: The holotype (Pl. 1, Figs. 1, 3) is an internal mould in slightly calcareous siltstone. It is broken, variably compressed, and partly embedded. The maximum length seen is 208 mm, of which 60 mm represents part of the body chamber. The maximum diameter seen adorally is 40 mm. The rate of increase is about 10 to 11 degrees. The body chamber is broken adorally, where a somewhat narrower portion, possibly from the same specimen, protrudes obliquely from the interior. The apicad end of the specimen is also broken and appears to be somewhat twisted. A portion of the mould occupying about a third of the total length reveals the siphuncle, the spindle shaped segments of which are 3.0 to 3.5 mm long and are expanded to the same width. The siphuncle is excentrically placed, but variably so because of the compression and some twisting. The septa are oblique. The longitudinal ornament (Pl. 1, Fig. 3) is represented by narrow striae 3 to 6 per mm, separated by flat elevations.

The paratype (Pl. 1, Fig. 4), preserved mostly as an internal mould in limestone, is sectioned longitudinally. It is broken at both ends, giving a maximum length seen of 119 mm. Its rate of increase is 11 degrees. The cross-section is circular, with an adoral diameter of 35 mm. The siphuncle of diameter 4.0 to 4.5 mm is excentrically placed at 11 mm from the nearest wall, where the diameter is 32 mm. The sutures appear to be not quite direct. The camerae are somewhat irregular in depth but on the whole vary from 2.5 mm adapicad to 5 mm adorally. There are fine longitudinal riblets where some patches of shell are still present; they are 5 to 6 per mm, separated by flat spaces. The siphuncle is filled mostly with darker material but some of the interior is finely crystalline. Dark material also occupies all of some of the first few camerae and what may be a very small remaining part of the body chamber. Otherwise the camerae are filled with

light brownish, and in a few places white, crystalline calcite, such that the presence of cameral deposits is unclear. There do, however, appear to be indications of pseudo-septa. The expanded siphuncular segments range from subspherical adapically to spindle shaped adorally. Septal necks are cyrtochoanitic. The more apicad segments bear annulosiphonate deposits, which have grown out from the septal necks as small tight bundles and show indications of layered structure. In fact, the internal structure here is remarkably similar to the *Pseudorthoceras* type illustrated by FLOWER (1939, p. 21, Fig. 3). The implication, following the Treatise (SWEET, 1964) is that this genus would fall into the Superfamily Pseudorthoceratacеae, rather than the Orthoceratacеae where the Subfamily Kionoceratinae is placed. I regard the erection of these two superfamilies as unsound. Within FLOWER's masterly treatment in his monograph on the Family Pseudorthceratidae (FLOWER, 1939) the possibility of various forms of septal neck and connecting ring, and various stages of their development in individual shells, are illustrated and described. These include a type of annulosiphonate deposit found also in *Michelinoceras* and its allies. As to the major subdivision, a similar situation once existed in trilobite taxonomy where one key character (the facial suture) was thought to allow division of the whole Class. The much better procedure of building the classification upwards and using a variety of characters was long since clearly recognised.

The most common mode of preservation of *Polygrammoceras bullatum* is as convex internal moulds (Pl. 1, Fig. 2), frequently with a brownish or ochreous coloration. These often show both sutures and fine longitudinal striae, the latter about 5 per mm. They have a characteristic shape like a blunt dagger. They are readily recognisable. I believe that the shell was unusually thin, giving rise so frequently to flattened or compressed fragments. There seems to have been particular weakness apicadly, resulting in breakage to the dagger like shape. The effect can be seen incipiently in the holotype (Pl. 1, Fig. 1). Epizoans, in particular small *Spirorbis*, are commonly found on these moulds (HOLLAND, 1971).

BLAKE (1882) discussed the ornament of *Orthoceras bullatum* as of two different kinds. He suggested that examples (internal moulds) in which there are striae must imply that there were original fine projecting ridges on the inside as well as the outside of the shell.

The common compression or flattening of the weak shells has made accurate measurements of rate of increase difficult. The figures of 10 to 11 degrees seen in the holotype, which does preserve some indication of the circular cross-section at its adoral end, and in the paratype have been confirmed in a number of other specimens.

Polygrammoceras bullatum var *pictoense* as illustrated and described by MCLEARN (1924, p. 155; Pl. 23, Figs. 1, 4, 5; Pl. 24, Fig. 9; Pl. 20, Fig. 19) has characteristics as in the British material. There is no need to retain the varietal name, particularly as Arisaig faunas are well known for their similarity to those in Britain.

Of the four species described by FOERSTE (1928) from Anticosti, the type species, *Polygrammoceras twenhofeli* is similar to *P. bullatum* but its rate of increase is less and its body chamber appears to be nearly cylindrical. Its camerae are relatively shallower and its longitudinal ornament is generally somewhat coarser. *P. ellisensis* is more coarsely ribbed but otherwise similar. *P. latolineatum* has a distinctly wider siphuncle. *P. chicottense*, too, has coarser longitudinal ornament, but in this case there are also transverse elements. These species, together with the British form, make a closely knit group, all with expanded siphuncles.

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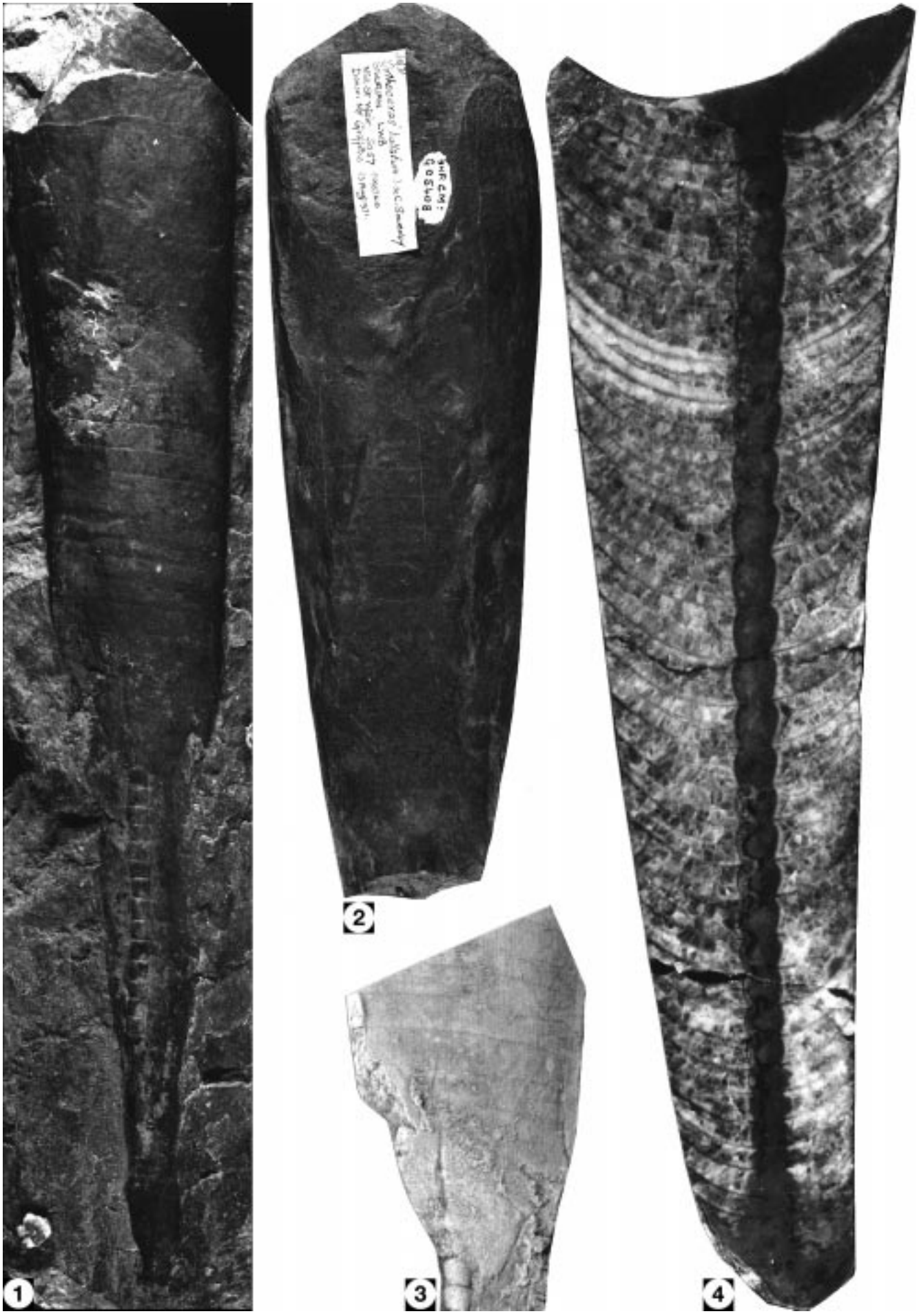
Plate 1

Polygrammoceras bullatum (J. DE C. SOWERBY, 1839).

Figs. 1,3: Holotype.
Ludfordian Stage, Ludlow Series, Ludlow, Shropshire.
BGS Geol. Soc. Coll. 6715.
Fig. 1: Internal mould.
× 1.
Fig. 3: Enlarged and heavily whitened portion to show longitudinal striations.
× 2.

Fig. 2: Typical preservation of internal mould.
SHRCM G 05408; Lower Whitcliffe Formation, Ludfordian Stage. Ludlow Series, Mill Street Weir, Ludlow, Shropshire.
× 1.

Fig. 4: Longitudinal section, ventral side to left with small banded annulosiphonate deposits in apicad half; more continuous white crystalline and dark lining probably secondary.
OUM C94 (paratype); Lower Bringewood Formation, Gorstian Stage, Ludlow Series, Ledbury, Herfordshire.
× 2.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