

Bajocian stephanoceratid ammonites and their stratigraphy from Dorset, UK, with reference to the work of András Galác

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Bajoci stephanoceratid ammonitesek és rétegtanuk Dorsetből (Egyesült Királyság) hivatkozással Galác András munkásságára

Összefoglalás

Az angliai Dorset területén felszínen lévő Inferior Oolite formációba tartozó alsó bajoci rétegekben rendszerint gyakoriak a stephanoceratid ammoniteszek, amelyek összehasonlíthatók a Dunántúli-középhegységéből származó ammoniteszegyűtésekkel. Utóbbiakat – köztük a *Lokuticeras*okat – GALÁCZ András tanulmányozta. Dorsetben a „*Lokuticeras* morfológiájú” példányok a Sauzei és a Humphriesianum zónák számos rétegében elfordulnak, és meghatározható volt az ezen ammoniteszeket tartalmazó biohorizontok faji összetétele. Dorsetben a *Lokuticeras*ok a Humphriesianum zóna Blagdeni szubzónájában és a Humphriesianum szubzóna legtetjén voltak a leggyakoribbak. A magyarországi maradványokkal való összehasonlítás érdekében három dorseti lelőhelyről ábrázoltunk példányokat. A *Lokuticeras rossbrunnense* típusfaj példányai gyakoriak a Humphriesianum és Blagdeni szubzónák határán. Az európai területekkel való párhuzamosítást segítő, a Blagdeni szubzóna legalsó biohorizontjaként bevezettük a *Lokuticeras rossbrunnense* biohorizontot. A korábbi publikált példányok kritikai értékelését is elvégeztük.

Kulcsszavak: bajoci, biosztratigráfia, Inferior Oolite, Lokuticeras, Stephanoceras

Abstract

The Inferior Oolite Formation of Dorset includes Lower Bajocian strata often rich in stephanoceratid ammonites comparable with assemblages from the rocks of the Transdanubian Central Range (W Hungary) that are the subject of research by András GALÁCZ, specifically *Lokuticeras*. In Dorset the stratigraphical occurrence of the ‘*Lokuticeras* morphology’ can be traced over a range of strata from the Sauzei and Humphriesianum zones and the assemblage composition of the biohorizons in which they occur identified. *Lokuticeras* is most abundant in Dorset in the uppermost Humphriesianum and Blagdeni subzones of the Humphriesianum Zone. Specimens from three Dorset locations are figured facilitating comparison with the Hungarian specimens. Type species *Lokuticeras rossbrunnense* is common at the Humphriesianum–Blagdeni subzonal transition. A new biohorizon is erected *Lokuticeras rossbrunnense* nov. as the lowest biohorizon of the Blagdeni Subzone facilitating correlating some areas of Europe. A critical review is made of previously published specimens and their affinities.

Keywords: Bajocian, biostratigraphy, Inferior Oolite, Lokuticeras, Stephanoceras

Introduction

Observations are presented regarding previously published data on some stephanoceratid ammonites from Hungary and England; the purpose is to present information from detailed field work in Dorset over the past thirty years that improves and clarifies the situation regarding the nomenclature, distribution in time, intraspecific variability and di-

morphism of this ammonite family in the Lower Bajocian. Ammonites from three Dorset localities are described.

The Sherborne area of England (*Fig. 1*) lies in a region of highly fossiliferous deposits of the Inferior Oolite Formation of the Aalenian to lowest Bathonian. Many abandoned quarries are present locally in a more or less east-west tract. The region is the source of numerous type species and genera, mostly ammonites described by S. S. BUCKMAN during

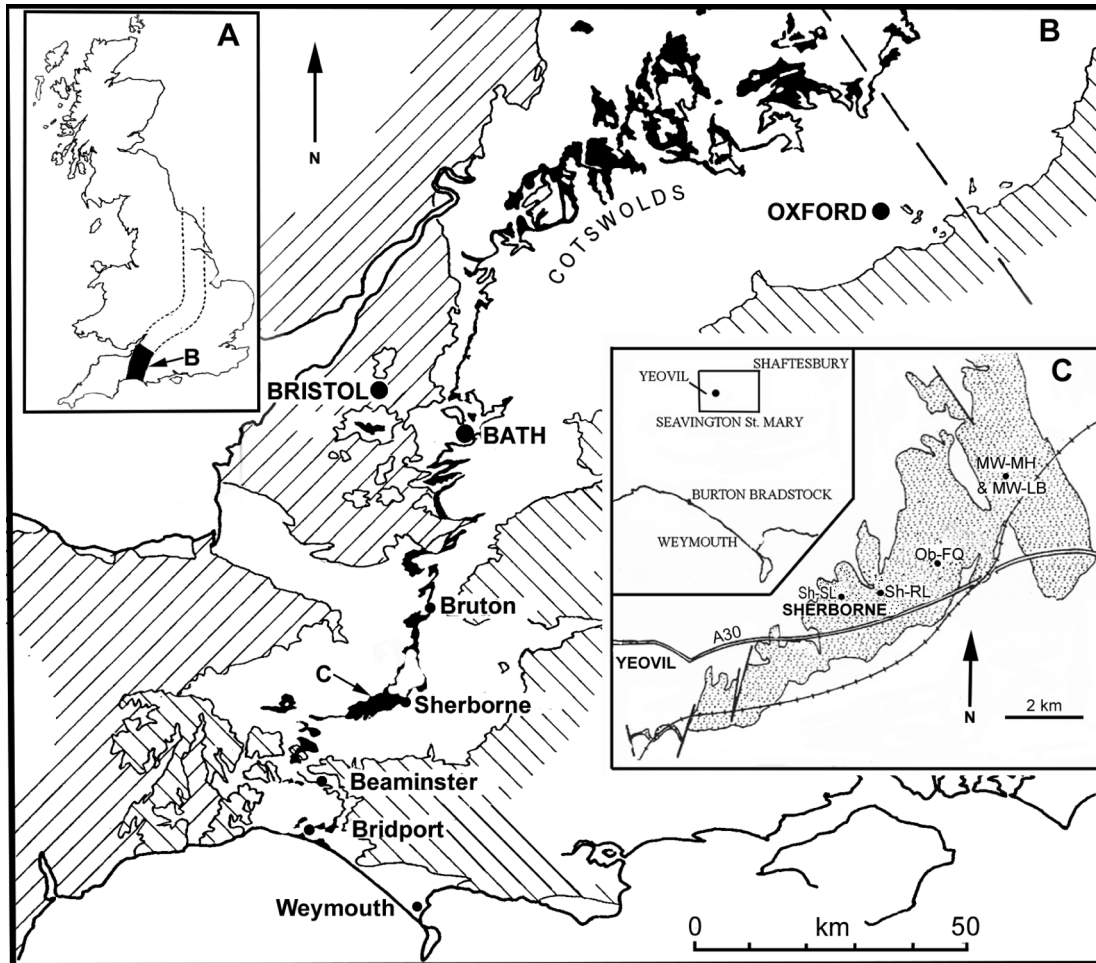


Figure 1. A. Sketch map of Britain (excluding Ireland) showing the outcrop of the Aalenian–lowest Bathonian of England. The solid black area is that shown in B. B. Outcrop of the Inferior Oolite Formation (solid) in southwest England. Diagonal shading to the west: pre-Jurassic rocks; diagonal shading to the east: post-Jurassic rocks. C. Outcrop of the Inferior Oolite Formation (dotted) in the Sherborne region. Localities are marked by a dot and code: Sh-SL Sherborne, Sandford Lane; Sh-RL Sherborne, Redhole Lane; Ob-FQ Osborne, Frogden Quarry; MW-MH Miller’s Hill SSSI and MW-LB Little Bradley, Milborne Wick

I. ábra. A: Az aalenii – alsó bathii rétegek előfordulása Nagy-Britanniában. A feketével jelzett terület a B ábrán látható. B: Az Inferior Oolite formáció kibukkanása (fekete) Délnyugat-Angliában. Az átlós árnyékolás nyugat felé a juránál fiatalabb kőzeteket jelöli. Az átlós árnyékolás kelet felé a juránál fiatalabb kőzeteket mutatja. C: Az Inferior Oolite Formáció (pontozott terület) a Sherborne régióban. A lelőhelyeket pontok és kódok jelölik: Sh-SL Sherborne, Sandford Lane; Sh-RL Sherborne, Redhole Lane; Ob-FQ Osborne, Frogden Quarry; MW-MH Miller’s Hill SSSI and MW-LB Little Bradley, Milborne Wick

his life (1860–1929). A zonal and biohorizon scheme is given here as *Fig. 2* for part of the Lower Bajocian.

The most westerly exposure included is at Sherborne, Redhole Lane, Clatcombe (ST 635 185) (Sh-RL) (*Fig. 3*) described by HUXTABLE (1999) and CHANDLER (2019) about which nearby locations were described by BUCKMAN (1893). Osborne, Frogden Quarry (ST 648 183) (Ob-FQ) (*Fig. 4*) is renowned from the researches of HUDLESTON & WOODWARD (1885); HUDLESTON (1887–1896) and BUCKMAN (1893, 1909–1930). The original quarry face is preserved as a Site of Special Scientific Interest (SSSI) (CHANDLER et al. 2013, 2014, 2017; LARWOOD & CHANDLER 2016). Milborne Wick, Miller’s Hill (MW-MH) (ST 653 205) (*Fig. 5*), also an SSSI is along a heavily overgrown lane known as Miller’s Hill Lane. Described here are specimens from Little Bradley (MW-LB) (ST 663 207) close to Miller’s Hill (HUXTABLE 2005, CHANDLER 2019). The Frogden and Milborne Wick locations are

included in the Geological Conservation Review (GCR) (COX & SUMBLER 2002).

Ammonites of the family Stephanoceratidae have been carefully recorded from the Lower Bajocian of Dorset and the Transdanubian Central Range (W Hungary). This account concerns only those from the Sauzei and Humphriesianum zones of Dorset. GALÁ CZ (1976, 1991, 1994) published on the occurrence and temporal distribution of lower Middle Jurassic ammonites, mainly stephanoceratids, and in particular the introduction of the genus *Lokuticeras* GALÁ CZ, 1994, which is the primary subject of this paper. *Lokuticeras* from the Lower Bajocian, Humphriesianum Zone, Humphriesianum Subzone to the Niortense Zone, Banksii Subzone of the Upper Bajocian were described. The occurrence of morphologically identical examples from the Lower Bajocian of Dorset is reported here over part of that range.

Stage/Substage		Zone	Subzone	biohorizon
Bajocian	Lower Bajocian	Humphriesianum	Blagdeni	<i>Teloceras coronatum</i>
				<i>Teloceras blagdeni</i>
				<i>Lokuticeras rossbrunnense</i> biohorizon nov.
			Humphriesianum	<i>Stephanoceras blagdeniforme</i>
				<i>Stephanoceras gibbosum</i>
				<i>Stephanoceras humphriesianum</i>
				<i>Pseudoteloceras labrum</i>
			Romani	<i>Chondroceras wrighti</i>
				<i>Chondroceras delphinum</i>
		Sauzei	Hebridica	<i>Nannina evoluta</i>
				<i>Stephanoceras rhytum</i>
				<i>Pseudoteloceras digbyi</i>
			Kumaterus	<i>Stephanoceras kalum</i>
				<i>Kumatostephanus kumaterus</i>

Figure 2. The stage, substage, zones and subzones of the Inferior Oolite Formation (pars). Ammonite biohorizons of the Lower Bajocian Sauzei–Humphriesianum zones of Dorset and Somerset, UK. Biohorizons are labelled by a characteristic guide fossil; the scheme is based on CALLOMON & CHANDLER (1990) amended here and introduces the rossbrunnense biohorizon nov

2. ábra. Az Inferior Oolite Formáció egy részének emelet, zóna és szubzóna szintű tagolása a Dorset és Somerset területén használatos ammonitesz-biohorizontokkal. A biohorizontokat a jellegzetes vezéralakok neve jelöli. A jelen munkában a rossbrunnense új biohorizonttal kiegészített táblázatot eredetileg CALLOMON & CHANDLER (1990) publikálta

The distribution of Aalenian – lowest Lower Bathonian ammonites in Dorset and Somerset has achieved significant progress since the introduction of the scheme of faunal horizons (biohorizons) by CALLOMON & CHANDLER (1990), with extension of the scheme to cover the Upper Bajocian and Lower Bathonian by CALLOMON & COPE (1995). The methodology of erection of the biohorizon scheme has been repeatedly described (CALLOMON & CHANDLER 1990; CALLOMON 1994, 1995; CALLOMON & COPE 1995).

The stratigraphical succession of the Inferior Oolite Formation in Dorset is that of richly fossiliferous, thin beds with omissions of strata on a very localized scale. These strata are heterogeneously condensed units, assumed, based on the close reproducibility of their assemblages at distant locations to be, in most cases, biohorizons isolated within the beds that are close to isochronous and contain contemporary assemblages of fossils (e.g., CHANDLER & CALLOMON 2009; CHANDLER et al. 2017, 2023). Excluding obviously reworked elements, these rock units represent biohorizons containing what is likely the closest to a palaeobiospecies, a segment of the evolving lineage in question.

The Hungarian succession such as at the Bakony Mountains is reported by GÉCZY (1967) and GALÁ CZ (1991, 1994) and consists of red nodular limestones in thin beds separated by gaps of unknown duration.

Specimens depicted in the figures herein are morpho-species; they are members of segments of evolving lineages labelled with suitable names rather than any attempt to re-classify them.

Abbreviations

[M], [m] Macroconch, microconch respectively. Specimen prefixed 'J' is stored at the Sedgwick Museum, Cambridge, UK; * type species, HT holotype, PT paratype; SSSI Site of Special Scientific Interest.

Locality codes and UK map references: Sherborne, Redhole Lane, Clatcombe (ST 635 185) (Sh-RL); Osborne, Frogden Quarry (ST 648 183) (Ob-FQ); Milborne Wick, Miller's Hill (MW-MH) (ST 653 205); Milborne Wick, Little Bradley (MW-LB) (ST 663 207). Map references are UK Ordnance Survey National Grid Reference System. ST refers to an area within which the locations are positioned. The six figure numerical reference locates a position to within 100 m.

Palaeontology

Suborder Ammonitina FISCHER, 1882
 Superfamily Stephanoceratoidea NEUMAYR, 1875
 Family Stephanoceratidae NEUMAYR, 1875
 Genus *Stephanoceras* WAAGEN, 1869

**Ammonites humphriesianus*
 J. de C. SOWERBY, 1825 [M]

It is not the aim here to offer any revision of the numerous generic and specific names introduced mostly by BUCKMAN (1909–1930) or to recommend how such taxa could be

SHERBORNE, REDHOLE LANE (Sh-RL)

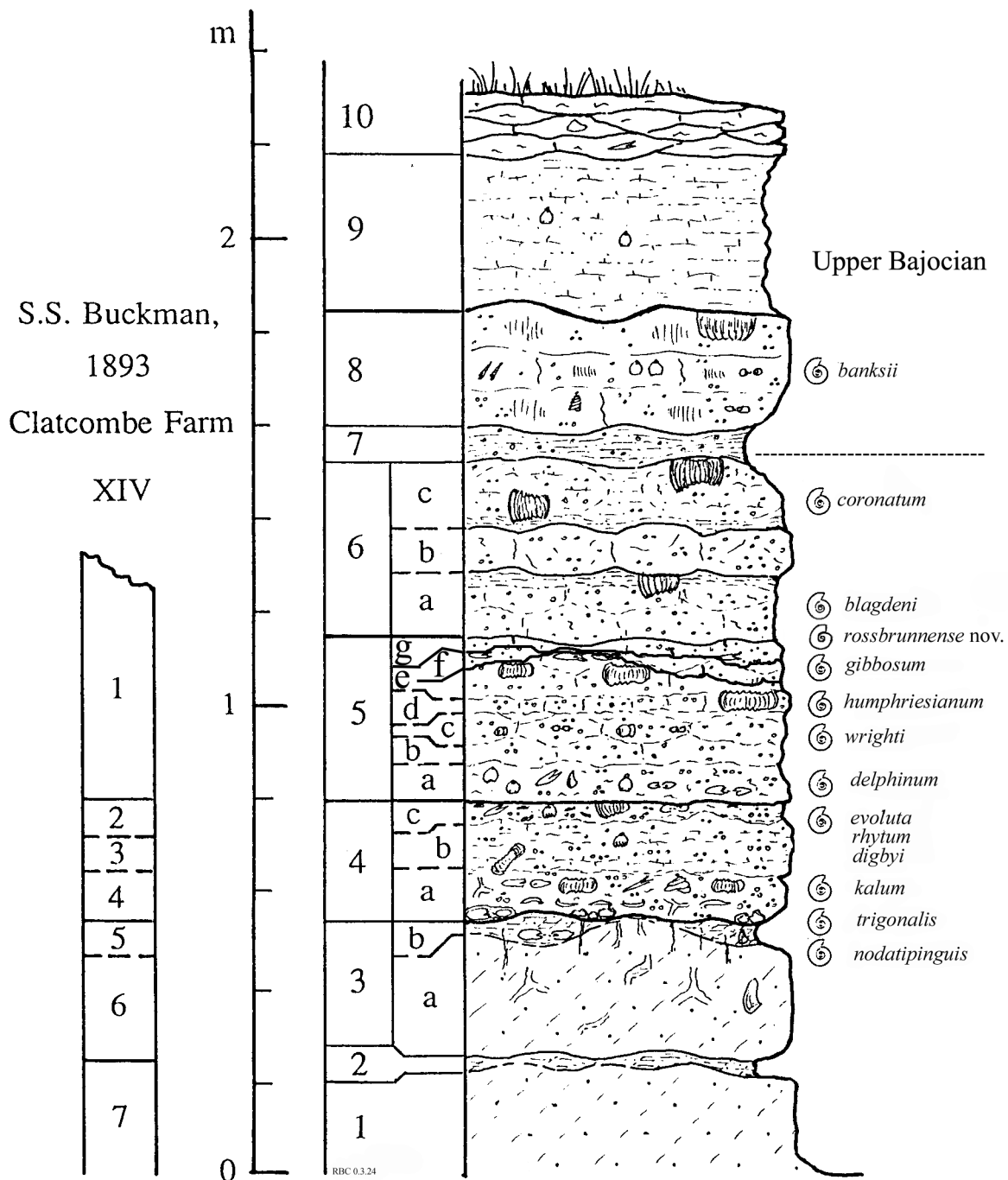


Figure 3. Diagrammatic representation through the Inferior Oolite at Lower Clatcombe, Redhole Lane. (Sh-RL). Horizons in italics and given by species name. BUCKMAN's (1893) section is shown on the left

3. ábra. Az Inferior Oolite a Lower Clatcombe, Redhole Lane (Sh-RL) szelvényben. A horizontokat a dőlttel szedett fajnevek jelölik. BUCKMAN (1893) szelvénye a bal oldalon

treated in a modern classification; however, it is now possible to state with certainty what occurs in each level representing the evolving family and what division, if any, is evident in the assemblages. Fig. 6 gives names of stephanoceratid, macroconch morphospecies found to date in the Dorset locations over part of the Sauzei to Humphriesianum zones. The difficulty in naming members of chrono-

lines that have taxa with long-established morphogeneric names included in their assemblages has recently been discussed for the Graphoceratidae (CHANDLER et al. 2023). The listing of numerous synonyms is avoided as homoeomorphy is prevalent in stephanoceratids at different stratigraphical levels and would only serve to distort the direct field evidence other than for precisely stratigraphically located specimens.

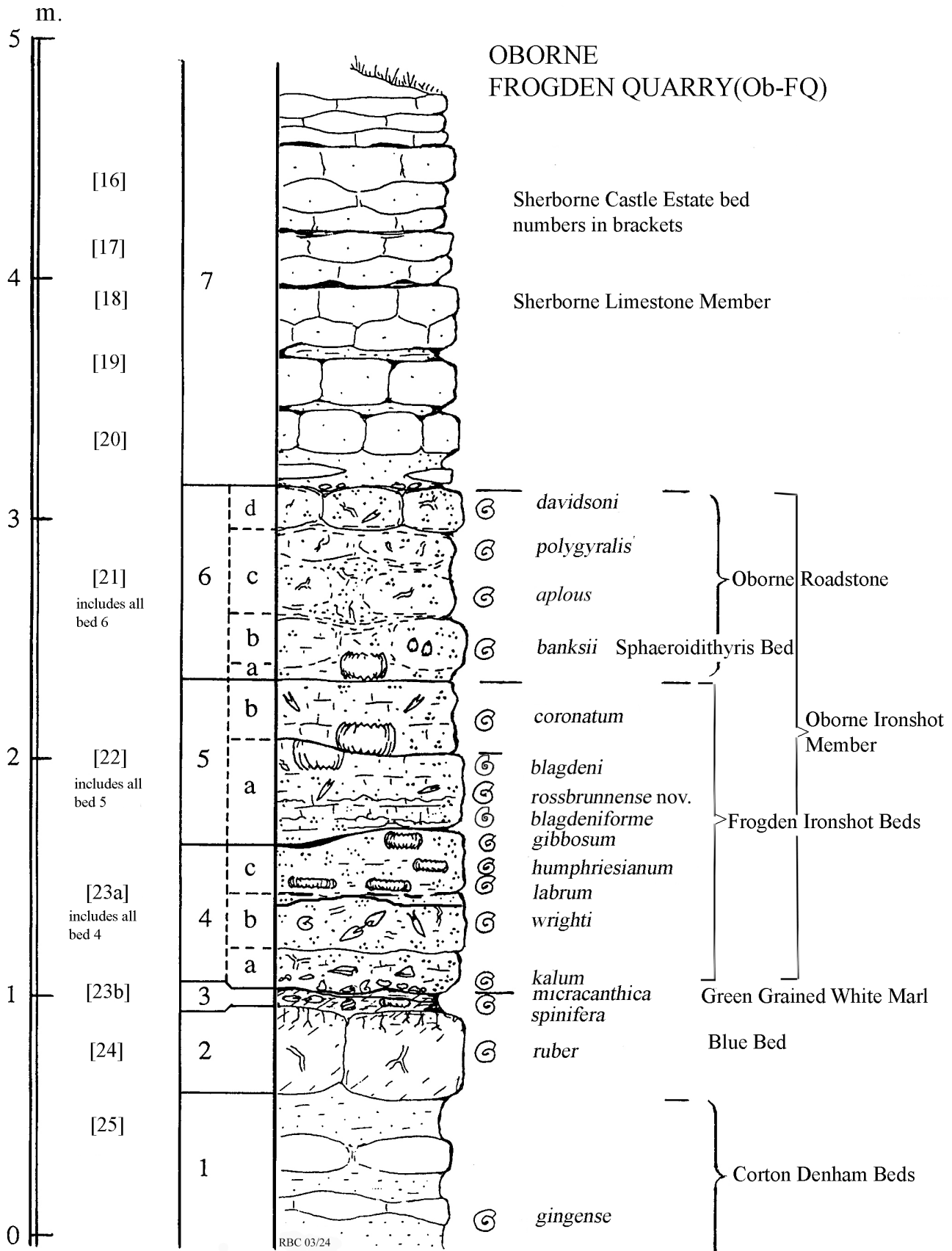


Figure 4. Diagrammatic representation through the Inferior Oolite at Frogden Quarry (Ob-FQ) after CHANDLER et al. (2014). Biohorizons in italics and given by guide species name. Sherborne Castle Estate quarry numbers on left

4. ábra. Az Inferior Oolite a Frogden Quarry (Ob-FQ) szelvényben CHANDLER et al. (2014) nyomán. A biohorizontokat a dőlttel szedett fajnevek jelölik. A Sherborne Castle Estate kőfejtő számai a bal oldalon

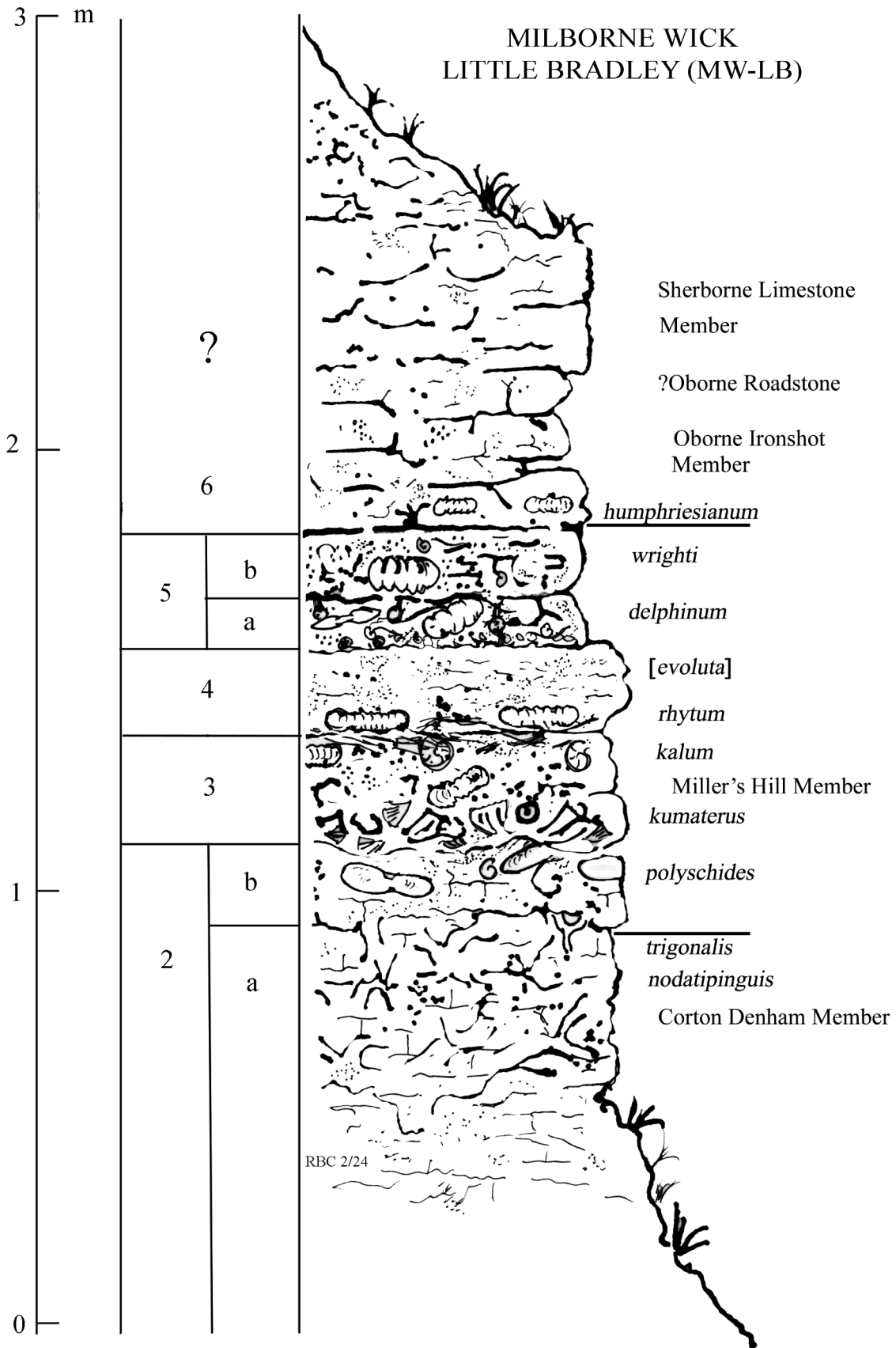


Figure 5. Diagrammatic representation through the Inferior Oolite at Little Bradley, Milborne Wick (MW-LB). The section is similar, but not identical to that at Miller's Hill (MW-MH) of COX & SUMBLER (2002). Biohorizons in italics and given by guide species name

5. ábra. Az Inferior Oolite a Little Bradley, Milborne Wick (MW-LB) szelvényben. A szelvény hasonló, de nem azonos a Miller's Hill (MW-MH) COX & SUMBLER (2002) félé szelvényvel. A biohorizontokat a dőlttel szedett fajnevek jelölik

ZONE	SUBZONE	Macroconchs
Humphriesianum	Blagdeni	<i>Lokuticeras fredericiromani</i> (ROCHÉ) (R), <i>Stephanoceras</i> (<i>Stephanoceras</i>) aff. <i>sturanii</i> PAVIA (O), <i>Teloceras blagdeni</i> (SOWERBY) (C) <i>Lokuticeras rossbrunnense</i> GALÁ CZ (O), <i>L. fredericiromani</i> (R), <i>S. sturanii</i> (O), <i>Stephanoceras leoniae</i> SCHMIDTILL & KRUMBEC (O), <i>Stephanoceras tenuicostatum</i> (HOCHSTETTER) (O), <i>T. blagdeni</i> (C)
	Humphriesianum	<i>Stephanoceras blagdeniforme</i> (ROCHÉ) (C), <i>L. rossbrunnense</i> & aff. (C), <i>L. fredericiromani</i> (R), <i>S. leoniae</i> (C), <i>Stephanoceras scalare</i> WEISERT (O), <i>Stephanoceras</i> (<i>Skirroceras</i>) <i>englandi</i> CHANDLER (O), <i>Stephanoceras zietenii</i> (QUENSTEDT) (O), <i>Stephanoceras gibbosum</i> (BUCKMAN) (C), <i>Stephanoceras humphriesianum</i> (J. DE C. SOWERBY) (C), <i>S. aff. sturanii</i> (O), <i>Stephanoceras triplex</i> WEISERT (O), <i>Kumatostephanus gibbosus</i> (BUCKMAN) (C) <i>L. aff. rossbrunnense</i> (O), <i>S. zietenii</i> (C), <i>St. (Sk.) aff. englandi</i> (O), <i>S. scalare</i> (C), <i>S. humphriesianum</i> (C), <i>S. aff. sturanii</i> (O), <i>Stephanoceras plicatissimum</i> (QUENSTEDT) (O), <i>Stephanoceras pyritosum</i> (QUENSTEDT) (C), <i>S. tenuicostatum</i> (O), <i>Stephanoceras hoffmanni</i> SCHMIDTILL & KRUMBEC (O), <i>Teloceras labrum</i> BUCKMAN (O), <i>Stephanoceras umbilicum</i> (QUENSTEDT) (C), <i>Stephanoceras mutabile</i> (QUENSTEDT) (C), <i>Stephanoceras plagium</i> BUCKMAN (O)
	Romani	<i>S. umbilicum</i> (QUENSTEDT) (O), <i>S. mutabile</i> (O), <i>S. aff. humphriesianum</i> (O), <i>S. scalare</i> (O), <i>S. aff. sturanii</i> (R), <i>S. zietenii</i> (O), <i>T. aff. labrum</i> (O) ? <i>Stephanoceras frechi</i> (RENZ), <i>S. aff. humphriesianum</i> (R) <i>S. aff. sturanii</i> (R), <i>Stephanoceras rochei</i> (MAUBEUGE) (O) <i>S. tenuicostatum</i> (R), <i>S. aff. scalare</i> (O), <i>Teloceras ellipticum</i> (MASCKE) (R)
Sauzei	Hebridica	<i>S. aff. macrum</i> (QUENSTEDT) (R), <i>S. rhytum</i> (BUCKMAN) (C) <i>Stephanoceras plicatum</i> (QUENSTEDT) (O), <i>Stephanoceras aff. pyritosum</i> (QUENSTEDT) (O), <i>S. aff. scalare</i> (R) <i>Pseudoteloceras digbyi</i> CHANDLER et al. (O)

Figure 6. The distribution of some stephanoceratid morphospecies from Redhole Lane, Frogden Quarry and Milborne Wick. Each Subzone is shown as an upper grey shaded part and a lower part without shading. The macroconch stephanoceratid morphospecies found from the three Dorset locations are shown by their occurrence in each part of the figure. The full name with author is given on first use only. Estimated abundance is indicated by (C) common, (O) occurs and (R) rare. It is to be stressed that the diagram only acts as a guide to what has been found based on comparison with published specimens. It is not a comprehensive list as much remains to be prepared and evaluated

6. ábra. Néhány stephanoceratid morphospecies a Redhole Lane, Frogden Quarry és Milborne Wick lelőhelyekről. A szubzónák felső része szürkével jelölve. A fajleíró nevét csak az első említéskor közöljük. Gyakorisági viszonyok: C: gyakori, O: előfordul, R: ritka

Genus *Lokuticeras* GALÁ CZ, 1994

Lokuticeras **rossbrunnense* GALÁ CZ, 1994

The type species is figured by GALÁ CZ (1994, pl. 1, fig. 1), a specimen from Lókút, Bakony Mountains, from the Humphriesianum Zone, Blagdeni Subzone; it is identical to specimens from the Sherborne area of Dorset from the *Stephanoceras humphriesianum* and *Stephanoceras gibbosum* biohorizons (e.g., *Pl. III, 4a–b*; *Pl. V, 3a–b*). Common examples occur in the base of the Blagdeni Subzone at Redhole Lane, where to date, the group is best represented in Dorset. Close matches for the paratypes of GALÁ CZ (1994, PT 1, pl. 1, fig. 2; PT 3, pl. 1, fig. 4; PT 2, pl. 2, fig. 1; PT 4, pl. 3, fig. 1) also occur and are depicted in *Pls. II–V*. The 4th paratype (J51767) is a Dorset specimen from Miller's Quarry Sherborne and is the most coarsely ribbed of the type series. The location of Miller's Quarry appears lost, but by matrix, it can only have come from a geographically restricted, narrow belt of strata, of the Osborne Ironshot Member, Frogden Ironshot Beds (CHANDLER et al 2014), Bed 4c belonging to the Humphriesianum Subzone, *humphriesianum* or *gibbosum* biohorizon from between Sherborne and Osborne. That specimen figured by GALÁ CZ (1994, pl. 3, fig.

1) as paratype 4 is refigured here from new photographs as *Pl. VI, 1a–b*. Similar additional specimens from Dorset are demonstrated to range as low as the Sauzei Zone and up to the Banksii Subzone. Only examples from part of that range are included here as some specimens await preparation.

Included in *Lokuticeras* GALÁ CZ, 1994 are macroconch species *Stephanoceras* (*Stephanoceras*) *sturanii* PAVIA, 1983 of the Humphriesianum/Niortense boundary and *Lokuticeras fredericiromani* (ROCHÉ, 1939) of the Blagdeni Subzone. The holotype of *St. sturanii* PAVIA is figured in PAVIA (1983 pl. 13, fig. 6; listed incorrectly in GALÁ CZ 1994 as pl. 14). PAVIA figures additional specimens from Bayeux (pl. 13, fig. 2) and another from Chaudon (pl. 13, fig. 4). The Dorset specimens figured herein (*Pl. IV, 3a–b*; *Pl. V, 2a–b*) are slightly different; therefore these have been listed as aff. or as a transitional form.

The profile of the mouth-border of many of these ammonites is similar to that depicted by J. BUCKMAN (1881, p. 64, text fig. 6). The microconch partners of *Lokuticeras* are placed in *Masckeites* BUCKMAN, 1920 and include *Masckeites *densus* BUCKMAN, 1920 of the Humphriesianum Zone and *Masckeites psilacanthoides* (SANDOVAL, 1983), Niortense Zone.

It should be clarified that the above are morphospecies that can be located to a specific range of biohorizons in Dorset at a number of locations. In all cases the observations of GALÁ CZ (1994) can be confirmed with the qualifications made below.

Discussion

This account is based on a large number of specimens collected *in situ*; however not all have yet been prepared in time for this work. Records of the stratigraphical distribution of ‘*Lokuticeras*’ morphology in Dorset appears to begin lower in the succession than in Hungary, first occurring in the Sauzei Zone or below. This may be due to earlier examples not so far being identified in Hungary, stratigraphic omission or an ecological factor. It may also be the case that if this ammonite group arrived via the ‘Hispanic Corridor’ (SADKI & MOUTERDE 1994) morphs leading to *Lokuticeras* may have inhabited western Europe slightly earlier. Examples of what GALÁ CZ considers included in *Lokuticeras* are quite widely reported across Europe (e.g., PAVIA 1983 for France, FERNÁNDEZ-LÓPEZ 1985 for Spain, CRESTA & GALÁ CZ 1990 for Hungary and Italy). A specimen figured by DIETZE (2010, pl. 4, figs. 3–4) from southern Germany has similar ribbing on the inner whorls to (pl. 3, fig. 1) of GALÁ CZ (1994) paratype 4 but has a broader whorl section and is less serpenticonic. All the macroconchs figured by GALÁ CZ (1994) lack a ventral view image therefore the interpretations here must take that into account.

In Dorset the first specimens collected to date that match the morphology of *Lokuticeras* [M & m] occur in the assemblage of the *rhytum* biohorizon of the upper part of the Sauzei Zone. They occur in the Romani Subzone and become relatively abundant in the lower Humphriesianum Subzone. They are most common (as observed by GALÁ CZ) in the uppermost Humphriesianum Subzone and persist at least to the *polygyralis* biohorizon of the Niortense Zone.

All the specimens have fine close ribbing, coronate innermost whorls, short primary ribbing and lack pronounced tubercles, some have tiny sharp spines. The most notable feature is the abundance of small macroconchs (e.g., Pl. III, Figs. 1–4; Pl. IV, Figs. 2a–b, 3a–b; Fig. 5. 2a–b, 3a–b) that show the features of adults with well-developed mouth-borders and lacking lappets. Such specimens are what CHANDLER (2019) referred to as mesoconchs. Taking only the range of morphological variability of *Lokuticeras* as described by GALÁ CZ in isolation, it is reasonable to consider, as GALÁ CZ concluded, that *Lokuticeras* forms a separate evolutionary lineage within the Stephanoceratidae; however this interpretation must be judged, based on the information presented here.

The Dorset specimens from the upper Sauzei Zone constitute a continuum, a plexus of morphology and size variability centred on *Stephanoceras rhytum*, the type of which has fine close ribbing of the inner whorls and similarity to *Lokuticeras*. *Stephanoceras* (*St.*) aff. *scalare* (Pl. IV, 3a–b) has morphology intermediate to *S.* aff. *sturani*, It is ar-

guable (as discussed by CHANDLER 2019) that the generic names *Skirroceras* or *Stephanoceras* can both be applied to the ammonites at this level as the plexus of variability ranges from stephanoceratids with depressed oval whorls sections approaching *Stephanoceras humphriesianum* to slender rather quadrate, very evolute *Skirroceras*. The line leading to *Stephanoceras* sensu stricto (**Ammonites humphriesianus* J. de C. SOWERBY, 1825 [M]), is present in the *rhytum* assemblage, as part of a continuum that can be traced back to the Aalenian from *Riccardiceras*. Furthermore, some of the more coarsely ribbed morphospecies (e.g., *Kumatostephanus*) likely originate from a different ancestor.

The size variability of complete adult macroconchs in the *rhytum* biohorizon and above is staggering, with small macroconchs of around 80 mm existing alongside shells of 350 mm, all displaying features of adulthood. A mesoconch specimen with *Lokuticeras* morphology identified as *Stephanoceras* aff. *pyritosum* (QUENSTEDT) from the Sauzei Zone is given in Pl. V, 1a–b. A further observation is that the larger examples develop coarser, more distant ribbing on the later whorls and sometimes spines or tubercles on the body-chamber. In all cases the ribbing persists to a short distance before the aperture. The mouth-border is flared with a constriction preceding the peristome.

Collections from Dorset from the Sauzei Zone to Blagdeni Subzone includes the *Lokuticeras* morphs within the intraspecific variability of the assemblage. The *Lokuticeras* morphology attains maximum abundance in the lowest Blagdeni Subzone and is the dominant stephanoceratid (excluding teloceratids). In the *blagdeniforme* and *blagdeni* biohorizons *Lokuticeras* persists as the only serpenticonic/subserpenticonic stephanoceratid alongside abundant ‘*Teloceras*-like’ forms. Further insight into the evolution of the morphogenus can be evaluated from specimens collected from three key Dorset locations

Redhole Lane is the most westerly exposure of strata of Humphriesianum Zone age relevant here. Further west, in a short distance at Sandford Lane (ST 628 178) the entire succession of the Humphriesianum Zone and almost all of the Niortense Zone is cut out beneath the Upper Bajocian. The outcrop at Redhole Lane is in an agricultural field and has been studied in temporary excavations (HUXTABLE 1999, CHANDLER 2019). Records from historical exposures nearby are by BUCKMAN (1893). Above the Sauzei Zone (Fig. 4) is a series of thin ironshot, oolitic limestones (Bed 5 & 6) representing the upper part of the Romani Subzone to the Humphriesianum Subzone; these are labelled 5a–g. Bed 6 is Blagdeni Subzone and contains common *Lokuticeras* in the lowest part. The beds are discontinuous across the area and are sometimes, locally, individually absent. New information regarding Beds 5 and 6 is now available shedding further clarity on the biostratigraphical division of this bed at Redhole Lane and Frogden Quarry. CHANDLER (2019, fig 13e) introduced the species *Stephanoceras* (*Skirroceras*) *englandi* HT, from Frogden Quarry, Bed 4c–5a transition (Fig. 4). The inner whorls of members of the type series closely resemble *Lokuticeras*; they are also close to GALÁ CZ

(1991, pl. 1, fig. 3) referred to as *Stephanoceras* sp. A number of examples of *S. englandi* have now been collected *in situ* from Redhole Lane and Frogden Quarry and their levels of occurrence can now be separated. The lower level at which the stouter ‘*Skirroceras*’ morphology of *S. englandi* is found is in the *humphriesianum* biohorizon (in the middle part of Bed 4c at Frogden) and includes large (300 mm +) *S. humphriesianum* and smaller *Lokuticeras*; this is the level of PT 4 of *L. *rossbrunnense* GALÁ CZ, 1994 with relatively common chorotypes of PT 4. The large *S. aff. englandi* are intermediate between *S. humphriesianum* and *Skirroceras* (Pl. I, 1a–b). Directly above at both Redhole Lane and Frogden Quarry is a bed of rotted limestone with specimens including some of the type series of *S. englandi*. These specimens are smaller than those below (c 150–250 mm or less) (Pl. I, 2a–b) and have rope-like narrow coiling and less pronounced close ribbing. They are accompanied by common *Lokuticeras* [M] at Redhole Lane (Pl. III, 1–4; Pl. IV, 1a–b, 2a–b; Pl. V, 3a–b) and lesser numbers at Frogden (Pl. II, 1a–b, 2a–b, 3a–b). They include diminutive examples (all c110 mm) of *L. rossbrunnense*, that themselves resemble small morphs of *S. englandi*. The same occurrence is seen at Frogden Quarry, but there *L. rossbrunnense* is less frequent and both *Kumatostephanus gibbosum* and *Teloceras* occur at the same level.

The microconch association remains more obscure. The specimen of *Masckeyites densus* [m] (Pl. I, 3a–b) is a fairly common form throughout the upper Humphriesianum and Blagdeni subzones and *Gerzenites rugosus* WESTERMANN [m] (Pl. V, Figs. 4a–b) occurs in the Humphriesianum Subzone. Finely ribbed examples such as *Germanites bicostatus* (WESTERMANN) [m] (Pl. IV, Fig. 4) occur in the Sauzei Zone.

The occurrence of ‘*Skirroceras*-like *Lokuticeras*’ in the Sauzei Zone in the plexus of forms in the *Stephanoceras rhytium* biohorizon (Pl. V, 1a–b) and in the Romani Subzone, *delphinium* biohorizon of Milborne Wick (Pl. IV, 3a–b; Pl. V, 2a–b) points to the origins of at least some *Lokuticeras* species in the Sauzei Zone from miniature members of the assemblage. Small macroconch ammonites (mesoconchs) are constituent members of stephanoceratid assemblages throughout the Bajocian and can also be identified in other families (e.g. sphaeroceratids, ootitids, perisphinctids). The smallest collected so far is Pl. II, 3a–b at 50 mm, smaller than some contemporary microconchs. They are pedomorphic members of the palaeobiospecies at the levels sampled, each being a miniature version of the normal size population. At some levels (e.g., *humphriesianum* biohorizon) there is indication of a trimodal size distribution (macroconchs, mesoconchs and microconchs). Testing this reliably, statistically, is challenging without knowing how many generations of ammonites are present in the time duration of a biohorizon. It is also likely that these ammonites could represent the extreme end of a highly variable palaeobiospecies with respect to size. FERNÁNDEZ-LÓPEZ & PAVIA (2016) have presented biological mechanisms to explain such size discrepancies. The upper levels of the occurrence of *Lokuticeras* are still in the early stage of study in Dorset;

L. rossbrunnense and spp. aff. rather than splitting-off towards the top of the Humphriesianum Zone evolve as surviving stephanoceratids with morphological changes including both an increase in size of the larger end members and evolution of others to *Cadomites* (see GALÁ CZ 1991, fig. 1). *L. rossbrunnense* occupies a stratigraphical position in Dorset where it is a common, characteristic, guide fossil in the uppermost Humphriesianum Subzone and lower Blagdeni Subzone. This range of occurrence is similar in Hungary and close matches to specimens that can be attributed to *Lokuticeras* can now be confirmed from collections made in Hungary (GALÁ CZ 1991, 1994), Hungary and Italy (CRESTA & GALÁ CZ 1990), Spain (FERNÁNDEZ-LÓPEZ 1985), Germany (DIETZE 2010), SE France (PAVIA 1983) and recently western France at La Grande Palisse, Nanteuil (Deux-Sèvres) in Bed 19b of the Blagdeni Subzone (LACROIX *pers. comm.*). Typical specimens centre on *L. rossbrunnense* which here is erected as the lowest biohorizon of the Blagdeni Subzone of the Humphriesianum Zone and included in the table of biohorizons (Fig. 2).

Conclusion

In Dorset the morphology of *Lokuticeras* can be traced back to the Sauzei Zone and possibly earlier. The morphology of the genus in Dorset constitutes part of the total stephanoceratid assemblage of biohorizons of the Humphriesianum Zone and in minor numbers in the Sauzei Zone. It becomes the dominant ammonite in the upper Humphriesianum Subzone/lowest Blagdeni Subzone for which a *L. rossbrunnense* biohorizon is erected herein. Specimens included in *Lokuticeras* have been widely reported across parts of Europe. Its persistence into higher strata gives rise to *Cadomites*. Much still needs to be clarified regarding the relationship of diminutive, but mature, small macroconchs of a number of taxa.

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Plate I – 1. tábla

- Fig. 1a–b. *Stephanoceras* (*Skirroceras*) aff. *englandi* CHANDLER [M] CT, WC6067, Bed 4c middle part, *humphriesianum* biohorizon.
- Fig. 2a–b. *St.* (*Sk.*) *englandi* [M] CT, WC6066, Bed 4d, *gibbosum* biohorizon.
- Fig. 3a–b. *Stephanoceras* (*Masckeites*) aff. *densus* (BUCKMAN) [m], WC0934, Bed 4c lower or middle part, *labrum* or *humphriesianum* biohorizon. Humphriesianum Zone, Osborne Ironshot Member, Frogden Ironshot Beds, Frogden Quarry, Osborne, Dorset.
- Scale bar Figs. 1–2 is 120 mm and Fig. 3 is 40 mm. A black star marks the last preserved suture.

- Fig. 1a–b. *Stephanoceras* (*Skirroceras*) aff. *englandi* CHANDLER [M] CT, WC6067, 4c réteg, *humphriesianum* biohorizont középső része.
- Fig. 2a–b. *St.* (*Sk.*) *englandi* [M] CT, WC6066, 4d réteg, *gibbosum* biohorizont.
- Fig. 3a–b. *Stephanoceras* (*Masckeites*) aff. *densus* (BUCKMAN) [m], WC0934, 4c réteg, alsó vagy középső része a *labrum* vagy *humphriesianum* biohorizontnak. *Humphriesianum* zóna, Osborne Ironshot Member, Frogden Ironshot Beds, Frogden Quarry, Osborne, Dorset.
- Méretarány: Figs. 1–2: 120 mm és Fig. 3: 40 mm. A csillag az utolsó megőrződött szutúrát jelzi.

Plate II – 2. tábla

- Figs. 1–4. *Stephanoceras scalare* WEISERT [M]. 1a–b. WC0311, Bed 4c middle part, Humphriesianum Subzone, *humphriesianum* biohorizon. 2a–b. WC0032 & 3a–b. WC2397, Bed 4b, Romani Subzone, *wrighti* biohorizon. WC2397 is the smallest [M] specimen found to date. Humphriesianum Zone, Osborne Ironshot Member, Frogden Ironshot Beds, Frogden Quarry, Osborne, Dorset. 4a–b. WC6072 *St.* (*L.*) *scalare*.
- Fig. 5a–b. WC6071 *Stephanoceras zietenii* (QUENSTEDT), both Bed 5a, *delphinum* biohorizon, Milborne Wick, Little Bradly, Humphriesianum Zone, Romani Subzone.
- Scale bar is 40 mm. A black star marks the last preserved suture.

- Figs. 1–4. *Stephanoceras scalare* WEISERT [M]. 1a–b. WC0311, 4c réteg, *Humphriesianum* szubzóna középső része, *humphriesianum* biohorizont. 2a–b. WC0032 és 3a–b. WC2397, 4b réteg, Romani Szubzóna, *wrighti* biohorizont. WC2397 a legkisebb valaha talált [M] példány. *Humphriesianum* zóna, Osborne Ironshot Member, Frogden Ironshot Beds, Frogden Quarry, Osborne, Dorset. 4a–b. WC6072 *St.* (*L.*) *scalare*.
- Fig. 5a–b. WC6071 *Stephanoceras zietenii* (QUENSTEDT), mindkettő az 5a rétegből, *delphinum* biohorizont, Milborne Wick, Little Bradly, *Humphriesianum* zóna, Romani szubzóna.
- Méretarány: 40 mm. A csillag az utolsó megőrződött szutúrát jelzi.

Plate III – 3. tábla

Figs. 1-3. *Stephanoceras scalare* WEISERT & aff. [M]. 1a-b. WC0320 *St. aff. scalare*, Bed 5d, 2a-b. WC2396 Bed 5d, 3a-b. WC0033 Bed 5d, *humphriesianum* biohorizon.

Fig. 4a-b. *Lokuticeras rossbrunnense* GALÁ CZ, Bed 5f, *gibbosum* biohorizon.

All Humphriesianum Zone, Humphriesianum Subzone, Sherborne, Clatcombe, Redhole Lane.

Scale bar is 40 mm. A black star marks the last preserved suture.

Figs. 1-3. *Stephanoceras scalare* WEISERT & aff. [M]. 1a-b. WC0320 *St. aff. scalare*, 5d réteg, 2a-b. WC2396 5d réteg, 3a-b. WC0033 5 réteg, *humphriesianum* biohorizont.

Fig. 4a-b. *Lokuticeras rossbrunnense* GALÁ CZ, 5f réteg, *gibbosum* biohorizont.

Minden példány Humphriesianum zóna, Humphriesianum szubzóna, Sherborne, Clatcombe, Redhole Lane.

Méretarány: 40 mm. A csillag az utolsó megőrződött szutúráját jelzi.

Plate IV – 4. tábla

Fig. 1a-b. *Lokuticeras aff. rossbrunnense* GALÁ CZ [M] WC6070 Bed 5e, *gibbosum* biohorizon.

Fig. 2a-b. *L. rossbrunnense* [M] WC0598 Bed 5d, *humphriesianum* biohorizon. Both Humphriesianum Subzone, Sherborne, Clatcombe, Redhole Lane.

Fig. 3a-b. *Stephanoceras (St.) scalare trans. sturani* PAVIA [M] WC2428 Bed 5a, *delphinum* biohorizon. Romani Subzone, Milborne Wick, Little Bradley.

Fig. 4a-b. *Germanites bicostatus* (WESTERMANN) [m] WC2223, Bed 4b, Sauzei Zone, Hebridica Subzone, *rhytum* biohorizon. Clatcombe, Redhole Lane. The specimen is attached to a specimen of *Dorsetensia*.

Scale bar is 40 mm. A black star marks the last preserved suture.

Fig. 1a-b. *Lokuticeras aff. rossbrunnense* GALÁ CZ [M] WC6070 5e réteg, *gibbosum* biohorizont.

Fig. 2a-b. *L. rossbrunnense* [M] WC0598 5d réteg, *humphriesianum* biohorizont. Mindkettő Humphriesianum szubzóna, Sherborne, Clatcombe, Redhole Lane.

Fig. 3a-b. *Stephanoceras (St.) scalare trans. sturani* PAVIA [M] WC2428 5a réteg, *delphinum* biohorizont. Romani szubzóna, Milborne Wick, Little Bradley.

Fig. 4a-b. *Germanites bicostatus* (WESTERMANN) [m] WC2223, 4b réteg, Sauzei zóna, Hebridica szubzóna, *rhytum* biohorizont. Clatcombe, Redhole Lane. A példány egy *Dorsetensia* példányával van összenőve.

Méretarány: 40 mm. A csillag az utolsó megőrződött szutúráját jelzi.

Plate V – 5. tábla

Fig. 1a-b. *Stephanoceras aff. pyritosum* (QUENSTEDT) [M] WC2670 Bed 4 Sauzei Zone, Hebridica Subzone, *rhytum* biohorizon.

Fig. 2a-b. *Stephanoceras (St.) aff. sturani* PAVIA [M] WC2427 Bed 5a, *delphinum* biohorizon. Romani Subzone 1-2 Milborne Wick, Little Bradley.

Fig. 3a-b. *Lokuticeras rossbrunnense* GALÁ CZ [M] WC2407 Bed 5g or 6a, *gibbosum* or *rossbrunnense* biohorizon, Sherborne, Clatcombe, Redhole Lane. A specimen of *Sphaeroceras* is adhering to the body-chamber.

Fig. 4a-b. *Gerzenites rugosus* WESTERMANN [m] WC0723 *humphriesianum* biohorizon, Osborne Wood adjacent to Frogden Quarry. 3-4: both Humphriesianum Zone and Subzone.

Scale bar is 40 mm.

Fig. 1a-b. *Stephanoceras aff. pyritosum* (QUENSTEDT) [M] WC2670 4. réteg, Sauzei zóna, Hebridica szubzóna, *rhytum* biohorizont.

Fig. 2a-b. *Stephanoceras (St.) aff. sturani* PAVIA [M] WC2427 5a réteg, *delphinum* biohorizont. Romani szubzóna 1-2 Milborne Wick, Little Bradley.

Fig. 3a-b. *Lokuticeras rossbrunnense* GALÁ CZ [M] WC2407 5g vagy 6a réteg, *gibbosum* vagy *rossbrunnense* biohorizont, Sherborne, Clatcombe, Redhole Lane. A példány egy *Sphaeroceras* lakókamrájával van összenőve.

Fig. 4a-b. *Gerzenites rugosus* WESTERMANN [m] WC0723 *humphriesianum* biohorizont, Osborne Wood a Frogden Quarry szomszédságában. 3-4: *Humphriesianum* zóna és szubzóna. A csillag az utolsó megőrződött szutúráját jelzi.

Méretarány 40 mm.

Plate VI – 6. tábla

Fig. 1a-b. *Lokuticeras rossbrunnense* GALÁ CZ [M] Sedgwick Museum, Cambridge J51767. 4th paratype of GALÁ CZ, 1994. Monk Collection. Miller's quarry, Sherborne. See text for details.

Scale bar is 50 mm. A black star marks the approximate position of the last preserved suture.

Fig. 1a-b. *Lokuticeras rossbrunnense* GALÁ CZ [M] Sedgwick Museum, Cambridge J51767. 4th paratype of GALÁ CZ (1994). Monk-gyűjtemény. Miller's quarry, Sherborne. Részletek a szövegben.

Méretarány: 50 mm. A csillag az utolsó megőrződött szutúra hozzávetőleges helyét jelzi.

Plate I – 1. tábla

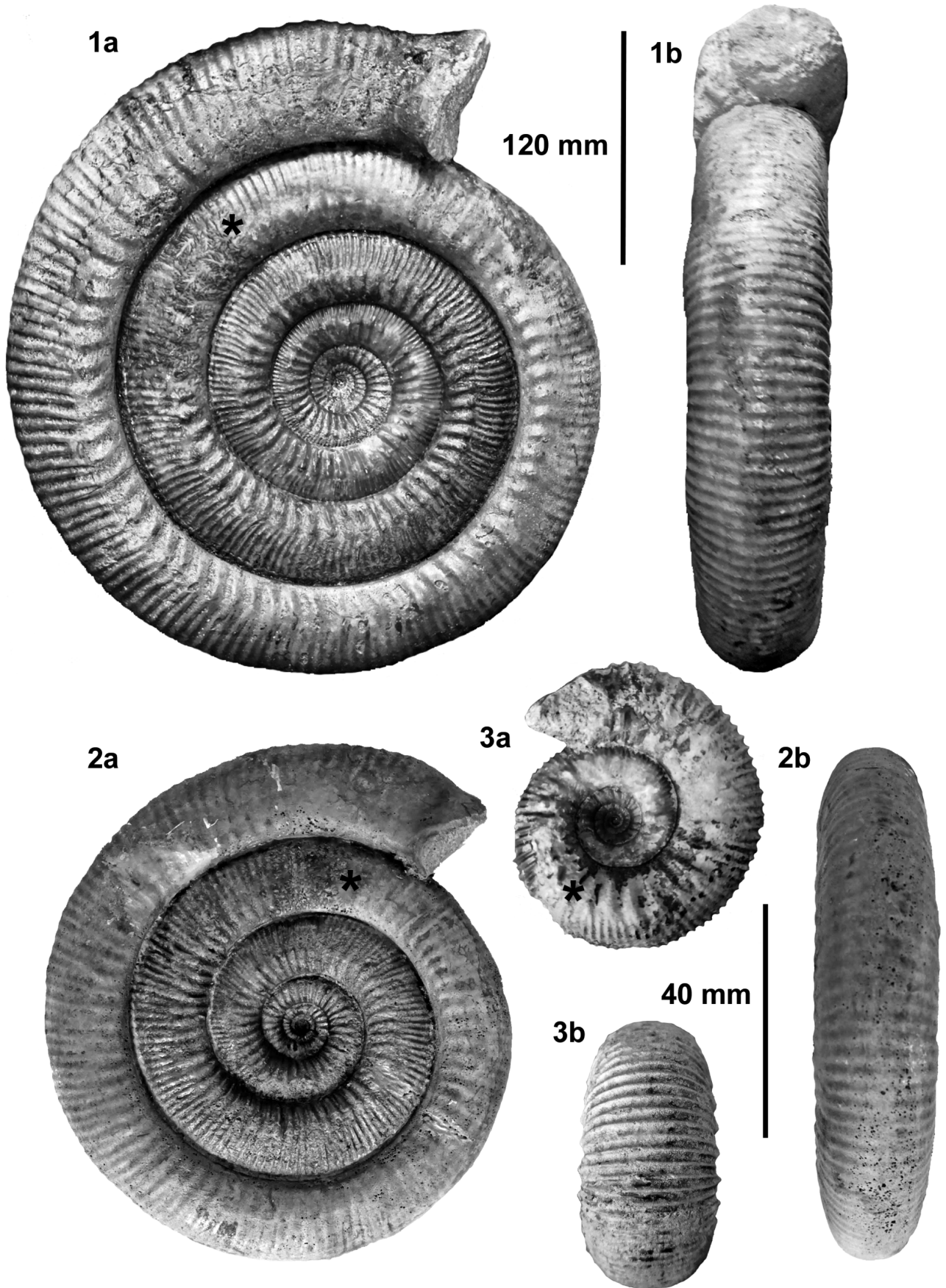


Plate II – 2. tábla

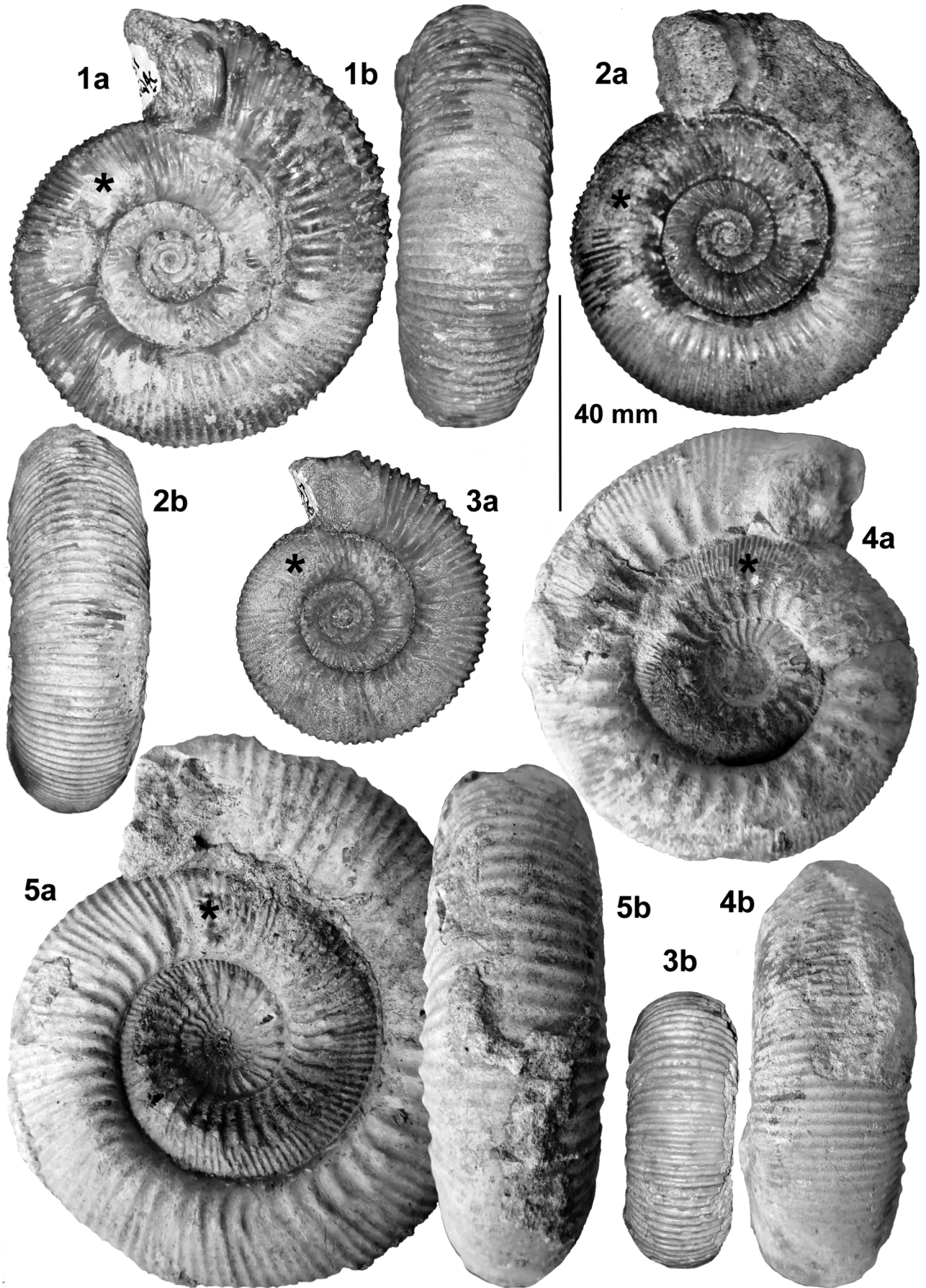


Plate III – 3. tábla

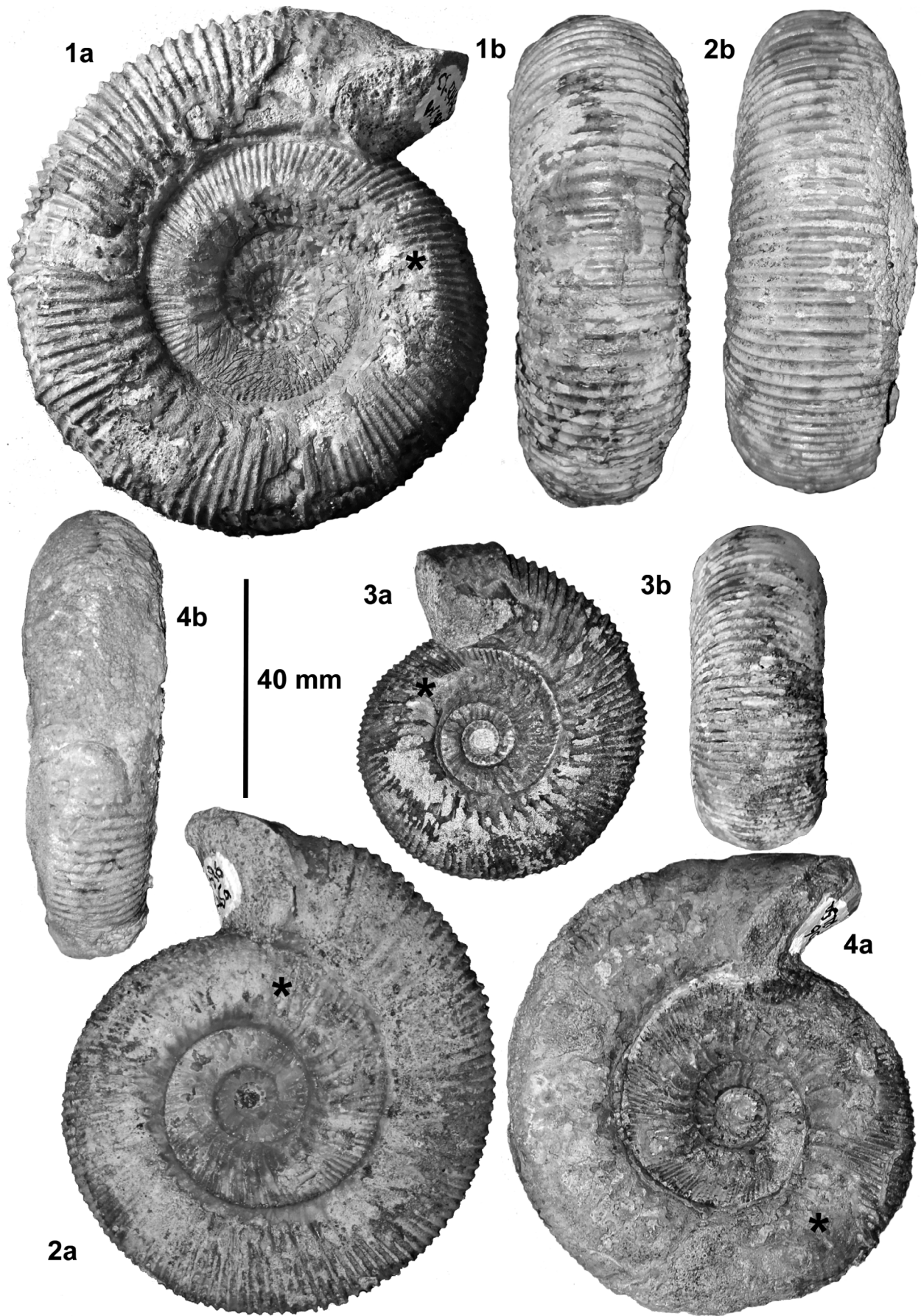


Plate IV – 4. tábla

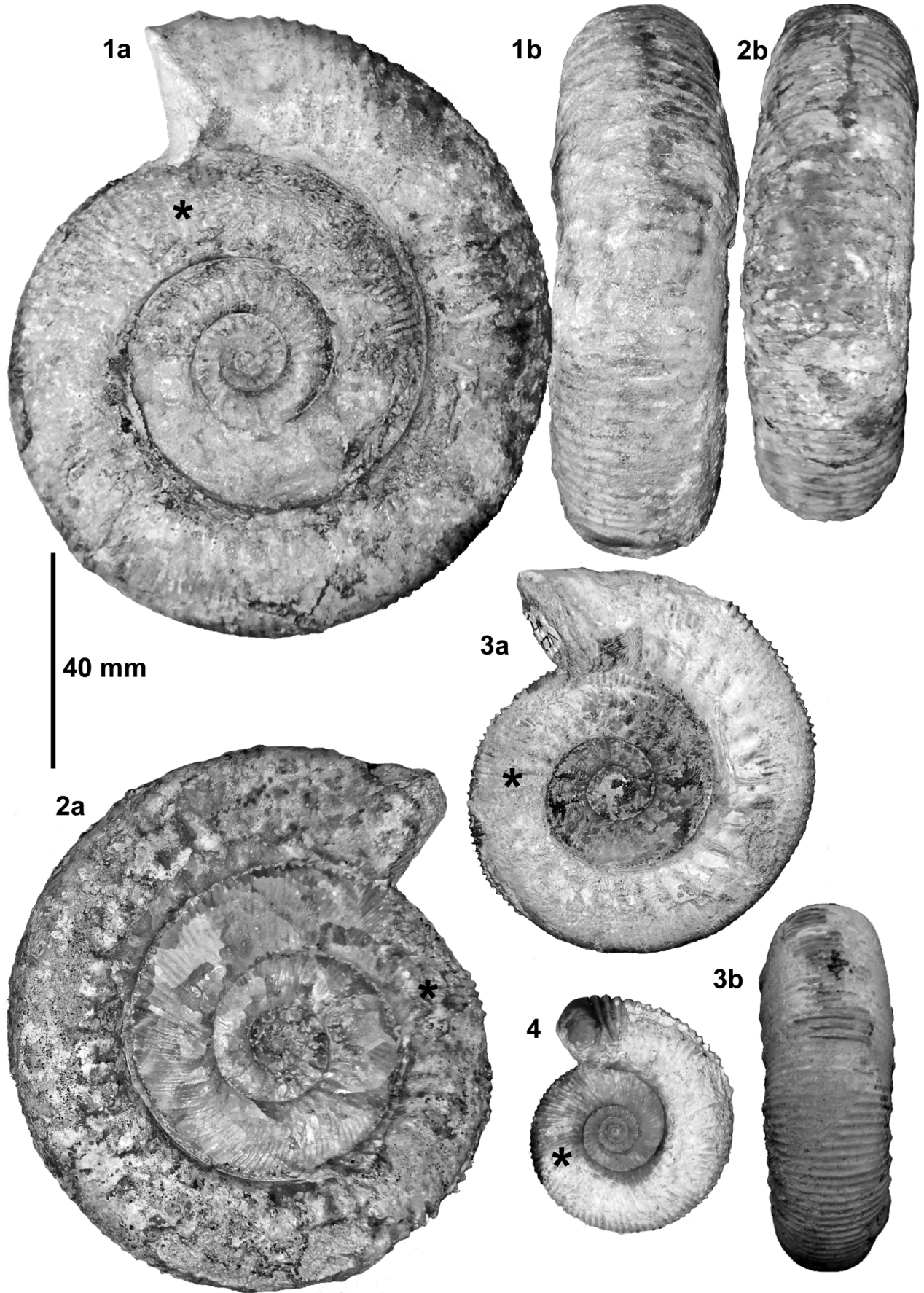


Plate V – 5. tábla

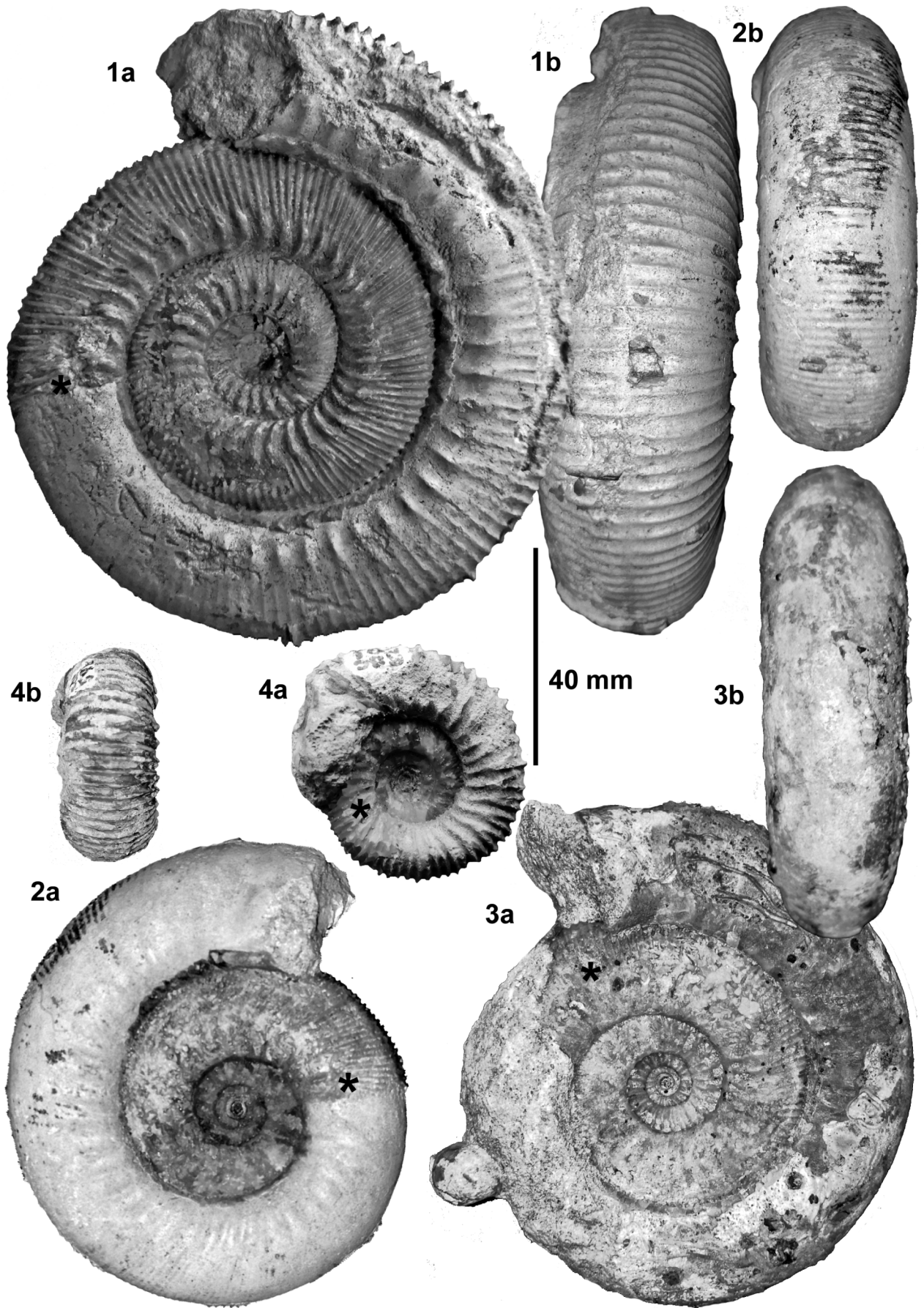
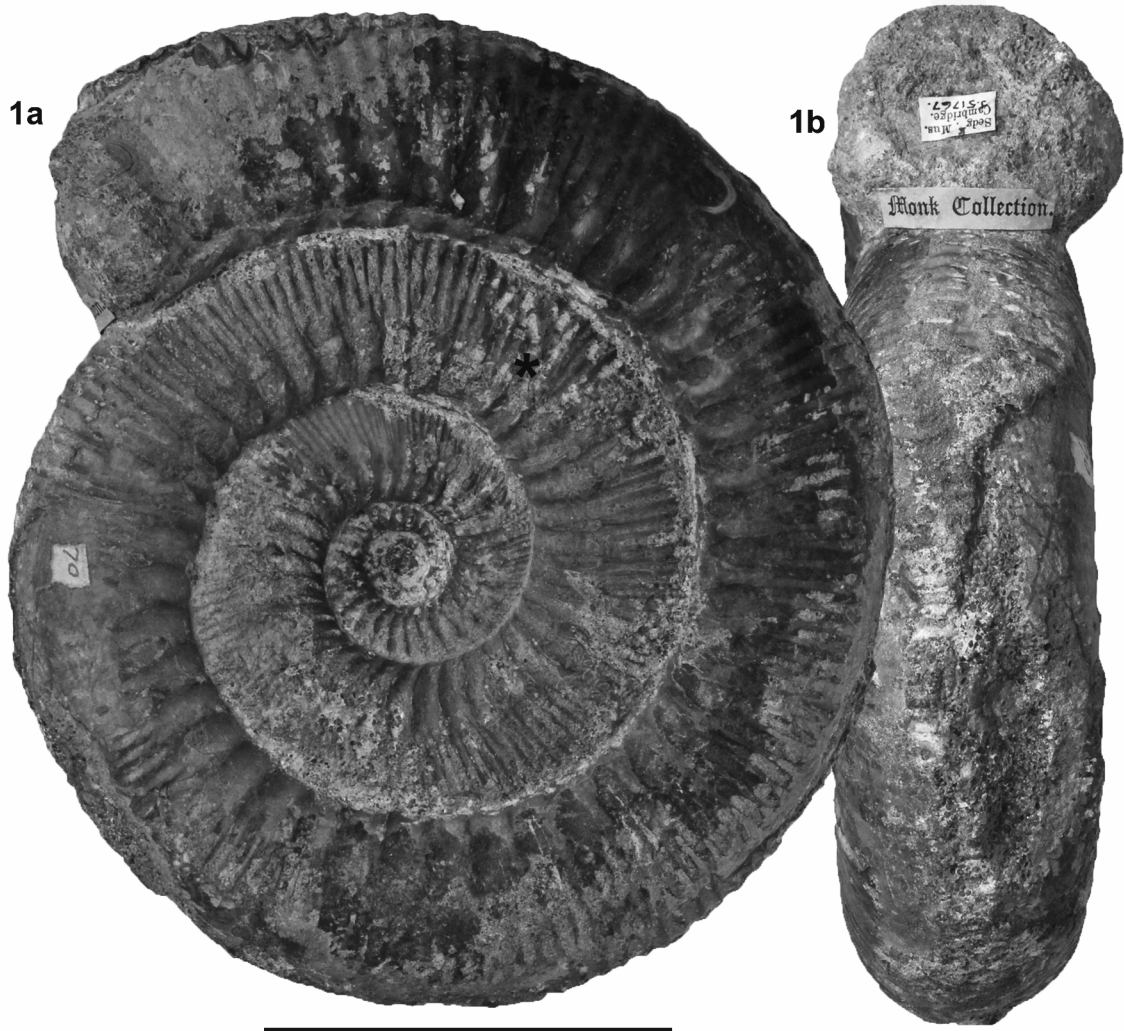


Plate VI – 6. tábla



50 mm