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RESEARCH ARTICLE

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A new giant nautilid species from the Middle Jurassic of Luxembourg and Southwest Germany

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Abstract

In comparison to other cephalopods such as ammonites and belemnites, nautilid shells are relatively rare fossils in Jurassic marine deposits and knowledge of their taxonomy is therefore still patchy. We describe herein a new species of *Cenoceras*, *C. rumelangense*, from the early Bajocian Humphriesianum Zone of Luxembourg and Southwest Germany. In Luxembourg, the type material occurs in the 'Marnes sableuses d'Audun-le-Tiche' unit, which yields other large-sized cephalopods, such as the largest known belemnite genus, *Megateuthis*. The new species reaches a remarkable size, with diameters up to 610 mm. Thus, it is amongst the largest known post-Triassic nautilids worldwide, together with *Paracenoceras giganteum* and *Paracenoceras ingens* from the Upper Jurassic. Additionally, we discuss some aspects of the taphonomy of these large shells deposited in a shallow marine setting.

Keywords Cephalopoda, Nautilida, Systematic palaeontology, Benthic islands

Introduction

Nautiloids are merely rare findings in the early Middle Jurassic rocks across Europe, but nonetheless their studies have a long tradition, dating back to the nineteenth century (e.g. Sowerby, 1815–1818; d'Orbigny, 1843; Quenstedt, 1845–1849; Morris & Lycett, 1850; Chapuis, 1858; Dumortier, 1874; Gemmellaro, 1886; Foord & Crick, 1890; Foord, 1891; Crick, 1898; Tagliarini, 1901). Subsequent authors revised and provided additional records of the early Middle Jurassic nautiloid taxa from western Europe (Alméras et al., 1998; Branger, 2004; Chirat & Rioult, 1998; Enay et al., 1994; Kummel, 1956; Rulleau, 2008; Tintant, 1993) and Saudi Arabia (Tintant 1987). The nautilids that evolved during and after the radiation of the Early Jurassic are difficult to classify due to their relative scarceness and their morphological similarity (Barroso-Barcenilla et al., 2016). Historically, they were mostly included in the basket genus *Cenoceras*, though later authors subdivided this group into several subgenera (e.g. Tintant, 1984). The fossil record of early Middle Jurassic nautilids in the north-western Tethys Realm is scarcely documented in the literature. Most species are based on poorly known type specimens first described in the nineteenth century (e.g. Crick, 1898; Foord & Crick, 1890; Morris & Lycett, 1850; Orbigny, 1843; Quenstedt, 1846–1849; Sowerby, 1816; Young & Bird, 1822; Zieten, 1830–1833) and revisions of theses pioneering works have been scarce with a few exceptions (Enay et al., 1994). Aside from the historical works documenting nautilids from the Middle Jurassic of north-western Tethys, some other occurrences have been described from this area more recently. Particularly, Branger (2004) and Rulleau (2008) reported material from France. Exceptionally large-sized nautilid shells have been reported both from the Bajocian of Southwest Germany (Dietl, 1995, 2013;

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Schweigert, 2021) and Luxembourg (Gross, 2005); these specimens, together with new unpublished findings, are revised herein and described as a new species.

Material and methods

We studied 18 specimens attributed to *Cenoceras rumelangense* n. sp., originating from the following collections:
MNHNL: Musée national d'histoire naturelle, Luxembourg.
SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany.
MEP: Musée Eugène Pesch, Lasauvage, Luxembourg.
MNM: Musée national des mines de fer, Rumelange, Luxembourg.
Geolor: Museum of the French amateur geologist association Geolor, Thionville, France.
Furthermore, for comparative reasons, we considered material described in the literature (Enay et al., 1994; Rulleau, 2008) and preserved in the following collections:
MNHN: Musée national d'histoire naturelle, Paris, France.
EPF: Espace Pierres Folles, Saint Jean-des-Vignes, France.
Our specimens have been measured according to standard methods (e.g. Rulleau, 2008). For comparison purposes, we also included material attributed to *Cenoceras* gr. *obesum* (Sowerby, 1816) and *Metacenoceras clausum* (Orbigny, 1843), with data taken from the literature (Enay et al., 1994; Rulleau, 2008).
The morphometric analysis (Figs. 1, 2) was performed on datasets referred to *C. rumelangense*, *C.* gr. *obesum* and *M. clausum*. First, we conducted an unconstrained ordination in the form of a principal component analysis (PCA) on all four descriptors in their absolute values (diameter, height, width, umbilical width) as well as on ratios of their descriptors (H/D, W/D, W/H, U/D). We chose a scaling 1 for the PCA representations because for the purpose of this study, we are more interested in interpreting the relationships amongst samples rather than amongst their morphometrical descriptors. Indeed, using this scaling, biplot distances amongst our samples are approximations of their Euclidean distances in multidimensional space (Legendre & Legendre, 2012). We concurrently evaluated the contribution of each eigenvalue to the correlations of the PCA (scree plot). Finally, we overlaid a dendrogram based on hierarchical agglomerative method using the weighted pair-group centroid method (WPGMC; Gower, 1967) on the PCA biplot to better interpret the distances between samples. We chose WPGMC because it avoids biases towards the over-represented C. *rumelangense* group (Legendre & Legendre, 2012). PCA analyses were run using the *vegan* (Oksanen et al., 2018) package in *R* (R Core Team, 2022).

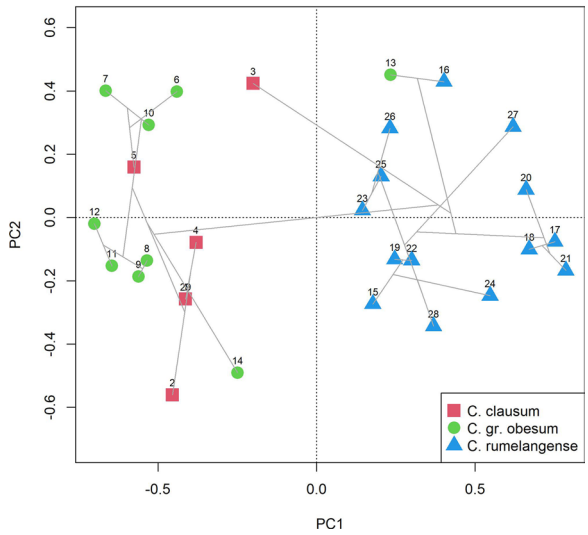

Fig. 2 PCA biplot for ratios of morphometric descriptor values (scaling 1). Clustering results are overlaid and represented by grey lines. Colour/shapes represent a priori grouping to species level

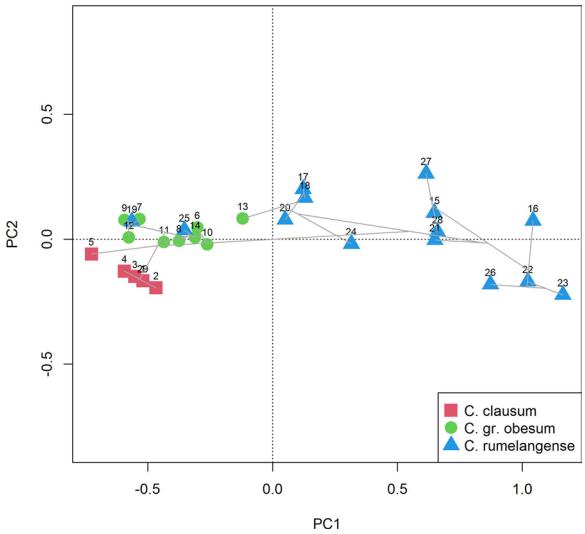

Fig. 1 PCA biplot for absolute morphometric descriptor values (scaling 1). Clustering results are overlaid and represented by grey lines. Colour/shapes represent a priori grouping to species level

Geological settings

Luxembourg

In southern Luxembourg, Middle Jurassic sediments (Aalenian to lower Bajocian) crop out along the French–Luxembourgish border (Fig. 3). The lower Bajocian series comprises five informally defined lithostratigraphic units (from bottom to top): 'Marnes micacées' (dom1), 'Calcaire d'Ottange' (dom2), 'Calcaire de Haut-Pont' (dom3), 'Calcaire d'Audun-le-Tiche' and 'Marnes sableuses

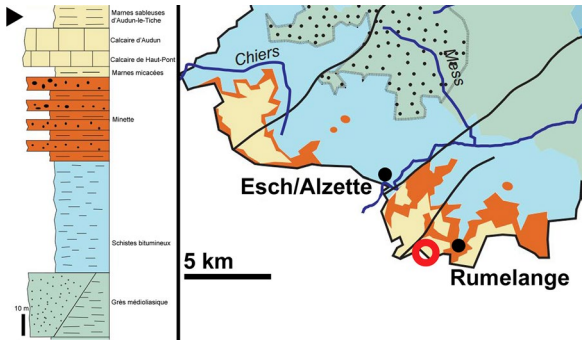

Fig. 3 Stratigraphic position (marked by a black arrow) and geographic location of the type locality (marked by a red circle) nearby Rumelange. Map of Southwest Luxembourg and stratigraphic log: Service géologique du Luxembourg (www.geology.lu)

d'Audun-le-Tiche' (dom4) (Fig. 3). The latter two crop out in a series of quarries on the plateau between the town of Rumelange and the French border, in an area called 'op der Heed' and 'op der hënneschter Heed' (Hary, 1970; Lucius, 1948). The 'Calcaire d'Audun-le-Tiche' comprises two facies, a bioclastic limestone and a coral reef facies (Lathuilière, 2005). These two facies can locally disappear, and in that case the 'Marnes sableuses d'Audun-le-Tiche' overlie directly the 'Calcaire de Haut-Pont' (Bintz, 2001). The reef facies has provided a rich invertebrate fauna including corals, brachiopods, bivalves, gastropods, and echinoderms (see Fayard et al., 2005 for an overview). This unit is separated from the overlying 'Marnes sableuses d'Audun-le-Tiche' by a hardground (Bintz et al., 1973). The latter unit is composed of an alternation of silt-rich carbonate beds and silt-rich marls. The unit denotes a change in environmental conditions, with a transgression and deeper marine conditions as compared to the shallow environment of the coral reefs (Lathuilière, 2005; Thiry-Bastien, 2002). Cephalopods are amongst the most common fossils, including ammonites (Gross & Weis, 2005; Hary, 1970; Sadki & Weis, 2023), belemnites (Weis, 2006; Weis & Gross, 2005; Weis & Mariotti, 2008) and nautilids (Gross, 2005), which are the subject of the present paper. This unit has been assigned to the Humphriesianum Zone due to findings of age-diagnostic stephanoceratid ammonites (Lucius, 1948; Stamm, 1976).

Baden-Württemberg, Germany

In Baden-Württemberg, Middle Jurassic deposits occur at the foothill of the Swabian Alb Mountains and in its foreland. The Bajocian of Swabia is made up of sandy limestones, clays with intercalated limestone beds and ferruginous oolites. The debris of the younger Upper Jurassic limestones mostly covers these deposits. Since the Bajocian rocks do not have any economic value, active clay pits or quarries do not exist and even in the past, only locally some parts of the section were temporarily quarried for building or pavement stones. The Bajocian of Swabia is subdivided into several formations (Bloos et al., 2006), the Wedelsandstein Formation at the base (formerly 'Braunjura Gamma'), followed by the Ostreenkalk and the Hamitenton formations (formerly 'Braunjura Delta'). In the southwestern part of the Swabian Alb, iron oolites become predominant and form the Gosheim Formation (Dietze et al., 2015). Towards the east and in adjacent Franconia, the Bajocian is represented by the highly condensed, partly iron-oolitic Sengenthal Formation (Dietze et al., 2017). The rich fossil content was described in classical monographs by Quenstedt (1856–1857) and Oppel (1857). Subsequently, Engel (1908) provided faunal lists of each formation ('Braunjura Gamma' and 'Braunjura Delta' correspond to the Bajocian). Ammonites, besides belemnites, bivalves, brachiopods, serpulids, and gastropods dominate the rich invertebrate fauna. In the middle Swabian Alb, an almost continuous section was exposed at Gruibingen during the construction of the motorway A8. At that occasion, the fossil content of the entire Middle Jurassic section was documented, however, with a clear focus on ammonite biostratigraphy (e.g. Dietl, 1988, 2006, 2007, 2013).

In contrast to Luxembourg, the Bajocian rocks of Swabia were deposited in a deeper marine shelf setting; scleractinian corals are restricted to a few locally developed thin horizons where they formed coral meadows (Bosch et al., 2013). The Ostreenkalk Formation is characterized by an alternation of clays, marly limestones and intervals of iron-oolitic marls and limestones containing abundant oysters (*Actinostreon*, *Liostrea*) and other thick-shelled bivalves (*Ctenostreon*) as well as giant belemnite rostra (*Megateuthis*). Stephanoceratids and other age-diagnostic ammonites date this formation into the Humphriesianum Zone. Nautilids, mostly represented by species of *Cenoceras* and *Metacenoceras*, are generally rare in the Bajocian of Swabia, but this may be due to the small outcrops and the focus on the collection of ammonites as the most attractive and iconic fossils within these beds. In the Ostreenkalk Formation of the Gruibingen section, the herein reported giant specimen was the only nautilid record.

Systematic palaeontology

Class Cephalopoda Cuvier, 1795
Subclass Nautilia nom. correct. Wade, 1988
Order Nautilida Agassiz, 1847

Family Cenoceratidae Tintant & Kabamba, 1983 (ex Nautilidae de Blainville, 1825).

Genus *Cenoceras* Hyatt, 1883

Type species. *Nautilus orbignyi* Prinz, 1906 (=*Nautilus intermedius* J. Sowerby, 1816 in Orbigny 1843, pl. 27), by original designation.

Remarks. There is great confusion about the nature, type horizon and stratigraphical range of *Nautilus intermedius* J. Sowerby, 1816, which has been controversially interpreted by numerous authors (for a recent overview see Țibuleac et al., 2020). Tintant (1984), who tried to trace the illustrated specimen in the Orbigny collection, reviewed the Early Jurassic representatives of the genus *Cenoceras*. He assigned a specimen of this collection originally labelled as *Nautilus striatus* to Sowerby's species *Nautilus intermedius*; however, this specimen has a much wider umbilicus than the specimen illustrated on Orbigny's plate 27, to which Hyatt (1883) explicitly referred when erecting his new genus *Cenoceras*. Tintant (in Enay et al., 1994) suspected that specimens were mixed up and that the illustration of plate 27 shows a chimaera by artificial combination of characters from various specimens of species of different ages and localities. Finally, he agreed that *Nautilus intermedius* sensu Orbigny was conspecific with *Nautilus intermedius* J. Sowerby, 1816. However, interpreting the specimen illustrated on Orbigny's plate 27 as a non-existent taxon would make Hyatt's genus *Cenoceras* invalid, since Tintant did not formally designate a type for *Nautilus orbignyi* amongst Orbigny's *Nautilus intermedius* specimens. Treating *N. orbignyi* Prinz as a "*nomen nudum*" as suggested by Tintant (1984) is impossible, because its holotype is by definition the illustrated specimen of Orbigny's plate 27.

Of course, it is well-known that the illustrations of Orbigny's plates are highly idealized and standardized (the apertures always pointing to the left), but he provided measurements of a concrete specimen, most likely of the illustrated one. Amongst the 15 surviving specimens in the Orbigny collection labelled as *Nautilus intermedius*, the closest morphological resemblance is with a specimen (MNHN-F-A02204) from the Toarcian of Avallon (Fig. 4) (Tintant in Enay et al., 1994). Tintant determined this specimen as *Cenoceras astacoides* (Young & Bird, 1822), a species originally described from the Toarcian of Yorkshire, United Kingdom (Howarth, 1962). MNHN-F-A02204 is the sole specimen of the surviving *Nautilus intermedius* material in Orbigny's collection that originates from the vicinity of a locality cited by d'Orbigny (Tintant in Enay et al., 1994). Hence, we conclude that MNHN-F-A02204 was indeed the specimen on which Orbigny's plate 27 is based and which was subsequently assigned to a new species by Prinz, (1906), *Nautilus orbignyi*. *Nautilus orbignyi* Prinz, 1906 is here considered a subjective junior synonym of *Nautilus astacoides* Young & Bird, 1822 and, more importantly, the widely used genus *Cenoceras* can still be used in the strict sense of Tintant. We concur with Tintant (1984) that *Nautilus intermedius* Sowerby, 1816 is a species from the Sinemurian. The illustration of the holotype, however, is a very schematic drawing. Obviously this holotype is untraceable, because Foord (1891, p. 192) referred to several specimens stored in the collection of the British Museum but explicitly not to Sowerby's illustrated specimen. Even the type locality of Sowerby's *Nautilus intermedius*, Keynsham in Somersetshire, was only cited with a question mark as a doubtful occurrence of this species. Tintant (in Enay et al., 1994) illustrated two nautilids of Orbigny's collection (MNHN-F-R09436 and MNHN-F-B48672) that he identified as *Cenoceras intermedium* (Sowerby, 1816), however, these specimens were originally labelled as *Nautilus striatus* Sowerby and did not belong to the series of *N. intermedius* in Orbigny's collection. Thus, replacing the type species of *Cenoceras* Hyatt, 1883 by *Nautilus intermedius* Sowerby, 1816 without legitimation by the International Commission of Zoological Nomenclature was a clear violation of the principles of zoological nomenclature (ICZN, 1999) and cannot be accepted.

Fig. 4 *'Nautilus intermedius* Sowerby', from the d'Orbigny collection (specimen MNHN-F-A02204); Toarcian of Avallon (photo: courtesy of Muséum national d'histoire naturelle, Paris)

***Cenoceras rumelangense* n. sp.** [Weis & Schweigert]
Figures 5, 6, 7, 8,9
1995 *Cenoceras* sp.: Dietl, p. 357, fig. 1.
2005 *Cenoceras* sp.: Gross, p. 58.
? 2008 *Cenoceras* gr. *obesum*: Rulleau, pl. 22, fig. 2 [only specimen EPF Baj74].
2013 *Cenoceras* sp.: Dietl, p. 20, fig. 24.
? 2016 *Metacenoceras* sp.: Grulke, p. 139, figs. 1&2.
2021 *Cenoceras obesum*: Schweigert, p. 9, fig. 14.
Derivation of name: The species is named after the town of Rumelange, a municipality in the southernmost part of Luxembourg that is widely known for its rich fossil findings from Toarcian to Bajocian rocks, including the herein described nautilids.
Holotype: Holotype is specimen MNHNL BM790 (Fig. 5).
Paratypes: 17 specimens from the Humphriesianum Zone of Rumelange (MNHNL: BM232, BM237, BM278, BM280, BM370, BM372, BM383, BM641, BM783, BM784, BM791, BM792, BM793; MEP1; MNM1; Geolor 1 & 2) and one specimen from the Middle Jurassic Ostreenkalk Formation (Humphriesianum Zone) of Gruibingen, Baden-Württemberg (SMNS 62245).

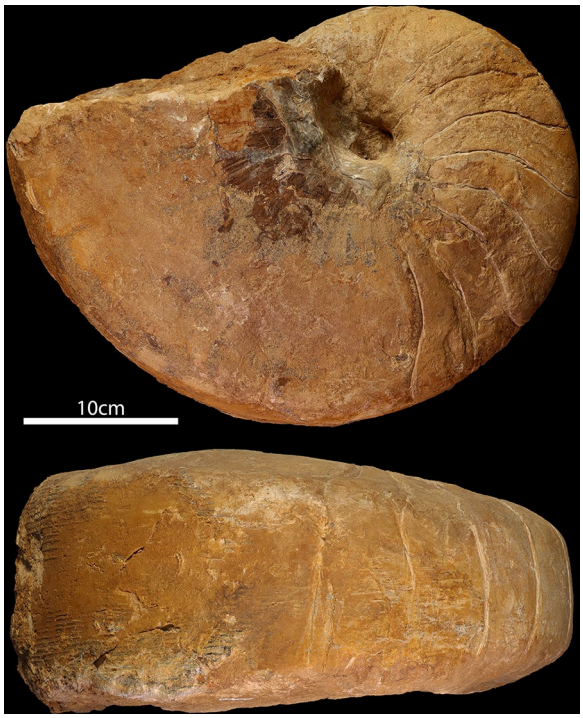

Fig. 6 *Cenoceras rumelangense* n.sp., paratype (specimen MNHNL BM383), 'Marnes sableuses d'Audun-le-Tiche', Humphriesianum Zone, Rumelange, Luxembourg

Fig. 5 *Cenoceras rumelangense* n.sp., holoytpe (specimen MNHNL BM790), 'Marnes sableuses d'Audun-le-Tiche', Humphriesianum Zone, Berenskaul, Rumelange, Luxembourg

Type locality: Rumelange, abandoned quarry site 'Berenskaul-Waisskaul' on the Luxembourgish–French border (Coordinates 49°27′12″N and 6°00′41″E; Bintz et al., 1973, p. 159) (Fig. 3).
Type horizon: 'Marnes sableuses d'Audun-le-Tiche' (dom4), lower Bajocian, Humphriesianum Zone.
Diagnosis: Giant-sized, narrow-umbilicate species of *Cenoceras* with strongly inflated subtrapezoidal whorl section, generally higher than wide; longitudinal striation on the flattened venter and on the outer third of the flank.
Description: The holotype (Fig. 5) is a steinkern with a few preserved remnants of the shell. The body-chamber occupies half of the last whorl. The last septa are more closely spaced, indicating that the specimen reached the adult age. The venter is distinctly flat and is ornamented with dense longitudinal striae that are particularly well developed on the body-chamber and which extend on the outer third of the flanks. The section of the body-chamber is markedly subtrapezoidal, compressed (compression index is 0.81 on the body-chamber and 0.77 on the phragmocone); the compression is more marked in younger whorls and less strong on the body-chamber but does not affect the lateral dimensions. The flanks are slightly rounded on the inner third (located towards the umbilicus) and distinctly flattened to slightly concave

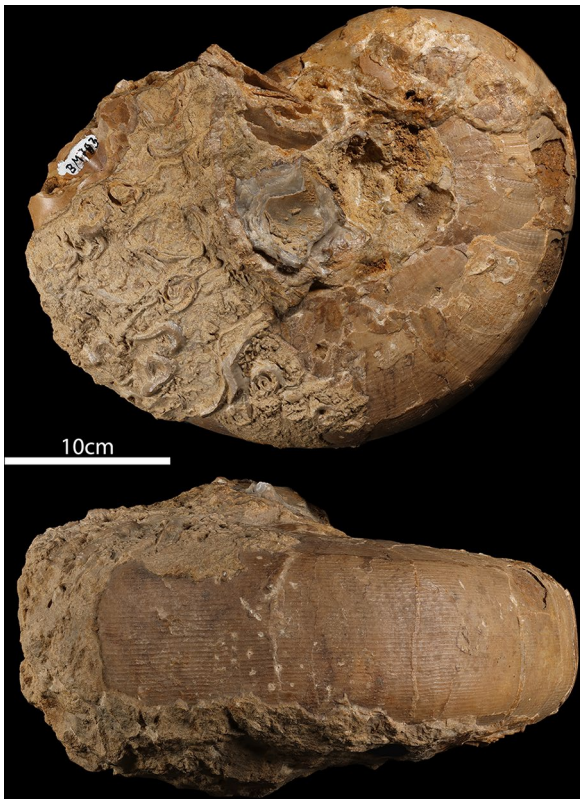

Fig. 7 *Cenoceras rumelangense* n.sp., paratype, inner whorl of a bigger specimen (specimen MNHNL BM783), 'Marnes sableuses d'Audun-le-Tiche', Humphriesianum Zone, Berenskaul, Rumelange, Luxembourg

Fig. 8 *Cenoceras rumelangense* n.sp., paratype, largest measured specimen (specimen MNHNL BM791), 'Marnes sableuses d'Audun-le-Tiche', Humphriesianum Zone, Berenskaul, Rumelange, Luxembourg

on the outer two thirds. The flanks are covered with fine falciform striae, and the outer third shows a reticulate ornamentation pattern. The phragmocone shows rather distant septa: the number of septa on the last whorl is $n = 10$. The lateral lobe is distinctly large and shallow (depth of the lateral lobe = 10 mm), and is followed by an even less profound ventral lobe. The latero-ventral saddle is rather distinctive. Traces of the siphuncle are not visible in this specimen.

Umbilicus: Throughout all ontogenetic stages the overhanging umbilicus remains open, with a well-rounded umbilical edge.

Flanks: Lower part gradually rising from the steep and overhanging umbilicus forming a well-rounded umbilical edge. Middle part of flanks form a trapezoidal section; upper part become slightly concave in the latest part of the adult body-chamber.

Venter: Venter is rounded only in the juvenile stage and soon becomes flattened by developing a prominent ventrolateral edge.

Suture line: On the flank, the suture line forms a single, relatively shallow lateral lobe, with its deepest part located in the outer third of the flank. From the saddle at the ventrolateral edge, it turns towards mid-venter in a right angle without forming an extra ventral lobe.

Ontogeny: Growth pattern lacks principal changes of coiling or other modifications during ontogeny, except the inflated whorl section gradually changing from being rounded in the juvenile stage to subtrapezoidal in the medium and adult stages. In the latest stage, the chambers and suture lines are narrowing thus indicating adult size.

Ornamentation: The almost uncompressed specimen from Swabia (Fig. 9) is the only one with a completely preserved calcitic replacement shell. The adult shell is ornamented with dense longitudinal striae both on the venter and on the outer third of the flank. The aperture does not exhibit any apertural modifications and crosses the venter in a straight way. Due to the shell preservation, the beginning of the body-chamber and the suture lines of the phragmocone cannot be traced.

Measurements and morphometrics: Various measurements and parameters of *C. rumelangense* specimens are reported in Table 1. We compared the data with measurements and parameters published for two coeval

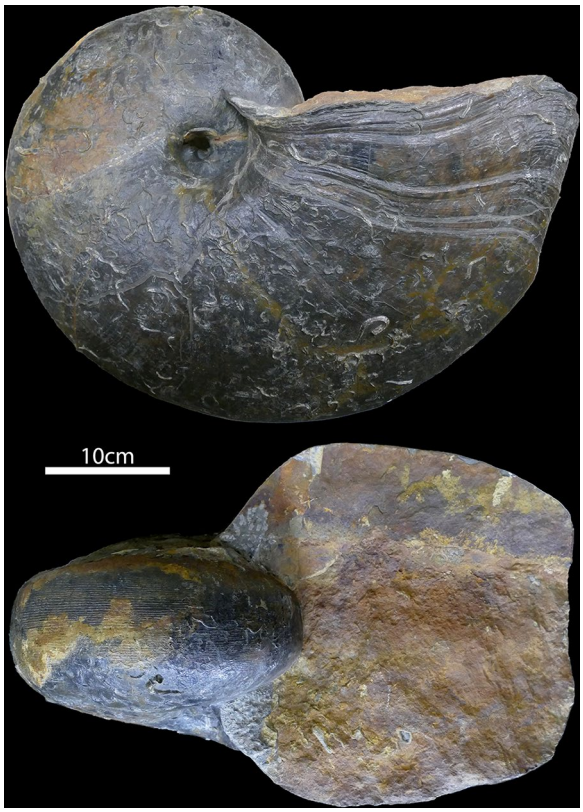

Fig. 9 *Cenoceras rumelangense* n.sp., paratype (specimen SMNS 62245), Ostreenkalk Formation, Humphriesianum Zone, Gruibingen, Southwest Germany

large-sized nautilid taxa: *Cenoceras obesum* (sensu Rulleau, 2008) and *Metacenoceras clausum*.

PCA biplot for absolute morphometric descriptor values (scaling 1)

Although the three groups seem separated in the biplot (Fig. 1), the eigenvalues showed that the first axis was explaining much more than the following axes for the absolute values PCA. This means that the *clausum* and *obesum* groups are closer to each other than they are to the *rumelangense* group. This is also supported by the clustering analysis (Fig. 1). Assuming that there are indeed three groups, the clustering analysis puts specimen EPF Baj74 (in Rulleau, 2008, p. 52) with the *rumelangense* group, not with the *obesum* group in which it was originally classified (Fig. 1). Also, the specimens attributed to the *rumelangense* group, MNHNL BM370 (sample 19) and MNHNL BM783 (sample 25), were clustered together with the *obesum* group.

PCA biplot for ratios of morphometric descriptor values (scaling 1)

Three groups are separated in the biplot (Fig. 2), the eigenvalues showed that the three first axes are relevant (see inset Fig. 1) for the ratio values PCA. Clustering results overlay well with PCA results and original grouping, aside from specimen EPF Baj74 (sample 13), which is associated with the *rumelangense* group again (Fig. 2).

For the PCA on absolute values, the proportion explained by the principal components 1 and 2 were 94% and 4%, respectively. For the PCA on absolute values, the proportion explained by the principal components 1 and 2 were 65% and 21%, respectively.

Remarks. In first view, the herein described *Cenoceras* seems to fit well with the description and illustration of *Nautilus obesus* Sowerby, 1816 (p. 124). However, the provided illustration is very schematic and, more important, the original of the illustrated specimen could not be traced (Foord & Crick, 1890). Thus, Foord and Crick (1890) re-interpreted this species based on further material. Interestingly, they noted that in one of the studied specimens they had assigned to Sowerby's species, the shell is preserved and it is said to have a shell showing only growth lines. In contrast, in our material with preserved shell, as mentioned above, a strong longitudinal striation is present at least in the ventral and ventrolateral part of the conch, most likely expanding to the entire conch in the juvenile stage as in other *Cenoceras* (s.str.) species. We therefore suspect that at least some of the material of *Nautilus obesus* sensu Foord & Crick does not represent *Cenoceras* s.str. but *Metacenoceras* Tintant, 1984 (*Metacenoceras*, previously considered a subgenus of *Cenoceras* was given full genus rank in Dietze et al., 2021. p. 48). This is corroborated by the fact that Foord and Crick (1890) included Orbigny's *Nautilus lineatus* in the synonymy of *N. obesus* Sowerby. For *Nautilus lineatus* Sowerby in Orbigny, Tintant (in Enay et al., 1994) introduced the new species *Cenoceras* (*Metacenoceras*) *moutierense* pointing out the differences with the incomplete specimen illustrated by Foord & Crick (1890, fig. 11) as *Nautilus obesus*. Although the determination of the latter was said to go back to the times of J. Sowerby, it is unknown whether it belonged to the type series. Moreover, this specimen has not preserved its shell and the entire body-chamber is missing. Although a conspecificity of our specimens with Sowerby's original *Nautilus obesus* cannot be ruled out, this is unprovable due to the apparent loss of the type, and consequently, we here regard *Nautilus obesus* J. Sowerby, 1816 as a *nomen*

Table 1 Measurements and parameters of *Cenoceras rumelangense* (unpublished), *Metacenoceras clausum* (data from Enay et al., 1994) and *Cenoceras*. gr. *obesum* sensu Rulleau (data from Rulleau, 2008)

Specimen	Data origin	n°	D	H	W	O	H/D	W/D	W/H	O/D
C. rumelangense (HT)	MNHNL BM790	15	450	270	220	54	0.6	0.49	0.81	0.12
C. rumelangense	MNHNL BM370	19	120	70	60	12	0.58	0.5	0.86	0.1
C. rumelangense	MNHNL BM641	17	355	195	110	38	0.55	0.31	0.56	0.11
C. rumelangense	MNHNL BM383	20	335	180	125	30	0.54	0.37	0.69	0.09
C. rumelangense	MNM 1	21	570	320	180	40	0.56	0.32	0.56	0.07
C. rumelangense	MEP 1	24	410	240	170	33	0.58	0.41	0.71	0.08
C. rumelangense	MNHNL BM232	18	350	195	120	37	0.56	0.34	0.62	0.11
C. rumelangense	MNHNL BM791	16	610	310	280	65	0.51	0.45	0.9	0.11
C. rumelangense	MNHNL BM793	22	600	350	300	50	0.58	0.5	0.86	0.08
C. rumelangense	MNHNL BM794	23	610	350	350	55	0.57	0.57	1	0.09
C. rumelangense	MNHNL BM783	25	175	98	100	18	0.56	0.57	1.02	0.1
C. rumelangense	SMNS 62245	26	535	290	308	48	0.54	0.58	1.06	0.09
C. rumelangense	Geolor 1	27	450	235	200	62	0.52	0.44	0.85	0.14
C. rumelangense	Geolor 2	28	460	280	230	50	0.61	0.5	0.82	0.11
M. clausum	Enay et al., 1994, p. 34	1	154	95	95	0	0.62	0.62	1	0
M. clausum	Enay et al., 1994, p. 34	2	168	110	104	0	0.65	0.62	0.95	0
M. clausum	Enay et al., 1994, p. 34	3	153	81	90	0	0.53	0.59	1.11	0
M. clausum	Enay et al., 1994, p. 34	4	129	77	82	0	0.6	0.64	1.06	0
M. clausum	Enay et al., 1994, p. 34	5	81	47	59	0	0.58	0.73	1.25	0
C. gr. *obesum*	Rulleau, 2008, p. 52	6	170	93	118	22	0.54	0.69	1.26	0.12
C. gr. *obesum*	Rulleau, 2008, p. 52	7	102	57	80	16	0.55	0.78	1.4	0.15
C. gr. *obesum*	Rulleau, 2008, p. 52	8	153	94	110	16	0.61	0.71	1.17	0.1
C. gr. *obesum*	Rulleau, 2008, p. 52	9	90	56	66	13	0.62	0.73	1.17	0.14
C. gr. *obesum*	Rulleau, 2008, p. 52	10	180	102	135	20	0.56	0.75	1.32	0.11
C. gr. *obesum*	Rulleau, 2008, p. 52	11	133	83	104	14	0.62	0.78	1.25	0.1
C. gr. *obesum*	Rulleau, 2008, p. 52	12	98	60	80	10	0.61	0.81	1.33	0.1
C. gr. *obesum*	Rulleau, 2008, p. 52	13	250	128	125	28	0.55	0.54	0.97	0.12
C. gr. *obesum*	Rulleau, 2008, p. 52	14	175	113	110	18	0.64	0.62	0.97	0.1

dubium. Rulleau (2008) illustrated several large-sized nautilids from the Humphriesianum Zone of France as *Cenoceras* ex gr. *obesum*. His material cannot be assigned to Sowerby's species for the same reasons. Comparing Rulleau's measurements with those of the herein described material, however, clearly indicates that his material differs significantly from ours and must represent another species, with the exception of specimen EPF Baj74, whose measurements fall into the variation of *C. rumelangense* as shown by our cluster analysis. Pending a verification of the original specimen in the Espace Pierres Folles collection, we tentatively include this specimen in our new species, with a question mark. We furthermore consider it likely that the specimens illustrated by Grulke (2016, p. 139) from the upper Bajocian of Frogden Quarry, Sherborne represent large-sized specimen of *C. rumelangense*. If confirmed, these records would represent the largest specimens known, with 700 resp. 750 mm of diameter (Grulke, 2016, p. 139).

Occurrence: *Cenoceras rumelangense* n. sp. occurs in the Humphriesianum Zone (lower Bajocian, Middle Jurassic) of Luxembourg and Southwest Germany (Baden-Württemberg). Unpublished data suggest a possible occurrence in coeval strata of North Switzerland (personal observation by GS). Clustering analyses performed in this study furthermore hints at the occurrence of the taxon in the Rhône Valley, France (specimen EPF Baj74 in Rulleau, 2008, p. 52). Unstudied specimens from Sherborne, UK, that were illustrated by Grulke (2016) might also belong to *C. rumelangense* and thus potentially extend the geographic occurrence towards the Northwest of Europe.

On the occurrence of 'giant' nautilids in the Jurassic

'Gigantism' is an ecologically important trait associated with competitive superiority; although it has been studied in specific cases, the general conditions at the origin of a very large body size remain still obscure (Vermeij,

2016). The term 'giant' or 'gigantism' is arbitrary, as any definition is comparative in itself; according to Klug et al. (2015), a giant species must fulfil the following three criteria: (1) species of the respective size should not have occurred all the time. There should be a low number of giant species; (2) adults of giant species have to be much larger than the average of their group; (3) the largest specimen(s) of the respective species should not show strong signs of pathology or abnormal growth.

Pathological gigantism (Manger et al., 1999) can be ruled out in the case of *C. rumelangense*, as none of the studied specimens shows any abnormalities in growth that would hint at a pathological development. In addition, there are several specimens that reach 500 mm diameter or more (Table 1), making the species outstanding by size not only for the genus *Cenoceras* but also in general for Mesozoic nautilids.

Living nautilids, namely *Nautilus pompilius*, *N. vitiensis, N. samoaensis, N. vanuatuensis* only rarely reach diameters larger than 200 m (Barord et al., 2023), *N. belauensis* and the questionable taxon *N. repertus* being credited with the largest shell diameters reaching up to 240 mm (Saunders, 1987). Compared to living nautilids, Mesozoic taxa reach considerably larger dimensions. Large-sized nautilids (> 300 mm) occasionally occur throughout the Jurassic. Already Zieten (1831) reported large-sized specimens from the Lower and Middle Jurassic of Swabia with diameters of "anderthalb Schuh" (*c.* 430 mm) and named them *Nautilites giganteus* Schübler. The collection of the National Museum of Natural History Luxembourg contains a large nautilid (330 mm; MNHNL n° SI340), ascribed to the genus *Cenoceras* from the 'Marnes et calcaires de Strassen' unit (Sinemurian, Lower Jurassic). The Stuttgart Natural History Museum houses a specimen of *Hemicenoceras arare* (Dumortier, 1869) from the early Pliensbachian of Swabia with a diameter of 350 mm (SMNS 70673). In the Middle Jurassic, Branger (2004) reported a large specimen (440 mm) of *Cenoceras mazardrikense* from the Callovian of western France. The specimens of *C. rumelangense* reported herein are thus considerably larger than these previously reported 'giant' nautilids.

The genus *Paracenoceras* Spath, 1927 is also known for some giant species, such as *Paracenoceras giganteum* (Orbigny, 1843) and *P. ingens* Tintant et al., 2002 from the Kimmeridgian (Upper Jurassic). Large-sized specimens of *Paracenoceras* spp. with diameters up to 500 mm are cited from southern Germany, Pomerania and France (Loesch, 1914; Kuhn, 1936; Tintant in Enay et al., 1994; Schweigert, 2021; Schlampp, 2022). Thurmann and Étallon (1861) noticed a diameter of 7 dm for *Nautilus giganteus*. Tintant et al. (2002) reported that some paracenoceratids from Switzerland could reach 600 mm or even more. However, the largest specimen measured by Tintant et al. (2002) was a *Paracenoceras ingens* of 522 mm diameter. To our knowledge, nautilids from the Cretaceous and younger ones did not reach diameters over 450 mm. Thus, the specimens of *C. rumelangense* n. sp. reported herein (Tab. 1) appear to be the largest post-Triassic nautilid documented so far in the scientific literature.

Taphonomical remarks

All of the herein studied specimens of *Cenoceras rumelangense* n. sp. show an extensive overgrowth of epifauna. Amongst the most common organism are serpulids (*Dorsoserpula lumbricalis*), small oyster shells (*Liostrea*) and bryozoans. Other bivalves, such as *Eopecten abjectus* (Phillips, 1829) are also present in some specimens. Typically, the epifauna is present on both flanks of the shell. An overview about benthic fauna from the 'Marnes sableuses d'Audun-le-Tiche' unit in Rumelange is given by Fayard et al. (2005).

In the specimen from Swabia (SMNS 62245), epizoans are represented by serpulids (*Dorsoserpula lumbricalis* [Schlotheim, 1820]) and bryozoans (*Berenicea*, *Kololophos*), whereas oysters are missing. Only the venter of the adult body-chamber is free of epifauna. This strongly points to a post-mortem overgrowth, when the empty shell was in an upright position at the seafloor forming a benthic island in a muddy substrate, otherwise the ventral area of the shell would have been overgrown as well. Similar observations were made in Lower Jurassic representatives of *Cenoceras* (Evans & King, 2019).

Conclusions

The study of previously undescribed giant nautilids from the lower Bajocian Humphriesianum Zone of Luxembourg and Southwest Germany allowed the identification of a new taxon of the genus *Cenoceras*, introduced herein as *Cenoceras rumelangense* n. sp. Clustering analysis support the distinction between *C. rumelangense* and coeval taxa *Metacenoceras clausum* (Orbigny, 1843) and *Cenoceras* gr. *obesum* (Sowerby, 1816 sensu Rulleau, 2008). *C. obesum* (Sowerby, 1816) is treated as *nomen dubium*. A comparison with measurements from the literature suggests that *C. rumelangense* is amongst the largest post-Triassic nautilids, together with *Paracenoceras* spp. from the Upper Jurassic. These large-sized shells also provided excellent support for encrusting organisms (serpulids, bryozoans, oysters and other bivalves), thus acting as so-called benthic islands.

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Author contributions
RW studied the specimens from Luxembourg, designed the study, and was a major contributor in writing the manuscript. GS studied the specimen from Germany and was a major contributor in writing the manuscript. JW carried out the statistical analysis and wrote the statistical method section. All authors read and approved the final manuscript.

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Declaration

Cometing interests
The authors declare that they have no competing interests.

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